METSÄNTUTKIMUSLAITOKSEN JULKAISUJA

COMMUNICATIONES
INSTITUTI FORESTALIS FENNIAE

MEDDELANDEN FRÅN SKOGSFORSKNINGSINSTITUTET I FINLAND
MITTEILUNGEN DER FORSTLICHEN FORSCHUNGSANSTALT IN FINNLAND
PUBLICATIONS OF THE FINNISH FOREST RESEARCH INSTITUTE
PUBLICATIONS DE L'INSTITUT DE RECHERCHES FORESTIÈRES DE LA FINLANDE

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HELSINKI 1975

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84

Holopainen, Viljo. 1974. Risto Olavi Sarvas in memoriam .... 1— 10

Lukkala, Aino. 1974. Risto Sarvaksen kirjallinen tuotanto. List of publications ..... 11— 17

84.1 Sarvas, Risto. 1974. Investigations on the annual cycle of development of forest trees. II. Autumn dormancy and winter dormancy. *Tiivistelmä:* Tutkimuksia metsäpuiden kehityksen vuotuisesta syklistä. Syys- ja talvihorros ..... 1—101

84.2 Leikola, Matti. 1974 Muokkauksen vaikutus metsämaan lämpösuhteisiin Pohjois-Suomessa. *Summary:* Effect of soil preparation on soil temperature conditions of forest regeneration areas in northern Finland ..... 1— 64

84.3 Lähde, Erkki. 1974. The effect of grain size distribution of natural and artificial sapling stands of Scots pine. *Selostus:* Maan lajitekoostumuksen vaikutus männyn luontaisten ja viljelytaimistojen kuntoon ..... 1— 23

84.4 Parviainen, Jari. 1974. Havupuiden latvakasvaimen ja neulasten vuotuisen kasvurytmin määrittäminen. Esimerkkisovellutus männyn jälkeläiskokeeseen. *Summary:* Determination of the annual growth rhythm of the terminal leader and needles of conifers. Application to a progeny test ..... 1— 27

84.5 Mälkönen, Eino. 1974. Annual primary production and nutrient cycle in some Scots pine stands ..... 1— 87

84.6 Rummukainen, Ukko. 1975. Männyn käpysadon ennustamisesta. *Summary:* On forecasting the cone crop of Scots pine .... 1— 26

84.7 Raulo, Jyrki & Koski, Veikko. 1975. Erilaisten rauduskoivujälkeläistöjen pituuskasvu Etelä- ja Keski-Suomessa. *Summary:* Height growth of different progenies of *Betula verrucosa* Ehrh. in South and Middle Finland ..... 1— 30

RISTO OLAVI SARVAS

IN MEMORIAM

1908—1974



Risto Sarvas

Risto Olavi Sarvas

in memoriam

Metsäntutkimuslaitoksen metsänhoidon professori Risto Olavi Sarvas, yksi Suomen metsätieteen näkyvimpiä henkilöitä, kuoli 66 vuoden ikäisenä huhtikuun 8 päivänä 1974.

Risto Sarvas syntyi 10. 2. 1908 Porissa. Hän suoritti metsänhoitajan tutkinnon Helsingin yliopistossa 1931 ja väitteli metsätieteen tohtoriksi 1944.

Sarvas toimi aluksi kolme vuotta valtion metsähallinnossa erilaisissa avustajan tehtävissä Pohjois-Suomessa, minkä jälkeen alkoi toiminta ylimmän metsäopetuksen ja metsäntutkimuksen saralla: vuodet 1934-38 yliopiston metsänhoidon assistenttina — tänä kautena kuitenkin sangen merkittävä lukuvuoden kestänyt opintomatka Saksaan Eberswaldin metsäkorkeakouluun — ja 1941-45 rintamapalvelun ohessa yliopiston metsänhoitajana. Jo ennen toista maailmansotaa (1938-39) Sarvas ehti toimia lyhyen aikaa Metsäntutkimuslaitoksen ylimääräisenä tutkijana ja v. 1945 hän palasi laitokseen uudestaan tällöin assistentin tehtävään. V. 1953 hänet nimitettiin Olli Heikinheimon jälkeen metsänhoidon tutkimusosaston professoriksi. Sitä ennen hän oli toiminut assistentin virkansa ohella kuusi vuotta myös Metsänjalostussäätiön toiminnanjohtajana.

Risto Sarvaksen elämäntyö on omistettu sangen ehyesti tiedemiehen kutsumukselle. Hänen suurtyönsä metsänhoitotieteen piirissä on ennen muuta Suomen metsien pääpuulajien uudistamistapahtuman syvällinen ja monipuolinen kartoittaminen. Alkuna näille tutkimuksille olivat jo 1930-luvulla suoritetut Lapin kuloalojen kasvillisuutta ja taimiston kehitystä koskevat, tunnustusta saaneet ja lupauksia herättäneet opinnäytetyöt.

Myöhemmin 1930-luvulla Sarvas ryhtyi — osittain käytännön taholta Metsäntutkimuslaitokselle esitettyjen toivomusten johdosta — tutkimaan harsintojen vaikutusta Suomen metsiin. Näiden tutkimusten — joista merkittävin oli väitöskirja »Tukkipuun harsintojen vaikutus Etelä-Suomen yksityismetsiin» (1944) — tulokset vaikuttivat osaltaan hakkuutapojen vähittäiseen tervehtymiseen 1940-luvun lopulta lähtien.

Sotien jälkeen Sarvas palasi jälleen uudistumistutkimusten pariin. Seurasivat mm. tutkimukset koivun uudistumisesta (1948) ja siemenpuuhakkuusta männikön uudistushakkuuna (1949). 1950-luvulla pääaiheeksi muo-

dostuivat metsäpuiden kukkimista ja siemensatoa koskevat ongelmat. Tämän erittäin mittavan tutkimustyön tuloksena ilmestyivät monografiat koivun (1952), männyn (1962) ja kuusen (1968) kukkimisesta, siemenen muodostumisesta ja leviämisestä, julkaisut, jotka alansa syvällisinä perusteita luotaavina esityksinä ovat saaneet tunnustusta yli koko maailman.

Näiden tutkimusten päätyttyä Sarvas paneutui 1960-luvun lopulla myöhäisen kautensa suureen tieteelliseen ponnistukseen: hän ryhtyi selvittämään puiden vuotuisen aikataulun, »periodin», etenemistä ja riippuvuutta ympäristötekijöistä. Sarjan v. 1972 ilmestynyt aktiivia periodia koskeva tutkimus ja vähän ennen tekijän kuolemaa valmistunut talvihorrosta koskeva osa muodostavat laajan, huolella kerättyyn aineistoon nojautuvan tieteellisen oppirakennelman, joka jo tähän mennessä on saanut osakseen laajaa kansainvälistäkin huomiota.

Erityisesti kukkimista ja vuotuisperiodia koskevilla tutkimuksillaan Sarvas on saattanut tietämyksen Suomen metsien pääpuulajeista aivan uudelle pohjalle. Nämä tutkimukset ovat jo tähän mennessä antaneet lähtökohtia monille käytännön sovellutuksille, virikkeitä uusille tutkimuksille ja kieltämättä myös tutkijoiden väliselle debatille. Kaikesta päättäen näiden suurtutkimusten hyödyntäminen on vielä aivan alkuvaiheessaan. On kuitenkin merkille pantavaa, etteivät vain tutkijat, vaan myös aikaansa seuraavat, valveutuneimmat käytännön miehet ovat näiden tutkimusten arvon oivaltaneet. Ne ovat suomalaisen metsätieteen arvokkaita pysyviä saavutuksia. Ne tarjoavat sitä paitsi puhuvan esimerkin siitä, kuinka omista, kansallisista tarpeista versonut tutkimus rikastuttaa myös kansainvälistä tieteen viljelyä.

Nyt esitetyn tutkimussarjan rinnakkaistyönä syntyi (1964) myös laaja dendrologian yliopistollinen oppikirja »Havupuut», osaksi omiin tutkimuksiin ja matkahavaintoihin sekä huolelliseen kirjallisuuden seulontaan perustunut puulajitiedon arvokas koostumus.

Risto Sarvaksen tutkijaprofiili on erinomaisen selväpiirteinen. Erityisesti metsien uudistamistapahtumaa ja vuotuista periodia koskevat tutkimukset valottavat sellaisinaan yhtä hänen tutkijakuvansa olennaista, kenties olennaisinta piirrettä: sinnikästä, määrätietoista pyrkimystä tiedon perusteisiin. Suhteellisen triviaaleista havainnoista tutkija eteni niissä yhä syvällisempään ja vaativampaan puiden elintoimintojen analyysiin. Jo tehtävään ryhtyessään hänen täytyi olla tietoinen siitä, että edessä on pitkä, vaivalloinen tie, mutta sitä ei Sarvas säikähtänyt, vaan hän eteni hellittämättömästi, askel askeleelta huolella laaditun aikataulun mukaan loppuun saakka, niin että viimeinen julkaisu saatiin painoon muutama viikko ennen hänen poismenoaan. Tuntui jopa siltä, että häntä kiehtoivat vaikeat tehtävät, että hän niiden parissa tunsi aidommin toteuttavansa tutkijan kutsumustaan.

Olisi kuitenkin virhe kuvitella, että nämä vaativat työt olisi toteutettu vain tahdon voimalla. Risto Sarvas kävi niihin käsiksi hyvin varustettuna.

Hän omasi alun alkaen suuret hengenlahjat sekä jo tutkijauransa alkuvaiheessa myös hyvät biologiset perustiedot, joita hän kartutti jatkuvasti ahkeralla opiskelulla sekä kotimaassa että ulkomailla. Hän on esimerkki tutkijasta, joka menestyksellä soveltaa perustieteiden metodeja ja oivalluksia metsätieteen ongelmiin.

Kolmas piirre Sarvaksen tutkijankuvassa on tukeva empiirinen ote. Hän oli syvästi kiintynyt tutkimuskohteeseensa metsään, viihtyi siinä ja innostui siitä jopa niin, että unohti monesti koealoillaan ajan kulumisen, unohti että päivä oli jo muuttunut illaksi ja että hän itse, työtoverit ja tutkimusapulaiset tarvitsivat ruokaa ja lepoa. Risto Sarvaksen metsä oli antoisa luonnonihme, mielenkiintoinen ja kiehtova, mutta hän käytti taitavasti hyväkseen myös laboratoriota ja sen välineistöä. Hän liikkui ahkerasti kaikissa Metsäntutkimuslaitoksen kokeilualueissa, mutta hänen mieluisin työympäristönsä oli Punkaharjun koeasema, missä metsä rikkaana ja moniilmeisenä ympäröi häntä ja missä — varsin vaatimattomiin huonetiloihin — oli onnistuttu saamaan välttämättömät tutkimusvälineet.

Sarvas koki tutkimuksen arvokkaana tehtävänä ja valitsi tutkijan kutsumuksen joutuessaan valintatilanteeseen v. 1962, jolloin Metsäntutkimuslaitokseen perustettiin ylijohtajan virka. Hän oli kuitenkin toiminut ansiokkaasti laitoksen johtajana kuuden vuoden ajan (1956-62). Näin hän saattoi sekä tutkijan että tutkimusjohtajan kokemuspohjalta tarkkailla aikansa tiedepoliittista kehitystä ja keskustelua. Hän seurasi sitä kiinteästi ja osallistui siihen hyvin harkituilla puheenvuoroilla. Hän toimi tieteen hyväksi myös eräissä valtion komiteoissa ja toimikunnissa, erityisesti metsäntutkimuskomiteassa (1957-60), valtion maatalous-metsätieteellisessä toimikunnassa (1960-66) sekä Pohjoismaiden välisessä metsäntutkimuksen yhteistyöelimessä (1972-74). Hän oli myös monien tieteellisten seurojen aktiivinen jäsen.

Tiedepolitiikassa Sarvaksen erityisen huomion kohteena oli tutkijayksilö, hänen toimintaedellytystensä ja työrauhansa turvaaminen sekä tutkijan työn mielekkyyden kokeminen aikana, jolloin tiedepolitiikka on voimakkaassa murroksessa, tutkija entistä kiinteämmässä hallinnollisessa ohjauksessa ja jolloin — siltä usein näyttää — jonkinlainen näennäistiede saa julkisuudessa enemmän arvostusta kuin vakava syvältä luotaava tutkimustyö.

Sarvas kuitenkin oivalsi tutkimustoiminnassa ajan haasteet. On tietynlainen paradoksi, että hän, alkuaan tyypillinen yksilösuorittaja, oli Metsäntutkimuslaitoksessa milteipä ensimmäisten joukossa kokoamassa eri tutkimusalojen edustajista työryhmää — metsänviljelyn tutkijaryhmää — ja suunnittelemassa toimintamalleja ryhmätyölle.

Risto Sarvas ei ollut rooli-ihminen. Tavanomaiset ajatusraiteet olivat hänelle yleensä vieraita eikä hän niitä seurannut, vaan muodosti käsityk-

sensä itsenäisen, usein kauan kestäneen harkinnan tuloksena. Hänen kannanottojaan erilaisissa päätöksentekotilanteissa sävytti monipuolinen lähtökohtien erittely ja pohdiskelu. Näin hän on jättänyt arvokkaita vaikutteita ei vain tutkijana, vaan myös tiedepoliittisena ajattelijana.

Metsäntutkimuslaitos, Suomen metsätiede ja metsätalous muistavat suuren kunnioituksen ja kiitollisuuden tuntein Risto Sarvasta, poikkeuksellisen mittavaa tiedemiestä.

Viljo Holopainen

Risto Olavi Sarvas

in memoriam

Risto Olavi Sarvas, Professor of Silviculture at the Forest Research Institute and one of the most outstanding personalities in Finnish forest science, died on April 8, 1974, at the age of 66.

Risto Sarvas was born in Pori on February 10, 1908. He graduated in forestry from Helsinki University in 1931 and defended his Doctoral Thesis in Forest Science in 1944. During the first three years of his career, Sarvas held various posts in the State Forest Administration in Northern Finland, after which he began his teaching and research activities in the field of advanced forestry. Between 1934 and 38 he held the post of assistant lecturer in silviculture at the University, during which time he spent a valuable study year at the Eberswalde Forestry University in Germany. Between 1941 and 1945, as well as serving at the front, he was the University Forest Officer.

Sarvas had already served for a short while (1938-1939) as a supplementary research worker at the Forest Research Institute, and in 1945 he returned to an assistantship at the Institute. In 1953, he succeeded Olli Heikinheimo as Professor and head of the Department of Silviculture. For six years during the time of his assistantship he managed the Foundation for the Improvement of Forest Trees.

Risto Sarvas's life was whole-heartedly devoted to the science of forestry. His principal contribution to silviculture was to further the understanding of the regeneration of the main Finnish tree species. The basis for this research was already laid in graduate work which he carried out in the 1930s on the vegetation and the development of seedling stands in fire-devastated areas in Lapland. The great promise shown in this early study received immediate recognition.

Later in the 1930s — partly owing to wishes expressed to the Forest Research Institute by practical foresters — Sarvas started to investigate the effect of selected cuttings on the Finnish forests. The most notable of the results was his doctoral thesis on »The effect of the selected cuttings of heavy timber on the privately-owned forests in South Finland» (1944). His findings contributed towards a gradual improvement in cutting practices from the late 1940s onwards.

After the war Sarvas returned to regeneration studies. Among other contributions, they led to a report on birch regeneration (1948) and on the seed-tree method of regeneration cutting for a pine stand (1949). In the 1950s his interest was caught by a new set of problems, research into which gave rise to monographs on the flowering, seed formation and seed dissemination of birch (1952), of pine (1962) and of spruce (1968). These thorough and penetrating publications have found recognition all over the world.

On completion of these studies Sarvas turned the main weight of his scientific effort to the investigation of the annual rhythm of trees and its dependence on environmental factors. The study of the active period of growth published in 1972 and the work on winter dormancy completed shortly before his death, form an extensive body of carefully assembled research material, the scientific value of which has already attracted widespread international attention.

As a result of his studies into the flowering of trees and their annual rhythm, Sarvas has given an entirely new dimension to our knowledge of the principal tree species of Finnish forests. His investigations have provided the starting point for much applied work, have stimulated new research and have stirred controversy among investigators. The application of these large-scale studies is clearly still in an early stage. It is significant that not only scientific workers but also progressive forest practitioners have realized the importance of these studies. They are lasting achievements of Finnish forest science, which also show how research which has sprung out of national needs can enrich scientific culture at the international level.

Side by side with his primary research, Sarvas published a substantial university textbook »The Conifers» (1964). This valuable compilation was based partly on the author's own research, partly on the keen observation made during his extensive travels and partly on a discriminating use of the literature in the field.

Risto Sarvas presents an extremely clear-cut picture of a research worker. The image is most clearly defined by his investigations into forest regeneration and the annual rhythm of tree development. They display his perseverance, his tenacity and the resolute effort that he always made to penetrate to the fundamentals of knowledge. From relatively trivial observations he advanced towards an increasingly profound and demanding analysis of the life processes of trees. On embarking upon this mission, he must have known that the road ahead was long and exacting. Nevertheless he advanced along it according to a carefully planned schedule step by step until the end. His last publication went to press a few weeks before his death. It seemed as if difficult tasks held a fascination for him and that he could satisfactorily fulfil himself by accepting their challenge.

Yet these exacting tasks were not carried out by will-power alone. Risto Sarvas was endowed with great mental ability and was well-equipped to tackle them. But he was aware of the constant need for industrious study both at home and abroad if his knowledge of biology was to be sustained and deepened. He is a good example of a research worker who successfully applies the methods and insight of the basic sciences to the problems of forestry.

A further characteristic of the image of Sarvas as a research worker is his firm empirical grasp. He was deeply attached to the subject of his studies, the forest. He was happy in it and was carried away by it. On his sample plots he was known to forget the passing of time, to forget that day had turned into evening and that he himself, his co-workers and research assistants needed food and rest. He was a frequent visitor to all experimental areas of the Forest Research Institute but the working environment that he loved most was the experimental station of Punkaharju. Here, where his extremely modest room was fitted with nothing but the indispensable research equipment, he was surrounded by all the riches and varying expressions of the forest.

Sarvas regarded research as a primary duty and when confronted with a choice, gave priority to it. Accordingly, in 1962, when a full-time directorship was established in the Forest Research Institute he chose research instead of administration. He had, however, commendably headed the institute for six years (1956-1962). This had given him the opportunity to review developments in scientific policy and to discuss them perceptively from his experiences both as researcher and research leader. Sarvas served his science on a number of State committees and boards, especially the Forest Research Committee (1957-1960), the National Research Council for Agriculture and Forestry (1960-1966) and the cooperative body of Inter-Scandinavian Forest Research (1972-1974). He was also an active member of several scientific societies.

Sarvas understood the challenge of his day and age in research work. In his approach to scientific policy, Sarvas devoted particular attention to the research worker as an individual and to ensuring his conditions of work in a peaceful environment, striving to make him realize the significance of research work during a period of great change in scientific policy-making, a period when the research worker is under increasingly rigid administrative supervision and when — so it often seems — some kind of pseudo-science receives more public appreciation than serious and fundamental investigation. It is something of a paradox that Sarvas, originally a typically individualistic worker, was almost among the first in the Forest Research Institute to form a team of representatives from various disciplines — the forest regeneration research group — and to plan activity models for team work.

Risto Sarvas was not a man to follow the herd. Conventional lines of thought were foreign to him and he never followed them. He was given to forming his own opinions after extensive deliberation, comprehensive analysis and assessment of the premises. The results were always distinctive and personal. He has thus left behind a valuable impression as a philosopher as well as a practitioner of his science.

Finnish forestry owes a great deal to Risto Sarvas. Members of the Finnish Forest Research Institute and his many friends and colleagues in all silvicultural walks of life will remember an exceptionally able scientist with feelings of great respect and gratitude.

Viljo Holopainen

Risto Sarvaksen kirjallinen tuotanto

List of publications

Luetteloinut — catalogued by Aino Lukkala

Lyhennyksiä — abbreviations

AFF = Acta Forestalia Fennica
MTA = Metsätaloudellinen aikakauskirja
Metsätaloudellinen aikakauslehti
MTJ = Metsätieteellisen tutkimuslaitoksen julkaisuja
Metsäntutkimuslaitoksen julkaisuja
Communicationes Instituti Forestalis Fenniae
SF = Silva Fennica
FF = Folia Forestalia

1937

Kuloalojen luontaisesta metsittymisestä. Pohjois-Suomen kuivilla kankailla suoritettu metsäbiologinen tutkielma. Referat: Über die natürliche Bewaldung der Waldbrandflächen. Eine Waldbiologische Untersuchung auf den trockenen Heideböden Nord-Finnlands. AFF 46.1, 146 s.

Havaintoja kasvillisuuden kehityksestä Pohjois-Suomen kuloaloilla. Referat: Beobachtungen über die Entwicklung der Vegetation auf den Waldbrandflächen Nord-Finnlands. SF 44, 64 s.

1938

Havaintoja Pohjois-Suomen kuloalojen kasvillisuuden kehityksestä. Luonnon Ystävä 42, s. 215—221.

Ilmavalokuvauksen merkityksestä metsätaloudessamme. Referat: Über die Bedeutung der Luftfotogrammetrie in unserer Waldwirtschaft. SF 48, 46 s.

Perä-Pohjolan kuloaloista ja niiden luontaisesta metsittymisestä. Metsälehti 6: 31, s. 4, 5.

1939

Ilmavalokuvauksen käyttäminen metsätaloudessamme. Die Photogrammetrie in unserer Waldwirtschaft. Maanmittaus, s. 237—247.

1940

Yksijaksoisen metsikön luontaisista kehityskausista. Die natürlichen Entwicklungsperioden der einschichtigen Bestände. MTA 58: 8, s. 79—83.

1941

Heikkotuottoisia metsiä polttohiilipuun hakkuilla kunnostamaan. Metsälehti 9: 1, s. 5—6.

1942

Havaintoja Syvärin varren metsistä. Metsälehti 10: 4, s. 6.

1944

Tukkipuun harsintojen vaikutus Etelä-Suomen yksityismetsiin. Referat: Einwirkung der Sägestammplenterungen auf die Privatwälder Südfinnlands. MTJ 33.1, 268 s.
Tukkipuun harsintojen vaikutus yksityismetsiimme. Metsälehti 12: 18, s. 5, 6.
Havaintoja kanervatyypin paljaaksihakkuualoilta. Observations from clear-cutting areas of *Calluna* type. MTA 61: 6/7, s. 122—126.

1945

Harsintahakkuiden vaikutus yksityismetsiemme tilaan. Metsälehti 13: 14/15, s. 10—11.
Puuston tiheys metsikön tunnuksena. MTA 62: 3, s. 80—84.
Metsikön siemensadon arvioimisesta. MTA 62: 12, s. 389—393.
Ilmakuvien käyttö metsätaloudessa. Metsäylioppilas, s. 3—5.

1946

Huomioita kaivospuun ja paperipuun määrämittahakkuilla käsitellyistä metsiköistä. Summary: Notes on stands cut for pitprops and pulpwood to minimum diameter. MTJ 33.2, 27 s.
Harsintahakkuiden vaikutus metsiemme ikäsuhteisiin. Metsäylioppilas, s. 16—18.
Koivun rodunjalostuksen mahdollisuuksista. Summary: Possibilities of birch breeding. Suomen paperi- ja puutavaralehti 28: 12, s. 188—191.

1947

Metsäpuiden rodunjalostuksesta. MTA 64: 1/2, s. 29—32.
Millaiset puut soveltuvat metsäpuiden rodunjalostuksen kantapuiksi. MTA 64: 10, s. 223—226.
Hurudana träd lämpa sig såsom stamträd för skogsträdens rasförädling? Skogsbruket 17: 11, s. 304—308.
Dendrologian kurssin työvihko. (Moniste). Dendrol. Editio II, 31 s.
Metsäpuiden rodunjalostuksesta. Työtehotietoa 10, 9 s.

1948

Metsän pintakasvillisuuden kuvaamisesta. MTA 65: 6, s. 186—190.
Tutkimuksia koivun uudistumisesta Etelä-Suomessa. Summary: A research on the regeneration of birch in South Finland. MTJ 35.4, 91 s.
Harsinnan ajatus kitkettävä ammattikunnastamme. MTA 65: 11, s. 325—328.
Harvennushakkuista. MTA 65: 12, s. 363—367.
Metsäpuiden rodunjalostuksesta. SF 64, s. 33—41.
Metsäpuiden rodunjalostuksesta. Suomen paperi-insinöörien yhdistyksen vuosikokouksessa 17. 4. 1948 pidetty esitelmä. Suomen paperi- ja puutavaral. 30: 17, s. 287—291 & Maatalous ja koetoiminta 3, s. 228—239.

1949

Puumaiset koivulajimme. MTA 66: 1, s. 9—13.
Siemenpuuhakkuu männikön uudistushakkuuna Etelä-Suomessa. Summary: Seed-tree cutting as a regeneration method in Scots pine forests of southern Finland. MTJ 37.5, s. 1—43.
Metsäpuiden rodunjalostus. Suuri Metsäkirja I, s. 180—189 ja Tapion Taskukirja, s. 137—142.
Huonokuntoiset metsät. Suuri metsäkirja I, s. 358—379.
Ulkomaiset puulajit ja niiden viljelymahdollisuudet Suomessa. (Yhdessä Lauri Ilvessalon † kanssa.) Suuri metsäkirja I, s. 156—179.
Forest genetics in Finland. III World Forestry Congress, Helsinki. Summaries of the Papers. Section I, s. 44—45. Bulletin No. 4.

1950

Tutkimuksia Perä-Pohjolan harsimalla hakattujen yksityismetsien uudistumisesta. Summary: Investigations into the natural regeneration of selectively cut private forests in Northern Finland. MTJ 38.1, s. 1—95.
The effect of light on the germination of forest tree seeds. Oikos 2: 1, s. 109—119.
Gallringarna och grundbeståndet. Skogsbruket 20: 3, s. 67—72.
Forest genetics in Finland. Actes du IIIe Congres Forestier Mondial. 3 rapports speciaux, s. 135—137.
Jättiläishaapa Helsingin kaupungissa. Summary: A triploid aspen in the town of Helsinki. MTA 67: 3/4, s. 98—100.
Kolme vuotta metsäpuiden rodunjalostustyötä Suomessa. Summary: Three years of tree breeding work in Finland. MTA 67: 6/7, s. 229—232.
Koivu suomalaisena metsäpuuna. Suomen luonto 9, s. 17—27.
Metsäpuiden siemenen hankkiminen ja käsittely. Tapion taimitarhakurssien luennot, s. 33—45. (Rotaprint).
Mitä harsiminen on ja minkä vuoksi se pilaa metsän? Metsätietoa 1, s. 3—6. (Liite Metsälehteen n:o 15).

1951

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INVESTIGATIONS ON THE ANNUAL CYCLE OF DEVELOPMENT OF FOREST TREES

II

Autumn dormancy and winter dormancy

RISTO SARVAS

† 8. IV. 1974

TUTKIMUKSIA METSÄPUIDEN KEHITYKSEN VUOTUISESTA SYKLISTÄ
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PREFACE

This investigation into autumn dormancy and winter dormancy was conducted abreast of the study of the active period forming part of the annual cycle of development of forest trees (Sarvas 1972). In the course of the investigation, I have become increasingly convinced that this cycle is an entity so well integrated that it seems hardly possible to investigate or survey any of its parts successfully if they are separated from the whole. It is entirely due to publication technique that the results of this investigation are issued in two separate volumes. Actually, a full description of this indivisible whole would require a third volume — a survey of the geographical variation in each of the three main parts of the cycle. But the data collected so far do not provide an adequate basis for a general survey of this question and this part of the study may have to be postponed for years.

Now that I am about to conclude my investigation of the annual developmental cycle of forest trees, which has continued for more than ten years, I wish to express my thanks to all those of my fellow workers who have participated in the task. The investigation has involved a great amount of work in the field and laboratory, as well as numerous calculations. Mr. *Olavi Helenius*, Forest Officer, Mr. *Veikko Silander* and Mr. *Jaakko Rokkonen*, Forest Technicians, have supervised the field work. Mr. *Alpo Luomajoki*, Ph.L., has participated significantly in the investigation of meiosis. The laboratory work has for the most part been done by Mr. *Pentti Manninen*. Mr. *Timo Ylitalo*, Forest Technician, has been in charge of the data processing and the other calculations involved. Miss *Katri Kallio* has drawn the diagrams and Mrs. *Aino Lukkala* has done the typing.

The manuscript was read by Professor *Max Hagman*, Professor *Paavo Juutinen*, and Dr. *Veikko Koski*, to whom I am indebted for many valuable suggestions.

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Helsinki, March 15, 1974. *Risto Sarvas*

Professor Risto Sarvas passed away on April 8, 1974 when this publication was still in the press. The proof has been read by his colleagues.

CONTENTS

	Page
Abstract	5
Introduction	8
Experiments in a controlled environment	11
Dormancy I	11
Definition of concepts and working hypothesis	11
Experimental determination of the rate of progress of dormancy I	16
Experimental method	16
Experiments with seeds	17
Experiments with seedlings	25
Experiments with cut twigs	27
Synthesis of experimental results	28
Length of dormancy I	32
Dormancy II	33
Definition of concepts and working hypothesis	33
Experimental determination of the rate of progress of dormancy II	33
Experiments with Larix sibirica	33
Experiments with Alnus incana	39
Synthesis of experimental results	42
Determination of the end of dormancy II	44
Length of dormancy II	47
Investigations in natural conditions	52
Introduction	52
Pattern of parcels in the course of development	56
Dormancy I	66
Dormancy II	73
Hardening and frost resistance	78
Review of literature	83
Concept of dormancy	83
Influence of environment on the onset and termination of dormancy	85
Discussion	89
Tiivistelmä	97
Literature cited	100

ABSTRACT

The author has divided the annual cycle of development of forest trees into three main parts: The active period, dormancy I (autumn dormancy) and dormancy II (winter dormancy). The results concerning the active period have been published earlier (S a r v a s 1972). The present investigation deals with dormancy I and dormancy II. The chief aim here, as in the study of the active period, has been to clarify in what way the progress of the cycle depends on environmental factors.

The progress of the cycle is essentially the outcome of a sequence of physiological phenomena in the apical and lateral meristems. The results obtained earlier (S a r v a s 1967, 1972) suggested that during the greater part of the cycle the moisture factor in these meristems is more or less optimal. As the progress of the cycle was observed in trees growing under natural conditions, it was not deemed necessary or even desirable, at least at this stage, to try to include the change in day length (photoperiod or nyctoperiod) in the model to explain the functional principle of the cycle. The pattern of progress of the cycle seems to be controlled largely by temperature and time.

In investigations on the dependence of the cycle on environmental factors it was possible in all the three main parts to make use of concepts that were alike in principle and research methods that were similar.

The equation which conveys, in concise form, the basic principle of the progress of the cycle at a constant temperature is as follows:

$$C_1 \rightarrow C_2 = v\,(T)\,(t_2 - t_1) \tag{1}$$

in which $C_1 \rightarrow C_2$ is the cycle interval between times t_1 and t_2, T a constant temperature and v (T) the rate of progress at temperature T. Where the temperature fluctuates, as in nature, the equation takes the following form:

$$C_1 \rightarrow C_2 = \int_{t_1}^{t_2} v\,(T(t))\,dt \tag{2}$$

For the sake of practical calculations, for instance, for automatic data processing programs, equation (2) can be approximated in the form

$$(3) \qquad C_1 \rightarrow C_2 = \sum_{i=1}^{n} v\,(T_i)\,\triangle t_i$$

in which i is the ith temperature measurement when the time measured between C_1 and C_2 has been divided into n equal parts.

The unit of a cycle interval has been defined as follows: the unit of interval is that interval through which the cycle progresses at a certain base temperature in one hour. This definition is applicable to all three main parts of the cycle, the active period, dormancy I and dormancy II. The same temperature could have been chosen as the base temperature for all three parts. However, for historical and practical reasons this was not done. The base temperature chosen for the active period was 2°C and the unit of this cycle interval was denoted p.u. (period unit). For dormancy I, 3.5°C was chosen as the base temperature and the unit of cycle interval was denoted ch.u. (chilling unit). The base temperature chosen for dormancy II was 2°C and the unit of cycle interval at this main part was denoted d.u. (dormancy unit).

From the definition of the unit of cycle interval and formula (1), the rate of progress of the cycle at any constant temperature can now be reckoned from the equation

$$(4) \qquad v\,(T) = \frac{h_P}{h_T}\ \text{c.u./h.}$$

where h_P is the time required for the cycle to pass through a given cycle interval at the base temperature P, and h_T the time required in the same cycle interval at temperature T. The result is expressed as c.u./h. (cycle units per hour).

The values for h_T at several different constant temperatures were determined experimentally for each of the three main parts of the cycle. These values were substituted in eq. (4) and the regression of the rate of progress of the cycle on temperature could be determined separately for each of the three main parts of the cycle. In general, these regressions seem to apply well to both the vegetative and the generative cycles.

These three regressions embody the first main principle concerning the progress of the cycle. The experimental data led to the formulation of two additional main principles: 1. the progress of the cycle is an irreversible phenomenon and 2. each of the three main parts of the cycle has its $\pm$ constant length expressed in its own units of cycle interval[1]); when the sum of the units amounts to this value, the cycle passes, without any special impulse, into the next main part.

[1]) Accordingly, length, as here used, does not refer to calendar time but rather to time weighted with temperature.

In this way the research concerned with the functional principle of the progress of the cycle crystallized into two main problems: 1. what is the form of the regression of the rate of progress of the cycle on temperature in each of the three main parts of the cycle and 2. how long is each main part (at the levels of the individual, the subpopulation and the population) expressed in the units of the particular main part of the cycle concerned. The results pertaining to dormancy I and dormancy II are seen in Figs. 5, p. 29, and 9, p. 43, and in Tables 13, pp. 71—72, and 10, pp. 49—50.

Investigations carried out in nature were largely focused on anthesis (dehiscence of pollen sacs) in subpopulations (stands) of different tree species. At this particular phase of the active period, when sampling at subpopulation (stand) level, it was possible to use recording devices which afforded great methodical advantages. The results were not incompatible with the principles presented above. In fact, they threw additional light on the details of the pattern of progress of the cycle. An observation of considerable importance is that in general, cells, in passing through a certain phase, do not show a normal frequency distribution but an irregular multimodal distribution. Thus they progress in »parcels» which form more or less separate groups at the start of dormancy II and continue to be observable until the end of the active period following dormancy II. The irregularity resulting from the parcels renders almost all sampling in research on the cycle very exacting.

The hardening phenomenon in forest trees, i.e. the development in autumn of a physiological stage resistant to frost, is actually beyond the scope of this study. Nevertheless, it has been possible to gain a rough idea of the general timetable of the hardening process and how it is related to the annual cycle of development.

INTRODUCTION

This study on the autumn and winter dormancies, like the earlier one concerning the active period (S a r v a s 1972), is confined to the investigation of physiological phenomena clearly included in the annual developmental cycle of forest trees. For instance, a state of dormancy that results from prolonged drought and is not annually recurrent, at least in the northern part of the temperate zone, is not covered.

Attention is concentrated on dormancy in buds. Investigation of a dormant stage possibly interrupting the activities of the cambium and the root had to be excluded from the study on account of the vast amount of work that would have been entailed. The so-called correlative inhibition (cf., e.g., R o m b e r g e r 1963 and L e i k e 1965) occurring during the initial phase of development of buds is not considered to be a true state of dormancy and has likewise been disregarded. Similarly, dormancy in seeds, which has received much attention in the literature on the subject, was not one of the main subjects of this study. However, because seeds are easier to use in experiments they have been given some attention.

The annual cycle of development of forest trees is divided into three main parts: the active period, autumn dormancy, and winter dormancy. In a detailed study of the active period (S a r v a s 1972), the beginning and end of this main part of the cycle were defined as follows: the active period begins when dormancy ends and ends when dormancy begins. This definition is admittedly loose, evidently because of lack of sufficient information. We have now come one step forward. Probably the most important finding made in the study concerning the active period is that the rate of progress of the active period depends almost exclusively on temperature and that the regression of the rate of progress of the active period on temperature is the same for all the tree species investigated and for all the different phases of the active period, provided that the variation of the other environmental factors falls within the range of variation of the natural habitat of the tree (population) concerned.

Dormancy may be defined as those parts of the annual cycle of development which generally coincide with autumn and winter in natural populations growing in natural habitats, and during which the temperature rela-

tions of the developmental processes are essentially different from those obtaining in the active period.

Of course, this definition, too, is far from perfect. However, it provides an objective criterion for the determination of whether a given meristem is in the active period or in dormancy.

Dormancy is clearly not a homogeneous state but composed of different stages. It has long been known that dormancy is more difficult to break in the beginning than towards the end of this stage. The resting condition is said to be deeper in the beginning than in the later phases. However, such a statement conveys little. It may be better to say that at the beginning a longer [1]) rest (the word rest in itself is, of course, not a very appropriate term) is required than later on. However, what is perhaps even more important is that the main change in the pattern of rest is probably not a gradual process but rather a single step of fairly short duration.

This last-mentioned view finds support in many observations at microscope level. A particularly concrete example is provided by meiosis in the microspore mother cells of *Larix* species. The transitional phase between pachytene and diplotene, i.e. between the active period and dormancy II, is short, particularly in the individual mother cell. Similarly, the transitional phase between diplotene and diakinesis, i.e. between dormancy II and the active period, is short. The same is true of the starch accumulating in the apical meristems of many tree species in the course of dormancy I; at the end of dormancy I the starch disappears during a short period.

As in an earlier paper (S a r v a s 1970), dormancy is here divided into two main stages, dormancy I (autumn dormancy) and dormancy II (winter dormancy). These terms were deliberately chosen to be as neutral as possible, because more descriptive ones would have tended to cause misunderstanding. In fact, a more neutral term would clearly be better than the word dormancy (for instance, the active period = stage CA (cycle A), and dormancy I = stage CB (cycle B), and dormancy II = stage CC (cycle C) but the time is probably not yet ripe for a terminological revision as radical as this.

The model of dormancy taken as the starting point of the present study resembles the one presented by P f e f f e r as long ago as 1904. P f e f f e r divided dormancy in buds into two stages, an autonomous and an aitionomous stage: »I Autonome Knospenruhe (auch häufig endonome, endogene, autogene), Austreiben der Knospen wird durch in den Knospen selbst liegende Ursachen gehemmt oder verhindert. II Aitionome Knospenruhe. Austreiben der Knospen wird nur durch äussere Ursachen (ungünstige Klimabedingungen) verhindert». P f e f f e r's autonomous dormancy may be identified,

[1]) Without doubt, the number of research workers holding a similar view about this important principle is increasing. For instance, W i t k o w s k a-Ž u k (1969, p. 385) uses the expression »less deep or shorter-lasting dormancy».

at least to some extent, with dormancy I as presented in this study, and his aitionomous dormancy with dormancy II of this study. However, in the course of this century it has become increasingly evident that all physiological phenomena are the outcome of interaction between the genotype and the environment. In principle, there are no truly autonomous physiological phenomena, i.e. physiological phenomena that are independent of the environment.

The purpose of the present study is to map out preliminarily and roughly the progress of autumn dormancy and winter dormancy, particularly that of the physical and physiological (antecological) characteristics of these states.

In the literature dealing with dormancy there often appear the terms dormancy release and chilling requirement. These terms are expressions of more or less precisely defined patterns of ideas relevant to dormancy. Evidently, they could be applied to the active period, too. We could speak of release of the active period and of the heat requirement of the active period. This kind of play with ideas is beneficial, for it clarifies the concepts now under discussion. When dealing with the active period, I did not, however, use these terms but instead spoke of the progress of the active period (= release of the active period) and of the length of the active period (= heat requirement of the active period). Thus, the difference lies in terminology alone. One of the goals of the present study was to construct as simple a model as possible of the whole cycle (of the sequence of physiological events in the cycle) and, therefore, in discussing dormancy, concepts and terminology that resemble those used earlier for the active period have been used, as far as possible. Thus, the expression dormancy release is replaced by progress of dormancy and instead of chilling requirement I refer to the length of dormancy (cf. footnote on page 6).

It is necessary to emphasize repeatedly the all too obvious fact that the annual cycle of development of forest trees, at least in temperate climates, reflects the adaptation of the trees and of the populations composed of them to the annual cycle of the local climate, i.e. the alternation of summer and winter. The trouble is that, because it is so obvious, this basic fact, despite its importance, has not always received due attention. One of the reasons for this may be that the term dormancy, in particular, has been used in reference to physiological phenomena that may not be connected, at least directly, with the annual cycle of development.

EXPERIMENTS IN A CONTROLLED ENVIRONMENT

Dormancy I

Definition of concepts and working hypothesis

For many tree species, especially at the onset of dormancy, exposure to cold is a prerequisite for the progress of dormancy; accordingly, somewhere between the end of the active period and the beginning of the next active period there is a stage in which development only progresses at low temperatures. This part of the cycle is termed dormancy I.

The classic experiment that establishes the existence of dormancy I is as follows. The experiment is started in late summer and continues till midwinter. At regular intervals during this period, twigs of certain individual trees are brought into a greenhouse maintained at a constant temperature between 10° and 18°C. Such treatment, known as forcing, induces flushing. As a rule, however, the twigs brought in before the autumn cold do not flush at all. Only after sufficient exposure to low temperatures outside can they be forced into flushing. Experiments of this type were made early in this century e.g. by M o l i s c h (1909). Since autumn 1969 they have formed part of the present investigation. The results obtained in the autumns of 1970 and 1972 are seen in Tables 1 and 2. The investigations covered the vegetative as well as the flower buds. It is perhaps well to emphasize that, after a minimum, specific to each tree species, the length of the forcing period is of no significance. In principle, all the twigs brought in for the purpose of forcing could be examined at the same time, for instance a month after the last lot of twigs was brought in. However, if this procedure had been used, analysis of the twigs brought in first would have been badly hampered by the effects of the long forcing period (for instance, buds would have withered). Therefore, several examinations were made during the forcing period. Of importance is not the length of the forcing period but the maximum percentage of buds that can be forced into the active period.

Different tree species were found to differ considerably in the cold required to terminate dormancy I, that is in the »chilling requirement» (Tables 1 and 2).

Table 1. Development of twigs brought into the greenhouse (17°C) from the forest at Punkaharju on successive dates in autumn 1970. Each tree species involved is represented by two individual trees and from each of these trees two twigs were taken each time. Buds were examined on Oct. 19, Oct. 28, Nov. 6, Nov. 12, Nov. 20, Nov. 27, and Dec. 10, 1970.

Material	Date and hour of day when the twigs were brought into the greenhouse							
	Sept. 28	Oct. 5	Oct. 12	Oct. 19	Oct. 26	Nov. 2	Nov. 9	Nov. 16
	7.25	8.30	10.40	13.00	13.40	13.50	15.00	•
	Maximum percentage of buds that reached in development the active period							
Alnus incana, local origin; Punkaharju LXII								
Male flover buds	0	0	50	100	100	100	100	100
Betula verrucosa, local origin; Punkaharju LIV								
Vegetative buds		0	0	100				
Male flower buds		0	0	100				
Female flower buds		0	0	100				
Larix decidua, origin unknown; Punkaharju 80								
Male flower buds	50	0	0					
Larix Gmelini, origin RSFSR, Sakhalin; Punkaharju 9								
Microspores	30	0	100	100	100			
Larix sibirica, origin unknown; Punkaharju 49								
Microspores	100	100	100	100	100	100	100	100
Populus tremula, local origin; Kerimäki, Silvola (near Punkaharju)								
Microspores			0	0	0	0	80	100
Chilling unit sum (cf. pp. 28—30) at canopy level, *Betula pubescens*, Punkaharju XIV	180	312	413	517	604	637	638	660

The length of dormancy I will be considered later on. However, at this point it is already well to mention that when the experiments described above were made, attention was attracted by the great topophytic variation displayed in the flushing of buds. As a rule, the buds on the older shoots of a twig flushed after a shorter period of exposure to cold than those on the younger shoots. Flushing was particularly late in the buds on the shoots of the current year. Earlier, Witkowska—Žuk (1969, p. 386) was among those who studied the wide topophytic variation during dormancy I.

Let us now state the working hypothesis as follows: 1. At the end of its active period, a given meristem enters dormancy I; 2. In dormancy I, the

Table 2. Development of twigs brought into the greenhouse (17°C) from the forest at Punkaharju on successive dates in autumn 1972. Each tree species involved is represented by two individual trees, and from each of these trees, two twigs were taken each time. Buds were examined on November 30, 1972 and January 12, 1973.

Material	Date and hour of day when the twigs were brought into the greenhous						
	Sept. 26	Oct. 3	Oct. 10	Oct. 17	Ost, 24	Oct. 31	Nov. 16
	10.00	9.50	7.50	7.50	8.00	8.00	15.45
	Maximum percentage of buds that reached in development the active period						
Abies sibirica, origin unknown; Punkaharju 45							
Microspores			0	0	54	100	100
Betula papyrifera var. neoalaskana, origin Canada, Alta., Cooking Lake; Punkaharju 118							
Vegetative buds			70	100	100	100	100
Betula pubescens, local origin; Punkaharju XIV							
Vegetative buds	0	0	15	100	100		
Betula verrucosa, local origin; Punkaharju LIV							
Vegetative buds	0	10	50	100	100	100	100
Larix decidua, origin unknown; Punkaharju 80							
Microspore mother cells	50	100	100	100	100	100	100
Larix Gmelini, origin RSFSR, Sakhalin; Punkaharju 9							
Microspore mother cells	0	100	100	100	0	100	100
Larix sibirica, origin unknown; Punkaharju 49							
Vegetative buds		10	50	80	100	100	100
Picea Abies, origin Finland, Lammi; Punkaharju LII							
Microspore mother cells	0	0	△	50	100	100	100
Populus tremula, local origin; Sääminki (near Punkaharju)							
Male flower buds			0	0	0	0	0
Chilling unit sum (cf. pp. 28—30) at canopy level, *Betula pubescens*, Punkaharju XIV							
	109	238	322	425	542	652	

cycle progresses only at relatively low temperatures; 3. As soon as the progress of dormancy I has terminated, the meristem enters dormancy II (where the cycle progresses at high temperatures, too, but the regression of the rate of progress on temperature is not the same as in the active period, cf. S a r v a s 1970).

This model immediately raises three questions: 1. What is the regression of the rate of progress of dormancy I on temperature? 2. How long is dormancy I? and 3. Is dormancy I a reversible or an irreversible chain of phenomena? These questions resemble those asked in connection with the active period, or, to be more precise, they have been framed in a similar way. Thus here, too, it seems possible to try to proceed by using similar concepts and experimental methods.

The investigation, like that concerning the active period, has been restricted to the reactions to environmental factors which are displayed by natural tree populations growing in their natural habitats. With this restriction, it may be assumed, initially at any rate, that the progress of dormancy I depends exclusively on time and temperature.

Let us further assume that at a constant temperature the progress of dormancy I is directly proportional to time. Then the rate of progress, v, is simply a function of temperature, T, i.e., $v = v(T)$. The cycle interval through which dormancy I has progressed at a constant temperature, T, can thus be expressed by the following equation:

$$d_1 \rightarrow d_2 = v(T)\,(t_2 - t_1) \tag{1}$$

in which d_1 and d_2 are two phases of dormancy I at times t_1 and t_2, and $d_1 \rightarrow d_2$ the cycle interval between phases d_1 and d_2.

The unit of cycle interval for dormancy I is defined as the cycle interval through which dormancy I progresses in 1 hour at a constant temperature of 3.5°C. This was chosen as the base temperature because, according to preliminary investigations, the progress of dormancy I is most rapid at this temperature, an even more important point being that between 3.0 and 4.0°C the rate of progress is least affected by temperature fluctuations. All the shortcomings attaching to the unit of cycle interval for the active period (Sarvas 1972, pp. 13 and 34) also apply to the unit of cycle interval for dormancy I, determined in this way. Below, this unit is termed the chilling unit and is denoted by the symbol ch.u.

Where the temperature fluctuates, as it usually does in natural conditions, the equation expressing the relation between the cycle interval and the temperature takes the form

$$d_1 \rightarrow d_2 = \int_{t_1}^{t_2} v(T(t))\,dt \tag{2}$$

where T (t) is the temperature at time t, and v (T) the rate of progress of dormancy I at temperature T.

For practical purposes, equation (2) can be approximated in the form

$$d_1 \rightarrow d_2 = \sum_{i=1}^{n} v(T_i)\,\Delta t_i \tag{3}$$

in which i is the ith temperature measurement counted from the beginning of the cycle interval $d_1 \rightarrow d_2$ when the interval has been divided into n equal parts.

We now observe that for reckoning the length of a given cycle interval, the only unknown is v. It is obvious that v can be determined experimentally (cf. p. 16). However, the practical difficulties involved may be expected to be greater than those faced in the corresponding task concerning the active period.

Above (as in the investigation of the active period), a set of concepts was used. The most important of these is the unit of cycle interval for a given genotype. However, it was not possible to define a unit common to all the genotypes, not even to those of the same species.

It is obvious that in the examination of dormancy I (as well as in the examination of the active period), other concepts based on a different approach can also be used. In studying the different possibilities, the first thing to be considered is what can be measured. As a matter of fact, the possibilities in this respect are very limited, at least for the time being. What can be measured are: 1. The period of time required for a given genotype (or a given population) to progress through a certain cycle interval at different constant temperatures and 2. The periods of time required for different genotypes (or populations) to progress through a certain cycle interval at the same constant temperature.

It is due to these limited possibilities that, whatever the concepts used, we ultimately end up working with relative values. Therefore the question arises of whether it is advisable to try to get round this fact, as has been done in this investigation, by defining the unit of cycle interval as absolute in form, when in actual fact it is not absolute. The examination of dormancy I and of the whole cycle could from the very start be based equally well or perhaps even better on the relative rates of progress of the cycle. However, as seen above, in this investigation another starting point was chosen, because it was hoped that the concepts that would arise from it would be easier to work with, even though the reasoning finally leads in a roundabout way to the same conclusion as would be reached more directly by using the relative rates of progress.

The results of the experiments given in Tables 1 and 2 show that in several species the termination of dormancy I has required less exposure to cold in the microspore mother cells than it has in the vegetative buds of the same twigs. This implies that the length of dormancy I is shorter in the flower buds than in the vegetative buds. A study of the microspore mother cells involves measurement of the length of dormancy I at cell level, whereas the time taken for the flushing of the vegetative buds is measured at bud level. It is possible that buds do not flush at the point when 50 % of

the primordial leaves have passed through dormancy I but rather when almost all the primordial leaves, including the apical ones, have proceeded from dormancy I to dormancy II. Furthermore, flushing of a vegetative bud signifies not only that both dormancy I and dormancy II have come to an end, but also that the active period has already made considerable progress. Accordingly, it is highly uncertain whether accurate observations concerning the length of dormancy I in the vegetative buds can be made on the basis of flushing. The difference between the lengths of dormancy I in the microspore mother cells and in the vegetative buds is not so great that the discrepancy is significant.

Experimental determination of the rate of progress of dormancy I

Experimental method

At this stage, almost the only thing we know about dormancy I is that, by definition, this part of the cycle does not, practically speaking, progress at temperatures above 10°C. This definition is based on observation, as was mentioned in the introduction, and must be used as a starting point when we seek to increase our knowledge.

It is appropriate to begin the investigation of dormancy I by clarifying how the rate of progress depends on temperature. Experiments can be made on cut twigs (on the vegetative or flower buds on them) or on seeds or whole plants. Since the variation within the material is likely to be large, several replicates are necessary. The procedure is as follows. From a large quantity (for example, several hundreds) of twigs, seeds or seedlings several matched sets are formed and divided into the requisite number of treatments and replications of treatments. For example, it is fairly easy to arrange experiments on 10 000—50 000 separate seeds. Such huge numbers greatly increase the accuracy of the results.

As regards the physiological state of the experimental material, it is only necessary to know that the active period has terminated but that dormancy I has not been completed. This can be tested in a pilot experiment by forcing a representative sample of the material before the experiment is begun for long enough at a constant temperature of, for instance, 15°C. Generally, at this temperature, if the material or some part of it is not yet in dormancy I, it will soon attain this stage. On the other hand, should it have passed through dormancy I, it would progress to the active period and, as a result, the buds on the twigs or seedlings would flush or the seeds would germinate.

The important point is that in principle it makes no difference which phase of dormancy I the experimental material has attained, as long as it is not too close to the end of dormancy I.

The practical difficulties encountered in carrying out experiments on dormancy I are largely due to lack of knowledge of any suitable, easily observable phases during this stage of dormancy. The same applies to dormancy II. Therefore, the effects of the different treatments (temperatures) given during dormancy I can be observed only after the experimental material has proceeded to the active period following dormancy II.

The experiments are divided into two parts: treatment and forcing. The treatments comprise different constant temperatures and different treatment periods. As a result of treatment, either all the material, or part of it or none at all progresses to dormancy II. By forcing the material after the treatment at a temperature high enough to prevent further progress of dormancy I and by prolonging the forcing for a sufficiently long time (long enough for the material to pass through dormancy II and reach the flushing phase in the active period), conclusions can be drawn regarding the proportion of the treated material that has passed through dormancy I as a result of the treatment.

Experiments with seeds

Although dormancy I in the apical meristems and dormancy in seeds have some characteristics in common, they obviously also differ fundamentally in many respects [1]). Often, their ecological functions are very different. Dormancy in seeds is not included in the annual cycle of development but forms part of the regenerative physiology of trees. In this study, experiments on dormancy in seeds have been made only for methodical reasons with a view to gaining a better understanding of the temperature relations of dormancy I in the apical meristems.

The relation between temperature and the progress of dormancy I can only be determined by measurement of the time required for some given experimental material to progress through a certain cycle interval belonging to dormancy I at different constant temperatures (provided that the other environmental factors are about the same at all the experimental temperatures). This is where the difficulty lies, because, as pointed out above, we have, at present, no knowledge of any physiological phases in dormancy I whose time-course can be observed. However, if we take randomized matched sets from material (e.g. a seed lot) that has previously undergone uniform treatment, we can presume that when the experiments are begun all these

[1]) E.g. dormancy in the apical meristems seems to have no counterpart in seeds. Hence, the term dormancy in seeds rather than dormancy I is used in reference to seeds.

sets are in the same physiological phase of dormancy I. And we shall take this phase (to be exact, the phase which 50 % of the experimental material has passed through when the experiment is begun) as the starting point for the cycle interval to be investigated. As the end point we shall take that phase in which 50 % of the material has passed from dormancy I to dormancy II or to the active period.

It is probable that investigations into the dormancy in seeds carried out in different parts of the world outnumber those made with any other plant organs. One reason for this is that dormancy in seeds is of considerable importance; for instance, in large seed-testing laboratories questions concerning dormancy inevitably arise. The seeming ease with which large quantities of seed can be handled in germination tests and with which statistically well-planned tests with this material can be arranged have, without doubt, tempted research workers to use seeds as research objects.

However, the seed forms a mysterious miniature world of its own which, despite the enormous amount of research concentrated on it, continues to be largely obscure. This involves a risk. In arranging experiments as well as in placing interpretations on them, the research worker is only too well aware that something essential may have been overlooked.

Earlier investigations have revealed that dormancy in seeds is achieved in different species in different ways, which involve different parts of the seed, and that, depending on the parts involved, dormancy often varies in character. In the present study, investigation has been concentrated on the phenomenon known as endogenous seed dormancy (cf., for instance, Villiers 1972, p. 229). Seed lots in which there was reason to suspect that dormancy was entirely or partly due to one of the following causes have here proved to be unsuitable as experimental material:

1. Retarded embryo development
2. Seed coat relatively impermeable to water and gases
3. Some mechanical obstructions that limit embryo development.

In investigating the general model of endogenous seed dormancy it seems appropriate to choose, as test objects, tree species having seed with rather a thin coat in which the embryo forms the major portion of the live seed, the endosperm's contribution being small. In Finland, the birches *Betula verrucosa* [1]) and *B. pubescens* are suitable for this purpose. For theoretical reasons, a third birch species, *Betula nana*, also growing autochthonously in Finland, deserves attention. The experiments were first begun with *Betula verrucosa* and *Betula pubescens*. It immediately became evident, however, that in the seeds of *Betula verrucosa*, dormancy was not well developed,

[1]) In the nomenclature of trees Rehder (1940) is mainly followed. In fact, *Betula verrucosa* Ehrh. is the only exception.

whereas the seeds of *Betula pubescens* displayed a strongly developed dormancy. Consequently, all experiments were made with seeds of *Betula pubescens*. The seeds of the birch are not seeds in the botanical sense of the word; they are nuts (or nutlets). Below, however, in accordance with common practice, the term seed is used, since there is no likelihood of confusion.

When dormancy in seeds is investigated the first questions to arise are surprisingly difficult to answer, viz. when should the experimental seeds be collected, and how should they be extracted from the catkins (temperature) and stored (humidity). Failure to apply the right preparatory treatment may ruin the experiment before it starts. For instance, at a high temperature at the time of extraction dormancy might be lost, and a low storage temperature might gradually release it.

The first experiments on dormancy in seeds were made in winter 1970/71. All the seeds used in these experiments, a total of several litres, were collected from a *Betula pubescens* tree growing at Punkaharju [1]), in the autumn, before the temperature started to drop below 10°C. Only catkins that were mature and had turned brown and partly opened were collected. This was a means to be sure that the active period had terminated and that the seeds were definitely in dormancy. Consequently, the seeds, when collected, were fairly dry and possibly less susceptible than moister seeds are to extraction at a high temperature. Extraction and final drying took place at room temperature (about 22°C). The seeds were stored at the same temperature.

Treatment of the seeds was carried out in incubators at different temperatures and for different periods. In each incubator, a thermoelement was connected to the multipoint recorder. Later on, the fluctuations in temperature that occurred during the treatment were determined from the tape in the recorder and the average treatment temperature was calculated. Generally, this deviated only a few tenths of a degree from the prescribed temperature.

With the particular needs of this investigation in mind, a germinator (Figs 1—3) was constructed, of dimensions suitable for ca. 200 birch seeds. The idea was that each treatment unit (replicate) should have its own small germinator.

Each germinator consists of 2 parts, a water reservoir (a large-sized drinking glass) and a germination tray (made from a disposable plastic Petri dish). The Petri dish and its cover are glued back to back. In the centre of the tray so constructed is a hole 2 cm in diameter made by burning. The other details are the same as in the Jacobsen germinator: a pad of blotting paper (filter paper), an interpad of stockinet and, underneath this, a cotton pad from which a lamp-wick is suspended.

[1]) The latitude and longitude of the experimental areas and some data on the experimental stands are given in Table 11, pp. 53—54.

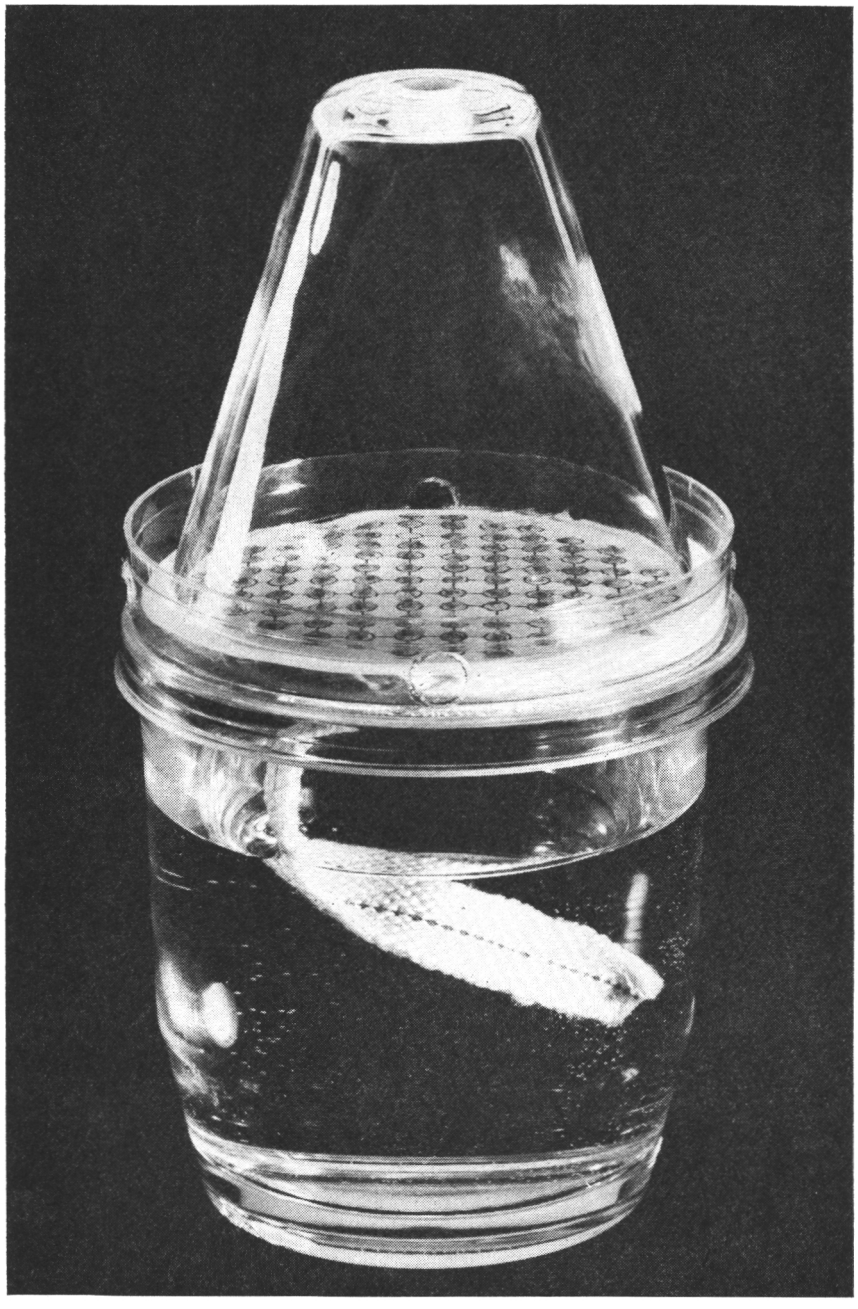


Fig. 1. The germinator used in experiments with seeds. The temperature under the bell jar was measured with thermoelements placed under the blotting paper or under a seed in such a way that the thermoelement was protected from radiation.

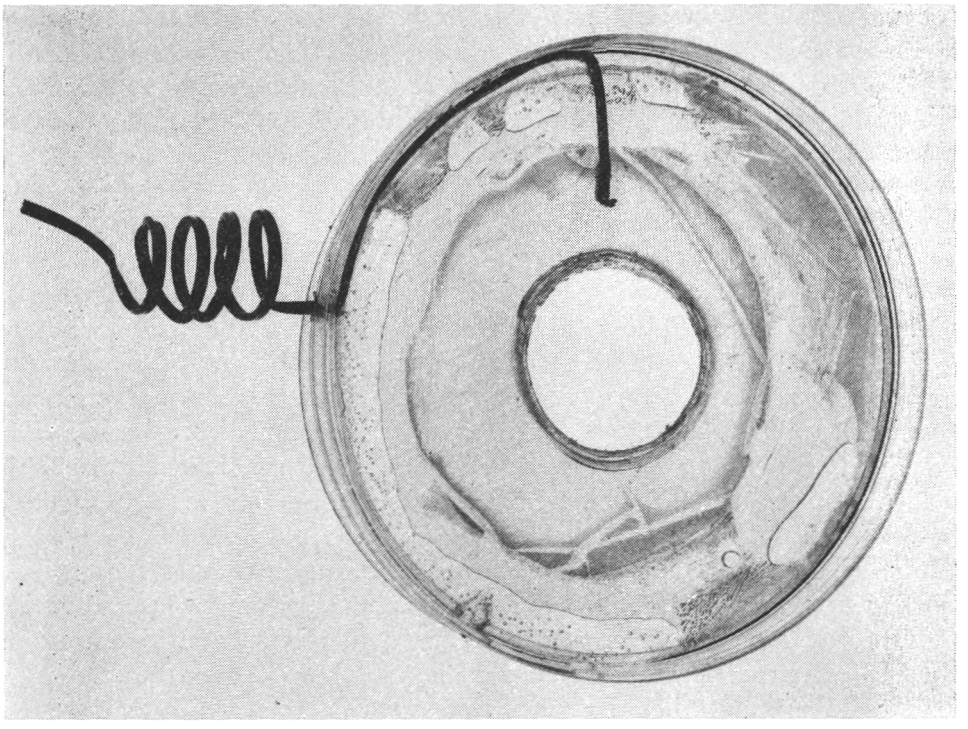


Fig. 2. Attachment of the thermoelement to the germinator. The thermoelement is led inside the germinator through a hole drilled in the side of the upper Petri dish functioning as a germination tray. The wire is glued to the floor of the tray and the end of the wire is bent upwards about 3 mm.



Fig. 3. Experiment to study the dependence of the rate of progress of dormancy in seeds on temperature. Germinative phase at 17°C. Punkaharju, spring 1971.
Photo by O. Oskarsson

The germinator facilitates the transfer of seed from the imbibition treatment to the incubators and then to conditions for forcing, so that the positions of replicates could be randomized at each transfer. Before the seeds were subjected to treatment, care was taken that their moisture content was maximal. Hence, 24 hours before the germinators were placed in the incubators the seeds were spread on the germination trays and immediately sprayed with water. During this imbibition treatment the temperature was 14°C.

All the treatments were carried out in artificial light, the intensity of which ranged between 1 500 and 3 000 lux. In the incubators the relative humidity of the air varied between 75 and 85 %.

The treatment temperature was measured with thermoelements connected to a multipoint recorder. The arrangement was made as stable as possible by gluing the wire from the thermoelement firmly to the bottom of the Petri dish; only a portion about 3 mm long at the tip of the wire was left unglued. This was then bent up at an angle of 90° with the tip touching the underside of a seed (Fig. 2). Comparative measurements indicated that the average temperature on the underside of the seed was 0.9°C higher than the air temperature measured (with a thermoelement protected from radiation) in the incubator, outside the germinator.

After treatment the seeds were transferred to a warmer temperature (14—18°C). As mentioned before, the method used here is based on the assumption that dormancy I does not progress at temperatures above 10°C. An important point to be considered here is that at very high temperatures (> 22°C) the dormancy of *Betula pubescens* seed is lost rapidly. On account of this, the germination temperature was kept approximately constant in each subseries of experiments, although it varied somewhat (from 14° to 18°C) between the different subseries. In addition to temperature, humidity was controlled by taking care that the relative humidity of the air in the germination room did not drop below 80 %. The seeds were sprayed with water every day.

Inspections were made once a day, starting at 16.00 h. A seed was considered to have germinated when the radicle was at least 3 mm long. At each inspection, the germinated seeds were removed and counted. A note was also made of the exact time of day. The experiments were discontinued after 3 weeks. The average percentage of empty seeds in the *Betula pubescens* samples used in the experiments proved to be 32.4 % and the germination percentage of well-stratified unsorted seed (filled and empty seeds) 65 %.

Subsequent compilation of the experimental results is seen in Fig. 4, which shows the results of one subseries of experiments 31/1972, conducted at 0.5°C. The graph is drawn on frequency paper. The horizontal axis shows the treatment periods at 0.5°C and the vertical axis the total germination

obtained by the end of a 3-week period at 17°C, expressed as a percentage of the highest value possible (65 %, cf. p. 22). In the diagram, each point represents the mean value of 3 replicates (comprising 200 seeds each, a total of 600 seeds). For each experimental procedure (position in the incubator, order of removal from the incubator, position in the warm phase) the replicates were randomized anew.

The experiment is largely based on the assumption that in the seed population under investigation the frequency distribution of the lengths of dormancy in seeds (the chilling unit sums required for termination of dormancy in seeds) is about normal. Fig. 4 shows that the scatter of plotted points can be well represented by a straight line. This may be taken to mean that the distribution really is about normal.

As Fig. 4 clearly shows, the longer the treatment period, the larger the percentage of the viable seed that has germinated. For example, after a 6-day treatment, only 19.0 % of the viable seed had passed from dormancy to the active period. A treatment period of 7.7 days was required for 50 % of the viable seed to pass from dormancy to the active period, and a treatment period of 10.9 days was needed for 95 % of the viable seed to proceed from dormancy to the active period. The standard deviation of the frequency distribution is considerable; Fig. 4 shows this to be 1.9 days, which in this case means that the variation coefficient is $1.9/7.7 = 24.6$ %.

However, the most important thing is that Fig. 4 shows the time that elapsed in the observed cycle interval of dormancy at 0.5°C. It is seen that 50 % of the viable seeds progressed from dormancy to the active period in 7.7 days after the beginning of the treatment. Since the beginning of the treatment was the starting point of the cycle interval under investigation, the average length of the entire cycle interval in question at this temperature is thus 7.7 days.

Without doubt, the rate of progress of dormancy in seeds also depends on environmental factors other than temperature. The moisture content of the seed, for instance, is of particular significance (cf., for example, Hari and Lehtiniemi 1972). In carrying out the present experiments, an effort was made to eliminate this effect by keeping the humidity close to the optimal level. It is possible, however, that these attempts were not altogether successful. The considerable variation that occurred between the different replicates of a certain treatment may have been due to differences in humidity.

The great significance of humidity should also be considered when the experimental results obtained here are applied to phenomena occurring in natural conditions. In the autumn and winter, when, from the point of view of temperature, dormancy in seeds has every chance to progress, the moisture content of the seed of several tree species is low. For instance, measurements

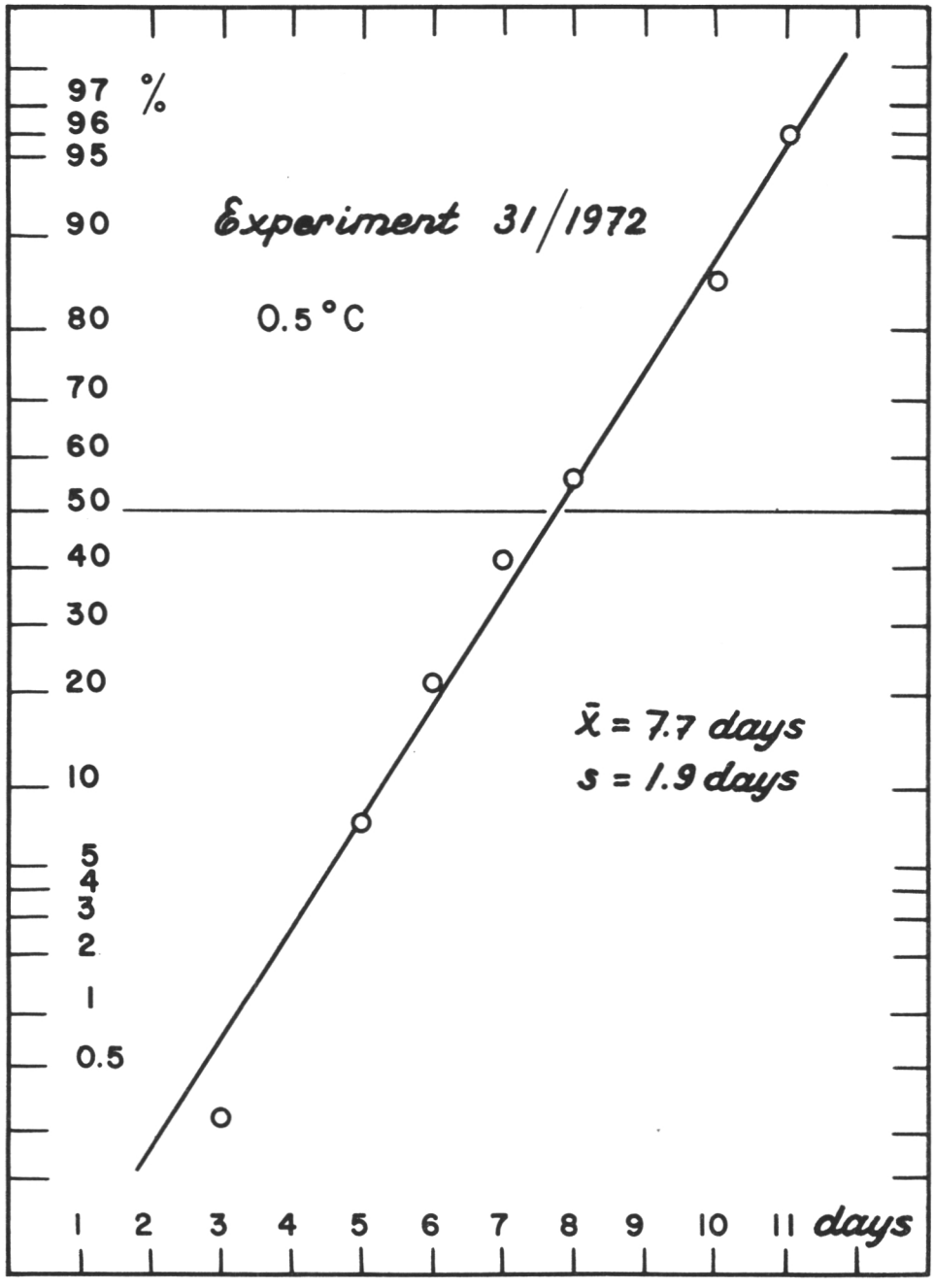


Fig. 4. The regression of the cumulative percentage of seeds that have passed through dormancy on the treatment period (at 0.5°C). The graph is drawn on frequency paper. The horizontal axis shows the treatment period and the vertical axis the percentage of the viable seeds that have germinated, following treatment, after exposure to a constant temperature of 17°C for 3 weeks. The seed: *Betula pubescens*, tree No. L, Punkaharju, collected in autumn 1970.

carried out at Punkaharju on October 13, 1971, indicate that the moisture content of seeds of *Pinus sylvestris* was only 9.5 %. Therefore, under natural conditions dormancy in seeds cannot be expected to progress as rapidly as it would if temperature were the only factor affecting progress.

In the foregoing, the progress of dormancy in seeds has been examined only at relatively low temperatures ranging between —1° and 20°C. It is well known, however, that high temperatures also release dormancy in seeds. Pilot tests made in the course of the present study indicate that when *Betula pubescens* seeds are exposed to temperatures above 23°C, dormancy can be overcome within about 24 hours.

The dependence of the progress of dormancy in seeds on temperature was investigated in five separate experiments conducted with *Betula pubescens* seeds. The results are compiled in Table 3. The results of calculations of the rate of progress of dormancy are also compiled in this table; they will be discussed later.

Experiments with seedlings

Dormancy can be investigated in seedlings, as in seeds, under controlled environmental conditions, without separating the experimental material from a whole to which it organically belongs, as happens, for instance, when cut twigs are studied. Of course, very possibly, perhaps even probably, the general pattern of dormancy I in the buds of small seedlings differs in many respects from the pattern displayed by seeds or by buds of mature trees; but another possibility is that the pattern is essentially similar in all these living cellular tissues. Before we resort to more complicated models, this last-mentioned possibility has to be tested.

The experiments with seedlings were arranged largely in the same way as those with seeds and the exposure of these two types of material to different constant temperatures was partly carried out simultaneously in the same incubators. After treatment the seedlings were grown in prickle boxes (natural light) in a greenhouse where the temperature fluctuated between 15° and 19°C.

In the experiments, balled seedlings 2—3 dm in lenght were used. Those of Scots pine were 1M + 1A [1]) roll seedlings and those of Norway spruce and birch were 1M + 1A paper pot seedlings. Before the experiments, the seedlings were stored in a greenhouse where, at a height of 1.5 m, the temperature fluctuated between 12° and 16°C. Unfortunately, during this 4-month period they were placed on the floor, where the temperature was lower. As a consequence, dormancy I in the buds had already progressed farther than was desirable at the start of the experiment.

[1]) 1M + 1A = plants grown one season in a plastic greenhouse and one year outdoors.

Table 3. Results of experiments clarifying the rate of progress of dormancy in seeds. The initial point of the cycle interval investigated ($d_1 \rightarrow d_2$) is that phase of dormancy which 50 % of the seed had passed through at the start of the experiment, and the end point is that phase at which 50 % of the seed had passed from dormancy to the active period.

No. of experiment	Relative humidity %	Illumination		Experiment began on	Treatment temperature °C	$d_1 \rightarrow d_2$ cycle interval, days		S	v (T) = $h_{3.5}/h_T$, ch.u./h.
		hrs.	lux			$h_{3.5}$	h_T		
Seed: *Betula pubescens*, Punkaharju, tree No. *a*, 1970									
31	75	8	1 300	9. 3. 72	0.5	5.0	7.6	1.9	0.66
					1.6	5.0	6.6	1.7	0.76
					4.0	5.0	5.1	1.2	0.98
					4.6	5.0	6.1	1.6	0.82
					7.0	5.0	9.7	2.6	0.52
					7.9	5.0	14.6	3.7	0.34
					10.3	5.0	—	—	0.0
32	80	8	3 000	13. 4. 72	—1.0	4.8	14.4	5.0	0.33
					3.1	4.8	5.2	1.5	0.93
					6.9	4.8	7.5	2.2	0.64
33	85	10	3 000	8. 5. 72	6.6	4.8	10.4	4.1	0.46
					7.3	4.8	11.7	4.5	0.41
Seed: *Betula pubescens*, Punkaharju, tree No. *a*, 1970, remaining seed lot									
34	85	10	3 000	29. 6. 72	3.6	4.8	4.8	3.0	1.0
					4.8	4.8	5.4	3.4	0.89
					7.8	4.8	11.3	7.5	0.43
					8.3	4.8	14.5	9.7	0.33
					9.0	4.8	46.5	32.0	0.10
Seed: *Betula pubescens*, Punkaharju, Sample stand No. L, random sampling of 7 trees, 1971									
35	85	10	4 000	28. 7. 72	4.0	4.8	4.9	3.3	0.98
					5.2	4.8	5.8	4.2	0.83
					6.5	4.8	7.5	5.3	0.64
					8.3	4.8	15.0	10.4	0.32
					9.2	4.8	22.5	15.4	0.21

When placed in the incubators for treatment the seedlings were almost bare-rooted, with their roots between damp sheets of newspaper. For forcing, the seedlings, planted in boxes containing fertilized (NKP fertilizer) milled peat, were placed on a table in the greenhouse. The seedlings were sprayed with water twice a day and inspected at the same time. As a rule, their development was slow.

The first experiment, carried out with *Betula pubescens* seedlings, began on February 1, 1972. The buds started to flush at the beginning of March. However, accurate dating of the flushing of the buds proved difficult and, therefore, a later developmental phase was used, the date when the annual

shoot reached a length of 1 cm. That is to say, if the shoot was less than 1 cm long, the observation was assigned a minus sign, and if its length was 1 cm or more, the observation was given a plus sign.

The observations were then treated in the same way as in the experiments with seeds. Frequency paper was used to determine the length of treatment time required at each temperature for the cumulative percentage of plus observations to rise to 50 % when the forcing time had been sufficiently long (about 1 month).

The results of this first pilot experiment are seen in Table 4. They will be examined in subsequent pages in connection with a consideration of all the results concerning the progress of dormancy I.

Table 4. Results of experiments on the rate of progress of dormancy I in the buds of seedlings. The initial point of the cycle interval investigated ($d_1 \rightarrow d_2$) is that phase of dormancy I which 50 % of the buds of the seedlings had passed through at the time when the experiment was begun, and the end point is that phase in which 50 % of the buds of the seedlings had passed from dormancy I to dormancy II.

No. of experiment	Relative humidity %	Illumination		Experiment began on	Treatment temperature °C	$d_1 \rightarrow d_2$, days		$v(T) = h_{3.5}/h_T$, ch.u./h
		hrs	lux			$h_{3.5}$	h_T	
Seedlings: *Betula pubescens*, origin Finland, Kolari								
6/72	80	8	1 500	1. 2. 72	1	2.0	4.0	0.5
					4		2.2	0.9
					6		2.9	0.7
					8		5.0	0.4
					12		—	—

Experiments with cut twigs

An attempt was also made to study the dependence of the rate of progress of dormancy I on temperature by experiments with twigs cut from mature trees. In fact, it was with such experiments that determination of the regression of the rate of progress of dormancy I on temperature was started.

However, the various difficulties that arose during these early experiments thwarted these attempts. The treatment had no effect at all on the development of either the vegetative or the flower buds.

Even now it is not clear what actually caused the failure of the experiments. A contributory factor was, without doubt, the unavoidable length of the experiment, as the small twigs did not remain vigorous till the end. With our greatly improved knowledge, these experiments could probably now be repeated in an essentially better way. Another possibility is that dormancy I only progresses if organic unity with the mother tree is pre-

served. The fact that the experiments made with large twigs were more successful than those carried out with small twigs lends support to this view.

This last-mentioned observation prompted the use of methods in which the material tested was not separated from the whole organism. Two alternatives were possible. Either 1. The experiments had to be made outdoors at the tops of standing trees by enclosing tips of branches in small incubators, or 2. The material chosen had to be so small that it could be placed, in its entirety, in growth chambers or incubators. In the present study, experiments were continued with seeds and seedlings.

Synthesis of experimental results

The limitation inherent in the unit of the cycle interval (the unit is different for each individual genotype) will have to be kept in mind when we proceed to combine the results on pages 23—27. Another thing to be remembered is that the different experiments did not relate to the same cycle interval. The end points of the cycle intervals investigated were, it is true, the same in all the experiments, i.e. the end point of dormancy I, but the starting points were different. These difficulties are overcome by expressing the experimental results in units of the rate of progress of dormancy I, which can then be combined. The combining is best done graphically, as in Fig. 5. The horizontal axis shows the constant temperatures from —4° to 12°C, and the vertical axis the rate of progress of dormancy I (ch.u./h.). All the values are for *Betula pubescens*. The oblique crosses refer to experiments with seeds and the circles to experiments with seedlings.

In shape, the free-hand curve fitted to the points resembles a normal frequency distribution. The most significant observation emerging from the experiments concerning dormancy I is that the scatter of points can be represented by a single curve of regular form, even though the experiments covered different genotypes of the species and different cycle intervals. This observation suggests that the regression of the rate of progress of dormancy I on temperature (Fig. 5) may have a fairly wide range of application. This view is further substantiated by those many empirical results (cf., e.g., Lamb 1948, Kriebel and Wang 1962, p. 127, Tumanov et al. 1964, Nienstaedt 1966, p. 374, and Wareing and Phillips 1973, p. 230) which have led to the conclusion that the release of dormancy I occurs only at temperatures below 10°C and reaches its maximum between 3—4°C. It should further be noted that the rates of progress of dormancy I measured in the seedling experiments do not deviate significantly from those measured in the seed experiments.

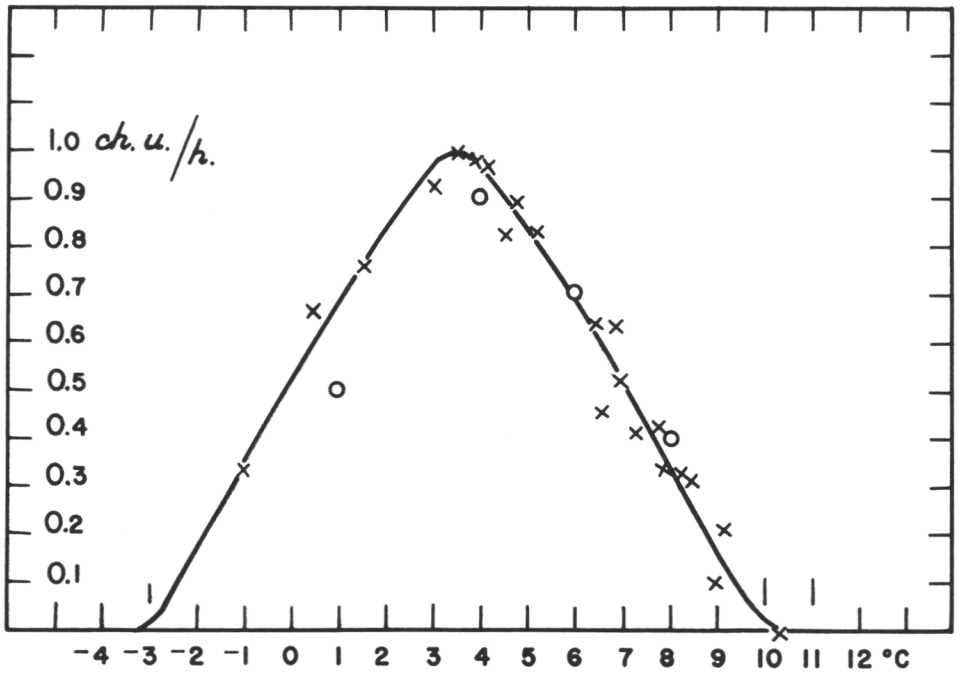


Fig. 5. Regression of the rate of progress (ch.u./h) of dormancy I on temperature (°C). All the experiments were made with *Betula pubescens*. The points denoted by oblique crosses refer to experiments with seeds and those denoted by circles to experiments with seedlings.

The diagram in Fig. 5 also shows some significant new features: the general shape of the curve is a typical optimal one. The peak is at ca. 3.5°C and from there the curve declines surprisingly steeply to left and right. Several previous authors have expressed the view that within a given temperature range the rate of release of dormancy I (true dormancy) does not depend on temperature. This view embodies the notion of certain temperature thresholds. The regression in Fig. 5 shows no evidence of thresholds. In addition, it reveals that at temperatures between —3° and 10°C the rate of progress of dormancy I depends strongly on temperature.

On the other hand, the data on which the regression is based are admittedly still scanty in many respects. Investigations will have to be continued with several different tree species and over periods that include all the different phases of dormancy I. This will take time and money.

Fig. 5 gives an accurate picture of the rate of progress of dormancy I at different constant temperatures between —4.0° and 10°C. Since these rates of progress are needed for a number of purposes, they are shown in Table 5 in respect of each full degree and each tenth of a degree. The cycle interval occupied by any phase during dormancy I can now, with the aid of Table 5,

Table 5. The rate of progress of dormancy I at different constant temperatures.

Full degrees C	Tenths of degrees, C									
	0	1	2	3	4	5	6	7	8	9
	Ch.u./h.									
—3	0.03	0.02	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.00
—2	0.17	0.15	0.13	0.12	0.10	0.09	0.07	0.06	0.05	0.04
—1	0.34	0.33	0.31	0.29	0.27	0.26	0.24	0.22	0.20	0.18
—0	0.52	0.50	0.48	0.47	0.45	0.43	0.41	0.39	0.37	0.36
0	0.52	0.54	0.56	0.57	0.59	0.61	0.62	0.64	0.66	0.67
1	0.69	0.70	0.72	0.73	0.75	0.76	0.77	0.79	0.80	0.82
2	0.83	0.85	0.86	0.87	0.89	0.90	0.91	0.93	0.94	0.95
3	0.96	0.98	0.99	0.99	1.00	1.00	1.00	0.99	0.99	0.98
4	0.96	0.95	0.94	0.93	0.91	0.90	0.89	0.87	0.86	0.85
5	0.83	0.82	0.80	0.79	0.77	0.76	0.75	0.73	0.72	0.70
6	0.69	0.67	0.66	0.64	0.62	0.61	0.59	0.57	0.56	0.54
7	0.52	0.50	0.48	0.47	0.45	0.43	0.41	0.39	0.37	0.36
8	0.34	0.33	0.31	0.29	0.27	0.26	0.24	0.22	0.20	0.18
9	0.17	0.15	0.13	0.12	0.10	0.09	0.07	0.06	0.05	0.04
10	0.03	0.02	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.00

be expressed in chilling units. It is only necessary to know the time required for dormancy I to pass through this phase at a given constant temperature. If, for instance, when a certain seed lot has been treated for 7.7 days at 0.5°C, 50 % of the seeds have passed from dormancy to the active period, the cycle interval for the phase under investigation (from the physiological state of the seed when the experiment was begun to the end of dormancy), expressed in chilling units, is $0.6 \cdot 7.7 \cdot 24 = 111$ ch.u. The same result will be obtained at all the other treatment temperatures between —3° and 9°C. The result will be the same even if the temperature fluctuates, as it generally does in a natural environment. In this case, the time has to be divided into periods (preferably of equal length) so short that during each of them the temperature is practically constant. If the time is divided into 1-hour periods, the cycle interval occupied by a given phase of dormancy I, expressed in chilling units, is obtained directly by summing up the rates of progress of dormancy I corresponding to the mean temperature of each hour (Table 5). In fact, all the ch.u. sums presented in this study have been reckoned in this way.

Thus we have clarified the environmental factor responsible for operating the innate physiological clock during dormancy I, and with this knowledge the progress of dormancy I can be simulated, provided that, under the conditions prevailing, the moisture content of the meristems remains about optimal. However, as regards the accuracy of temperature measurements, simulation of dormancy I is even more demanding than simulation of the active period. This is because the entire progress of dormancy I occurs within such a narrow temperature range that fluctuations in temperature

Table 6. Moisture content of male flower catkins of *Alnus incana*. Punkaharju, sample stand LXII, tree No. 181.

Date	Water %	Date	Water %	Date	Water %
1971		6. 9	67	8. 2	54
14. 1	57	14	65	17	55
21	57	21	63	23	56
28	61	28	60	29	54
4. 2	59	5. 10	57	8. 3	48
11	60	12	57	14	54
18	58	19	57	21	49
25	58	26	58	28	55
4. 3	58	2. 11	59	4. 4	55
11	57	9	56	11	64
18	58	16	55	19 [1]	42
25	58	23	57	25	37
31	61	1972			
7. 4	66	3. 1	55		
15 [1]	69	11	53		
22	58	18	55		
26	31	25	55		
29	25	1. 2	55		

[1]) Onset of anthesis.

of even 1 or 2 degrees bring about significant changes in the rate of progress. In fact, measurements have revealed that if simulation is to succeed at all, the temperature must be measured quite close to the material tested; the best results are obtained when the temperature is measured inside the organ (e.g. the bud) investigated.

The progress of the entire cycle is largely made up of physiological phenomena in the apical and lateral meristems. Those good services which the physiological clock simulating the progress of the active period has afforded without our paying much attention to the moisture factor, suggest that, during the active period, the moisture content in the apical as well as the lateral meristems of forest trees is kept close to the optimal level. Whether this is also true during dormancy I remains, for the time being, uncertain. For instance, measurements of fluctuations in the moisture content of male flower catkins of alder (Table 6) suggest that this may not be the case. (At the same time, however, attention is attracted by the fact that throughout the autumn, winter and spring, fluctuations in the moisture content are small, significant changes only taking place just before flowering). Measurement of the moisture content of the meristematic cells themselves is hardly feasible. Thus, in applying the concept of the physiological clock to dormancy, it is well to bear in mind that the moisture factor may complicate the picture.

Length of dormancy I

Although the exact end-point of the active period has proved difficult to determine, conclusions regarding the start of progress of dormancy I can nevertheless be drawn. This is because when the active period terminates, particularly in summers that are warmer than average, the apical meristems remain at the zero point of dormancy I until the temperature drops below 10°C. From this it further follows that, particularly in autumns that follow warm summers, the cumulative chilling unit sum (reckoned from the middle of August, for example) closely corresponds to the progress of dormancy I.

For instance, the experiments described above (pp. 11—13) involving twigs that were brought into the greenhouse (17°C) for the purpose of forcing, reveal that in 1970 when the first lot of twigs was brought in (Sept. 28, cf. Table 1, p. 12), dormancy I had already progressed 180 ch. u., and in 1972 (Sept. 26, cf. Table 2, p. 13), 109 ch.u. On the other hand, since we can determine from Tables 1 and 2 the approximate date (and the ch.u. sum, too) at which dormancy I had come to an end, it is possible to draw at least tentative conclusions about the total length of dormancy I.

By combining the information contained in Tables 1 and 2 the following approximate values are obtained (the tree species are listed in alphabetical order):

Abies sibirica, origin unknown; Punkaharju 45	540 ch.u.
Alnus incana, local origin; Punkaharju LXII	420 »
Betula papyrifera var. neoalaskana, origin Canada, Alta., Cooking Lake; Punkaharju 118	310 »
Betula pubescens, local origin; Punkaharju XIV	420 »
Betula verrucosa, local origin; Punkaharju LIV	400 »
Larix decidua, origin unknown; Punkaharju 80	140 »
Larix Gmelini, origin RSFSR, Sakhalin; Punkaharju 9	190 »
Larix sibirica, origin unknown; Punkaharju 49	150 »
Picea Abies, origin Finland, Lammi; Punkaharju LII	420 »
Populus tremula, local origin; near Punkaharju	630 »

In a subsequent section, in which the cycle model constructed in the course of this study is compared to natural phenomena, the total length of dormancy I will be re-examined, and revised and more exact data (Table 13, pp. 71— 72) on it will be furnished.

Dormancy II

Definition of concepts and working hypothesis

Investigation of dormancy II has been based on the observation, made in the course of the pilot study (S a r v a s 1970), that the dependence of the progress of dormancy on temperature is not the same in the earlier and later phases of this stage. This simple observation raised two questions: 1. What is the relation between the progress of the cycle and temperature in the latter part of dormancy and 2. How far back, starting from the end of dormancy, does the regression of the rate of progress of dormancy on temperature stay essentially the same. We immediately realize that the latter question also includes the problem of where to place the zero point of the second stage of dormancy.

In clarifying how the progress of dormancy II depends on temperature (and time) the same experimental technique can be used as in the investigation of the active period (S a r v a s 1970) and dormancy I.

As the unit of cycle interval in dormancy II let us choose that interval through which dormancy II progresses in 1 hour at a constant temperature of 2°C. The reason for defining the unit in this particular way is to have a unit that facilitates comparison with the active period. The unit of cycle interval in dormancy II is termed the dormancy unit (d.u.). If we express the time in hours, as we did in observing the active period and dormancy I, the rate of progress, v, is expressed in units of d.u./h. The calculation of the rate of progress can be based on the general equation (4), p. 6.

Experimental determination of the rate of progress of dormancy II

E x p e r i m e n t s w i t h L a r i x s i b i r i c a

In the investigation of dormancy great methodical difficulties are encountered in almost all phases. Reference has already been made to a difficulty that applies to the entire period of dormancy, namely that we do not yet know of a single physiological phase (cardinal phase) of dormancy marked by events from which it can readily be determined whether this phase has been passed through or not. On this account, practically everything we know

about dormancy is based on more or less indirect evidence. But, even if indirect evidence has to be accepted, the data used must be accurate. Consequently, every effort has to be made to find a physiological event which, from the point of view of research on dormancy, is comparatively easy to observe. For example, meiosis in the microspore mother cells of *Larix* species offers several suitable events.

In *Larix* species (including, at least, *L. sibirica*, *L. decidua*, *L. Gmelini* and *L. occidentalis*) meiosis in the microspore mother cells begins in the autumn at about the time when the needles begin to turn yellow but stops in the diplotene phase even when the weather is warm and environmental factors appear favourable for the continuance of meiosis. In natural populations, the microspore mother cells winter in diplotene and meiosis terminates in early spring. Obviously, on attaining diplotene, the mother cells become dormant (dormancy II [1]) and when they continue their development from diplotene to diakinesis dormancy is broken. This view is supported by the observation that while in diplotene, the mother cells are able to survive many degrees of frost, whereas before diplotene and particularly after it they are remarkably sensitive (cf., for instance, Eriksson 1968).

Let us assume that dormancy II terminates when the mother cells attain diakinesis. In other words, we consider that while in diplotene the mother cells are in dormancy II and while in diakinesis they are in the active period. In microscope preparations the line between diplotene and diakinesis is clear-cut with few transitional phases. Thus, we have an event by which we can determine with great accuracy whether or not dormancy II has terminated. Furthermore, *Larix* species offer the particular advantage over several other alternatives that at this stage the branchlets bearing male flower buds lack needles and are almost straight and unbranched, all of which greatly facilitates the handling of large quantities of twigs in small incubators. Dissecting out the pollen sacs from the microsporangiate buds is easy. The chromosomes are large enough to be observed under a microscope at fairly low magnification and yet not so large as to make observation difficult.

In investigations on how the rate of progress of dormancy II depends on time and temperature it is not necessary to observe the development of dormancy II from beginning to end, but rather the mother cells should be examined in one of the phases in the middle or at the end of dormancy II. This is an important methodical point, because it means that the experiments do not have to cover the whole of dormancy II (the longer lasting the experiment, the longer will the material tested be exposed to various disturbances and complications).

[1]) This stage of dormancy is expressly dormancy II — there is no need for exposure to low temperatures for progress to occur at this stage. Exceptionally, in *Larix* species the microspore mother cells pass through dormancy I before the onset of meiosis.

The procedure was so planned that each series of experiments comprised branchlets from a single tree. In this way genetic variation was eliminated but this did not mean that the material was uniform, for environmental variation (including topophytic variation) proved to be very great, as will be seen from the data below. The only way to overcome this variation was to take a large number of branchlets and mix them thoroughly before treatment. The number of twigs collected for one series of experiments had to be so large that about 20 male flower buds were available for every fixation. Each series, as a rule, comprised about 10 different treatment temperatures, and from each treatment at least 15 fixations were made. Thus the number of branchlets required for each experiment amounted to about 800—1 000. Often, this meant that all the branchlets of a tree had to be used.

At first, about 50 mother cells were investigated from each bud. In view of the variation within the bud, this number is too small to give a true picture of the situation in the bud. And yet, investigation of 50 mother cells per bud meant that about 100 000 mother cells had to be investigated in each series of experiments. Because it looked as if the investigation would come to a halt as a result of excessive microscopic work, the procedure was improved at an early phase of this investigation as follows. From each of the buds included in one fixation (20 buds) about the same number of pollen sacs were dissected out and combined into a squash. In this way the number of microscope slides involved was reduced to almost one-twentieth (to about 5 000 mother cells per series) of the number previously required.

Also, during the work it proved necessary to develop a method that ensured that the buds required for each experiment were definitely randomized. The buds on the basal half of the shoots were, as a rule, in more advanced developmental phases than those situated on the apical portion of the shoots. This particular aspect of the topophytic variation was the cause of most of the difficulties encountered in sampling.

As has become apparent from the foregoing, the different treatment temperatures were mostly produced by incubators. The temperature could be maintained at the desired level to within ± 0.5°C. The temperature was monitored continuously by means of a thermoelement attached to a multipoint recorder. On completion of the experiment, the mean temperature prevailing in the incubator during the treatment was calculated from the data obtained in this way to the nearest 0.1°C.

The relative humidity of the air was checked only by making occasional tests to ensure that it continued to be over 70 %. There was no illumination in the incubators. Thus, except for a few comparative experiments made in artificial light (3 000 lux), the experiments were carried out in almost total darkness.

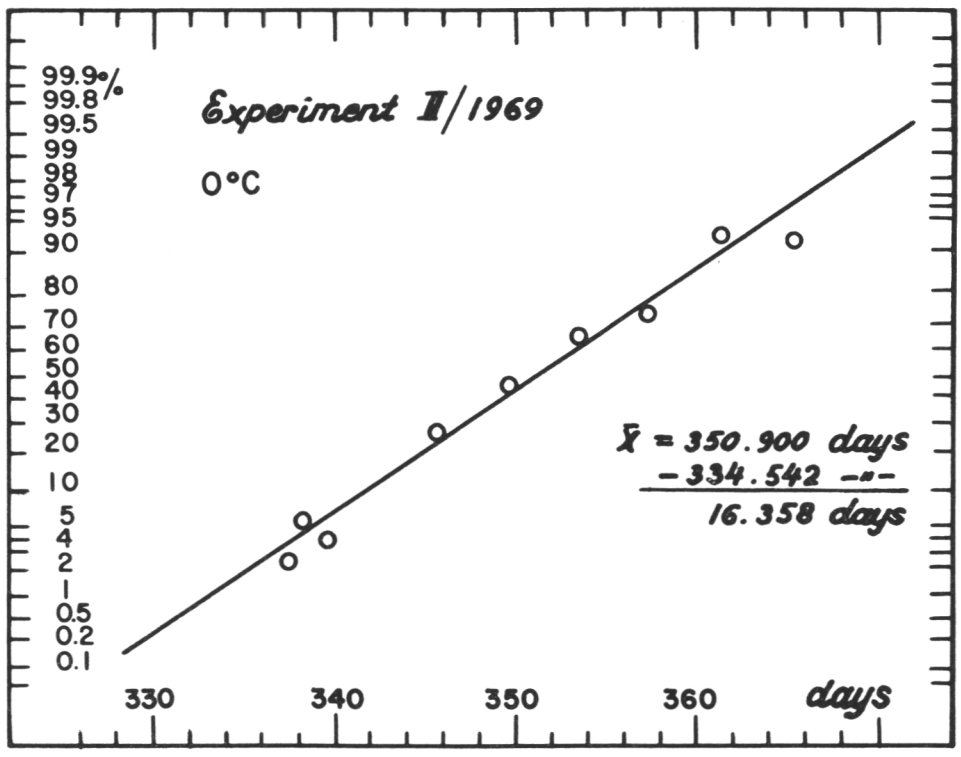


Fig. 6. An example of how the lapse of time at 0°C for progress through a certain cycle interval of dormancy II was reckoned in microspore mother cells of *Larix sibirica*. The beginning point of the cycle interval investigated was that particular phase of dormancy II through which 50 % of the mother cells had passed when the experiment was started, and the end point was the diakinesis phase of meiosis. The experiment was started at 334.542 days.

The branchlets were taken from trees in winter when temperature was fluctuating between —5° and —10°C. Therefore, before they were placed in the final treatment temperatures, they were gradually warmed up to about 2°C. This pretreatment lasted 1—2 days.

The microscope results were plotted on frequency paper. The horizontal axis shows the treatment period and the vertical axis indicates the total percentage of the mother cells in the fixation concerned that were in different postdiplotene phases (i.e. the cumulative frequency of attainment of diakinesis). Calculation of the treatment periods and the plotting of the data obtained on frequency paper were made much easier by using decimal time (full days counted from the beginning of the year, with hours and minutes expressed as decimal parts of 24 hours to 3 decimal places) instead of calendar time. As an illustration of this procedure, the data obtained concerning microspore mother cells treated at $\pm$0°C are shown in Fig. 6.

Table 7. The rate of progress of dormancy II at different constant temperatures. The experiments were made with the microspore mother cells of *Larix sibirica*. The initial point of the cycle interval (d_1 — — d_2) investigated in each experiment was that particular phase of dormancy II through which 50 % of the mother cells had passed when the experiment was begun, and the end point that particular phase of meiosis at which 50 % of the mother cells had passed beyond diplotene. Experiment I was begun on December 1, 1969, at 13.00 (334.542 days), experiment II on March 2, 1970, at 15.55 (60.663 days), and experiment III on March 6, 1970, at 7.40 (64.319 days).

Experiment I

Treatment temperatures, °C									
0.10	1.9	2.2	4.0	4.3	5.2	6.7	7.2	8.2	10.0
Lapse of time in the cycle interval, days									
16.36	13.26	11.76	9.31	6.86	7.06	5.86	5.51	3.74	3.46
v, d.u./h.									
0.85	1.06	1.19	1.50	2.08	1.98	2.39	2.54	3.74	4.40

Experiment II

Treatment temperatures, °C					
2.5	4.1	5.8	11.2	13.6	17.6
Lapse of time in the cycle interval, days					
8.348	6.948	5.348	2.647	2.687	1.824
v, d.u./h.					
1.444	1.735	2.276	4.550	4.510	6.600

Experiment III

Treatment temperatures, °C			
5.0	11.2	13.8	25.9
Lapse of time in the cycle interval, days			
5.72	2.201	2.081	1.138
v, d.u./h.			
2.0	4.49	4.56	8.69

The scatter of points has been fitted with a free-hand straight line, from which it is easy to read with great accuracy the time required for 50 % of the mother cells to progress to postdiplotene. It can be seen that 50 % was attained at 350.900 days (counted from 0.00 hours on January 1). The experiment was begun at 334.542 days; the treatment time required for 50 % of the mother cells to progress to postdiplotene is thus 350.900—334.542 = 16.358 days.

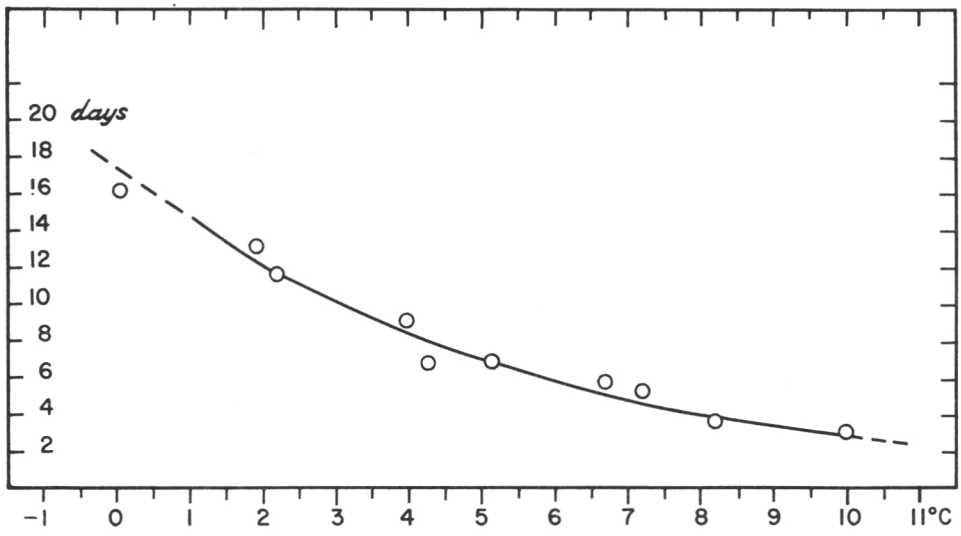


Fig. 7. The lapse of time at different constant temperatures in a given cycle interval. The experiment was made with the microspore mother cells of *Larix sibirica*. The initial point of the cycle interval investigated is that particular phase of dormancy II through which 50 % of the mother cells had passed when the experiment was started and the end point that particular phase in which 50 % of the mother cells had passed beyond the diplotene phase of meiosis. The experiment was started on December 1, 1969.

The results of all the treatments have been obtained in this way. They are seen in Table 7 (this table also includes the corresponding rates of progress of dormancy II, which will be reviewed in subsequent pages).

Let us now recall the definition of the cycle interval of dormancy II: the unit interval of dormancy II is the cycle interval through which dormancy II progresses in one hour at 2°C. However, none of the treatment temperatures of the experiment described here was exactly 2°C. The time required for the progress of dormancy II at a temperature of exactly 2°C can be found by plotting the experimental results graphically. This is also beneficial, because the graph illustrates the variation within the series. The free-hand curve fitting the points is shown in Fig. 7. From this it appears that at 2.0°C the time required for dormancy II to terminate is 12.1 days = 290.4 hours. We now denote the rate of progress of dormancy II at 2°C by 1.0. As is easily seen, the rates of progress (d.u./h.) at other experimental temperatures can be obtained by dividing 290.4 by the times (expressed in hours) required to attain postdiplotene at these temperatures. The results for each of the three separate experiments are shown on the lowermost rows in the respective sections of Table 7.

The outcome was a surprise. When the experiment was begun, it was anticipated that at high temperatures the rate of progress of dormancy II

would be comparatively slow. The result indicated, however, that the opposite was true: the higher the temperature, the faster the progress of dormancy II.

Even a superficial comparison of the results in Table 7 indicates that where the temperature ranges overlap the results of the three experiments are reasonably consistent.

At the highest temperature, 25.9°C, disturbances occurred during meiosis, and caution is necessary in interpreting the results obtained. Furthermore, an experiment made at 2°C failed, because fixation was delayed, and as a result, the time required at 2.0°C had to be extrapolated from the results obtained in the two previous experiments.

Despite their deficiencies, the results of this series of »warm-weather» experiments are important. They indicate that high temperatures do not accelerate the progress of dormancy II nearly so effectively as they accelerate the progress of the active period. In natural habitats the progress of dormancy II in the microspore mother cells of *Larix sibirica* mostly occurs at temperatures below 15°C and, therefore, it is not surprising that the process should be disturbed at temperatures above 20°C.

To contrast with the set of warm-weather experiments, a set of particularly cold weather experiments was also conducted with the microspore mother cells of *Larix sibirica*. The temperatures involved were —10.9°, —2.8°, —1.3° and 5.0°C. The time required for dormancy II to terminate at 2°C, 11.0 days, was determined by interpolation. The experiments conducted at —10.9 and —2.8°C failed because, when dormancy II came to an end, the mother cells were badly injured, and were resorbed. (This does not, however, warrant the conclusion that the mother cells become injured at a temperature of —2.8°, for, as a result of the long treatment period, the temperature in the incubator unavoidably fluctuated between —3.7° and —1.2°C.) At —2.8°C, the time required for dormancy II to come to an end (50 %) was $24 \times 49.52 = 1\,189$ hours. The rate of progress was thus $(24 \times 11.0) : 24 \times 49.5 = 0.22$ d.u./hour.

Experiments with Alnus incana

It would be reasonable to suppose that in every tree species and even in every meristem of the same individual tree, the rate of progress of dormancy II depends in a different way on time and temperature. However, complying with the general principle adopted in this study, we shall start out from the simplest assumption possible, namely that the relationship is similar in every

case. Experiments were made in an effort to clarify whether or not this simple model should be replaced by a more complicated one. Experiments were conducted with *Alnus incana* expressly to elucidate this question.

In the natural habitats of *Alnus incana* the development of the microsporangiate catkins of this species is already so far advanced in the autumn that in the spring the pollen sacs of the anthers are ready to dehisce almost immediately after the release of dormancy II. Much earlier, when the tree is still in dormancy II, the catkins swell, their axes lengthen and fissures appear between the scales. It is fairly easy to decide for each catkin whether or not there are fissures between the scales in the mid-part of the catkin. In the following, catkins that have developed fissures are referred to as opened catkins. A microsporangiate catkin in which the scales had just become separated was preserved in 50 % alcohol and used as a criterion. Catkins in which the fissures were narrower were noted as minus observations and those with fissures equally wide or wider scored as plus. In a series of observations of this kind, the sum of the plus scores at each inspection indicates the frequency sum of opened catkins at that moment.

The experiments were arranged as follows. From a single tree of *Alnus incana* with abundant microsporangiate catkins, branchlets about 50 cm long were collected in the early spring of 1971. These were exposed, in groups with about 150 catkins, to 10 different constant temperatures. Thus, the total number of catkins required for one set of experiments was approximately 1 500. Before the treatments, all the branchlets to be used in the experiments were mixed thoroughly and laid out in a row. From the row, branchlets were picked at random to form 10 sets, each comprising the required number of catkins (about 150).

Thus, when the experiment began each set had, on the average, attained the same developmental phase of dormancy II. This phase (we have no exact knowledge of it, but this is immaterial) was thus the starting point of the cycle interval to be measured. The end point was the phase of dormancy II at which 50 % of the catkins had opened.

When the rate of progress of dormancy II is investigated, the opening of the male catkins of *Alnus* affords two significant methodical advantages as compared with *Larix:* observation is less laborious and inspection does not destroy the catkins. The latter advantage greatly enhances the efficiency of the experiment.

The twigs were brought indoors from about —10°C. They were first kept at —2°C for 24 hours and then taken to a room where the temperature was 2°C. The assorting was done in this room.

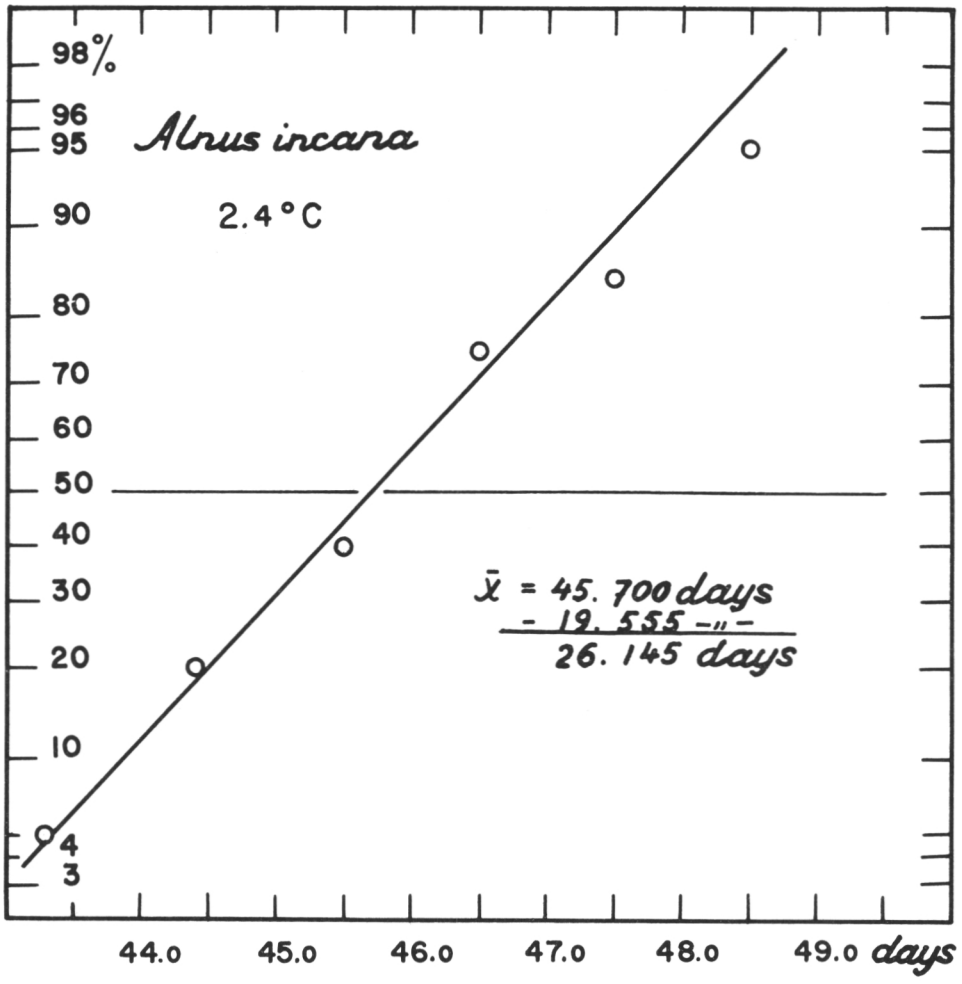


Fig. 8. Result of an experiment with *Alnus incana* at 2.4°C. The starting point of the cycle interval investigated was that particular phase of dormancy II passed through by 50 % of the microsporangiate catkins at the time the experiment was started and the end point that phase in which 50 % of the catkins displayed fissures. The experiment was started at 19.555 days in 1970. The lapse of time in the cycle interval investigated was 26.145 days.

The treatments were carried out in two separate series of experiments in the incubators used in the *Larix* experiments described above. The results were treated in the same manner as in the *Larix* experiments. Fig. 8 is presented as an example of treatment of the data.

The results of experiments conducted with *Alnus incana* have been compiled in Table 8. In the next section they will be compared with the results of experiments conducted with *Larix sibirica*.

Table 8. Rate of progress, v, of dormancy II at different constant temperatures. The experiments were made with microsporangiate catkins of *Alnus incana*. In each experiment the starting point of the cycle interval ($d_1 \rightarrow d_2$) investigated was that particular phase of dormancy II through which 50 % of the catkins had passed when the experiment started and the end point that phase in which 50 % of the catkins were opened. Experiment I was started on Jan. 20, 1970, at 12.30 (= 19.521 days) and experiment II on Feb. 13, 1970, at 9.10 (= 43.382 days).

Experiment I

Treatment temperatures, °C			
2.4	3.6	6.7	11.5
Lapse of time in the cycle interval, days			
26.15	19.17	10.23	5.77
v, d.u./h.			
1.09	1.50	2.81	5.0

Experiment II

Treatment temperatures, °C						
0.0	2.7	3.8	5.5	11.1	12.3	17.1
Lapse of time in the cycle interval, days						
31.66	15.95	10.95	9.07	4.45	3.88	2.75
v, d.u./h.						
0.594	1.18	1.72	2.07	4.22	4.84	6.84

Synthesis of experimental results

Data from the experiments conducted with *Larix sibirica* and *Alnus incana* were synthesized graphically. The rates of progress of dormancy II, v (d.u./hour), calculated from the experimental results, have been plotted against temperature (Fig. 9). It is seen that the data for these two tree species can be represented by the same curve. This is an important observation, for it signifies that the data obtained are compatible with the simple working hypothesis advanced at the beginning, namely, that for several or, perhaps, many tree species the rate of progress of dormancy II depends in a similar manner on temperature.

It can further be seen that the regression of the rate of progress of dormancy II on temperature resembles the corresponding regression in the active period (cf. Sarvas 1972, p. 31). Particularly, at temperatures below 8°C, the regressions are almost identical. At higher temperatures, dormancy II seems to progress at a slower rate than the active period. The number of experimental results obtained at high temperatures is comparatively small and, therefore, it remains somewhat uncertain whether this difference between dormancy II and the active period is due merely to shortcomings of the experimental methods.

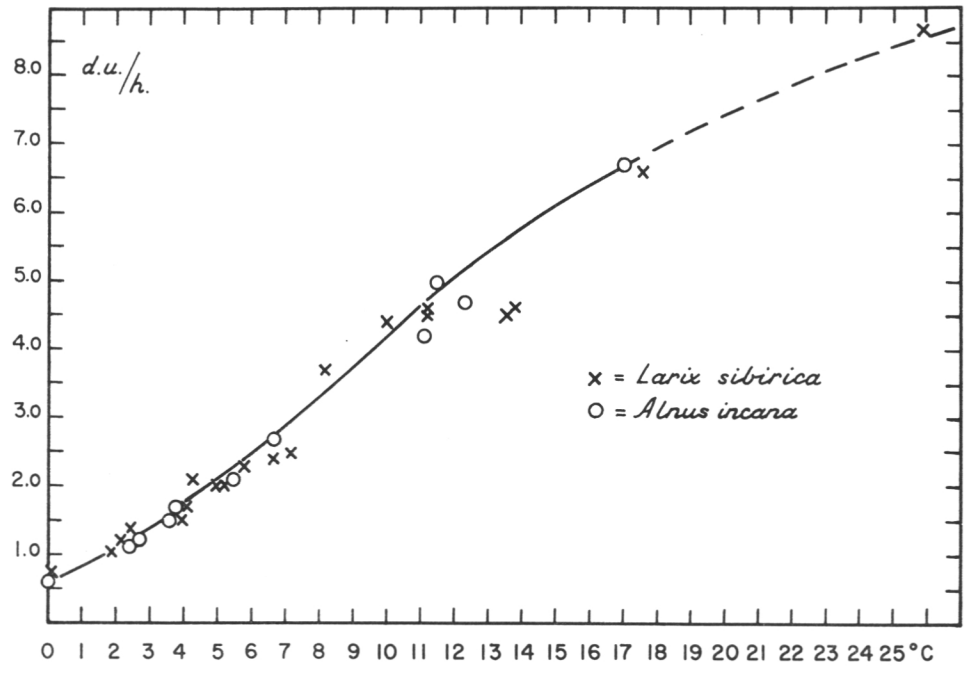


Fig. 9. The rate of progress of dormancy II, expressed in d.u./h., at different constant temperatures

This last-mentioned question was elucidated to some extent by the *Larix* experiments. In these experiments, meiosis in the microspore mother cells was observed not only until the mother cells had passed through dormancy II (the diplotene phase) but till the tetrad phase. Since the p.u. sum required for the active period of *Larix sibirica* to progress from diakinesis to the tetrad phase had been clarified in the investigations on the active period, it could now be tested whether, in the experiments concerning the progress of dormancy II, meiosis had progressed according to the normal rate for the active period once dormancy II (diplotene) was completed. This had indeed been the case.

In the Finnish climate the temperature is usually below 8°C during most of the time when the autochthonous tree species are in dormancy II. However, almost every year the temperature rises transiently above 8°C during this period, and remains high for a few hours or even a few days. Therefore, when high temperatures are involved accurate prediction of the end of dormancy II must be based on the regression shown in Fig. 9. For even handier reckoning, the rates of progress of dormancy II at different constant temperatures are presented in Table 9 for every full degree and every tenth of a degree. These figures were obtained from the regression curve shown in Fig. 9.

Table 9. The rate of progress of dormancy II, d.u./h. at constant temperatures.

Full degrees C	Tenths of degrees, C									
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
	D.u./h.									
Below —3	0	0	0	0	0	0	0	0	0	0
—3	0.24	0.23	0.22	0.22	0.21	0.20	0.20	0.19	0.19	0.18
—2	0.32	0.31	0.31	0.29	0.28	0.28	0.27	0.26	0.25	0.25
—1	0.42	0.41	0.41	0.39	0.38	0.37	0.36	0.35	0.34	0.33
—0	0.57	0.55	0.53	0.52	0.50	0.49	0.48	0.46	0.45	0.43
+0	0.57	0.59	0.60	0.63	0.64	0.66	0.67	0.69	0.71	0.73
1	0.76	0.77	0.78	0.81	0.84	0.85	0.87	0.91	0.94	0.97
2	1.00	1.01	1.02	1.05	1.08	1.11	1.12	1.13	1.18	1.23
3	1.25	1.27	1.29	1.33	1.39	1.40	1.43	1.46	1.48	1.51
4	1.57	1.60	1.62	1.68	1.71	1.76	1.79	1.85	1.88	1.90
5	1.96	1.99	2.02	2.07	2.13	2.18	2.21	2.27	2.30	2.35
6	2.41	2.44	2.52	2.55	2.60	2.66	2.72	2.77	2.83	2.88
7	2.91	3.00	3.05	3.11	3.16	3.25	3.30	3.36	3.39	3.47
8	3.51	3.26	3.62	3.70	3.75	3.83	3.88	3.92	4.00	4.06
9	4.12	4.18	4.23	4.28	4.34	4.40	4.45	4.50	4.55	4.61
10	4.66	4.71	4.76	4.81	4.86	4.91	4.96	5.01	5.06	5.10
11	5.14	5.19	5.23	5.28	5.32	5.36	5.40	5.44	5.48	5.52
12	5.55	5.59	5.63	5.66	5.70	5.73	5.76	5.79	5.82	5.86
13	5.89	5.91	5.94	5.97	5.99	6.02	6.05	6.07	6.10	6.12
14	6.15	6.17	6.19	6.22	6.24	6.26	6.29	6.31	6.34	6.36
15	6.38	6.40	6.42	6.44	6.46	6.48	6.50	6.53	6.55	6.57
16	6.58	6.60	6.62	6.64	6.66	6.68	6.69	6.71	6.73	6.75
17	6.76	6.78	6.79	6.81	6.83	6.84	6.86	6.87	6.89	6.90
18	6.92	6.93	6.95	6.96	6.98	6.99	7.00	7.02	7.04	7.06
Above 18. 9 .	7.06	7.06	7.06	7.06	7.06	7.06	7.06	7.06	7.06	7.06

Determination of the end of dormancy II

The beginning of dormancy II is identical with the end of dormancy I, as has been stated above. Determination of the end of dormancy I, although often laborious, does not involve great methodical difficulties. The situation is different with regard to the end of dormancy II. According to the model of the cycle presented earlier, the active period begins immediately after dormancy II has terminated. But here we cannot avoid running into a difficulty, namely that the zero point of the active period has not as yet been resolved (cf. S a r v a s 1972, p. 72).

Only limited possibilities exist for accurate determination of the point at which dormancy II ends and the active period begins. In respect of the microspore mother cells of *Larix* species this is easy, for dormancy II appears to end in that physiological phase of development in which meiosis progresses from diplotene to diakinesis. Obviously, generally applicable biochemical methods would be the best (cf., e.g., K u p i l a - A h v e n n i e m i 1966 and the literature cited). However, as established in the previous section, in dormancy II and in the active period meristems react differently to high temperatures and it is this difference in their reaction that now provides the first generally applicable method, even though a laborious one.

Determination of the zero point can now take place as follows. Let us study the end of dormancy II in the microspore mother cells of *Picea Abies*. Easily determinable phases of dormancy II or of the active period would make suitable starting points. However, since none of the former phases are detectable, let us start from one belonging to the latter group, for instance, the metaphase I of meiosis. The investigation can be made at either the individual or the population level. In early spring, when the microspore mother cells are still in dormancy II, about 50 twigs 30—50 cm long, with abundant male flower buds, are taken from a *Picea Abies* tree (or subpopulation) to be investigated. The twigs are divided at random into two matched sets, one of which is forced at a high temperature (for instance, 18°C) and the other kept at a low temperature (for instance, 9°C). Development of the buds is followed by making observations from time to time. When meiosis sets in, regular fixing is begun. The »warm-weather» series is fixed at 12-hour intervals and the »cold-weather» series at 24-hour intervals, until metaphase I has been passed through in both series. Each fixation comprises about 20—30 buds which are prepared in one squash. From this squash some 300—500 mother cells are investigated. Whether metaphase I has been attained or not is determined for each mother cell. Those mother cells that are in this phase or have passed beyond it are given the plus sign and those that have not yet attained it, the minus sign. Each fixation shows the number of mother cells that have attained metaphase I and thus gives one frequency sum. All the frequency sums obtained in this way are plotted on frequency paper against the lapse of time between the beginning of the experiment and fixation, and lines are fitted to the points for the »warm-weather» and the »cold-weather» series. The average time required for the attainment of metaphase I can now be read accurately from the fitted lines. Let us denote these periods of time by t.

The rate of progress of dormancy II in the »warm-weather» series is denoted by d_1 and in the »cold-weather» series by d_2, and the corresponding rates of progress of the active period by a_1 and a_2. The time required for dormancy II to terminate in the »warm-weather» series is denoted by x_1 and in the »cold-weather» series by x_2. We now obtain the following two equations:

$$d_1 x_1 = d_2 x_2 \tag{4}$$

$$a_1 (t_1 - x_1) = a_2 (t_2 - x_2) \tag{5}$$

Both sides of the latter equation indicate, in terms of a p.u. sum, the cycle interval between the zero point of the active period and the metaphase I of meiosis, which is exactly what we wish to know. We can thus solve the pair of equations with regard to either side of the latter equation. The

result is (we denote the p.u. sum of the cycle interval between the zero point of the active period and metaphase I by $\triangle a$, and the d.u. sum of the cycle interval between the beginning point of the experiment and the zero point of the active period by $\triangle d$):

$$(6) \quad \triangle a = a_2 (t_2 - x_2) = a_1 a_2 \frac{(d_1 t_1 - d_2 t_2)}{d_1 a_2 - d_2 a_1}$$

After t_1 and t_2 have been determined experimentally, the right-hand side of the equation comprises only known values.

The pair of equations can, of course, also be solved for $d_2 x_2$ (the d.u. sum of the remaining dormancy II). We then obtain

$$(7) \quad \triangle d = d_2 x_2 = d_1 d_2 \frac{(a_2 t_2 - a_1 t_1)}{d_1 a_2 - d_2 a_1}$$

This method of calculation can be made even clearer by the following concrete example: The study was made on a stand of *Picea Abies*, No. LII, at Punkaharju Exp. Station (origin of seed Lammi). The investigation was carried out in winter 1970/71 at population level (10 randomized dominant trees). The temperatures were $T_1 = 9.9°$ and $T_2 = 18.1°C$. Forcing of branchlets was begun on January 18 at 16.40 h. In both series fixing was carried out about three times in 24 hours. Each time, 20 randomized male buds (2 buds from each tree) from each of the two treatments were fixed. One squash (comprising about the same number of pollen sacs from each of these 20 buds) was made from each fixing. From each squash, three preparations were made, and 300 mother cells were examined. These were selected by applying the line survey method (the width of the line was the same as the field of vision in the microscope). The results were treated graphically on frequency paper. The horizontal axis of the graph showed the time lapse (expressed in decimal time) between the beginning of forcing and the time of fixing, and the vertical axis the percentage of plus observations (the metaphase I or a later phase of meiosis). The two scatters of points were fitted with free - hand straight lines.

From these lines, at the 50 % ordinates, one could then read the average periods of times required to attain metaphase I. They were: $t_1 = 17.80$ days and $t_2 = 7.86$ days.

For the parameters employed in formula (6) we obtain the following values:

$a_1 = 4.93$ p.u. (Sarvas 1972, Table 7, p. 39)
$a_2 = 13.83$ p.u. (» » » » » »)
$d_1 = 4.61$ d.u. Table 9, p. 44

$d_2 = 6.93$ d.u. Table 9, p. 44
$t_1 = 17.80$ days
$t_2 = 7.86$ »

Calculations gave the following result: $\triangle a = 1\,526$ p.u.

To test the validity of this result let us study the time course of meiosis in the spring of 1970 in an individual tree of *Picea Abies* belonging to the same subpopulation (cf. S a r v a s 1972, p. 38, Fig. 15). Other observations showed that this particular tree was about average as regards the rate of progress of the active period.

In the *Picea Abies* subpopulation concerned, the screen p.u. sum (S a r v a s 1972, p. 57) of the cycle interval of the active period between the first observable signs of meiosis (phase B) and the metaphase I of meiosis is 1 120 p.u. (Phase B = condensation of chromatin in the cell nucleus; from phase B to leptotene about 350 p.u. and from leptotene to metaphase I about 770 p.u., totalling, from phase B to metaphase I, about 1 120 p.u.). Transformed to a bud p.u. sum (cf. S a r v a s 1972, p. 58), this is about 1 500 p.u. It is seen that this interval is about the same as that measured for the whole subpopulation between metaphase I and the zero point of the active period. From this we conclude that in the microspore mother cells of *Picea Abies*, the end of dormancy II coincides with the initial signs of meiosis. In *Larix* species meiosis is at an apparent standstill all through dormancy II, remaining in the diplotene phase. In *Picea Abies* in the autumn the active period of the microspore mother cells can be speculated to end in the phase immediately preceding meiosis. We have now achieved a significant methodical advance regarding the cycle investigation: in addition to *Larix* species, we can now, at least, in regard to the microspore mother cells of *Picea Abies* determine directly by microscopy when dormancy II has come to an end and the active period has begun. An interesting question is, of course, whether the other *Picea* species behave similarly.

Termination of dormancy II can also be viewed from within dormancy II. From formula (7), p. 46, it can be calculated how much is left (expressed as a d.u. sum) of dormancy II at a certain time when dormancy II is still in progress. Calculations of this kind are useful when the aim is to estimate the total length of dormancy II.

Length of dormancy II

Now that the beginning and end points of dormancy II are known, determination of the total length of dormancy II would not be expected to present much difficulty. In practice, however, there are still many problems to be overcome. All measurement techniques concerning the annual cycle

of development of forest trees are still subject to considerable shortcomings which lead to errors. For instance, attempts to measure bud temperature at canopy level with a degree of accuracy that satisfies the exacting requirements of physiology and statistical analysis encounter almost insurmountable difficulties. Owing to great variation between buds, the temperature must be measured in at least 5 buds. The measurements must be carried out accurately and regularly, without a single gap, all through the year. Any failure means a delay of one or several years. Another point to be borne in mind is that, as a result of geographical variation, the length of dormancy II probably varies considerably. From all this it follows that for the time being our information about the total length of dormancy II is only tentative. The methods of estimation are described below.

The total length of dormancy I (ch.u. sum) can be estimated roughly on the basis of the greenhouse experiments discussed earlier (p. 11). The results obtained in this way can furthermore be refined with a method that will be discussed in subsequent pages (pp. 66—73). Since dormancy I, in terms of calendar time, is short as compared with the other two main phases of the cycle, the cumulative errors associated with it are likely to be fairly small. Consequently, the end point of dormancy I or beginning point of dormancy II is the particular phase of the entire cycle that can be determined most accurately.

In experiments to determine the end point of dormancy II, the difficulties presented by different tree species vary in magnitude. The method of forcing described above produces good results only when the forcing period is not too long. With this method the end point of dormancy II in the microspore mother cells is much easier to determine e.g. in *Picea Abies* than in *Pinus sylvestris* and the results are more reliable. This determination is even more difficult in *Alnus* and *Betula* species. Below, *Picea Abies* is the first object of study.

The length of dormancy II can also be reckoned by a different method. It has already been established (p. 47) that in *Picea Abies* the end point of dormancy II coincides with the phase at which the microspore mother cells proceed to meiosis. This conclusion finds support in the observation that in this phase a great deal of starch accumulates in the mother cells (but disappears at the diplotene phase of meiosis, at latest). The appearance of starch can probably be interpreted as a visible sign that the protoplasm changes from the state specific to dormancy II to the state specific to the active period. Observations of the initiation of meiosis in the microspore mother cells of *Picea Abies* (as well as of many other tree species) have been carried out during several years and in many different localities as part of this investigation, and the results obtained can thus be used in calculations concerning the length of dormancy II.

Table 10. Data on the length of dormancy II. In each subpopulation (stand) 10 randomized trees were sampled.

Material	Dormancy II				Autumn	Spring	Total
	Onset		End				
	Year	Day, month	Year	Day, month	D.u. (in buds)		
Abies sibirica, origin unknown; Punkaharju 45							
Microspore mother cells	1972	29. 9.	1973	9. 4.	2 263	657	2 920
Alnus incana, local origin; Punkaharju LXII							
Starch in microspores	1970	9. 10.	1971	9. 4.	1 164	344	1 508
Leaf buds	1973	27. 9.	1974	16. 4.	1 402	1 198	2 600
Betula papyrifera var. neoalaskana, origin Canada, Alta., Cooking Lake; Punkaharju 118							
Starch in microspores	1970	3. 10.	1971	9. 5.	1 510	1 875	3 385
Betula pubescens, local origin; Punkaharju L							
Starch in microspores	1970	7. 10.	1971	9. 5.	1 331	1 950	3 281
Betula verrucosa, local origin; Punkaharju LIV							
Starch in microspores	1970	21. 10.	1971	21. 4.	1 531	1 520	3 051
Leaf buds	1973	17. 9.	1974	2. 4.	1 862	834	2 696
Juniperus communis, local origin; Punkaharju 38							
Microspore mother cells	1972	25. 9.	1973	31. 5.	2 522	4 370	6 892
Juniperus communis, local origin; Rovaniemi XXX							
Microspore mother cells	1971	31. 8.	1972	13. 6.	2 694	4 120	6 814
Larix decidua, origin unknown; Punkaharju 27							
Diplotene phase in microspore mother cells	1971	26. 10.	1972	12. 4.	629	655	1 284
	1972	1. 11.	1973	29. 3.	917	907	1 824
Leaf buds	1973	26. 9.	1974	27. 3.	1 368	557	1 925
Larix Gmelini, origin RSFSR., Sakhalin; Punkaharju 9							
Diplotene phase	1972	5. 10.	1972	3. 12.	960	—	960
Leaf buds	1973	26. 9.	1974	30. 1.	1 368	46	1 414
Larix sibirica, origin unknown; Punkaharju 49							
Diplotene phase in microspore mother cells	1972	14. 9.	1973	24. 3.	3 637	133	3 770
	1973	23. 8.	1973	21. 9.	2 776	—	2 776
Leaf buds	1973	10. 9.	1974	31. 3.	2 194	728	2 922
Picea Abies, origin Finland, Lammi; Punkaharju LII							
Microspore mother cells	1969	6. 10.	1970	4. 4.	1 840	1 190	3 030
» » »	1970	4. 10.	1971	27. 4.	1 428	1 340	2 768
» » »	1972	10. 10.	1973	18. 5.	1 656	1 400	3 056
Leaf buds	1973	23. 9.	1974	7. 4.	1 550	1 095	2 645
Picea Abies, local origin; Rovaniemi XVIII							
Microspore mother cells	1972	29. 9.	1973	11. 4.	933	764	1 697

Table 10. (contin.)

Material	Dormancy II				Autumn	Spring	Total
	Onset		End				
	Year	Day, month	Year	Day, month	D.u. (in buds)		
Picea Abies, local origin; Kittilä, Pallasjärvi IV							
Microspore mother cells	1972	18. 9.	1973	21. 5.	1 104	1 361	2 465
Picea Omorika, origin Serbia; Punkaharju 358							
Leaf buds	1973	14. 9.	1974	2. 4.	2 034	818	2 852
Pinus Banksiana, origin Canada, Saskatchewan; Punkaharju D 51							
Microspore mother cells	1972	20. 9.	1973	13. 5.	3 004	2 710	5 714
Pinus Cembra (probably var. *typica*), origin unknown; Punkaharju 100							
Microspore mother cells	1970	25. 9.	1971	2. 6.	1 787	5 200	6 987
Pinus contorta var. latifolia, origin Canada, Br.Col., Long Lake For. Res; Punkaharju 99							
Microspore mother cells	1972	29. 9.	1973	15. 5.	2 315	2 800	5 115
Pinus Mugo var. rostrata, origin Switzerland, Engadine; Punkaharju 235							
Microspore mother cells	1972	5. 10.	1973	22. 5.	1 979	3 750	5 729
Pinus Peuce, origin Bulgaria, Pirin Mts.; Punkaharju 306							
Microspore mother cells	1970	25. 9.	1971	3. 6.	1 765	5 700	7 465
Pinus sylvestris, local origin; Bromarv III							
Microspore mother cells	1972	30. 9.	1973	7. 5.	3 670	2 840	6 510
Pinus sylvestris, local origin; Punkaharju XLV							
Microspore mother cells	1970	26. 9.	1971	12. 5.	1 608	2 400	4 008
» » »	1971	15. 9.	1972	18. 5.	2 898	2 400	5 298
» » »	1972	30. 9.	1973	11. 5.	2 211	2 770	4 981
Pinus sylvestris, local origin; Rovaniemi XXIX							
Microspore mother cells	1971	31. 8.	1972	27. 5.	2 795	2 000	4 795
» » »	1972	2. 9.	1973	26. 5.	3 513	2 000	5 513
Pinus sylvestris, local origin, Kittilä; Pallasjärvi I							
Microspore mother cells	1972	31. 8.	1973		2 847	2 000	4 847
Populus tremula, local origin; Tuusula XXXIII							
Microspore mother cells	1964	1. 11.	1965	2. 4.	1 029	576	1 605
Leaf buds	1973	7. 10.	1974	25.2	$1\,16^{0}$	540	1 700
Quercus Robur, origin Finland, Bromarv, Framnäs; Punkaharju 90							
Microspore mother cells	1972	28. 9.	1973	20. 5.	2 343	3 353	5 696
Thuja occidentalis, origin Canada, Ontario; Punkaharju 19							
Microspore mother cells	1972	21. 9.	1973	8. 2.	2 936	80	3 016

The results obtained are compiled in Table 10. As regards *Picea*, *Abies* and *Larix* species, the results find support in determinations based on forcing at two different temperatures. For *Betula* and *Alnus* species, the calculations are based on the assumption that the first appearance of starch in the microspores in the spring marks the end of dormancy II.

From the compilation it can be seen that between the different tree species there are great differences in the length of dormancy II. This is true even of species growing autochthonously in the same locality.

In comparing different tree species with one another it should also be recognized at once that it is hardly advisable to study the lengths of dormancy I and dormancy II as separate entities. They seem to be inseparably coupled together and the integrated whole so formed has become adapted to the local climate. Furthermore, the greatly varying evolutionary backgrounds of the different tree species may also be of essential significance. Thus, for the time being, there can be little point in speculating on the ecogenetic significance of the differences between the lengths of dormancy II in the different tree species. Obviously, when comparisons are made between different populations of the same tree species, continentality and oceanity, to which reference is often made, are concepts too inexact to be useful. What is probably of decisive importance is the d.u. sum in the climatic cycle between the first warning (a certain ch.u. sum) of the approach of winter and the first intense frost (below —10°C). Another d.u. sum deserving notice is the one between the end of the actual winter (continuous freezing weather) and the last hard frosts.

INVESTIGATIONS IN NATURAL CONDITIONS

Introduction

When more information, particularly quantitative information, has accumulated regarding the annual cycle of forest trees, we shall stand a better chance of clarifying the extent to which natural phenomena conform to the model of the cycle constructed on the basis of experimental evidence.

Surprisingly, at the present moment, anthesis [1]), the male flowering of forest trees, is of interest in this respect. It has been shown earlier (S a r v a s 1970) that in dormancy II the regression of the rate of progress of the cycle on temperature closely resembles the corresponding regression in the active period; the most important difference found so far is that in dormancy II, at temperatures above 10°C, progress is slower than in the active period. However, during dormancy II, i.e. late in the autumn and early in the spring, the temperature seldom rises above 10°C. Hence, in natural conditions, there is generally little difference between the patterns of progress during dormancy II and during the active period. From this it follows that a study of anthesis cannot to any noteworthy degree elucidate dormancy II. On the other hand, the progress of dormancy I and the progress of the active period depend on temperature in very different ways: the rate of progress of dormancy I reaches its peak at low temperatures (1°—6°C), whereas the active period practically comes to a standstill at low temperatures. At high temperatures (above 10°C) the situation is reversed: dormancy I almost comes to a standstill, whereas the higher the temperature, the more rapidly the active period progresses.

The general pattern of cumulation of a ch.u. sum is visualized if we examine it by means of a graph on a scale where the horizontal axis shows the cumulative p.u. sum and the vertical axis the 24- or 12-hour ch.u. increments divided by the p.u. increments for the same lengths of time. Fig. 10 is an example of a graph of this kind.

[2]) The general situation in late summer and in autumn, in terms of period units and chilling units, can be illustrated by means of 30-year temperature

[1]) In this investigation the term anthesis refers only to male flowering, even though the original Greek word denotes flowering in general. Female flowering is referred to in this study by the term gynesis.

[2]) The text within brackets was inserted in a gap in the proof. It was written according to the notes of the author.

Table 11. General information on sample stands.

Location	Sample stand No.	Geographical		Altitude m.	Stand			
		Latitude	Longitude		Years when measured	Age years	Dominant height m.	Trees per ha
Abies sibirica Ledeb.								
Punkaharju	45	61°48.6′	29°18.4′	102	1967	76	20.0	584
Alnus incana (L.) Moench.								
Kerimäki	540	61°51.7′	29°17.9′	101	1967	49	17.3	688
Punkaharju	LXII	61°48.1′	29°18.3′	81	1967	41	15.4	545
Betula papyrifera var. neoalaskana (Sarg.) Raup.								
Punkaharju	118	61°50.0′	29°19.5′	83	1960	32	13.0	1 437
Betula pubescens Ehrh.								
Tuusula	12	60°21.6′	25°01.9′	45	1967	49	17.3	496
Punkaharju	XIV	61°48.8′	29°19.2′	85	1971	44	19.3	400
»	L	61°48.5′	29°19.5′	90	1967	67	20.1	320
»	LX	61°45.5′	29°20.0′	83	1967	41	16.7	624
Vilppula	153	62°02.8′	24°30.1′	120	1967	65	18.5	375
Rovaniemi	XVII	66°20.8′	26°37.5′	170	1967	120	14.3	554
Betula verrucosa Ehrh.								
Hammarland	III	60°14.4′	19°44.0′	10	1962	34	17.7	624
Bromarv	VI	60°02.8′	23°02.5′	5	1967	55	21.1	317
Helsinki, Ilmala	167	60°12.3′	24°54.9′	32	1961	56	19.9	
Kerimäki, K.	543	61°48.4′	29°24.5′	86	1967	63	24.9	332
Punkaharju	LIV	61°49.0′	29°17.9′	90	1967	56	23.9	197
Rovaniemi	XXI	66°21.3′	26°45.2′	114	1967	110	18.2	324
Corylus Avellana L.								
Punkaharju	I	61°48.7′	29°18.4′	90	1973		2.5	·
Juniperus communis L.								
Rovaniemi	XXX	66°20.5′	26°41.0′	230	1973	38	1.5	·
Larix decidua Mill.								
Punkaharju	27	61°48.4′	29°18.8′	90	1966	39	22.8	428
»	80	61°49.0′	29°17.9′	93	1968	92	32.7	171
Larix Gmelini (Rupr.) Litv.								
Punkaharju	9	61°48.4′	29°18.8′	90	1966	40	22.7	350
Larix sibirica Ledeb.								
Punkaharju	49	61°49.0′	29°18.4′	106	1968	77	26.5	192
Vilppula	16	62°04.1′	24°29.6′	165	1967	66	22.2	348
Picea Abies (L.) Karst.								
Bromarv	I	60°02.4′	23°02.4′	27	1967	123	26.8	297
Tuusula	XXX	60°21.3′	25°01.6′	53	1967	88	23.6	496
Punkaharju	LII	61°48.8′	29°19.5′	92	1967	93	23.3	515
Rovaniemi	XVIII	66°20.6′	26°40.4′	182	1967	124	18.7	632
Picea Omorika (Panĉic) Purkyne								
Punkaharju	358	61°48.6′	29°19.7′	90	1968	36	11.9	1 335
Pinus Cembra L.								
Punkaharju	100	61°48.8′	29°19.3′	88	1967	44	14.9	680

Location	Sample stand No.	Geographical		Altitude m.	Stand			
		Latitude	Longitude		Years when measured	Age years	Dominant height m.	Trees per ha
Pinus contorta var. latifolia S.Wats.								
Punkaharju	99	61°48.2′	29°19.7′	89	1972	47	21.4	575
Pinus Mugo var. rostrata (Ant.) Hoopes								
Punkaharju	235	61°48.6′	29°18.4′	105	1958	29	7.6	1 370
Pinus Peuce Griseb.								
Bromarv	40	60°02.2′	23°03.1′	40	1973	49	14.8	814
Punkaharju	306	61°48.4′	29°19.6′	88	1967	37	13.5	1 132
Pinus sylvestris L.								
Eckerö	I	60°11.4′	19°34.3′	33	1962	132	16.3	780
Bromarv	II	60°02.2′	23°02.9′	41	1967	81	17.4	372
»	III	60°02.9′	23°02.5′	35	1967	60	21.7	360
Tuusula	XXXII	60°21.3′	25°01.2′	70	1967	141	19.8	252
Heinola	566	61°07.1′	26°00.9′	133	1972	129	24.0	116
Punkaharju	I	61°48.0′	29°18.1′	91	1967	144	29.3	232
»	XLV	61°48.9′	29°18.3′	106	1967	116	22.2	328
Kerimäki	XX	61°50.7′	29°22.7′	99	1967	99	29.5	212
»	XXXIII	61°50.4′	29°22.7′	92	1967	152	24.4	264
Vilppula	2 a	62°03.8′	24°29.4′	130	1967	187	24.7	521
Kuorevesi	XXIII	62°01.4′	24°48.0′	110	1967	99	26.3	236
Kajaani	546	64°17.5′	27°40.6′	132	1967	136	21.2	212
Rovaniemi	XXVII	66°21.4′	26°44.2′	118	1967	109	22.8	376
»	XXIX	66°20.7′	26°38.3′	165	1966		21.2	196
Quercus Robur L.								
Punkaharju	90	61°48.8′	29°18.8′	96	1967	42	15.0	1 038
Thuja occidentalis L.								
Punkaharju	19	61°48.1′	29°18.1′	97	1968	43	8.0	155

averages of given dates. Fig. 11 gives an example of such an analysis. The data are based on measurements made at Punkaharju in southern Finland during 1940—1970. The horizontal axis shows the dates concerned and, above each date, the number of days that had elapsed up till then, counted from January 1. Curve 1 shows how the daily increments of the p.u. sum (the vertical axis) keep decreasing in magnitude until they end some time in December. Obviously, the period units accumulating towards the end of the year fail to have an effect on the active period, because low temperatures destructive to active tissues occur at the same time. Curve 2 indicates the daily increments of chilling units. Curve 3 shows the average accumulation of a chilling unit sum. Corresponding curves for a different climatic region would, of course, be quite different in appearance. For instance, if a continental climate were involved, curve 1 would decline much more steeply and curves 2 and 3 would remain shorter.

The curves in Fig. 11 can be applied for estimating the average time course of events. For instance, a genotype whose active period has been

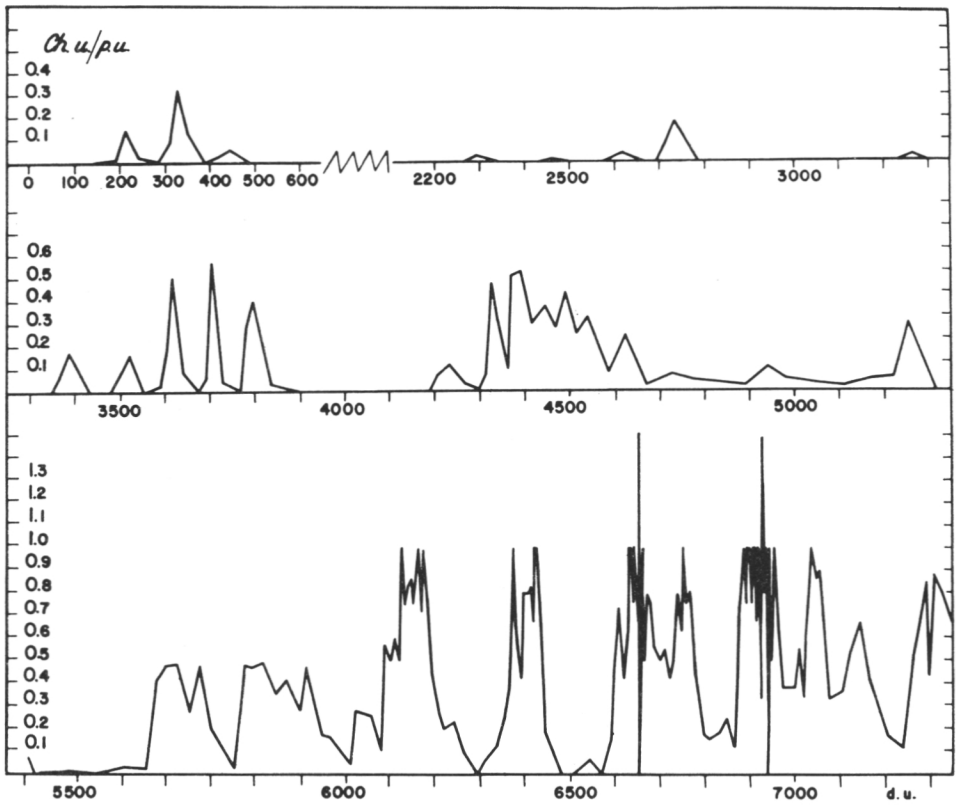


Fig. 10. Example of 12-hour increments to the cumulative ch.u. sum, calculated per p.u. increment resulting from the same length of time. The horizontal axis shows the cumulative p.u. sum reckoned from Jan. 1. Punkaharju, *Alnus incana*, sample stand No. LXII, year 1971

completed before the end of August and whose dormancy I is equal to 300 ch.u. will pass from dormancy I to dormancy II on October 1. However, should the active period not terminate until the end of September and dormancy I would be equal to 300 ch.u., dormancy II would start on October 25, and so forth.

If the temperature decreased gradually every year as the average temperature does, it would be possible to describe, e.g., the passing of all the male flower buds of a population from the active period to dormancy I and further to dormancy II as a single wave. This distribution is partly responsible for the variation found in anthesis within a population the following spring.]

Generally, the onset of winter does not consist of a sudden change from warm to cold weather or of a gradual fall in temperature, but rather of an interchange of warm and cool spells lasting a few days or even a week. The

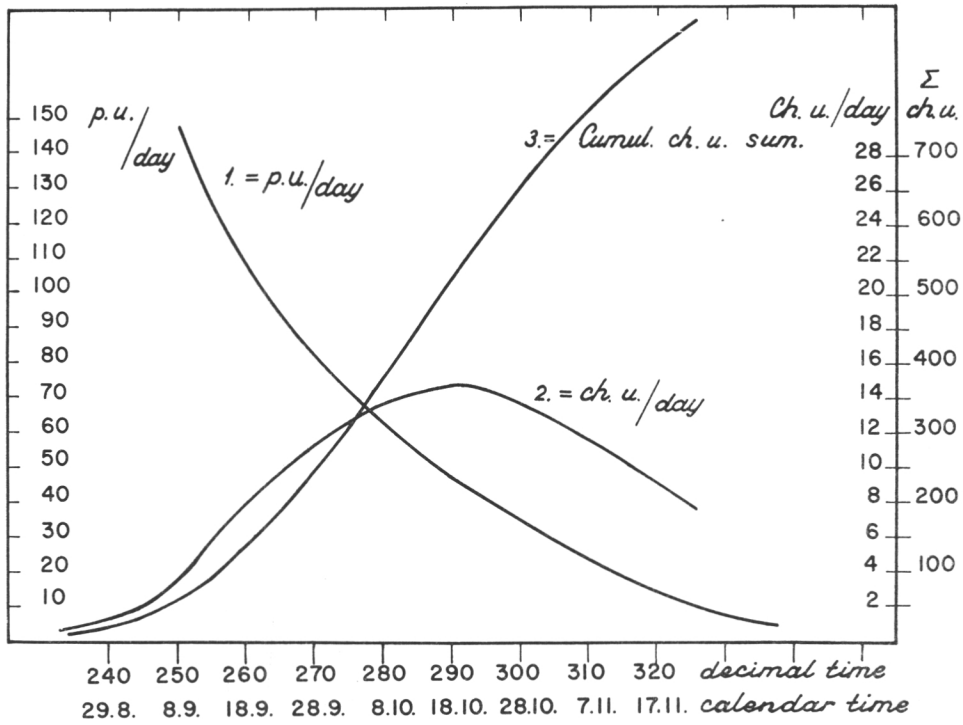


Fig. 11. Development in the autumn of some climatic parameters relevant to dormancy I. Computation is based on temperature measurements in Punkaharju during the years 1940—1970.

closer the approach to winter, the shorter and less frequent are the warm periods and the colder and longer the cool periods.

Thus, the weather characteristic of the autumn will be reflected in the sequence of anthesis the following year. The subject is discussed in the next section.

Pattern of parcels in the course of development

To start with, let us confine our examination to the microspores of *Betula pubescens*. In this species microsporogenesis occurs at such an early phase in the latter half of the summer that in most years the microspores are fully developed before the end of August. At this time, the temperature in southern Finland has not, as a rule, fallen below 10°C. According to the model of the cycle adopted in this study, the microspores, on completion of the active period, pass immediately and unconditionally into dormancy I. Hence, even if the microspores have developed at such different rates in the active period, they all accumulate at the zero point of dormancy I, without progressing to the later phases of the cycle until the temperature drops below 10°C.

From what has been stated before (p. 12) we know that even between the different microspores of one tree there are large differences in the length of dormancy I. Some microspores need exposure to cold for a short period, whereas others have to encounter cold for a long period before they are able to pass into dormancy II. From this it follows that those microspores in which dormancy I is short may pass into dormancy II as a result of the first cold spell. In dormancy II their cycle immediately begins to progress, slowly at low and more rapidly at high temperatures (including temperatures above 10°C). As a result of the next cold spell, those microspores in which dormancy I is a little longer advance to dormancy II, and so forth. In the meantime, however, those microspores that passed first into dormancy II have gained a certain lead. Thus, the microspores do not, as a rule, pass in a single wave from dormancy I into dormancy II but in a series of waves or »parcels» that are more or less detached. These »parcels» can later be distinguished in the course of anthesis (i.e. in the frequency distribution of the p.u. sums of the pollen catches) that displays a multimodal rather than a normal pattern of distribution.

As regards investigations of the cycle, anthesis affords several advantages, one being that at population level sampling with self-recording pollen samplers is comparatively easy. This method has been described in several previous publications (S a r v a s 1962, pp. 26—27, 1968 pp. 14—17) and details are not needed here. It is enough to point out that the data presented below are mean values of results of pollen catch measurements carried out with three self-recording pollen samplers in each stand, and that the temperature readings refer to measurements made inside buds or in the air inside meteorological screens in sample stands at or immediately above the dominant height.

The basic aim of the following examination is to predict from the temperature conditions of the autumn what the distribution of the p.u. sums of the pollen catches will be like in anthesis the following spring. For this purpose, several values have to be known: the frequency distribution of the ch.u. sums for the total length of dormancy I, the mean value $\bar{x}$ of this frequency distribution and its standard deviation s.

Experiments carried out in 1970 and 1972 showed that microsporangiate catkins opened, on an average (50 %), when the chilling unit sum in nature amounted to about 420 ch.u. This figure was taken as the starting point for a detailed analysis.

Experiments on the length of dormancy I, conducted with *Betula pubescens* seeds, also threw some light on the matter; the large standard deviation in the frequency distribution of the ch.u. sums for the total length of dormancy I was an observation of great importance.

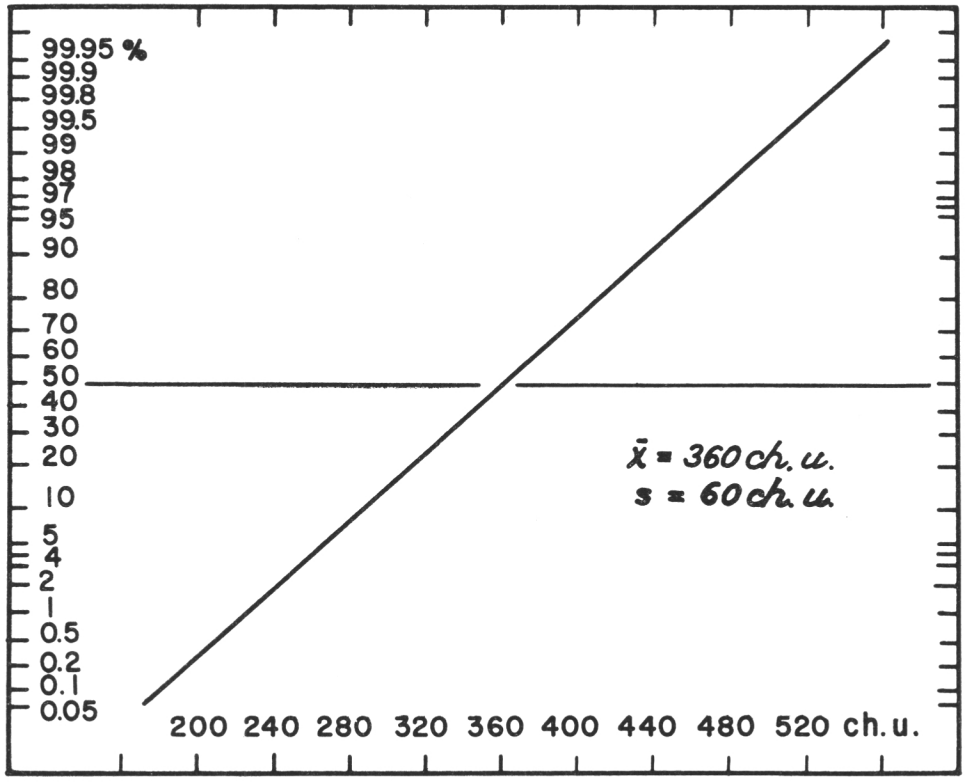


Fig. 12. The cumulative frequency distribution of the lengths (= chilling unit requirements) of dormancy I in the microspores of *Betula pubescens* (origin local, Punkaharju L); $\bar{x}$ = 360 ch.u., s = 60 ch.u.

The detailed statistical analysis was made as follows: several alternate $\bar{x}$ and s values were tested, the $\bar{x}$ values were tested at 20 ch.u. intervals, from 500 ch.u. downwards, and the s values at 20 ch.u. intervals, from 200 ch.u. downwards. The values used in these calculations were air temperature measurements made at canopy level in 1970, bud temperature measurements made at the same time in a nearby *Pinus sylvestris* stand, and pollen catch measurements made with three self-recording pollen samplers in *Betula pubescens* stand L, Punkaharju, in the spring of 1971. A rather difficult analysis led to the following conclusion: the mean value of the length of dormancy I is $\bar{x}$ = 360 ch.u., and the standard deviation of the frequency distribution, s = 60 ch.u.

Let us now see what kind of predictions can be made concerning the pollen catch from these base values. Fig. 12 and Table 12 illustrate how the calculations were carried out. In Fig. 12 the distribution of ch.u. sums for the total length of dormancy I in the microspores of *Betula pubescens* is

Table 12. Example of the calculation of the frequency distribution of the d.u. sums of those microspores that have passed from dormancy I to dormancy II. *Betula pubescens*, Punkaharju L, autumn 1970 (cf. Fig. 12, p. 58).

1	2	3	4	5	6	7
Day and month	Ch.u. sum at 24 h.	Passed from d I to d II		D.u. sum at 24 h.	Addition per day d.u.	Passed from d I to d II per d.u.
		Cumulative	Per day			
		%				
26. 9	151	0.0	—	0	—	0.00
27	172	0.1	0.1	38	38	0.00
28	191	0.3	0.2	74	36	0.01
29	209	0.6	0.3	128	54	0.01
30	224	1.2	0.6	192	64	0.01
1. 10	239	2.2	1.0	252	60	0.02
2	257	4.3	2.1	307	55	0.04
3	277	8.5	4.2	354	47	0.09
4	299	15.5	7.0	384	30	0.23
5	322	26.2	10.7	421	37	0.29
6	342	38.1	11.9	468	47	0.25
7	358	48.4	10.3	526	58	0.18
8	373	58.4	10.0	590	64	0.16
9	381	63.4	5.0	675	85	0.06
10	390	68.9	5.5	756	81	0.07
11	397	73.0	4.1	845	89	0.05
12	416	82.1	9.1	896	51	0.18
13	432	88.2	6.1	915	19	0.32
14	445	92.0	3.8	930	15	0.25
15	461	95.2	3.2	949	19	0.17
16	477	97.3	2.1	989	40	0.05
17	489	98.3	1.0	1 062	73	0.01
18	505	99.2	0.9	1 119	57	0.02
19	516	99.5	0.3	1 196	77	0.00
20	530	99.8	0.3	1 262	66	0.00
21	544	99.9	0.1	1 327	65	0.00
22	562	100.0	0.1	1 359	32	0.00
23	572	100.0	—	1 370	11	0.00

drawn on frequency paper. The horizontal axis shows the cumulative ch.u. sum and the vertical axis shows the percentage of the microspores that have passed from dormancy I to dormancy II. Table 12 gives an example of how the frequency distribution of the p.u. sums of the pollen catches has been predicted for the following spring. The basic idea in this calculation is that after the microspores have passed from dormancy I to dormancy II, the frequency distribution of their d.u. and p.u. sums will not undergo any appreciable changes, at least not in general pattern. In other words, we calculate the frequency distribution of the d.u. sums of microspores at the beginning of dormancy II and conclude that the following spring the frequency distribution of the p.u. sums of the pollen catches will be similar as regards general pattern. The 2nd column of Table 12 gives the cumulative ch.u. sum that has been calculated from that date at the end of August when the temperature dropped below 10°C the first time. From this we see how high the ch.u. sum has risen by the end of each day (at 24 h.), and the

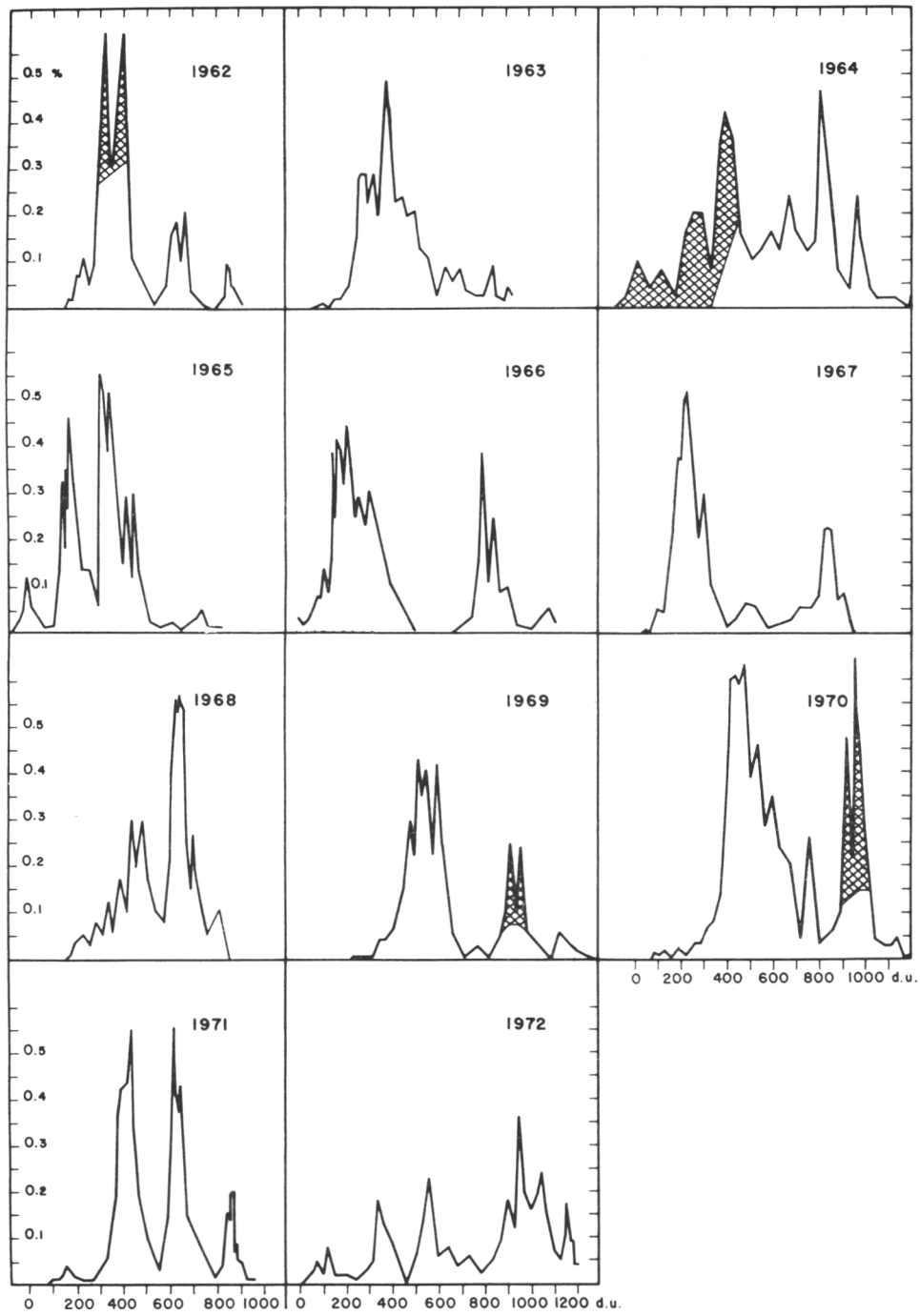


Fig. 13. *Betula pubescens*, Punkaharju, sample stand L, the frequency distribution of the d.u. sums of the microspores at the onset of dormancy II in the autumns of 1962—1972. The calculation was based on measurements of air temperature at canopy level. The total length of dormancy I is $\bar{x}$ = 360 ch.u., and the standard deviation of the frequency distribution is s = 60 ch.u.

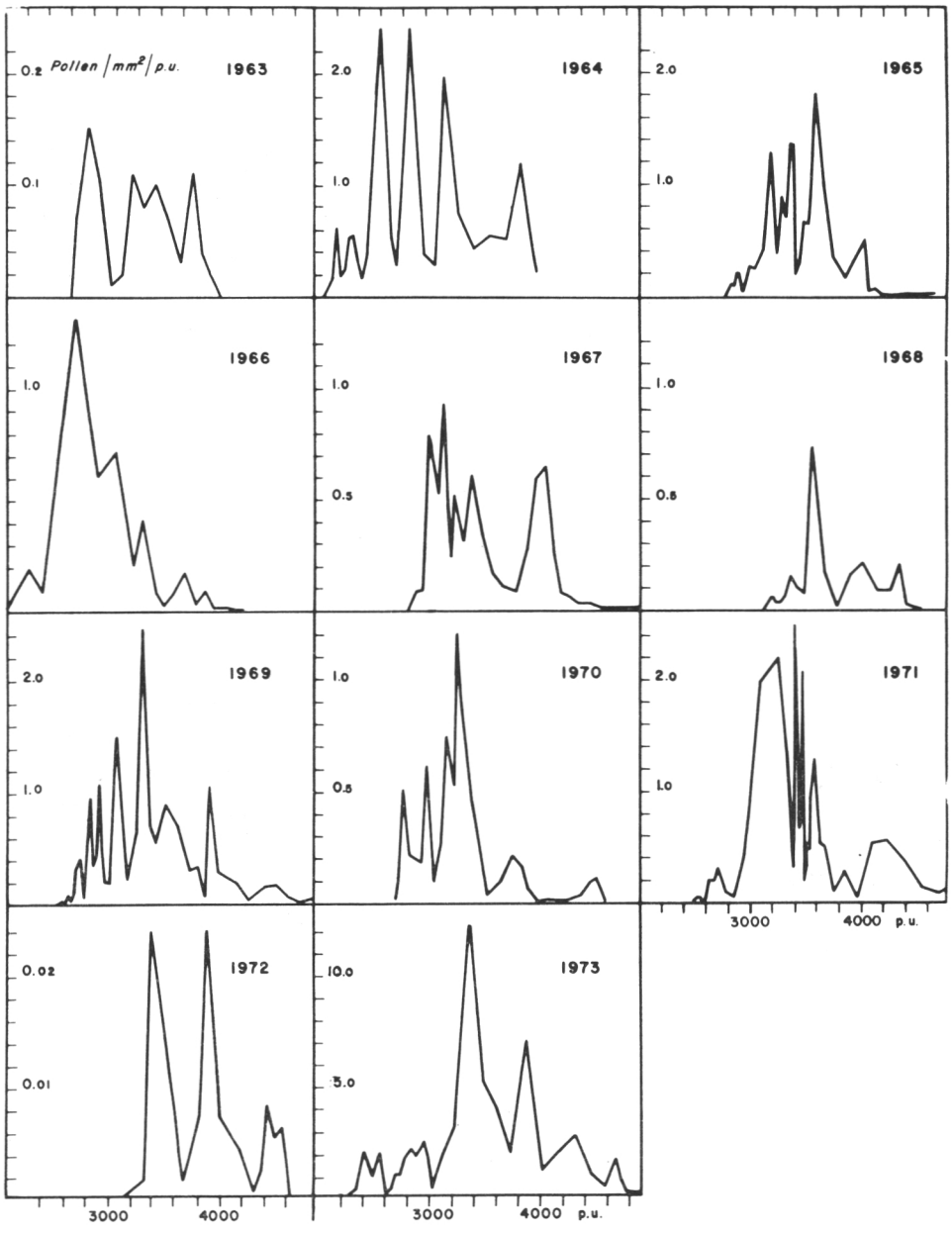


Fig. 14. *Betula pubescens*, Punkaharju, sample stand L, the frequency distribution of the p.u. sums of the pollen catches in 1963—1973. The pollen catches were measured with self-recording pollen samplers and drawn as 12-hour means.

ordinate corresponding to this value on the abscissa can be read from Fig. 12. Thus we find the cumulative percentage of microspores that have passed to dormancy II by the end of each day (the 3rd column; in the example we observe the progress of 1 000 microspores.) The difference between the cumulative values for two consecutive days is the number of microspores that have passed to dormancy II daily (the 4th column). The 5th column shows the cumulative d.u. sums of these days reckoned from that point in time when the first microspores passed to dormancy II (or the reckoning can start from any arbitrary day before the onset of dormancy II). In the 6th column are the daily d.u. additions, and the 7th column shows the number of microspores that have passed to dormancy II daily, reckoned per d.u. [1])

Figs. 13—14 show the frequency distributions of the d.u. sums of the microspores at the start of dormancy II, calculated in the manner described above, as well as the frequency distributions of the p.u. sums of the pollen catches measured in the forest. It was found that during the autumn, winter and spring low temperatures destroy a portion of the microspores. In fig. 13 the shaded portions of the d.u. frequency distributions represent microspores that have probably been destroyed.

A similarity is seen between the frequency distributions of the d.u. sums of microspores and the corresponding frequency distributions of the p.u. sums of the pollen catches in the forest. In spite of many differences in minor details, the frequency distributions show the same main features.

Attention is also drawn to the irregularity of the pattern of the frequency distributions and the great variation from year to year. This is exactly what was expected in the introduction to this section. And the fact that the irregularity in the d.u. sum distributions of microspores in the autumn is repeated $\pm$ unchanged in the p.u. sum distributions of pollen catches the following spring adds to the convincingness of the comparison. It is hardly an exaggeration to say that this test of the cycle model, which, as a matter of fact, does not concern dormancy I alone but, more or less, the entire model of the cycle, is a particularly stringent one, especially since it has been extended to cover eleven consecutive years in the same stand.

However, the data available are very much more extensive than this. In connection with the present study, during more than ten years, a total of several hundred frequency distributions of p.u. sums of the pollen catches of several different tree species have been measured with self-recording pollen samplers. Thus, in this form the tests can be intensified almost indefinitely. However, these data can be used for other purposes besides checking the validity of the model of the cycle. They can be used in studies on the flowering phenomenon itself and the annual variation displayed by it. The inten-

[1]) The numbers of microspores that have passed to dormancy II daily have been reckoned expressly per d.u., because we are unable to make calculations for equidistant d.u. intervals. For the same reason, the pollen catch values have been calculated per p.u.

tion is to revert in greater detail to this matter in a subsequent study on the annual variation in the abundance of flowers.

Let us revert to the comparison of the frequency distributions of the d.u. and the p.u. sums of microspores (Figs. 13 and 14). When examination is concentrated on details, significant quantitative differences can be noted. In the frequency distributions of the p.u. sums the intervals between the corresponding peaks are generally about 1.5 times as long as in the frequency distributions of the d.u. sums. This cannot be due to the difference in the p.u. and d.u. scales, which are based on dissimilar regressions of the rate of progress of the cycle on temperature. This dissimilarity becomes significant only at temperatures above 10°C, which are rare in late autumn and early spring. The cause will thus have to be sought elsewhere. What is it that happens between the end of dormancy I and anthesis that causes this quantitative difference?

In fact, from what we know of the progress of the active period a quantitative difference like this is understandable. At an early phase of this investigation of the cycle (S a r v a s 1967, pp. 223—224), it became evident that the later the stage of the active period at which a physiological phenomenon occurs, the larger is the standard deviation of the frequency distribution of the d.d. (or p.u.) sums, particularly if the phenomenon involved is investigated at population level. The reason for this increasing variation is that different genotypes react differently to the thermal factor. The population consists of individuals which progress in the active period at a rapid or a slow rate or at rates that are between these two extremes. The farther the active period has progressed, the longer is the lead which the rapidly progressing individuals have gained over the slowly progressing ones, and so the standard deviation of the frequency distribution keeps steadily increasing as the active period progresses.

In a local tree population at Punkaharju the pollen sacs of the anthers of *Betula pubescens* dehisce, on an average, at $\bar{x} = 2\,210$ p.u. (mean value for 11 years). For instance, the pollen sacs of the anthers of *Alnus incana* dehisce much earlier ($\bar{x} = 750$ p.u.) and those of *Pinus sylvestris* much later ($\bar{x} = 4\,650$ p.u.). Therefore, the difference between the standard deviation of the frequency distribution of the d.u. sums of the microspore mother cells and that of the frequency distribution of the p.u. sums of the pollen catches (and thus the difference between the corresponding peak values too) may be expected to be smaller for *Alnus incana* than for *Betula pubescens*. Similarly, this difference for *Betula pubescens* may be expected to be smaller than the corresponding difference for *Pinus sylvestris*. This important subject will be discussed in greater detail on pages 73—77.

It may be well to state at this point that the comparison of the frequency distributions of the d.u. sums of microspores and the frequency distributions

of the p.u. sums of the pollen catches gives no grounds for supposing that when dormancy I passes to dormancy II the change in the regression of the rate of progress of the cycle on temperature is gradual. On the contrary, the comparisons carried out strongly support the view that the changes that the tree undergoes when passing from one main part of the cycle to the next occur within a short transition period. Apart from this, the results obtained in the course of this study bear a certain resemblance to the view presented on several occasions by V e g i s (cf., for instance, 1963, 1965). V e g i s held it characteristic of the different stages of dormancy that the effective temperature range widens or narrows from one stage to another.

Let us now proceed to examine several species instead of one. In many tree species, as in *Betula pubescens*, the active period of the flower buds ends a good while before the end of the growing season (in southern Finland, towards the end of August). If for these tree species the length of dormancy I is the same or almost the same as for *Betula pubescens*, the frequency distribution of the p.u. sums of their pollen catches may be expected to be divided into the same parcels as in *Betula pubescens*. In other words, in many tree species the microspores or microspore mother cells pass from dormancy I to dormancy II at approximately the same time in the autumn, and it is therefore to be expected that the frequency distributions of the p.u. sums of the pollen catches will display a certain similarity in spite of the fact that flowering occurs at different times in the spring and under different weather conditions. However, it is evident from the foregoing that the length of dormancy I differs in most tree species and there is no reason why the standard deviation of the frequency distribution of the ch.u. sums of dormancy I should be the same either.

The second tree species to be examined here is *Picea Abies*. Although this species, too, flowers fairly early in the spring, it is about one or two weeks behind *Betula pubescens* and thus flowers under different weather conditions.

The investigations on *Picea Abies* were carried out in sample stand No. LII at Punkaharju. The mean length of dormancy I in this stand was found to be $\bar{x} = 333$ ch.u. and its standard deviation $s = 60$ ch.u. The frequency distribution was thus almost the same as in the *Betula pubescens* stand described above. The frequency distributions of the p.u. sums of the pollen catches for the years 1966—1973 are seen in Fig. 15 (in 1972 the stand did not flower). On comparison of these frequency distributions with those of the p.u. sums of the pollen catches of *Betula pubescens* presented in Fig. 14, considerable similarity can be seen between the same years (on the other hand, there are substantial differences between the different years). Thus, in this respect, too, the expectation based on the model of the cycle is borne out well. It is surprising to note, here too, how very little the weather condi-

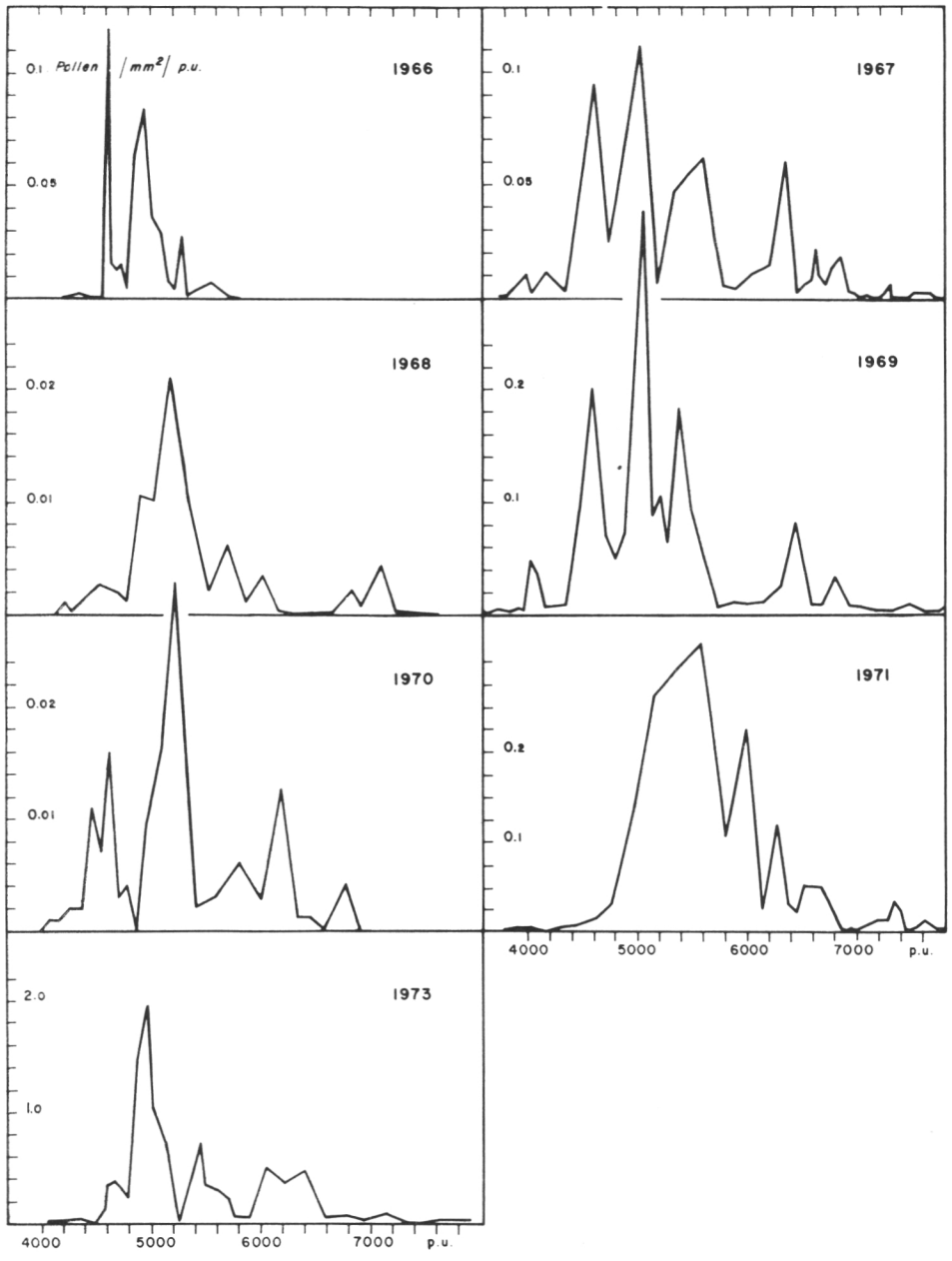


Fig. 15. *Picea Abies*, origin Lammi, Punkaharju sample stand LII. The frequency distribution of the p.u. sums of the pollen catches in 1966—1969, 1970, 1971 and 1973 (no flowers in 1972). The pollen catches were measured with self-recording pollen samplers and drawn as 12-hour means.

tions at the time of flowering affect the main features of the frequency distribution of the p.u. sums of the pollen catches, and how far this is preconditioned the autumn before.

The question of the parcels can be approached from yet another angle. In the model of the cycle employed in this study the parcels are assumed to exist already at the very onset of dormancy II. They should thus be observable, at least in theory, in any of the phases of the cycle between the starting point of dormancy II and the end of the active period. For instance, the meiosis of the microspore mother cells affords several developmental phases suitable for examination in this respect. As an example of how this principle is applied, the frequency distribution of metaphase I of meiosis in the microspore mother cells of *Larix sibirica* for 1972 is presented (Fig. 16) on the p.u. scale, and so is the corresponding frequency distribution of the p.u. sums of the pollen catches in sample stand No. 49 at Punkaharju. A qualitative resemblance can be noted between these two frequency distributions: neither of them is a typical normal distribution curve but rather they consist of four separate »parcels». Thus, we proceed from the assumption that the pattern of parcels in the progress of annual development can be discerned at the start of dormancy II and that it subsequently characterizes dormancy II and the entire active period. In particular, this means that generally the frequency distributions of the d.u. and p.u. sums do not conform to a normal frequency distribution in any phases of dormancy II or the active period, and often deviate from it considerably. This again is a source of considerable difficulty in almost all investigations concerned with the cycle and makes very large samples necessary.

Dormancy I

On pages 11—13, a description was given of a forcing method which can be used for estimating the approximate length of dormancy I. Some preliminary measurements were also given.

It is obvious that the measurements relating to the frequency distribution of the p.u. sums of the pollen catches clarified in the two preceding sections afford a new and more accurate method for determining the length of dormancy I. This method has the further advantage of being based exclusively on measurements made in natural conditions, for results obtained with laboratory methods alone always carry a considerable risk of error.

The new method applied and explained in the foregoing consists in comparison of the ch.u./p.u. diagram drawn on the basis of the temperature conditions of the autumn with the frequency distribution of the p.u. sums of the pollen catches measured in the spring. The comparison is carried out

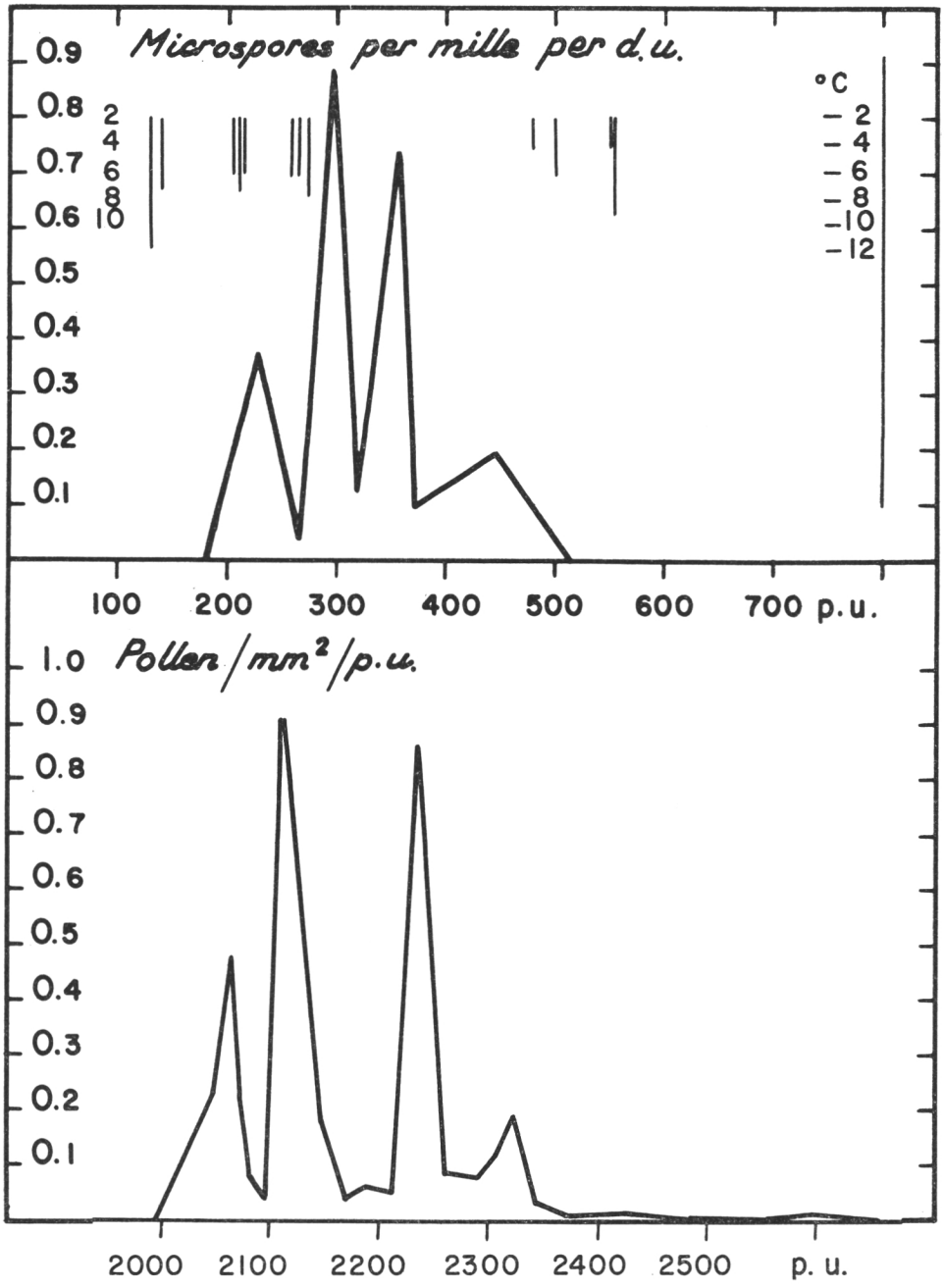


Fig. 16. The frequency distribution of the p.u. sums of metaphase I of the microspore mother cells (upper section of the figure) and the frequency distribution of the p.u. sums of the pollen catches (lower section of the figure). *Larix sibirica*, Punkaharju 49, 1972.

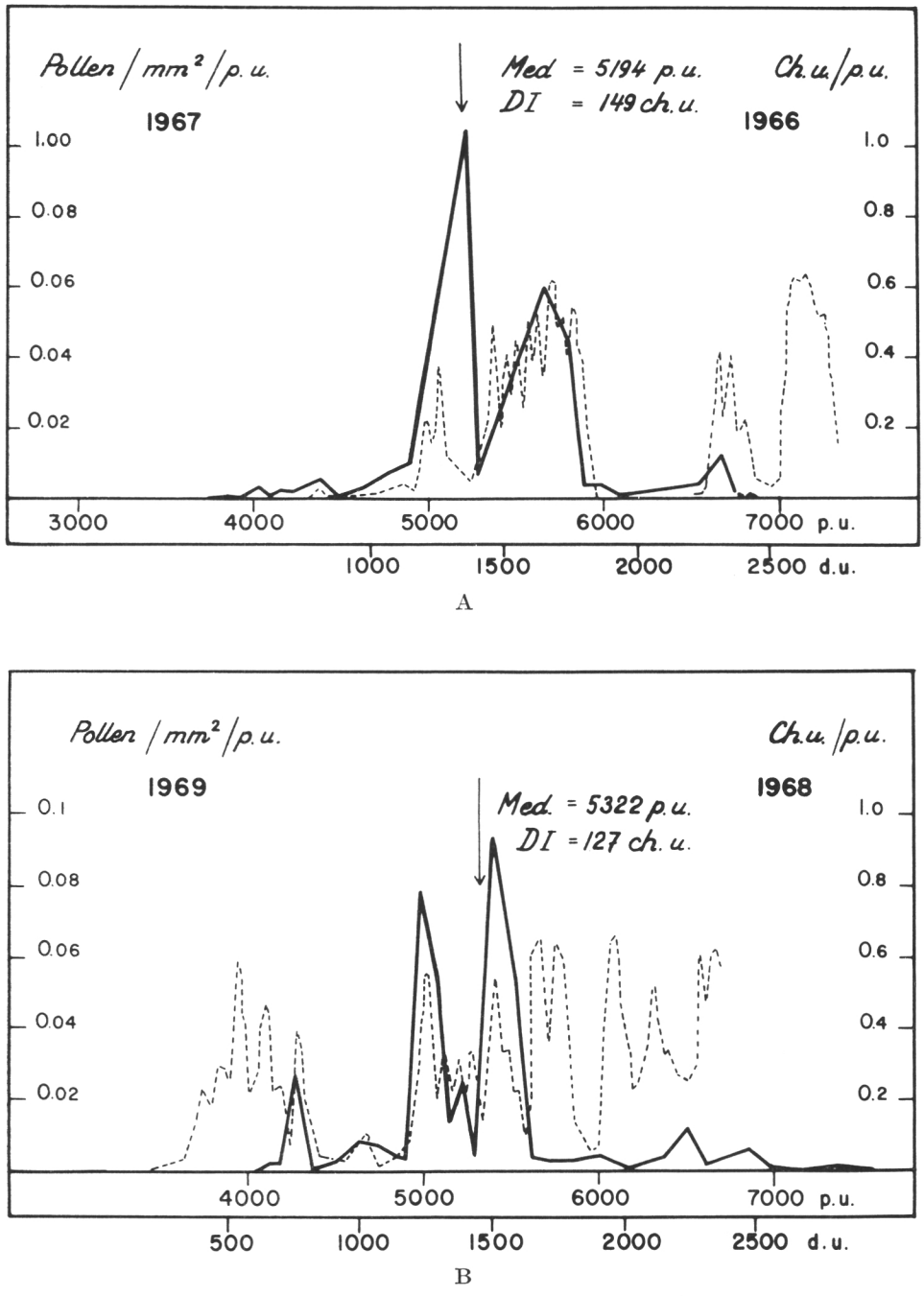
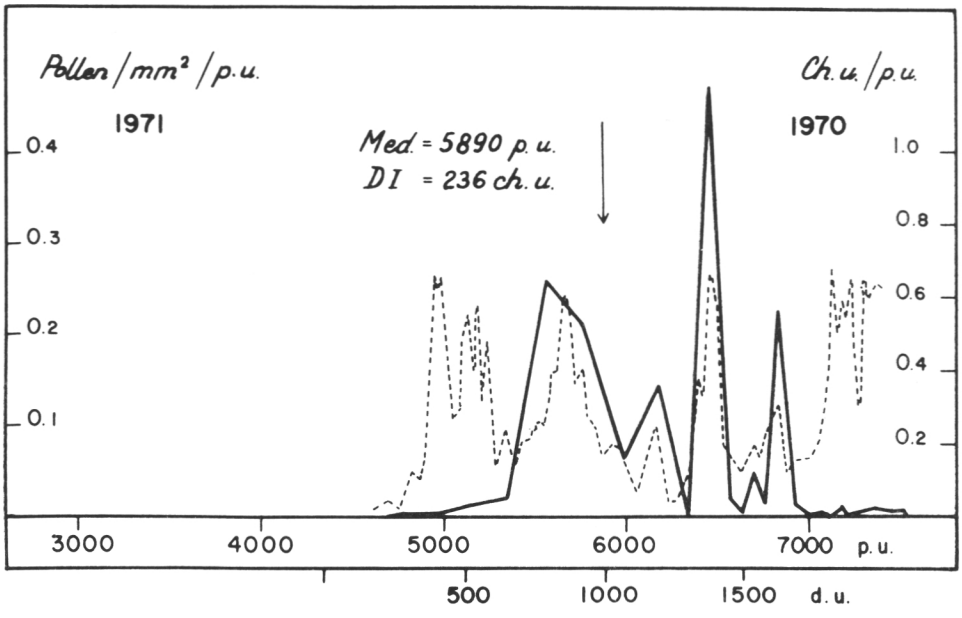
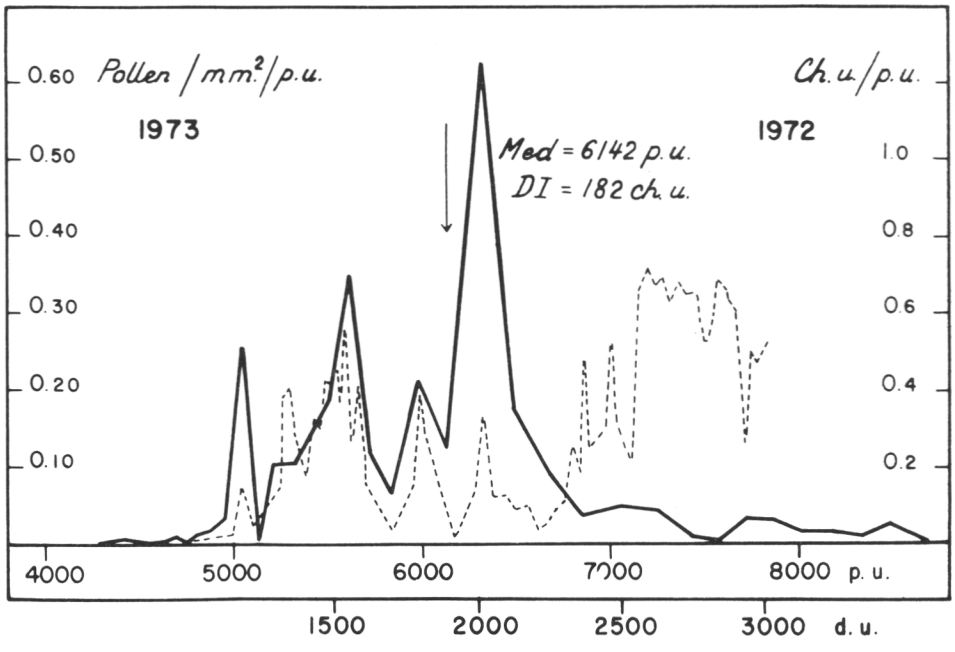


Fig. 17. An example of the relationship existing between the daily additions to the ch.u. sum and the frequency distributions of the p.u. sums of the pollen catches. *Abies sibirica*, Punkaharju, sample stand 45.


Pollen / mm² / p.u.
1971
Med. = 5890 p.u.
DI = 236 ch.u.
Ch.u./p.u.
1970
0.4
0.3
0.2
0.1
1.0
0.8
0.6
0.4
0.2
3000
4000
5000
6000
7000 p.u.
500
1000
1500 d.u.

C


0.60 Pollen / mm²/p.u.
1973
Med = 6142 p.u.
DI = 182 ch.u.
Ch.u./p.u.
1972
0.50
0.40
0.30
0.20
0.10
1.0
0.8
0.6
0.4
0.2
4000
5000
6000
7000
8000 p.u.
1500
2000
2500
3000 d.u.

D

as follows: In the frequency distribution of the p.u. sums of the pollen catches the median value of the distribution is marked. For the ch.u./p.u. diagram the date corresponding to the median is determined (by placing one diagram on top of the other; Fig. 17 illustrates this procedure). The cumulative ch.u. sum for that date shows the average length of dormancy I (to put it more precisely, this is its meadian value; however, supposing that the frequency distribution of the ch.u. sums of the length of dormancy I is mostly normal, it can be considered that the median value and the mean value are of approximately the same magnitude). — The results obtained have been compiled in Table 13.

These results substantiate the earlier findings that in different tree species there are very considerable differences in the length of dormancy I. Among the 25 tree species investigated dormancy I was found to be short in *Larix sibirica*, *Pinus Peuce*, *Pinus Cembra*, *Larix Gmelini*, *Larix decidua*, *Pinus sylvestris* and long in *Populus tremula*, *Alnus incana*, *Corylus Avellana*, *Betula pubescens*. In most cases the length falls within the range 50—350 ch.u.

For some tree species measurements were carried out in several subpopulations growing either in the same locality or in different parts of Finland. The results suggest that different subpopulations, even in the same locality, differ significantly in the length of dormancy I. On the other hand, the differences between the different geographical origins are relatively small. Moreover, in general the length of dormancy I is slightly shorter in the populations of northern Finland than in the populations of the same species in southern Finland. Another significant and even surprising observation is that in the populations of the coastal area in S.W. Finland, dormancy I appears to be almost as short as in the populations of northern Finland.

In Table 13, the wide range of year-to-year variation in the length of dormancy I (the large mean errors of the mean values) attracts attention at once. The reason for this variation would seem to be that in most years only part of the population takes part in the flowering process. However, the question is so complicated that a detailed examination of it is out of the question here. Evidently, estimates of the total length of dormancy I based on measurements made in years of abundant flowering best reflect the situation in the entire population. These results may be expected to be of the same order of magnitude as those obtained with the forcing method. They are also likely to give the best picture of the length of dormancy I in the vegetative buds. — Numerous tentative data on the length of dormancy I in different tree species have been published earlier in studies on dormancy (cf., for instance, K á r p á t i and K á r p á t i 1961 and the literature cited therein). However, owing to different concepts and, above all, lack of a clearly defined unit for the chilling requirement, these valuable data are

Table 13. Data on the length of dormancy I. Subpopulation (stand) level.

Species and origin	No. of years	$\bar{x}$ [1] ch.u.	s_1 [2]	Capacity, ch.u.	s_2 [2]
Abies balsamea, origin Canada, New Brunswick; Tuusula 275	3	206		195	17
Abies sibirica, origin unknown; Punkaharju 45	7	171±14.5	38	236	60
Alnus glutinosa, local origin; Tuusula 3	2	405		407	30
Alnus incana, local origin; Punkaharju LXII	7	406±12.2	32	390	80
» » » » Kerimäki 540	10	426± 5.6	18	417	95
Betula papyrifera var. neoalaskana, origin Canada, Alta., Cooking Lake; Punkaharju 118	5	272± 6.3	14	280	35
Betula pubescens, local origin; Tuusula 12	6	248± 6.8	16	246	53
» » » » Punkaharju L	9	345±12.3	37	359	60
» » » » Punkaharju XIV	10	363±14.6	47	352	60
» » » » Punkaharju LX	10	355±11.4	36	363	65
» » » » Vilppula 153	4	344		324	50
» » » » Rovaniemi XVII	6	215±16.7	40	241	40
Betula verrucosa, local origin Hammarland III	4	247		287	45
» » » » Bromarv VI	6	238±23.4	56	294	20
» » » » Helsinki, Ilmala 167	5	294±10.1	22	324	10
» » » » Punkaharju LIV	6	229±14.9	39	257	40
» » » » Kerimäki 543	8	250±14.6	41	285	50
» » » » Rovaniemi XXI	7	220±14.3	37	248	32
Corylus Avellana, origin Finland, Bromarv; Punkaharju No. 1	2	434		434	25
Juniperus communis, local origin; Punkaharju 38	1	142		142	
» » » » Rovaniemi XXX	6	93±11.3	27		
Larix Gmelini, origin RSFSR, Sakhalin; Punkaharju 9	3	122		150	
Larix decidua, origin unknown; Punkaharju 80	5	149±16.0	35	169	35
Larix sibirica, origin unknown; Punkaharju 49	7	20± 4.1	11	9	3
» » » » Vilppula 16	3	16			
Picea Abies, local origin; Bromarv I	7	308±15.4	40	375	75
» » » » Tuusula XXX	6	339±27.8	67	395	60
» » » » Tuusula XXXIV	6	256±18.5	45	387	
» » » » Heinola 565	6	258±25.7	62	208	90
origin Finland, Lammi; Punkaharju LII	7	343±13.2	34	300	70
» » local origin; Rovaniemi XVIII	5	319±33.3	73	230	73
» » » » Kittilä III	2	230			
Picea glauca, origin Canada, Alta., Olds; Punkaharju 221	1	194		194	20
Picea mariana, origin Canada, New Brunswick, St. John; Punkaharju 217	4	151		160	45

[1]) mean and standard error.
[2]) Standard deviations of the ch.u. sums calculated as described on p. 73.

Table 13. (contin.)

Species and origin	No. of years	$\bar{x}$ ch.u.	s_1	Capacity, ch.u.	s_2
Picea Omorika, origin Serbia; Punkaharju 358	1	170		170	25
Pinus Banksiana, origin unknown; Bromarv 106 ..	1	69		69	12
» » » » Bromarv 139 ..	1	89		89	15
Pinus Cembra, probably var. typica, origin unknown; Punkaharju 100	8	170±17.1	51	179	60
Pinus contorta var. latifolia, origin Canada, Br. Col., Long Lake, 1 380 m; Punkaharju 99	8	178± 4.5	13	154	45
Pinus Mugo var. rostrata, origin Switzerland, Engadine; Punkaharju 235	1	325		325	75
Pinus Peuce, origin Bulgaria, Rila Mt.; Bromarv 40	7	111±12.2	30	106	50
» » » » Pirin Mt.; Punkaharju 306	10	94±16.2	51	110	45
Pinus sylvestris, local origin; Eckerö I	4	96±27.7	55		
» » » » Bromarv II	9	102±13.9	31		
» » » » Bromarv III	9	102± 8.3	25		
» » » » Tuusula XXXII	5	106± 4.2			
» » » » Heinola 566	6	167±27.2	65	292	55
» » » » Punkaharju I	10	148±17.1	56	220	75
» » » » Punkaharju XLV ...	11	146±22.3	74	255	60
» » » » Kerimäki XX	9	133±17.0	56	233	75
» » » » Kerimäki XXXIII ..	7	147±19.4	58	230	65
» » » » Kuorevesi XXIII ...	4	154±26.7	64		
» » » » Kajaani 546	6	133±20.3	54	215	
» » » » Rovaniemi XXVII ..	8	87±17.6	50	200	
» » » » Rovaniemi XXIX ...	7	93±20.1	57	227	
Populus tremula, local origin; Tuusula XXXIII, clonal stand	6	403±26.9	66	450	45
Quercus Robur, origin Finland, Bromarv, Framnäs; Punkaharju 90	8	118± 8.2	23	106	50
Thuja occidentalis, origin Canada, Ontario; Punkaharju 19	6	109± 5.1	12	113	15

more qualitative than quantitative in character. Consequently, comparison of the present results with those published earlier does not seem beneficial here. It would, without doubt, only lead to prolonged speculations.

The next step is to examine the standard deviations of the ch.u. sum distributions of the lengths of dormancy I. A rough value can be obtained when the mean error of the mean value is reckoned. However, since calculations of the mean value are generally based on only a few measurements the

standard deviation is only a rough estimate. There is, however, another, more accurate method. In the foregoing it was shown that the frequency distribution of the p.u. sums of the pollen catches of the following spring can be predicted in the autumn from the prevailing temperature conditions (p. 66). It follows that the frequency distribution of the p.u. sums of the pollen catches can be used for retrospective calculation of the ch.u. distribution of the microspores (or their mother cells) at the end of dormancy I. But, of course, this method can only give good estimates for the standard deviation of the total length of dormancy I if it is based on the p.u. distributions of pollen catches in years of abundant flowering. Table 13 gives an estimate of the standard deviations calculated in both ways: s_1 indicates the standard deviation obtained directly from the calculation of the mean value, and s_2 that estimated retrospectively from the frequency distribution of the pollen catches in years of abundant flowering (»capacity years».)

Dormancy II

Surprisingly enough, the pollen catch measurements afford an opportunity for drawing some conclusions about the methodically difficult dormancy II.

As was pointed out earlier, comparison of the ch.u./p.u. diagrams drawn on the basis of the weather conditions of the autumn and the corresponding diagrams of the pollen catch (for instance, Fig. 17, p. 68—69) revealed that the similarity between them is qualitative rather than quantitative. Particularly for tree species which require a high p.u. sum to flower the interval (e.g. between two peaks) in the frequency distribution of the pollen catches was considerably larger than the corresponding interval in the ch.u./p.u. diagram. Let us study this point more closely. Information on the mean values of the frequency distributions of the pollen catches of different tree species and on the ratio between the corresponding intervals in the frequency distributions in spring and autumn is given in Table 14. Fig. 18 is a diagram based on these figures.

Let us first confine our study to tree species growing autochthonously in southern Finland. As can be seen from Fig. 18, a straight line can be fitted to the points representing them and this intersects the y axis at approximately 1.0. This result can be interpreted as meaning that the larger the p.u. sum at which flowering occurs, the more the interval between two given points has expanded since it was measured at the start of dormancy II. The equation of the regression line,

$$y = 1.0 + 0.00039x, \tag{8}$$

indicates the amount of this expansion.

Table 14. The ratio (p.u./d.u.) between corresponding intervals in the frequency distribution of the p.u. sums of pollen catches and the frequency distribution of the d.u. sums of microspores (or microspore mother cells) at the start of dormancy II. Only years of abundant flowering have been included.

No.	Species and origin	Sample plot	Year of flowering	Anthesis, Med. p.u.	P.u. / D.u.
1	*Abies sibirica*, origin unknown	Punkaharju No. 45	1973	5 473	2.8
2	*Alnus incana*, local origin	Punkaharju No. LXII	1973	764	1.1
3	*Betula papyrifera var. neoalaskana*, origin Canada, Alta., Cooking Lake	Punkaharju No. 118	1966	596	1.37
4	*Betula pubescens*, local origin	Punkaharju No. L	1965	2 278	1.8
5	*Betula verrucosa*, local origin	Punkaharju No. LIV	1966	651	1.34
6	*Larix sibirica*, origin unknown	Punkaharju No 49	1968	1 905	1.2
7	*Picea Abies*, origin Finland, Lammi	Punkaharju No. LII	1973	3 654	2.2
8	*Pinus Cembra*, origin unknown	Punkaharju No. 100	1965	7 044	3.0
9	*Pinus Peuce*, origin Bulgaria, Pirin Mt.	Punkaharju No. 306	1971	6 728	3.0
10	*Pinus sylvestris*, local origin	Punkaharju No. XLV	1971	4 676	3.2
11	*Pinus sylvestris*, local origin	Rovaniemi No. XXVII	1972	4 102	2.0
12	*Quercus Robur*, origin Finland, Bromarv, Framnäs	Punkaharju No. 90	1965	3 037	2.0
13	*Thuja occidentalis*, origin Canada, Ontario	Punkaharju No. 19	1971	483	1.05

In the diagram (Fig. 18) the points representing some foreign tree species and the autochthonous tree species in the northern marginal zone indicate that the expansion phenomenon is less pronounced in these populations than in the autochthonous species in the optimal zone. This is taken to indicate that in the marginal populations the length of the active period, expressed in p.u., is subject to less genetic variation.

As regards dormancy II, the most important observation is that the regression line in Fig. 18 passes approximately through the point $x = 0$, $y = 1.0$. This is interpreted to mean that the ratio investigated does not increase during dormancy II (at the end of dormancy II, for instance, the standard deviation of the frequency distribution is almost the same as at the beginning of dormancy II.)

The above phenomenon is perhaps elucidated in a still more concrete manner by the data compiled in Table 15 and the diagram in Fig. 19, based on these data. In this figure, the data relate to a single *Pinus sylvestris* subpopulation, sample stand XLV, Punkaharju. The frequency distributions

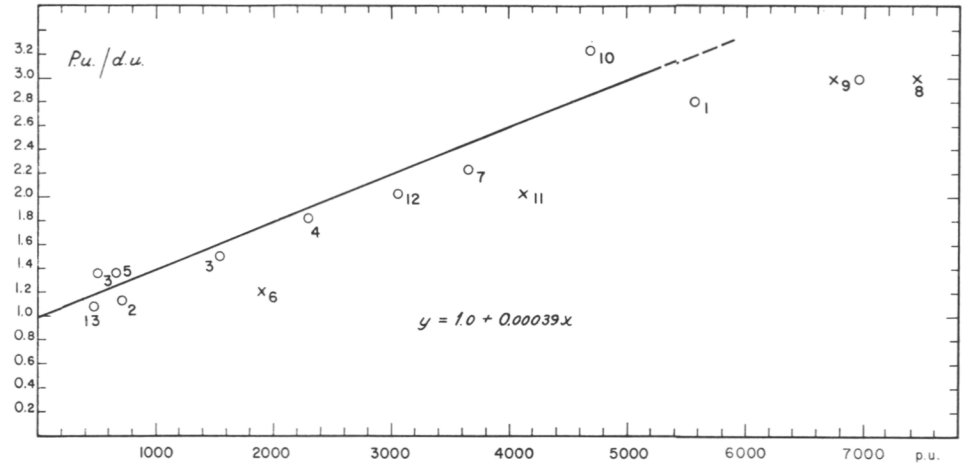


Fig. 18. The ratio (p.u./d.u.) between corresponding intervals in the frequency distribution of the p.u. sums at a certain physiological phase of the active period and in the frequency distribution of the d.u. sums at the start of dormancy II. The horizontal axis shows the average ($\bar{x}$) p.u. sums of the examined phases of the active period. Subpopulations originating in marginal zones are marked with oblique crosses. The figures refer to Table 14, p. 74.

of the p.u. sums of some readily observable physiological phases were sampled at subpopulation level and the standard deviations of these frequency distributions were reckoned. The line representing the regression of the ratio of the standard deviations (p.u./d.u.) on the mean p.u. sum passes through the point x = 0, y = 1.0, or close to it.

Thus, here, too, the standard deviation obviously begins to increase only around the zero point of the active period rather than at the zero point of dormancy II which in Fig. 19 is represented by x = —5 900, y = 0.

These observations greatly strengthen the view that in its physiological character dormancy II is completely different from the active period.

Table 15. Ratio (s/s_0) between the standard deviation, s, of the frequency distribution of the p.u. sums of a certain physiological phase in the active period and the standard deviation, s_0, of the frequency distribution of the d.u. sums of the zero point of dormancy II. *Pinus sylvestris*, Punkaharju, sample stand No. XLV. The s of the frequency distribution of the d.u. sums for the zero point of dormancy II is 150 d.u.

No.	Phase of active period	Year	$\bar{x}$ (p.u.)	s (p.u.)	s/s_0
1	Metaphase I of meiosis in microspore mother cells	1972	745	155	1.03
2	Dehiscence of pollen sacs of anthers	1964	4 400	450	3.0
3	Stalk of female cone bent to horizontal position	1968	6 211	600	3.87
4	Syngamy	1964	8 900	680	4.53
5	Embryo filling 60 % of embryo cavity	1966	23 911	1 540	10.3

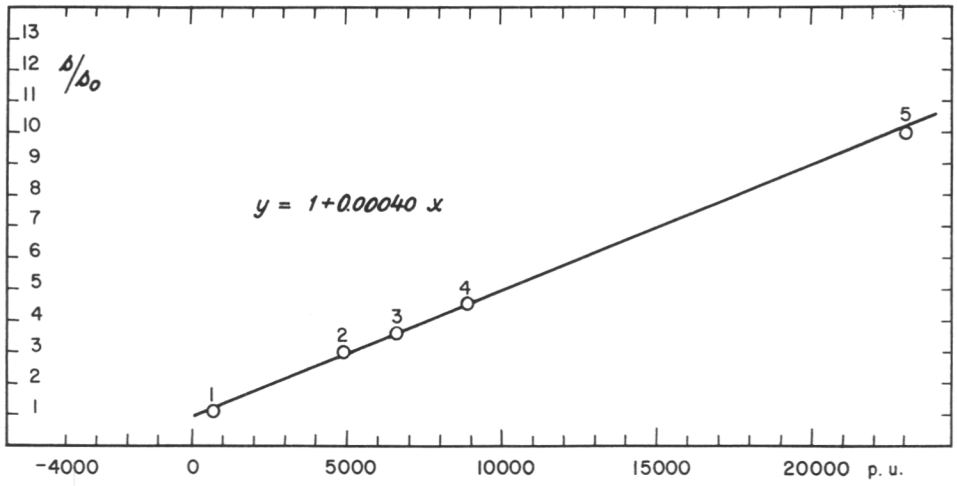


Fig. 19. The ratio (s/s_0) between the corresponding intervals (one standard deviation) in the frequency distribution of the p.u. sums at a certain physiological phase of the active period and in the frequency distribution of the d.u. sums at the start of dormancy II. The horizontal axis shows the average ($\bar{x}$) p.u. sums of the phases examined. The figures refer to Table 15, p. 75. *Pinus sylvestris*, Punkaharju, sample stand No. XLV.

The result given by equation (8) resembles a preliminary result obtained earlier (S a r v a s 1967, pp. 223—224) for the same relationship. It was then established that the regression of the standard deviation of the frequency distribution of the p.u. sums of the pollen catches on the mean value of the frequency distribution complies with the equation

$$y = 0.944 + 0.0577\ X \tag{9}$$

in which y is the standard deviation of the frequency distribution of the p.u. sum of a given phase of the active period and X the mean value of this distribution. It was further established that equation (9) can easily be approximated in the form of a rule of thumb that is easy to remember: the standard deviation of the frequency distribution is about 6 % of the mean value of the distribution. — True, at that time the research was limited by lack of information: simulation of the progress of the active period was based on the d.d. (degree days) principle, and that particular point of time in the spring when the mean temperature of the day rose above 5°C for the first time was chosen as the zero point of the active period. We now know that the progress of the active period can be simulated much better by using the p.u. (period unit) principle (which does not involve thinking in terms of threshold values) and that the zero point of the active period is determined in accordance with the termination of dormancy II.

Despite the conceptual differences between the earlier and the present treatments, it is interesting to try to compare the present result with the one obtained earlier.

The comparison can, for instance, be based on the following equation:

$$k = s_0 K \tag{10}$$

in which k indicates the variation coefficient ($s/\bar{x}$) of a certain physiological phenomenon belonging to the active period (thus corresponding to the method of examination applied in equation (9)) and K the angle coefficient of equation (8) in the particular case shown in Fig. 19, p. 76, in which s_0 is the same (150 d.u.) for all observational values.

By substituting $s_0 = 150$ in equation (10) we obtain

$$k = 150 \times 0.00040 = 0.06 \tag{11}$$

We now note that equation (8) (p. 73) conforms to the same rule of thumb as was found earlier: the standard deviation of the frequency distribution is about 6 % of the mean value of the distribution.

In view of the conceptual differences between the earlier and the present examinations, such close conformity is actually surprising. As was demonstrated earlier (S a r v a s 1972, pp. 60—66), in the major portion of the active period the d.d. principle simulates the progress of the cycle surprisingly well. The comparison now made further suggests the conclusion (important from the practical point of view) that the 5°C threshold value, in addition, simulates the zero point of the active period with an accuracy sufficient to meet the requirements of many practical purposes.

HARDENING AND FROST RESISTANCE

The process of hardening in trees and the development of resistance to (very) low temperatures are phenomena outside the scope of this study. However, as the investigation advances, it has become increasingly clear that no logical model of the annual cycle of development of forest trees can be constructed without due regard to the process of hardening and the development of frost resistance. For acquisition of adequate frost resistance during the coldest season appears to be the fundamental ecological function of the whole annual cycle of development.

The methods suitable for an investigation of the process of hardening and the development of frost resistance differ greatly from those used in this investigation (cf., for instance, Aronsson and Eliasson 1970 and the literature cited). Thus, a detailed study of this matter would have meant a considerable increase in the number of measurements required and it has seemed necessary, for the time being, to be content with superficial observations and existing knowledge.

In several studies concerned with hardening and the development of frost resistance (cf., for example, Tumanov 1931, Tumanov and Krasavtsev 1955, 1959, Leike 1965, Weiser 1970) the conclusion has been reached that in the apical and lateral meristems, resistance to frost is developed in two consecutive and essentially different stages. For instance, according to Tumanov, the first stage coincides with that climatic period in the autumn when the temperature fluctuates mainly between 5° and 0°C. As regards biochemistry, it is a characteristic of this stage that soluble carbohydrates accumulate in the living cells. The second stage coincides with that period of the autumn and early winter when the temperature seldom rises above 0°C. The second stage is characterized by physiological phenomena that cause the water content of living cells to decrease and the cytoplasm to solidify.

The observations made and the data obtained in the course of the present study largely agree with these findings. The first stage in the hardening process distinquised by Tumanov and Leike coincides to a great extent with dormancy I as described in this study and the second stage with the early phases of dormancy II. For instance, Tumanov et al. (1964)

state that »Thirty days are sufficient for the first hardening phase in dormant birch and white acacia at 0°C (whether in light or dark)». On the ch.u. scale developed in the present study (Table 5), 30 days at 0°C is equivalent to $30 \cdot 24 \cdot 0.52$ ch.u. = 374 ch.u. which is close to the result obtained here for dormancy I in the apical meristems of *Betula pubescens* (p. 71). In the present study, another point that has attracted attention is the difference, important in principle, between the first and second stages, i.e. that the physiological processes characteristic of the first stage are largely irreversible, whereas those characterizing the second stage are reversible (details will be given below).

In the following, the term hardening refers to the phenomena belonging to the first stage, and the development of resistance to (very) low temperature refers to the second stage.

It should be noted that the physiological processes included in the active period also make an important contribution towards hardening and the development of resistance to very low temperatures. The nutritional state of a tree at the end of the active period depends largely on how favourable environmental conditions were during the course of the active period. Where the nutritional balance is poor, or perhaps even negative, the accumulation of soluble carbohydrates in the meristematic cells, regarded by Tumanov and others as a biochemical process characterizing the acclimation phenomenon, is likely to be inadequate. This probability can at least be speculated on. Many observations confirm the view that a good nutritional balance improves frost resistance.

When the hardening process and frost resistance are examined, consideration of the active period is also necessary from another and perhaps even more important point of view. Obviously, those apical and lateral meristems that by the autumn and on the threshold of early winter have not completed their active period cannot proceed to dormancy (either dormancy I or dormancy II) and may thus be unable to undergo the normal hardening process. During the autumn and winter frosts they are still in the active period and will, sooner or later, at least in the severe Finnish winter, become injured or even freeze to death.

When (pp. 57—63) the predictions pertaining to the frequency distribution of the d.u. sums of microspores passing from dormancy I to dormancy II, made on the basis of laboratory experiments, were compared with the corresponding frequency distributions of the pollen catches measured in natural conditions it was possible to make observations regarding the frost resistance of living meristematic cells while they were in dormancy I. These observations indicated that in dormancy I resistance to frost is somewhat better than in the active period. While even temperatures below —3°C are usually fatal in the active period, the critical temperature in dormancy I

seems to be somewhere between —7° and —10°C. For instance, at Punkaharju on October 27, 1966, when they were close to the end of dormancy I, the pollen grains of *Alnus incana* did not become injured even though the temperature at canopy level dropped to a minimum of —7°C.

Even though resistance to frost may be a little better in dormancy I than in the active period, it is important to note that for withstanding the severe climatic conditions in Finland it is poor. Here it may be noted that Leike (1965), from his investigations on frost resistance, came to the conclusion, at first sight paradoxical, that at the beginning of winter (in dormancy I), when »dormancy was at its deepest» (true dormancy!), the frost resistance of living cells was relatively poor.

In this context the observations made concerning the accumulation and depletion of starch reserves are relevant (Sarvas 1972, p. 94). Particularly, during dormancy I the accumulation of carbohydrate (starch) in the meristematic cells appears to be an irreversible phenomenon. The fact that the starch dwindles soon after it accumulates is not an indication of reversibility but a sign that it is converted to other, soluble carbohydrates. This conversion, in contrast, seems to be reversible to some extent: in samples fixed at temperatures above 0°C the amount of starch seen is greater than in samples fixed at temperatures below the freezing point. The interaction found (cf., for instance, Leike 1965) between leaf-fall and the progress of dormancy I in the apical meristems further suggests that irreversibility may even be a fairly general characteristic of the physiological processes included in dormancy I (at least, the yellowing of leaves and leaf-fall are irreversible).

Resistance to very low temperatures, by contrast, develops gradually and is only acquired during dormancy II. Some observations concerning the microspore mother cells shed light on this process. Male flower buds of *Larix sibirica* and *Larix decidua* were fixed during mild weather (between 0° and 5°C) and also during a hard frost (between —15° and —30°C) in the early winter of 1971. It could then be seen that the mother cells that had been fixed in intense frost were very different in appearance from those fixed in mild weather (cf. Fig. 20). In frosty weather, the mother cells were irregular and shrivelled in form, the nuclear membrane was not distinct, as it is in mild weather, and no dark spots characteristic of the chromosomes at the diplotene phase could be distinquished. However, when the mild weather (temperature around 1°C) returned, even in midwinter, the mother cells resumed their typical mild-weather appearance.

These observations show that the mother cells in dormancy II are not inert but react readily to changes in temperature. It can be speculated that as the frost becomes more intense the mother cells undergo changes which gradually increase their resistance to frost. As the weather becomes milder

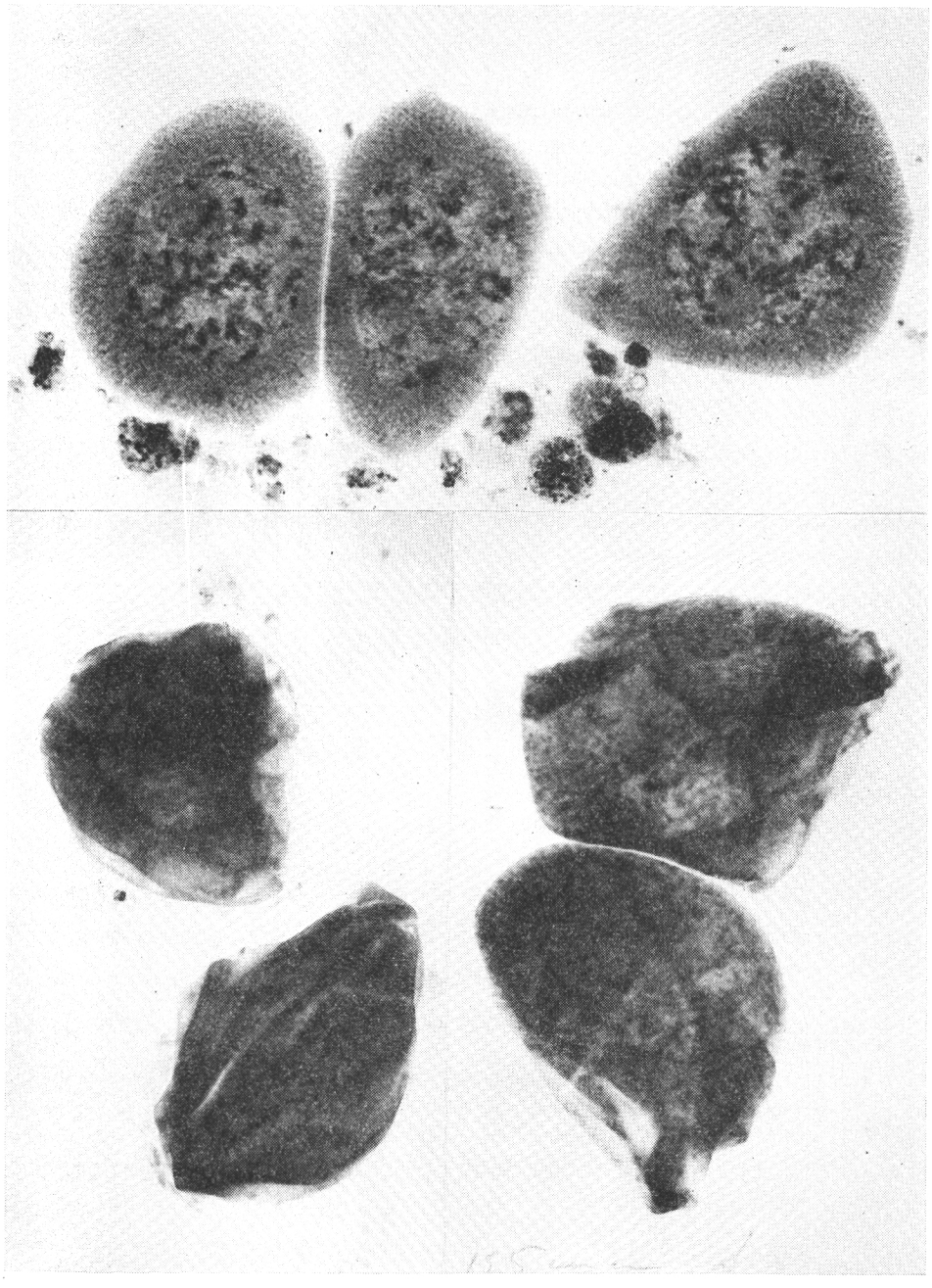


Fig. 20. Microspore mother cells of *Larix sibirica* (Punkaharju, sample stand No. 8). The twigs were cut off the tree at 14 h. on November 23, 1971. Some of the male buds were fixed immediately (the lower section of the figure), whereas others were first forced at 2°C for 2 days and then fixed (the upper section of the figure).

the resistance to frost weakens again. Thus, the increase and decrease in resistance to frost in dormancy II means that these physiological phenomena are reversible.

Also, resistance to frost remains poor if, on account of exceptional weather conditions in the autumn, dormancy II comes to an end before the onset of winter, and as a result the meristems involved in the progress of the annual cycle pass into the active period. This is accompanied by a gradual decrease in frost resistance. Such a situation although rarely seen among autochthonous tree species, which are well adapted to the local climate, may well arise where tree populations native to a continental climate are grown in an oceanic climate.

REVIEW OF LITERATURE

Concept of dormancy

The literature concerned with dormancy in trees is so vast that even a brief general survey is out of the question here. Moreover, several good reviews are already available (D o o r e n b o s 1953, R o m b e r g e r 1963, and L e i k e 1965). Here, the data obtained and the conclusions reached in the present study will be considered in relation to those of earlier investigations.

On the basis of the definitions presented by P f e f f e r (1904) and M o l i s c h (1909), L e i k e (1965) divided dormancy into three main parts: »I korrelative Knospenhemmung (Molisch 1909), Austreiben der Knospen wird durch in der Pflanze, aber ausserhalb der Knospen liegende Ursachen (z.B. Blätter) verhindert, syn. summer dormancy (Doorenbos 1953), II autonome Knospenruhe (Pfeffer 1904), Austreiben der Knospen wird durch in den Knospen selbst liegende Ursachen gehemmt oder verhindert, syn. winter dormancy (Doorenbos 1953), III aitionome Knospenruhe (Pfeffer 1904), Austreiben der Knospen wird nur durch äussere Ursachen (ungünstige Klimabedingungen) verhindert, syn. imposed dormancy (Doorenbos 1953)».

At first glance, this division seems logical and appropriate. But a closer examination raises the question of whether the difference between autonomous rest in buds and aitionomous rest has been correctly understood. In both cases, the release of dormancy depends, of course, on factors present in the bud (genes, enzymes, hormones, and inhibitors) and on environmental factors. The idea that the release of autonomous rest (true dormancy) is more dependent on factors within the bud than is the release of aitionomous rest (imposed dormancy) does not seem justified. What are the »ungünstige Klimabedingungen» which alone would induce aitionomous rest? A low temperature (below —3°C), without doubt, would be one of the most important. As soon as the temperature rises above —3° or, at least, when it rises above 5°C, the release of aitionomous rest occurs. But on similar grounds it could be suggested that the release of autonomous rest is only prevented by unfavourable environmental factors (e.g. temperatures above 10°C and, possibly, a short photoperiod). Thus, for diagnostic purposes the concepts of

autonomous and aitionomous rest do not seem very helpful. On the other hand, correlative inhibition, as defined by Molisch, is clearly distinguishable from autonomous and aitionomous rest as a stage that is clearly defined. Correlative inhibition is in a special position in another respect, too. Here, if anywhere, dormancy is an inappropriate term, for in the greater part of that particular cycle interval where correlative inhibition prevails, the apical meristems in the buds are vigorously active (in the active period), producing an increasing number of leaf initials in the upper portion of the apical dome. Cf. Leike, p. 477: »Korrelative Hemmung und Ruheperiode betreffen im wesentlichen das Streckungswachstum der Knospen, während gerade zu dieser Zeit wichtige Differenzierungsvorgänge ablaufen, die bei günstigen Aussentemperaturen auch in der tiefsten Ruhe nicht völlig unterbrochen werden». Thus, no overall rest period is involved, but correlative inhibition only prevents the buds from flushing. In the present study, correlative inhibition has not been regarded as one of the main stages of the cycle. According to the model of the cycle developed in the course of this study, correlative inhibition is a physiological stage in the active period of apical meristems to which a given cycle interval has been assigned.

As briefly mentioned in the Introduction, the term winter dormancy refers in the present study to the cycle interval between the end of dormancy I (autumn dormancy) and the beginning of the next active period. Winter dormancy defined in this way is not identical with the condition as defined by Doorenbos (syn. true dormancy). The closest equivalent to Doorenbos's winter dormancy is the dormancy I stage defined in the present study. The dormancy II stage, as defined here, would obviously be included in aitionomous rest in Leike's system and in imposed dormancy in the system applied by Doorenbos. However, there is a great difference in principle between imposed dormancy as defined by Doorenbos and the dormancy II distinguished in the present study. Although dormancy II, like the active period, starts to progress as soon as the temperature exceeds —3°C, the cells have to meet a d.u. sum requirement specific to each population (similar to the ch.u. sum requirement of dormancy I) before they pass to the active period. If one wishes to use the concept of imposed dormancy, its application should, as shown by the results obtained in the present study, be limited to cells that have reached the active period but are kept inactive, at least seemingly, by low temperatures (below —3°C) or other environmental conditions that are unfavourable during that period.

At this point it should be noted that the term winter dormancy as applied by Doorenbos is attended by a serious and generally recognized flaw: as a rule, dormancy I does not occur in winter but in autumn and, moreover, usually in the first rather than in the second half of autumn. The term is thus very misleading. On account of this the term autumn dormancy has been

used in the present study as a descriptive synonym for dormancy I and the term winter dormancy has been applied only to dormancy II, which really does occur in the actual winter.

In several publications concerned with dormancy (for instance, S a m i s h 1954, V e g i s 1964, 1965) autonomous rest in buds has been divided into three phases: I preliminary rest (predormancy), II midrest (true dormancy) and III after-rest (postdormancy)[1]). This subdivision is based on the notion that »rest becomes deeper and deeper» until it reaches a maximum, then grows shallower and shallower until it is broken. Such a mode of thought is a very natural consequence of the use of the term dormancy, with its subconscious suggestion of parallels between this condition and, for instance, the rest that man enjoys in the form of sleep. This concept is contrasted with the hypothesis that within a given main part of the cycle (for instance, the entire autonomous rest) the mode of reaction of a given meristematic tissue to environmental factors is practically unchanged and that the transitional phases between the different main parts of the cycle (for instance, between autonomous and aitionomous rest) are brief, although not necessarily so brief as to form thresholds. The data accumulated in the course of the present study have led to the adoption of this latter alternative.

Influence of environment on the onset and termination of dormancy

The influence of environmental factors on the onset and termination of rest in buds has attracted much attention. The most difficult question is which are the environmental factors (or the factor) that induce autonomous rest in buds. This question has already been discussed in the first part of the present study on the active period, because the end of the active period and the beginning of dormancy I are in many respects the same thing. Reference is, therefore, made to this earlier review (S a r v a s 1972, pp. 70—76). However, it may be well to touch upon the question briefly here, too.

Several results of laboratory experiments have been interpreted to mean that the shortening of day length in the autumn is one of the most important environmental factors, if not the only one, to which the plant reacts in such a way that in certain meristems the cycle passes from the active period to dormancy (cf., for instance, T u m a n o v et al. 1964).

On the other hand, it has been suggested that the significance of photoperiod (or nyctoperiod) may have been exaggerated and believed to apply

[1]) It is difficult to see whether these three phases have counterparts in the cycle model presented in this study. Preliminary rest would perhaps correspond to the initial part of dormancy I defined in the present study, i.e. that part in which dormancy I stays at the zero point as a result of high temperature. Midrest would apparently correspond to dormancy I (autumn dormancy) and after-rest to dormancy II (winter dormancy).

too widely. For instance, Leike (1965, p. 480) states: »Die ökologische Bedeutung der photoperiodischen Regulierung des Einsetzens der Ruheperiode wird häufig überschätzt. Für Gehölze der Klasse C ist sie von vornherein nicht vorhanden. Bei Pflanzen der Klassen A, B und D muss berücksichtigt werden, dass bei vielen Gehölzen die Ruheperiode in unseren Breiten bereits im Juni/Juli beginnt, zu einer Zeit mit mehr als 16 Std. Sonnenlicht und mindestens 18 Std. photoperiodisch wirksamer Helligkeit am Tag. Das bedeutet aber, dass für viele Gehölze die photoperiodische Induktion der Ruheperiode nur eine rein theoretische Möglichkeit ist, die am nätürlichen Standort niemals genutzt werden kann, da die Ruheperiode aus inneren oder anderen Gründen längst eingesetzt hat, bevor photoperiodisch induktive Bedingungen aintreten . . . Es ist aus diesem Grunde eigentlich irreführend, unter natürlichen Bedingungen von einer Kurztagsinduktion der Ruheperiode zu sprechen, da bestenfalls ein verkürzter Langtag wirksam werden kann». The view of Wareing and Phillips (1973) seems to be largely similar.

As has been stated previously, the starting point for the present study was the working hypothesis that for a certain genotype the active period of a particular meristem or meristem type terminates each year, on an average, at about the same p.u. sum, which means that the meristem in question immediately passes to dormancy I (its initial stage, zero point). However, in principle, this working hypothesis is applicable only to trees growing in their natural habitat. If this condition is not met, for instance, when exotics or foreign populations (origins) of indigenous species are transferred to an essentially different habitat, photoperiod may become an important factor. The marginal populations of autochthonous tree species are, to some extent, comparable to exotics, for generally, even in their natural habitats, they are no longer fully adapted to one or several of the environmental factors (cf. Sarvas 1970).

The data obtained by different research workers concerning the release of autonomous rest in buds and the conclusions drawn by them are in much better accord than the data concerning the beginning of rest. It is generally agreed that in nature the release of autonomous rest in buds occurs at temperatures below 10°C. The cold requirement is often expressed as the total length (for instance, in hours) of the time required for dormancy to progress from its start to the end phase at a temperature of 7°C or lower (cf., for instance, Weinberger 1950, p. 122, Doorenbos 1953, p. 9, Wareing and Phillips 1973, p. 230). Such a definition regarding the cold requirement comes near to the concepts adopted in the present study. The most important difference is that in the present study experimental measurements have shown that different weights should be assigned to temperatures below 10°C (the time required for the release of autonomous rest, dor-

mancy I, has to be weighted with temperature and the weights for different temperatures have to be found by experimentation in a controlled environment). The highest value, 1.0, has been assigned to a temperature of 3.5°C, and lower values have been calculated for temperatures below and above this — the appropriate value for temperatures of —3° and 10° being 0.03.

A review of the situation by Wareing (1956), largely based on his own investigations, merits special attention. Discussing laboratory experiments conducted by several researchers, Wareing concluded (p. 192) that »In species with monopodial habit the onset of dormancy under short-days is marked by the formation of a terminal resting bud, and in those with sympodial habit it involves abscission of the shoot apex. It appears that short-day treatment generally induces a state of winter dormancy in resting buds, which (except in *Fagus sylvatica)* can be broken by chilling». Wareing further emphasized (pp. 207—208) that results obtained in this way cannot be extended to apply to phenomena in nature: »It need hardly be pointed out, however, that the demonstration of photoperiodic responses in relation to experimentally controlled day length conditions does not imply that such effects will necessarily occur in nature. — — — Indeed, of the considerable number of species which have been found to show hastened dormancy under experimental short-day conditions, probably only a small proportion show extension growth actually subject to photoperiodic control in nature». Wareing also discussed the possibility underlined in the first part of this study that small seedlings, particularly those 1 year old, and mature trees may in many respects behave in fundamentally different ways (p. 208): »Thus, conclusions regarding mature trees cannot be arrived at by extrapolation from the photoperiodic behaviour of the seedlings».

In studies concerned with chilling requirements, considerable differences have been found between different species and even between different genera of the same species (cf., for instance, Weinberger 1950, Perry and Wang 1960, Kriebel and Wang 1962, Nienstaedt 1967). For instance, for *Picea species* (Nienstaedt 1967, p. 67) the chilling requirement at 4.4°C seems to vary from 2 (from 1?) to 4 weeks.

Laboratory experiments have shown that autonomous rest in buds is also broken as a result of a long photoperiod. The extent to which the photoperiod affects phenomena in nature is not yet clear. As Worral and Mergen (1967, p. 735) aptly remark: »Because photoperiod in a specific area is constant on any date from year to year, providing cloud-cover is ignored, control of the breakage of dormancy by photoperiod alone should ensure that »spring» would always arrive on the same date. On the contrary, it is well known that there is a wide year to year variation in date of breakage of dormancy». (The same applies to onset of dormancy!)

It should be emphasized that the dormancy II stage, as defined in the present study, has attracted hardly any attention at all in the literature. This stage of the cycle has generally been included in the aitionomous rest in buds (imposed dormancy). This is understandable, for in dormancy II there is no chilling requirement and, therefore, it is difficult to find a definition by which to distinguish dormancy II from the active period (in the present study, dormancy II has been distinguished from the active period by the difference in the regression of the rate of progress of the cycle on temperature in these two stages). However, in this stage there is a dormancy unit sum requirement resembling the chilling unit sum requirement in dormancy I. And what is even more important is that dormancy II is the true winter dormancy in the proper sense of the word, expressly because it appears to be the only part of the cycle in which resistance to very low temperatures (below —15°C) can be developed; moreover, dormancy II is the particular stage of the cycle in which trees spend the actual winter, the coldest part of the annual climatic cycle.

DISCUSSION

The general features of the model of the annual developmental cycle of forest trees has by now acquired a more definite form. The entire annual cycle so clearly distinguishable in the development of forest trees, particularly in the temperate climatic zone, can be interpreted as a manifestation of the internal physiological clock of the plant, the timing of which depends primarily on temperature.

It has proved appropriate to divide the cycle into three main parts: 1. the active period, 2. dormancy I (autumn dormancy) and 3. dormancy II (winter dormancy). During each of these main parts progress is determined by a different timing mechanism (as shown by the regressions of the rate of progress of the cycle on temperature). Without doubt, moisture, too, plays an important role; however, in the apical meristems the variation in moisture within each of the main parts of the cycle appears to be slight. On the other hand, there may possibly be differences between the main parts that are more significant and have to be considered when the entire cycle is examined.

The model of the cycle has been constructed largely from measurements of the rate of progress of the cycle in a controlled environment. For purposes of quantitative treatment of the data it has proved useful to define a unit for the cycle interval. According to the general definition (p. 6), this unit refers to the cycle interval through which the cycle progresses in one hour at the base temperature. For historical and methodical reasons, the base temperatures for the three different parts of the cycle were chosen in slightly different ways. However, the final outcome is that in the different parts of the cycle, the base temperature is almost the same, 2° and 3.5°C. In the active period, the unit of the cycle interval has been assigned the symbol p.u. (period unit), in dormancy I, the corresponding symbol is ch.u. (chilling unit) and in dormancy II, d.u. (dormancy unit).

In the model of the cycle now constructed, the progress of each of the main parts of the cycle continues until the sum of the units has reached a certain total: the active period ends at a specific p.u. sum and the cells (and meristems) on whose activity the cycle depends pass automatically to dormancy I. This, in turn, ends at a specific ch. u. sum and the cells pass to dormancy II, which, again, ends at a specific d.u. sum and the cells pass to

the next active period. Thus, functioning on two simple principles, timing dependent on temperature and the ± constant sum of units required for each of its main parts, the cycle continues indefinitely.

This model can also be described as follows: to break out of dormancy I a tree must be exposed to a certain chilling unit sum, specific to each species, population, and individual, reckoned from the beginning of dormancy I. Correspondingly, to emerge from dormancy II it must experience a certain dormancy unit sum, reckoned from the beginning of dormancy II, and to reach the end of the active period it must be exposed to a certain period unit sum, reckoned from the beginning of the active period.

The dormancy I (autumn dormancy) defined in this study is largely the same as the winter dormancy defined by Doorenbos (1953) or the true dormancy defined by Samish (1954). On the other hand, for the dormancy II (winter dormancy) distinguished in this study, it is difficult to find any clear counterpart in the literature (but see Perry 1971, p. 30). The opinion generally held was probably that dormancy I was succeeded by a state called imposed dormancy, i.e. a state that initiates the active period as soon as environmental factors become favourable. However, the present study has revealed that dormancy I is generally succeeded by a phase of the cycle where this does not occur. A characteristic of this phase is a given dormancy unit requirement (which corresponds to the chilling unit requirement of dormancy I). Not until this requirement (release of dormancy II) has been met will the meristems pass to the active period, where at first, as a result of low external temperatures, which often continue at this time of year, it may enter real imposed dormancy. Dormancy II differs from dormancy I in that the former becomes released not only at low temperatures but also at temperatures above 10°C (cf. Perry 1971, p. 30: »warm temperature requirement»).

Here it is important to note that in principle no parts of the cycle are static in the true sense of the word. And, on the other hand, the cycle may come to a seeming standstill in any of its three main parts: in the active period and dormancy II this happens when the temperature drops below —3°C, and in dormancy I when the temperature rises above 10° or drops below —3°C. Thus, the terms, such as rest, dormancy, etc., that have been used (and are used even in the present study) are seen to be highly misleading.

It is also illogical to maintain that in some of its main parts the cycle comes to a seeming standstill on account of internal factors and in others as a result of unfavourable weather conditions. The converse of the latter statement is, of course, true, i.e., in a certain stage environmental factors are to be considered unfavourable if the cycle does not progress (for instance, temperatures above 10°C are unfavourable during dormancy I) and favourable when the cycle progresses appropriately from the ecological point of view.

Previously, it has been stressed that a logical model of the cycle can hardly be constructed unless the basic ecological function of the cycle is considered in conjunction with the experimental evidence: the physiological cycle represents, above all, the adaptation of trees to the climatic cycle of the habitat where they evolved.

At this stage of the investigation, it is clear that one of the fundamental functions of the timing and total length of the active period is to strengthen the competitiveness of an individual and a species by ensuring that the particular part of the climatic cycle favourable to vegetative physiological processes is fully utilized. Another important function of the active period is to ensure the survival of the individual (and the species) by taking care that winter does not interrupt any of the vital functions (i.e. these have to come to an end in good time before the onset of winter). It is obvious that these two functions, maximal utilization of the particular season favourable for vegetative processes and minimizing of the risk presented by winter, are in opposition to each other.

Similarly, dormancy II, winter dormancy, can be regarded as having two functions: it must ensure the survival of an individual and a species in the coldest part of the climatic cycle in a zone where the temperature almost invariably drops below —20° and often even below —30°C. And, regarding the competitiveness of a species, it is important to ensure that winter dormancy does not interrupt or retard the vegetative processes of a species more than is really necessary from the point of view of adequate frost hardiness. These two functions, which in fact are similar to those involved in the active period, except that they have a different starting point, are likewise opposed. And here, too, the final outcome must be a compromise. However, this calls for a more detailed discussion.

Obviously, the length of dormancy II (the d.u. sum specific to the species and genus concerned) is so adjusted that dormancy II does not end in the spring so early as to involve a risk or so late as to make the price of elimination of the risk unreasonable; in other words, the active period is not shortened by dormancy II more than is absolutely necessary.

Termination of dormancy II depends not only on the length of dormancy II but also on the time when it begins. For instance, should dormancy II begin immediately after the active period has terminated there would be a risk that in very warm growing seasons dormancy II would end before the onset of winter, leaving the trees without protection from frost. The problem of the beginning of dormancy II is solved ingeniously by dormancy I: dormancy II does not begin until the temperature has remained below 10°C for some time. In this way, the start of dormancy II is rendered independent of the p.u. sum of the past summer. This is obviously one important function of dormancy I. Dormancy I thus ensures that the physiological stage

during which the tree is resistant to cold begins at the appropriate season; the length of dormancy II, the d.u. sum specific to the species and genus, ensures that protection ends at an appropriate time.

Dormancy I obviously has another function in the cycle in addition to the one described above. As an illustration of this function let us picture a model of the cycle in which only the active period and dormancy II alternate in accordance with the principles stated above. In a certain autochthonous population let us then examine two individual trees, one belonging to a genotype with a short active period, the other to one with a long active period. Let the total length of the active period of the former be 20 000 p.u. and of the latter 25 000 p.u. Since there is hardly any reason to assume a correlation between the total lengths of the active period and dormancy II, we will further assume that for these two trees the total length of dormancy II is the same, for instance, 2 000 d.u. In addition, let us assume that in a given year P_1 the physiological cycle is well synchronized with the climatic cycle. In year P_2 the difference in the p.u. sums of the ending times of the active periods of the genotypes under examination has risen to 10 000 p.u., in year P_3 to 20 000, and so forth. It is obvious that in a few years' time a situation would arise where the cycle of either one (or both) of the genotypes would be poorly synchronized with the climatic cycle.

Such an increasing discrepancy between the physiological and climatic cycles does not arise because dormancy I comes between the active period and dormancy II. For instance, in the imaginary model of the cycle pictured above, the short-active-period genotype ends its active period at 20 000 p.u. and the long-active-period genotype at 25 000 p.u., but only after the ch.u. sum has risen to a total of, say, 300 ch.u. do they simultaneously pass into dormancy II. Thus, dormancy I carries out at least two important functions yearly: 1. it ensures the onset of dormancy II at an appropriate time and 2. every autumn it reduces to a minimum the large variation arising during the active period between the different genotypes with regard to the progress of the cycle.

The cycle is often illustrated by means of a circle on which the relative lengths of the different parts of the cycle are marked (Fig. 21). In an illustration like this the first-mentioned function of dormancy I can be represented with a wavy line. Dormancy I is like a bellows which permits extension and compression according to need. To be more specific, the length of dormancy I expressed in chilling units is, at least broadly speaking, the same every year, but the p.u. sum of the period of time involved varies greatly; in warm summers it is large and in cold summers small.

From the synchronization effected by dormancy I it follows that at the zero phase of dormancy II the differences between the different individual trees (genotypes) in one population as regards the progress of the cycle are

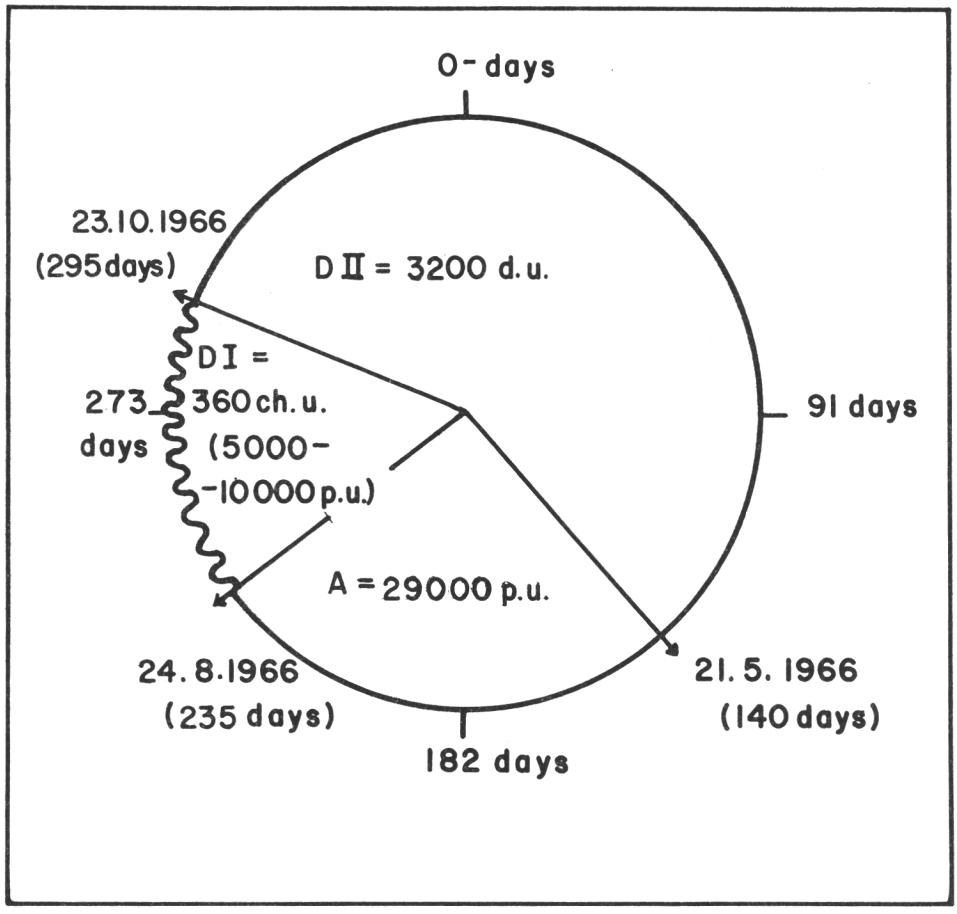


Fig. 21. Diagram representing the annual cycle of development of the generative meristems of *Betula pubescens* (origin Punkaharju). The scale of the circle is calendar time. A = active period, D I = dormancy I, and D II = dormancy II. The wavy portion of the circumference, representing dormancy I, demonstrates the particular characteristic of the cycle that even though the length of dormancy I is constant when expressed in chilling units, this length varies when it is expressed in period units (i.e. between 5 000 and 10 000 p.u.).

reduced to a minimum. On account of this, if one wishes to name a natural zero point for the cycle, the zero point (starting point) of dormancy II is without doubt the best choice. This zero point is not a very sharp one either, for, as seen when discussing the pattern of parcels during the course of development (p. 57), there is considerable variation even as regards the start of dormancy II. Thus, the synchronization (adjustment of the clocks) accomplished by dormancy I is not perfect. Even so, the natural zero point of the cycle is in the autumn, and not in the spring as has traditionally been thought. Here lies, without doubt, one of the causes of the difficulties that

have interfered with earlier attempts to solve the problem of the zero point of the active period.

In this connection it is well to view the entire cycle from yet another angle. In the foregoing it has already been shown that in all three main parts of the cycle, the regression of the rate of progress of the cycle on temperature is similar at low temperatures (between —3° and 4°C), but that at high temperatures (above 10°) there are great differences between these stages. These differences become more evident when all three regressions are drawn on the same scale (Fig. 22). A study of Fig. 22 reveals a certain resemblance between these regressions and the view presented by V e g i s in several papers (e.g. 1948, 1965) that dormancy in forest trees is characterized by changes (narrowing and broadening) in the effective temperature range; from Fig. 22 it is seen that as the cycle progresses from the active period to dormancy I the effective temperature range narrows greatly and when the cycle progresses to dormancy II and further to the active period, the effective temperature range broadens.

In the foregoing it has been established as characteristic of the active period as well as of dormancy II that by their timing and length they simultaneously achieve two conflicting goals: 1. the most efficient utilization of the part of the climatic cycle that is favourable for vegetative processes, which ensures good competitiveness and 2. the most efficient protection against a winter that comes either exceptionally early or exceptionally late, which guarantees the immediate survival of the individual. These two goals can hardly be achieved simultaneously without a compromise in which the physiological clock has been made to synchronize accurately with the climatic cycle. Obviously, evolution has arranged for the risk involved to be as high as possible without being fatal. This must inevitably mean that the genetic variation in the length of the active period, dormancy II and dormancy I is probably large, particularly for tree species with a wide geographic range. In the present study this variation, too, has been followed, even if on a small scale only. The question is so complex, however, that it will have to be treated separately.

In the present investigation, interest has been concentrated particularly on the autumn dormancy and winter dormancy of flower and vegetative buds. Dormancy in seeds has been included in the examination only because it has afforded methodical advantages as compared with that in buds. There has been no attempt to obtain an overall picture of dormancy in seeds. It must be underlined that for the most part the ecological functions of dormancy in the apical meristems and in seeds are very different. In the apical meristems of most of the tree species of temperate climate these functions of dormancy are very similar. In seeds, again, they are very different in different tree species and, owing to this, manifest a great variety of physio-

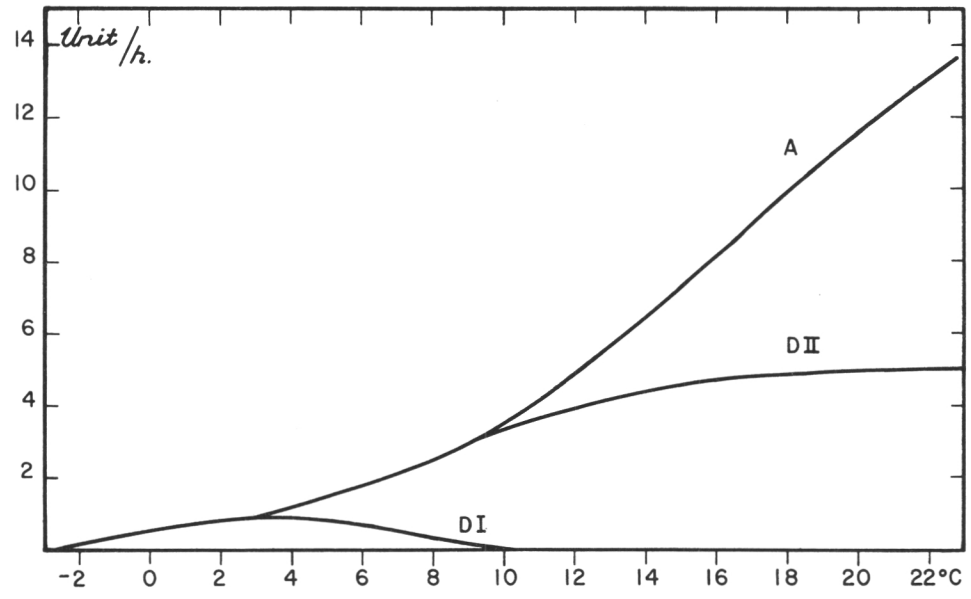


Fig. 22. The regression of the rate of progress of the different main parts of the cycle on temperaturel reduced to the same scale (in all these main stages the unit of cycle interval is that cycle interva, through which the cycle progresses at 3.5°C in one hour). A = the active period, D I = dormancy I and D II = dormancy II.

logical solutions. The most important feature that the ecological functions of dormancy in the apical meristems and in seeds have in common is perhaps that abscisic acid evidently plays an important role in both of them. This may, in fact, be the reason why in this investigation the regression of the rate of progress of dormancy I on temperature could be determined by using seeds rather than buds as study material.

During the latter half of the last century, the usefulness of so-called temperature sums for scientific purposes was often the subject of rather heated discussions between phenologists and plant physiologists. The phenologists were for and the plant physiologists against the use of temperature sums. The plant physiologists won (cf., e.g., P f e f f e r 1904, p. 269), of course, for, basically, the problem was one of plant physiology. Time has passed and today one might ask whether their triumph was not something of a Pyrrhic victory. In any case, as a result of this, the investigative approach based on temperature sums remained in almost complete disuse for several decades. In the light of the present investigation, it is evident that both parties to the discussions were partly right and partly wrong.

Scientific efforts were unavoidably concentrated on the active period (in the present study, too, at first), because information on the rest of the cycle was scanty, and much time was wasted on largely fruitless discussions concerning threshold values (this was the case in the present study too). Also, the solution of the zero point problem by an investigation of the active period alone was almost impossible.

However, the temperature sum approach, though outmoded, is used in biology, even at the present moment, in a disguised form, to a greater extent than one unfamiliar with the subject would be inclined to think. For instance, use of the concept of the so-called thermal growing season and references to chilling requirements are tantamount to this. In reality, the temperature sum approach is nothing but recognition of the fact that in several of the problems faced in biology the need almost inevitably arises for a single parameter to denote the joint effect of time and temperature.

The most important difference between the principle employed in the present study and those used earlier is the following. Earlier, different temperature sum calculation methods were chosen by some kind of rule of thumb, and the validity of the results was tested by comparison with observations made in nature. In the present investigation, the dependence of the progress of the three main phases of the cycle on the environmental factors was first clarified experimentally and this evidence was used to construct parameters denoting the joint effect of the environment (time and temperature) during the successive stages of the cycle.

Tiivistelmä

Tämä metsäpuiden vuotuisen kehityksen talvihorrosta käsittelevä tutkimus on rinnakkaistutkimus aikaisemmin julkaistulle, vuotuisen syklin aktiivia periodia koskevalle osalle. Tekijä on pyrkinyt luomaan kokonaiskuvan kehityksen vuotuisesta syklistä, ja tästä syystä tutkimus niin kentällä kuin laboratoriossakin on ollut jakamaton kokonaisuus, jonka eri osia on tutkittu suuressa määrin samanaikaisesti. Tulosten julkaiseminen kahtena erillisenä niteenä on puhtaasti julkaisutekniikan sanelema ratkaisu.

Metsäpuiden fysiologiaa, ekologiaa ja genetiikkaa koskevassa tutkimuksessa metsäpuiden vuotuisen kehityksen sykli on tullut yhä enemmän avainasemaan; se on suuressa määrin terra incognita, jonka eteen monen tärkeän, välittömästi käytännön metsätaloutta palvelevan tutkimussektorin eteneminen uhkaa pysähtyä. Tällaisia ovat mm. metsäpuiden taimien talveentumista ja talveentamista sekä talvivarastointia koskeva tutkimus, metsäpuiden siemensadon niin sadon määrää kuin laatua koskevien tarkkojen ennusteiden laatiminen, siemenhorrosta koskevat selvitykset, siemenen siirtoa koskevat kysymykset ja koko se laaja metsägenetiikan ala, joka tavalla tai toisella sivuaa metsäpuiden geneettistä sopeutumista luonnolliseen ympäristöönsä.

Tutkimus lähtee siitä toteamuksesta, että metsäkasvillisuuden, erityisesti puuston, vuotuisen kehityksen sykli on kaikilta osiltaan erinomaisen täsmällisesti synkronoitu puuston eri komponenttien kesken [1]). Nousee esiin kysymys, mikä on sen fysiologisen kellon periaate, joka vastaa tästä synkronoinnista. Tämä on tutkimuksen keskeinen ongelma.

Syklin kaikkia osia on voitu käsitellä periaatteessa samanlaisella käsitteistöllä ja samantapaisella tutkimusmenetelmällä.

Syklin eteneminen on ennen kaikkea ketju fysiologisia tapahtumia puun apikaaleissa ja lateraaleissa meristeemeissä. Saadut tutkimustulokset viittaavat siihen, että näissä meristeemeissä kosteustekijä on enemmän tai vähemmän optimaalinen suurimmassa osassa sykliä. Ilmeisesti tämä on eräs selitys siihen, että syklin eteneminen näyttää olevan suuressa määrin vain

[1]) On syytä samalla todeta, että tämä synkronointi ei ole mikään itsestään selvä automaatio; on yleisesti tunnettua, että m.m. monien troopillisten puiden, esim. troopillisten Pinus-lajien, kohdalla ei tällaista synkronointia ole — ei liioin alhaisia lämpötiloja, eikä ehkä syyshorrosta.

ajan ja lämpötilan valvonnassa. Tässä tutkimuksessa valon, erityisesti päivän pituuden vaikutus on jäänyt avoimeksi; toistaiseksi ei kuitenkaan ole näyttänyt tarpeelliselta, tai edes hyödylliseltä, liittää päivän pituutta syklin toimintaperiaatetta koskevaan malliin.

Perusyhtälö, joka tiivistetyssä muodossa sisältää syklin etenemistä vakiolämpötilassa koskevan perusidean, on seuraava:

$$S_1 \rightarrow S_2 = v\,(T)\,(t_2 - t_1) \tag{1}$$

jossa $S_1 \rightarrow S_2$ tarkoittaa ajankohtien t_1 ja t_2 välistä sykliväliä, T vakiolämpötilaa ja v (T) syklin etenemisnopeutta lämpötilassa T. Milloin lämpötila jatkuvasti vaihtelee, kuten luonnon oloissa, yhtälö saa muodon

$$S_1 \rightarrow S_2 = \int_{t_1}^{t_2} v\,(T(t))\,dt \tag{2}$$

Tämä taas voidaan käytännön laskuja, esim. ATK-ohjelmia varten, likiarvioida muotoon

$$S_1 \rightarrow S_2 = \sum_{i=1}^{n} v\,(T_i)\,\triangle t_i \tag{3}$$

jossa i on i:nnes lämpötilanmittaus, kun S_1:stä S_2:een kulunut aika on jaettu n:ään (yhtäsuureen) osaan.

Syklivälille määritellään yksikkö seuraavasti: yksikköväli on se sykliväli, jonka sykli etenee tietyssä peruslämpötilassa 1 tunnin kuluessa. Tämä määritelmä soveltuu syklin kaikkiin kolmeen pääosaan, aktiiviin periodiin, syys- ja talvihorrokseen. Peruslämpötilaksi olisi voitu kaikissa syklin kolmessa pääosassa valita sama lämpötila. Näin ei tietyistä historiallisista ja käytännöllisistä syistä kuitenkaan ole tehty.

Kaavoissa 1—3 on v ainoa tuntematon. Se voidaan määrittää kokeellisesti mittaamalla tiettyyn sykliväliin ($S_1 \rightarrow S_2$) erilaisissa vakiolämpötiloissa (T) kulunut aika ($t_2 - t_1$).

Syklivälin yksikön määritelmän ja kaavan (1) perusteella syklin etenemisnopeus missä tahansa vakiolämpötilassa voidaan tämän jälkeen laskea kaavasta

$$v\,(T) = \frac{h_P}{h_T}\ \text{s.y./t} \tag{4}$$

jossa h_P tarkoittaa sitä aikaa, mikä kyseiseen sykliväliin kuluu peruslämpötilassa P ja h_T sitä aikaa, joka kuluu lämpötilassa T. Tuloksen dimensio on s.y./t = syklivälin yksiköitä/tunnissa.

Yhtälön (1) lisäksi tässä tutkimuksessa koko syklin toimintaperiaatetta koskevaan ajatusmalliin kuuluu kaksi muuta tärkeätä periaatetta: 1. syklin eteneminen tapahtuu irreversiibelisti, 2. syklin kullakin kolmella pääosalla, aktiivilla periodilla, syyshorroksella ja talvihorroksella on meristeemilajille ja genotyypille ominainen vakiopituus tämän pääosan syklivälin yksikköinä lausuttuna; kun tämä vakiopituus on kumuloivasti summautunut täyteen, sykli siirtyy ilman mitään erityisiä impulsseja seuraavaan pääosaansa.

Näin syklin toimintaperiaatetta koskeva tutkimus pelkistyy kahdeksi pääongelmaksi: 1. millainen on syklin etenemisnopeuden ja lämpötilan riippuvaisuussuhde erikseen kussakin syklin kolmessa pääosassa ja 2. miten pitkä kukin päävaihe on (yksilö- tai populaatiotasolla) kyseisen päävaiheen syklivälin yksikköjen määränä lausuttuna.

Syyshorroksen syklivälin yksiköksi on valittu se sykliväli, jonka syyshorros etenee yhden tunnin aikana +3.5°C lämpötilassa. Etenemisnopeuden riippuminen lämpötilasta, laboratoriokokeisiin perustuen, nähdään graafisesti kuvassa 5, s. 29 ja diagrammista otettuja arvoja taulukossa 5, s. 30. Tulokset syyshorroksen pituutta koskevista mittauksista, joita on suoritettu sekä koti- että ulkomaisilla puulajeilla, nähdään yhdistelmänä sivuilla 71—72.

Talvihorroksen syklivälin yksiköksi on valittu se sykliväli, jonka talvihorros etenee yhden tunnin aikana +2°C lämpötilassa. Etenemisnopeuden riippuminen lämpötilasta nähdään kuvassa 9, s. 43 ja siitä otettuja arvoja taulukossa 9. Talvihorroksen pituutta koskevat laskelmat on yhdistetty taulukkoon 10, s. 49.

Kokeellisia tuloksia verrattiin luonnossa suoritettuihin mittauksiin. Nämä vertailut osoittivat, että luonnossa tehdyt mittaukset eivät olleet antaneet tuloksia, jotka olisivat olleet ristiriidassa tässä tutkimuksessa kehitetyn syklimallin kanssa. Paitsi tätä, nämä vertailut valaisivat monipuolisesti asetetun syklimallin yksityiskohtia.

Vaikkakaan metsäpuiden talveentumistapahtuma, se on, syksyllä tapahtuva talvenkestävän fysiologisen tilan muodostuminen, ei varsinaisesti ole kuulunut tämän tutkimuksen piiriin, talveentumistapahtuman yleisestä aikataulusta ja sen liittymisestä kehityksen vuotuiseen sykliin on voitu muodostaa entistä täsmällisempi käsitys.

Syklin yleisessä ekologis-geneettisessä tarkastelussa todetaan, että fysiologinen sykli on ilmeisesti kaikilta osiltaan hyvin pitkälle mukautunut kunkin puupopulaation luonnollisen kasvupaikan ilmastolliseen sykliin. Aktiivin periodin kohdalla tästä yleensä syntyy maantieteellisesti etelä-pohjoissuuntainen gradientti ja sekä syys- että talvihorroksen kohdalla gradientti ilmaston mantereisuus-mereisyys suunnassa. Vaikkakin syys- ja talvihorroksen fysiologis-ekologiset tehtävät ovat hyvin erilaiset, näyttää siltä, että maantieteellinen mukautuminen on tapahtunut syklin näiden osien integroituna kokonaisuutena.

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METSÄNTUTKIMUSLAITOKSEN JULKAISUJA 84.2
COMMUNICATIONES INSTITUTI FORESTALIS FENNIAE 84.2

MUOKKAUKSEN VAIKUTUS METSÄMAAN LÄMPÖSUHTEISIIN POHJOIS-SUOMESSA

MATTI LEIKOLA

EFFECT OF SOIL PREPARATION ON SOIL TEMPERATURE CONDITIONS OF FOREST REGENERATION AREAS IN NORTHERN FINLAND

SUMMARY IN ENGLISH

HELSINKI 1974

IBSN 951-40-0134-6

Valtion Painatuskeskus/Arvi A. Karisto Osakeyhtiön kirjapaino
Hämeenlinna 1974

ALKUSANAT

Tämä tutkimus on yksi edesmenneen professori RISTO SARVAKSEN johdolla vuonna 1969 aloitetuista Metsäntutkimuslaitoksen metsänviljelyn tutkijaryhmän Pohjois-Suomen erikoistutkimuksista. Käsillä oleva julkaisu esittelee vuosina 1970—1973 suoritettujen maan lämpötilan termoelementtimittausten tuloksia. Muut lämpötilahavainnot on tarkoitus julkaista myöhemmin.

Lämpötilan mittauslaitteiden asennuksessa avusti ja vuoden 1970 kenttätöiden valvonnasta vastasi metsäteknikko PEKKA SUOLAHTI. Mittausten valvojana toimi vuosina 1971—1973 metsäteknikko JAAKKO ROKKONEN, joka myös on johtanut lämpösummien laskentaa. Mt. SUOLAHTI on piirtänyt julkaisun kuvat ja hän on muutoinkin avustanut sen painokuntoon saattamisessa. Kivalon koealan maan raekoostumustiedot on luovuttanut käyttöön koko tutkimuksen ajan kiinteässä yhteistoiminnassa ollut maat.metsät.lis. EINO MÄLKÖNEN. Käytetyn venäjänkielisen kirjallisuuden on kääntänyt metsänh. KULLERVO ETHOLÉN ja englanninkielisen tiivistelmän on kääntänyt rva MARJA DETHLEFSEN.

Käsikirjoituksen ovat lukeneet prof. SARVAKSEN ja lis. MÄLKÖSEN lisäksi fil. kand. JYRKI RAULO ja maat.metsät. kand. ELJAS POHTILA. He ovat tehneet varteenotettuja huomautuksia esitykseen.

Lausun parhaat kiitokset työssä avustaneille, erityisesti kaikille koealueilla toimineille mittaajille.

Helsingissä elokuussa 1974

Matti Leikola

SISÄLLYSLUETTELO

Sivu

1. Johdanto 7
2. Tutkimusaineisto ja menetelmä 9
   21. Koealueet 9
   22. Koealueiden maa 13
   23. Maan lämpötilan mittaus 14
      231. Mittauskaudet 14
      232. Mittauslaitteet 14
      233. Mittaussyvyys 16
      234. Mittarien lukumäärä 17
      235. Mittausajankohdat 18
   24. Lämpösummien koostaminen 19
   25. Mittausvuosien edustavuus 22
3. Tutkimustulokset 24
   31. Käsittelemättömän maan lämpöolot 24
   32. Käsittelyn vaikutus maan lämpöoloihin 27
      321. Laikutus 27
      322. Vaotus 30
         3221. Metsäauraus 30
         3222. Lautasauraus 34
      323. Jyrsintä 36
      324. Muu maan käsittely 39
4. Tulosten tarkastelua 42
5. Tiivistelmä 45
6. Kirjallisuusluettelo 47

Summary 53

1. JOHDANTO

Pohjois-Suomessa 1950- ja 1960-luvuilla suoritettujen metsänviljelyiden ennalta odottamattoman huono menestyminen paljastui vv. 1969—1970 toimeenpantujen taimistoinventointien eräänä päätuloksena (SOLIN 1970, ETHOLÉN 1971, 1972). Jo varttuneiden taimistojen kuolemista on yritetty selittää monin eri tavoin. Selvään ja yhdenmukaiseen kantaan ei kuitenkaan ole päädytty, vaan kysymys on laajentunut monitahoiseksi ilmastolliseksi, maantieteelliseksi, geneettiseksi, metsänhoidolliseksi ja metsänsuojelulliseksi kokonaisongelmaksi VALTANEN (1969, 1970, 1971, LÄHDE 1970, 1971, LÄHDE ja SILTANEN 1973, JALKANEN 1971, NOROKORPI 1971, POHTILA 1972, 1974). Tämä on nostanut voimakkaana esiin tarpeen tehostaa metsänviljelyn tutkimusta, erityisesti taimien elinympäristön monipuolista kartoitusta Lapissa. On tunnettu, että metsänviljelyn tuloksia kyetään parantamaan vain selvittämällä entistä tarkemmin eri kasvutekijät, niiden vaikutus taimien menestymiseen sekä edelleen metsänhoidollisten toimenpiteiden vaikutukset taimien elinympäristöön.

Eräänä varteen otettavana taimien kehitystä pohjoisilla leveysasteilla haittaavana ekologisena tekijänä on usein tuotu esiin maan alhainen lämpötila, joka suoranaisesti heikentää juurten toimintaa ja kasvua sekä välillisesti vaikeuttaa taimien ravinnetaloutta hidastamalla humuksen ja karikkeiden hajoamista maassa (esim. HESSELMAN 1927, AALTONEN 1940, TAMM 1940). Koska erilaisilla maanmuokkausmenetelmillä tiedetään voitavan muuttaa mm. maan pintakerroksen lämpöoloja, yleisesti on toivottu taimien elinympäristö voitavan tätä kautta saattaa niiden menestymiselle suotuisammaksi (mm. AUTIO 1965, VALTANEN 1968, SIRÉN 1969, RITONIEMI 1970, PIRINEN 1972).

Moneen muuhun ekologiseen tekijään verrattuna maan lämpötilaa on tutkittu verrattain vähän. Tietojen puute on ollut hyvin selvä erityisesti Pohjois-Suomen metsänviljelyalojen kohdalla. Tärkeitä kotimaisia julkaisuja ovat mm. KERÄSEN (1920) lumen ja maan lämpötilan mittaukset Sodankylässä vv. 1915—1917. FRANSSILA (1945, 1960, 1962) on käsitellyt lämpötilan mittauksen metodiikkaa ja erilaisten maalajien lämpöoloja Lapissa useassa julkaisussaan. Ilmatieteen laitoksella on myös ollut säännöllistä maan lämpötilan mittaustoimintaa Sodankylässä mm. vv. 1957—1960, sekä edelleen vuodesta 1962 lähtien (RAPELI 1969, RESULTS ... 1969). SIRÉN (1955 b) on julkaissut tuloksia lämpötilan mittauksista paksusammaltyypin kuusikoissa ja koivikoissa. Aivan

viime vuosina on tietoa Pohjois-Suomen metsänviljelyalojen lämpöoloista kertynyt enemmän. Maininnan ansaitsevat tässä yhteydessä ÄIKÄKSEN (1969), KOIVURINTEEN (1970), PENTTISEN (1970) sekä TURTIAISEN ja VALTASEN (1970) selvitykset. Pelsonsuon hallakoeasemalla on maan lämpöolojen vuotuisa kehitystä seurattu perusteellisesti, ja tuloksia ovat esitelleet ennen kaikkea PESSI (1956, 1957 a, 1957 b, 1958) ja VALMARI (1967, 1970). Vastaavia tuloksia Etelä-Suomesta ovat viime vuosina julkaisseet mm. HEIKURAINEN ja SEPPÄLÄ (1963), HUIKARI ja PAARLAHTI (1967) sekä MÄLKÖNEN (1972).

Ruotsissa ovat ODIN (1964, 1974) ja PERTTU (1970) julkaisseet Norrlannissa tehtyjen mikroilmastotutkimusten tuloksia. KOHH (1970) on suorittanut maan lämpötilan mittauksia Keski-Ruotsin metsäaurausaloilla, ja SÖDERSTRÖM (1959, 1974) on tutkinut taimien juurten kasvua ja maan lämpötilaa muokatussa ja koskemattomassa maassa. Myös BÄRRINGin (1967) laajaan peltojen metsittämistutkimukseen sisältyy mittauksia eri tavoin käsitellyn maan lämpöoloista. Aiheeseen liittyvistä norjalaisista tutkimuksista on mainittava ennen kaikkea MORKin tutkimus lämpöolojen vaikutuksesta kylvösiemenen itämiseen (1933) sekä hänen julkaisunsa Hirkjolenin tunturimetsissä vv. 1932—1967 tehdystä ekologisesta mittaustoiminnasta (1968), ja BJORin (1965, 1971, 1972), BRAEKKEN (1972) sekä BERGANin (1974) maan lämpötilaa ja vesitaloutta käsittelevät perusteelliset tutkimukset.

Myös Neuvostoliitossa on erilaisen maan käsittelyn vaikutusta metsämaan lämpöoloihin tutkittu intensiivisesti. Runsaasta kirjallisuudesta voi tässä yhteydessä esimerkkeinä mainita vain SHUBINin ja POPOVin (1959) tutkimukset metsänviljelytekniikasta Etelä-Karjalassa sekä KURAJEVin ja SESTAKOVin (1970) sekä BÉZDENÉZNYHin (1970) selvitykset maan fysikaalisten ominaisuuksien muuttumisesta aurauksen jälkeen. Monipuolisen kuvan maan lämpö- ja kosteusoloista sekä niiden merkityksestä havupuiden taimien alkukehitykselle antavat STRATONOVITSin (1966) sekä ORLOVin ja KOSELKOVin (1971) oppikirjat.

Tätä tutkimusta suunniteltaessa pidettiin erittäin tärkeänä havaintojen ulottamista koko roudasta vapaan kauden ajalle. Kirjallisuuden perusteella kyetään kyllä ainakin pääpiirtein hahmottamaan maan pintakerroksen lämpötaseen malli esim. erilaisten säätyyppien vallitessa (mm. ODIN 1969, LAITINEN 1970, BJOR 1972), mutta avoimeksi jää, millaisen kasvuympäristön eri tavoin käsitelty maa metsäpuiden taimille tarjoaa, kun asiaa tarkastellaan koko roudasta vapaan kauden ongelmana. Päähuomio oli siis syytä kiinnittää uudistusalojen maan lämpöolojen koko kesäkauden aikaiseen tarkasteluun.

Tämän julkaisun tarkoituksena on esitellä tuloksia vv. 1970—1973 Pohjois-Suomessa kahdella maanmuokkausalueella suoritetuista maan lämpötilan mittauksista. Tutkimuksen kohdetta, maan lämpötilaa, käsitellään ennen kaikkea metsänviljelyn onnistumiseen vaikuttavana tekijänä. Mittausten ennakkotuloksia on esitelty suppeasti kahdessa edeltävässä tiedonannossa (LEIKOLA 1971 a, 1972).

Metsämaan muokkausta koskeva terminologia on suomen kielessä vielä jonkin verran vakiintumaton (esim. MÄLKÖNEN 1972). Tässä esityksessä käytetään ensisijassa metsähallituksen ohjekirjeessä kangasmaiden uudistusalojen maankäsittelystä (OHJEKIRJE ... 1973) esitettyjä määritelmiä, jotka ovat Pohjois-Suomessa yleisessä käytössä.

2. TUTKIMUSAINEISTO JA MENETELMÄ

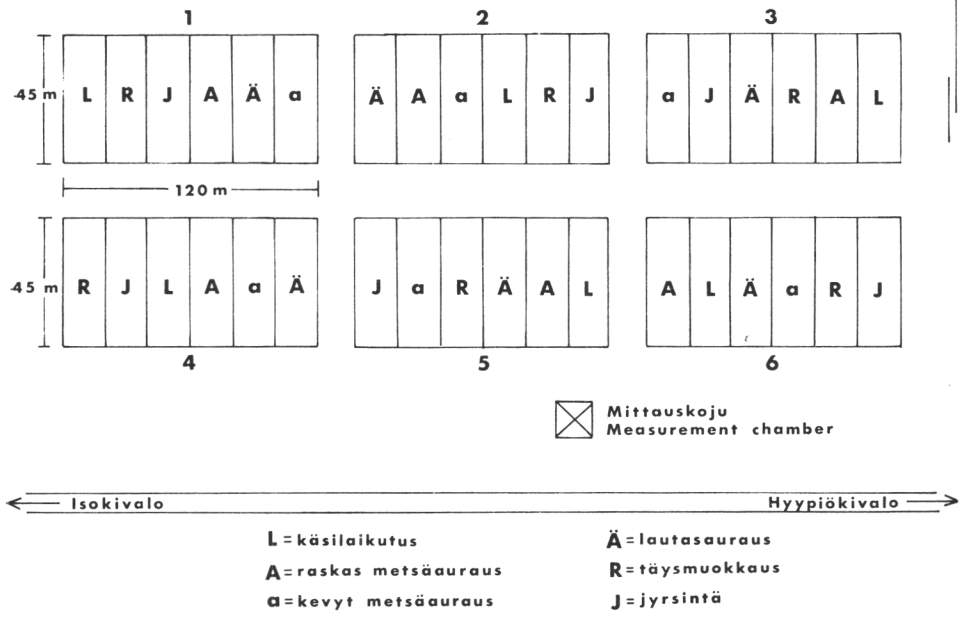
21. Koealueet

Maan lämpötilan mittaukset suoritettiin kahdella maanmuokkauskoealueella, joista eteläisempi sijaitsee Rovaniemen maalaiskunnassa, metsäntutkimuslaitoksen Kivalon kokeilualueessa (66° 17′ P; 26° 40′ I; 292 m mpy) ja pohjoisempi Sodankylän pitäjässä, metsähallinnon Sodankylän hoitoalueen Vaalolehdossa (67° 51′ P; 26° 38′ I; 232 m mpy). Koealueista Kivalo edustaa Etelä-Lapin topografisesti korkeita seutuja ja Vaalolehto Keski-Lapin tasankomaata.

Kivalon koealue perustettiin vuonna 1970. Paikalla kasvanut vanha paksusammalkuusikko hakattiin talvikautena 1969—1970, ja koe perustettiin toukokesäkuussa 1970. Koejärjestelyssä käytettiin ns. split-plot järjestelyä, jossa ruutujen koko oli 45 × 15 m. Pääkäsittelyinä oli kuusi erilaista maankäsittelytapaa ja alakäsittelyinä lannoitus kolmella tasolla (kuva 1). Lannoitteina käytettiin Thomasfosfaattia ja kalkkikiveä. Lannoituksen vaikutusta ei kuitenkaan käsitellä tässä yhteydessä.

Maan käsittely suoritettiin kesäkuussa 1970 seuraavasti (laitteista esim. SUOMALAISTA ... 1970):

- Laikutus: Billnäs-suokuokkaa käyttäen miestyönä.
- Raskas metsäauraus: KLM-240 metsänviljelyauralla käyttäen vetokoneena Caterpillar D-7 telaketjutraktoria; vakoväli 4 m.
- Kevyt metsäauraus: KLM:170 metsänviljelyauralla käyttäen vetokoneena Caterpillar D4/70 telaketjutraktoria; vakoväli 4 m.

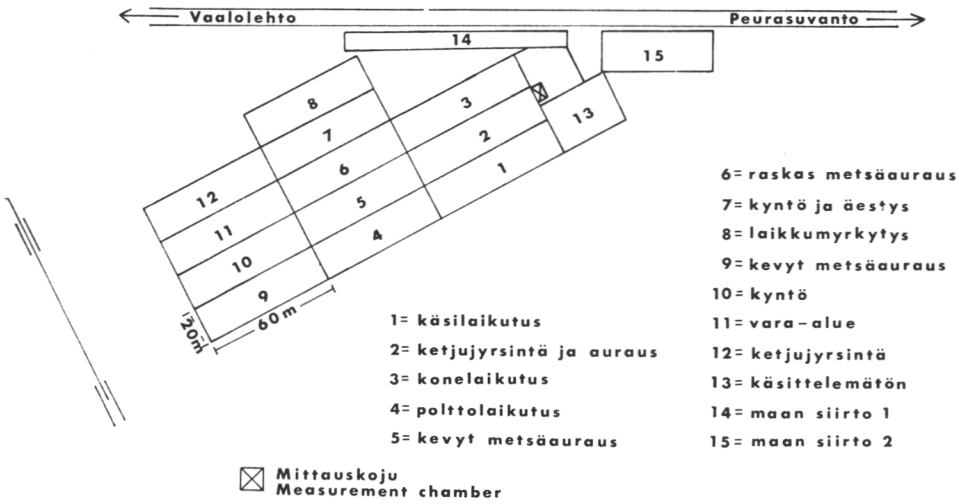


Kuva 1. Kivalon koealue.
Fig. 1. Kivalo experimental area. Explanation: L = hand scalping, A = heavy reforestation ploughing, a = light reforestation ploughing, Ä = disk ploughing, R = full site preparation, J = drum rotary tilling.

— Lautasauraus: TTS-metsä-äkeellä käyttäen vetokoneena Varmer Farmet-metsätraktoria.
— Täysmuokkaus (ristiinauraus): Ylö-metsänviljelyauralla muokaten koeala tristiin kahteen suuntaan käyttäen vetokoneena Fordson-maataloustraktoria.
— Rumpujyrsintä: TTS-metsäjyrsimellä MJ-1 käyttäen vetokoneena Belarus-maataloustraktoria; jyrsinjälkien (leveys 40 cm) väli 2 m.

Maan käsittely suoritettiin Kivalossa aina ruutujen pituussuuntaan, joten laitteiden työjäljen suunta oli suoraan etelästä pohjoiseen.

Vaalolehdon koealue perustettiin vuosina 1969—70. Aiemmin kuusta kasvanut, jo 1950-luvulla aukeaksi hakattu alue jaettiin yhtä suuriin 20 × 60 m ruutuihin, joilla suoritettavat maan käsittelyt arvottiin (kuva 2). Maan käsittely suoritettiin metsähallituksen kehittämisjaoston toimesta keväällä 1970 lukuunottamatta raskasta metsäaurausta, joka tehtiin jo syksyllä 1969. Polttolaikutus ja laikkumyrkytys suoritettiin syksyllä 1970. Käsittelyt, joilla mitattiin maan lämpötilaa olivat seuraavat (Pohjola 1971):



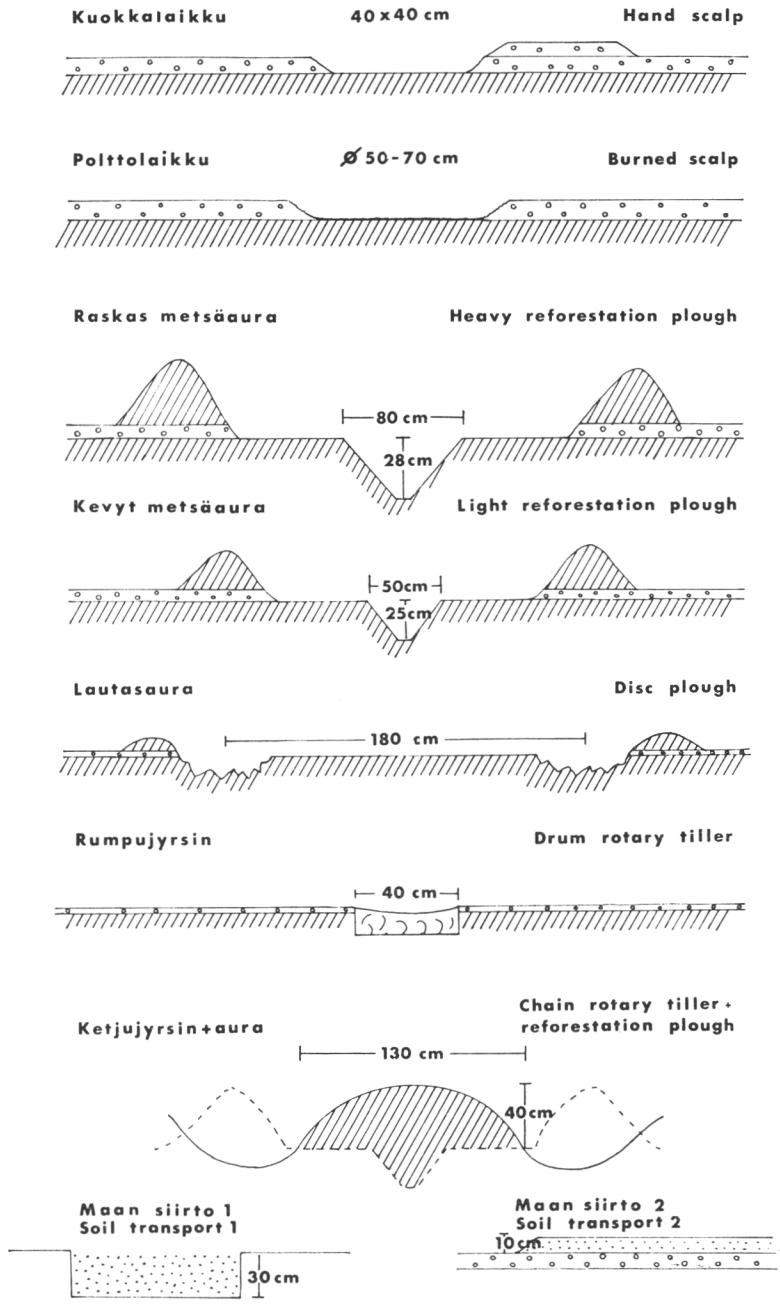
Kuva 2. Vaalolehdon koealue.
Fig. 2. Vaalolehto experimental area. Explanation: 1 = hand scalping, 2 = reforestation ploughing and chain rotary tilling, 3 = machine scalping, 4 = scalp burning, 5 = light reforestation ploughing, 6 = heavy reforestation ploughing, 7 = ploughing and harrowing, 8 = scalping by herbicides, 9 = light reforestation ploughing, 10 = ploughing, 11 = spare area, 12 = chain rotary tilling, 13 = no soil treatment, 14 = soil transport 1, 15 = soil transport 2.

— Käsilaikutus: Billnäs suokuokkaa käyttäen miestyönä.
— Konelaikutus: kantokoukulla käyttäen vetokoneena Ford County-maataloustraktoria.
— Polttolaikutus: moottoriselkäruiskulla, johon oli yhdistetty liekinheitinsuutin. Poltetun alan halkaisija 50—70 cm.
— Raskas metsäauraus: PP-1/220-metsänviljelyauralla käyttäen vetokoneena Caterpillar D-7-telaketjutraktoria.
— Kevyt metsäauraus: KLM-170 metsänviljelyauralla käyttäen vetokoneena Caterpillar D4/70-telaketjutraktoria.
— Ketjujyrsintä: auraus KLM-170-metsänviljelyauralla käyttäen vetokoneena Caterpillar D4/70-telaketjutraktoria. Aurausjälki muokattiin KLM-ketjujyrsimellä käyttäen vetokoneena Ford County-traktoria.

Maan käsittely suoritettiin Vaalolehdossa ruutujen pituussuuntaan, joten laitteiden työjäljen suunta oli idästä länteen.

Maansiirtokokeita tehtiin syksyllä 1970 Vaalolehdossa kahdella ruudulla seuraavasti:

— Ruudun alalta kuorittiin 30 cm kerros pintamaata pois ja tilalle siirrettiin noin 30 cm vahvuinen hietakerros (maan siirto 1).
— Ruudun päälle levitettiin noin 10 cm vahvuinen hiekkamoreenikerros (maan siirto 2).



Kuva 3. Profiilikuvat erilaisista maan käsittelyistä.
Fig. 3. Profiles of different kinds of soil treatment.

Eri tavoin käsiteltyihin ruutuihin kylvettiin keväällä 1971 mäntyä ja istutettiin männyn ja kuusen paljasjuurisia sekä paakkutaimia. Ennakkotuloksia viljelykokeista ovat esittäneet mm. POHJOLA (1971) ja SOLISMAA (1973).

22. Koealueiden maa

Kivalon ja Vaalolehdon koealueiden maan keskimääräinen raekoostumus on esitetty taulukoissa 1 ja 2. Kumpikin koealue on perustettu moreenimaalle; Kivalossa päälajitteena on hieta ja Vaalolehdossa hiesu.

Haluttaessa verrata koealueiden maan raekoostumusta Pohjois-Suomen käytännön metsänviljelyalueiden maahan, erään tarkastelupohjan tarjoaa hienojen lajitteiden ($\leq$ 0.2 mm) osuus koko pintamaasta:

	Lajitetta $\leq$ 0.2 mm
Kuusenistutusalat, keskimäärin[1]	40 %
Kuusen luontainen uudistaminen, keskimäärin[1]	46 %
Männynistutusalat, keskimäärin[2]	61 %
Männyn luontainen uudistaminen, keskimäärin[2]	46 %
Kivalon koealue, keskimäärin	63 %
Vaalolehdon koealue, keskimäärin	60 %

[1] MUTKA 1974
[2] LÄHDE ja SILTANEN 1972

Yleisesti voidaan tämän perusteella sanoa, että sekä Kivalon että Vaalolehdon koealueet ovat maan hienojen lajitteiden kokonaismäärässä hyvin lähellä Lapissa männyn istutuksiin keskimäärin käytettyjä maita. Männyn luontaiseen uudistamiseen sekä kuusen uudistamiseen on yleensä valittu edellistä huomattavasti karkearakeisempia maita.

Humuksen paksuus vaihteli Kivalossa kasvillisuuden laikuttaisuudesta ym. johtuen. Keskimäärin humus oli 5 cm paksua. Vaalolehdossa maata peitti miltei yhtäjaksoinen karhunsammalkerros, joten siellä humuksen paksuuden vaihtelu oli vähäisempää. Humuksen keskimääräinen paksuus oli 4 cm.

Taulukko 1. Kivalon koealueen maan keskimääräinen raekoostumus.
Table 1. The average composition of soil particle size in Kivalo experimental area.

Maakerros, cm *Layer of soil, cm*	Lajite, % *Class of soil particle size, %*				
	> 2.0 mm	2—0.2 mm	0.2—0.02 mm	0.02—0.002 mm	< 0.002 mm
0—10	16.1	24.7	48.9	8.1	0.9
10—20	15.4	21.6	50.8	10.3	1.9
20—30	27.6	21.0	40.4	9.4	1.7
30—60	25.7	18.3	43.5	11.0	1.5

Taulukko 2. Vaalolehdon koealueen eri tavoin käsitellyn maan keskimääräinen raekoostumus (SOLISMAA 1973).
Table 2. The average composition of soil particle size in plots prepared in different ways in Vaalolehto (Solismaa 1973).

Käsittely, Maakerros, cm *Treatment, Layer of soil, cm*	Lajite, % *Class of soil particle size, %*			
	> 2.0 mm	2.0—0.2 mm	0.2—0.06 mm	< 0.06 mm
Laikutus — *Scalping*				
0—10	24.4	18.5	19.8	37.3
10—20	17.5	22.8	20.5	40.2
20—30	15.0	24.8	22.1	38.1
Polttolaik. — *Scalp burning*				
0—10	32.2	18.3	18.3	31.1
10—20	18.7	21.3	19.6	40.4
20—30	20.3	22.3	20.1	37.4
Rask. metsäauraus — *Heavy reforestation ploughing*				
0—10	22.0	15.9	20.4	41.7
10—20	17.9	16.7	21.0	44.4
20—30	22.8	14.2	19.1	43.9
K-jyrs. — *Chain rotary tilling*				
0—10	36.4	14.0	17.5	32.1
10—20	30.9	16.2	16.9	35.9
20—30	23.7	20.2	19.6	36.6

23. Maan lämpötilan mittaus

231. Mittauskaudet

Taulukossa 3 on esitetty Kivalon ja Vaalolehdon maanmuokkausalueiden lämpötilan mittauskaudet havaintovuosina 1970—1973. Kummallakin koealueella tehtiin ensimmäisenä kesänä (Kivalossa v. 1970 ja Vaalolehdossa vuonna 1971) koemittauksia menetelmän kehittämiseksi. Myöhemmin pyrkimyksenä oli seurata maan lämpöoloja aloittaen mittaukset jo ennen kuin routaantunut maa osoitti ensimmäisiäkään sulamisen merkkejä ja jatkaa mittaustoimintaa seuraavaan syksyyn aina roudan ja pysyvän lumipeitteen tuloon saakka. Tästä syystä mittauskausien pituudet eri vuosina poikkeavat hieman toisistaan. Kuitenkin voidaan todeta, että mittauskaudet kattoivat vähintäin koko sen ajanjakson, jolloin maa oli sulana (vrt. KUUKAUSIKATSAUS . . . 1970—1973).

232. Mittauslaitteet

Pääosa maan lämpötilan mittauksista tehtiin termoelementtejä käyttäen. Menetelmää on käytetty ekologisessa tutkimuksessa jo kauan, ja Suomessakin

Taulukko 3. Maan lämpötilan mittauskaudet Kivalon ja Vaalolehdon koealueilla vuosina 1970—1973.
Table 3. Measurement periods at the experimental areas of Kivalo and Vaalolehto in the years 1970—1973.

Koealue, Havaintovuosi *Experimental area Observation year*	Mittakausi — *Measurement period*			Huom. *Notes*
	Alkoi *Beginning*	Loppui *End*	Kesto, vrk *Duration, days*	
Kivalo				
1970	08.01	10.30	91	
1971	05.10	10.27	170	
1972	05.15	10.13	150	
1973	05.28	10.10	136	
Vaalolehto				
1971	07.21	09.30	71	
1972	05.17	09.29	134	toukokuussa klo 8.00—22.00
1973	05.29	09.28	123	*In May 8 a.m.—10 p.m.*

on termoelementeistä kertynyt runsaasti kokemusta (esim. KERÄNEN 1920 VAARTAJA 1949).

Tutkimuksessa käytetyt termoelementtikaapelit olivat 1.3 mm läpimittaista muovipäällysteistä kupari- ja konstantaanijohtoa, tyyppimerkinnältään CONCORD 1W.2P4. Mittauslaitteena käytettiin Rubicon Instruments Inc'n valmistamaa lämpötilakalibroitua käsipotentiometriä, malli no 2715B, mittaustarkkuus 15 μv 23° C lämpötilassa. Käytännössä laitteiden tarkkuus vaihteli 0.5° - 1.0° C lämpötilasta ym. riippuen.

Termoelementtimittauksen rinnalla käytettiin Kivalossa ja Vaalolehdossa Lambrecht'in valmistamia kaksianturista termografeja, malli n:o 257 (mittausalue —35° C - +45° C), sekä maan lämpötilan mittaamista varten suunniteltuja, taitettuja lasisia minimi- ja maksimilämpömittareita. Näillä laitteilla tehtyjen mittausten tulokset esitellään toisaalla.

Yleisiä vaatimuksia kaikille maan lämpötilan mittauksessa käytettäville antureille ovat mm. seuraavat:

— Anturin tulee olla kooltaan riittävän suuri, jotta sen ja maahiukkasten välillä vallitsisi hyvä, välitön kosketusyhteys.
— Anturin tulee olla muodoltaan ja rakenteeltaan sellainen, että se pysyy hyvin paikoillaan.
— Anturi tulee asettaa siten, että maan rakennetta muutetaan mahdollisimman vähän. Vettä johtavien kanavien muodostaminen samoin kuin ilman liike anturin ympäriltä tulee estää (esim. PLATT ja GRIFFITHS 1964, TAYLOR ja JACKSON 1965).

Termoelementtianturit muodostettiin juottamalla kupari- ja konstantaanijohtimet noin 2 cm matkalla yhteen hopeajuotoksella. Näin tehty anturi osoittautui kuitenkin hieman liian pieneksi, ja vuonna 1972 molempien koealueiden kaikki anturit varustettiin 5 cm pitkillä ja 7 mm läpimittaisilla messinkisylintereillä, jotka täytettiin mehiläisvahalla ja suljettiin lopuksi tiiviisti kutistusmuovilla. Kaikki termoelementtianturit asetettiin halutulle syvyydelle mittauspaikan viereen kaivetun kuopan kautta, jonka tasoitettuun seinämään teräväkärkinen anturi painettiin. Kaapeli johdettiin maassa noin 50 cm matkan, jonka jälkeen se ankkuroitiin lujasti maahan painettuun muovikeppiin. Tämän jälkeen kaapeli johdettiin maan päällä mittauskojuun, jossa varsinainen mittaus tapahtui.

Mittauskojuna käytettiin Kivalossa lasikuituista lämmitettävää työmaasuojaa ja Vaalolehdossa puista 8 hengen asuntokämppää. Mittaus tapahtui kummallakin koealueella samalla tavalla. Potentiometrillä mitattiin vuorotellen jokaisen anturin lämpötila ja merkittiin se muistiin. Vuodesta 1972 lähtien käytettiin mittauksessa anturikanavien vaihtoon Croydon Precision Instruments'in valmistamaa valintakytkintä, malli no SP2/P/MB, jossa on tilaa 50 anturikanavalle. Potentiometrin lukemisen apuna käytettiin suurennuslasia.

233. Mittaussyvyys

Mittaussyvyyden valitseminen on erittäin tärkeätä, sillä maan lämpöolot vaihtelevat suuresti mm.syvyyden mukaan. Viime vuosikymmenien aikana metsämaan lämpötilan mittauksissa on yleisesti noudatettu World Meteorological Organization'in suositusta vakiosyvyyksiksi: 5, 10, 20, 50 ja 100 cm maan pinnasta. Kun kyseessä on paljas ja tasainen, humuksesta vapaa maan pinta, kuten lähes aina ilmatieteellisissä selvityksissä, ei epäselvyyttä juuri synny. Milloin maata kuitenkin peittää epätasainen kasvillisuuskerros ja vaihtelevan paksuinen orgaaninen aines, tämä on syytä ottaa huomioon tavalla tai toisella. Tarjolla on kolme erilaista tapaa perustason määräämiseksi (vrt. esim. FRANSSILA 1960):

1. Humuskerroksen ja kivennäismaan välistä rajaa pidetään usein mittausten perustasona (0-taso), sillä tämä raja on useimmiten selvä, paikallaan pysyvä ja jotakuinkin yksikäsitteinen (esim. TURTIAINEN ja VALTANEN 1970). Suuria vaikeuksia on kuitenkin vertailujen tekemisessä eri mittauspaikkojen välillä, varsinkin mikäli metsikön humuskerroksen vahvuus vaihtelee. Muokkaamattoman ja muokatun maan lämpöolojen vertaamisessa tämä 0-tason määräämistapa ei olekaan suositeltava.

2. Maanpinnan säteilytasetta tutkittaessa ainoana perusteltavissa oleva mittauksen perustaso on energeettisesti toimiva pinta (esim. KULMALA 1970, LAITINEN 1970). Soiden lämpöolojen selvityksissä, jolloin luonnollisista syistä ei ole mielekästä valita perustasoksi turpeen pohjaa vaan pinta, tämä tapa on

lähes yksinomainen (esim. HEIKURAINEN ja SEPPÄLÄ 1963). Tämä vaihtoehto johtaa kuitenkin käytännössä usein vaikeuksiin, sillä metsämaassa sammal- ja varpukerros on siinä määrin epätasainen, että mittauksen perustasosta käytännössä muodostuu kolmiulotteinen avaruustila. Osaksi tästä syystä useissa kivennäismaan lämpötilan mittauksissa varpu- ja sammalkerroksen pinta onkin hyljätty, mutta näin tehden on myös etäännytty maan lämpöolojen selvittämisen energeettisesti lujasta pohjasta ja siirrytty sopimukseen perustuvan määrittelyn tielle.

3. Koska metsäntutkijoille maan lämpötila on usein mielenkiinnon kohteena puiden ja taimien menestymisen kannalta, eräs järkevä vaihtoehto on sitoa tarkastelu siihen tasoon (maakerrokseen), jossa suurin osa taimien tai täysikokoisten puiden juuristoista kulkee. Näin tulisi maan lämpötilan mittauksen perustason muuttua koealueen maantieteellisen sijainnin perusteella, mieluimmin vielä puulajin ja metsikön iänkin mukaan (vrt. esim. KALELA 1955, PAAVILAINEN 1966, LÄHDE ja SILTANEN 1973).

Tässä tutkimuksessa maan lämpötilan mittauksen perustaso on määritetty käyttäen pääasiallisempana perusteena toimivaa pintaa (menettely 2). Maan pintana (0-taso) on muokatuilla mailla käytetty paljastetun kivennäismaan pintaa, ja humuspeitteisillä mailla sammalkerroksen ja humuksen rajakohtaa, missä elävät sammaleet loppuvat. Metsämaata peittävässä sammalkerroksessa esiintyvät yleensä kaikkein äärevimmät lämpötilat, joten se tässäkin mielessä on lähinnä toimivan pinnan käsitettä (esim. BJOR 1972, BERGAN 1974). Koska istutustaimien keskusjuuriston valtaosa kulkee Lapissa 7—15 cm:n päässä maan pinnasta (LÄHDE ja SILTANEN 1973, MUTKA 1974) valittiin syvyys 5 cm 0-tasosta alaspäin pääasiallisimmaksi mittaussyvyydeksi. Muutamia mittaussarjoja perustettiin lisäksi Kivaloon syvyyksille 1, 5, 10 ja 15 cm.

234. Mittarien lukumäärä

Moreenimaa on tunnetusti epähomogeenista, eivätkä sen lämpöooloja tasaavat ominaisuudet ole mitenkään hyvät esim. ilmaan verrattuna (BERÉNYI 1967 ym.). Vaihto tasottaa ilman lämpötilan mikrovaihteluita suuresti, joten usein vain vähäinen määrä lämpömittareita on tarpeen esim. metsäntutkimuksen kannalta riittävän tarkkuuden ja yleistettävyyden saavuttamiseen (esim. SARVAS 1962, 1968).

Mittarien lukumäärä määritetään ekologisessa tutkimustyössä yleistä havaintopisteiden lukumäärän osoitusmenettelyä noudattaen: erilaisilla ennakoivilla kokeilla estimoidaan mittauslaitteiden lukemien vaihtelun standardipoikkeama, ja tästä edelleen vaaditun mittaustulosten tarkkuuden (keskiarvon keskivirheen) riippuvuus mittarien lukumäärästä. Näin voidaan perustaa mittaussarjoja, joiden keskimääräiset vaihtelurajat on sovittujen virherajojen sisällä (esim. HOFMANN 1965).

Edellä kuvattua yleistä menettelyä hankaloittaa muutama maan lämpötilan mittaukseen liittyvä erikoispiirre. Tiedetään, että rinnakkaisten lämpötilahavaintojen standardipoikkeama on riippuvainen myös ilman ja maan lämpötilan välisestä erosta; ts. se vaihtelee systemaattisesti sääsuhteiden ja vuodenajan mukaan (FRANSSILA 1960). Kun myös tiedetään, että pintakasvillisuuden laikkumainen vaihtelu ja karikkeiden ym. esiintyminen on suurena syynä homogeenisenkin metsämaan lämpöolojen vaihteluun (esim. BJOR 1971), joudutaan uuteen vaikeuteen, sillä tämä ei noudata tilakoordinaatistossa satunnaista mallia, vaan kasvien välinen kilpailu ym. vuorovaikutussuhteet tuovat mukaan voimakkaan systemaattisuuden (esim. CAIN ja CASTRO 1959, KERSHAW 1964). Kun tiedämme, että esim. sademäärän jakaantuminen metsässä on epätasaista (esim. PÄIVÄNEN 1966, LEIKOLA 1971 b), ja että maan kosteussuhteilla on hyvin suuri merkitys sen lämpöolojen jakaantumiselle (esim. BJOR 1965), on selvää, että maan lämpötilan mittauksen havaintopisteiden lukumäärän moitteeton määrittäminen on jo sinänsä laajaa erikoistutkimusta vaativa ongelma.

Aihetta käsittelevistä tutkimuksistä FRANSSILAN (1960) työ on kiinnostavin. Muutamana esimerkkinä voidaan mainita, että EMT-männikössä Pohjois-Sodankylässä humuksen ja kivennäismaan rajassa 10 mittarilla mitattu maan päivittäisen maksimilämpötilan standardipoikkeama oli keskimäärin 2.9°C, ja minimilämpötilan vastaava tunnus 0.50° C. Aapasuolla vastaavat tunnukset 10 sm syvyydessä maan pinnasta olivat suuruudeltaan 1.81° C ja 0.84°C. Vastaavassa selvityksessä, joka on suoritettu ojitetulla suolla Etelä-Suomessa, vaihtelu on ollut vieläkin suurempaa (HEIKURAINEN ja SEPPÄLÄ 1969).

Jotta saataisiin suuntaa antava kuva, miten suurta anturien lukumäärää kohtuulliseen luotettavuustasoon pääseminen vaatisi, laskettiin Vaalolehdon koealueen käsittelemättömän maan keskimääräisille lämpösummille vv. 1972—1973 a.o. tilastolliset tunnukset (vrt. taulukko 4). Vuotuisen lämpösumman keskiarvo oli seitsemällä termoelementtianturilla mitattuna 605 l.s-yksikköä. Anturien välinen standardipoikkeama oli 73.7 yksikköä ja keskiarvon keskivirhe 27.7 yksikköä. Em. keskiarvon vaihteluväli oli siten 605 $\pm$ 5.3 (= 9 %) yksikköä.

Jos kuitenkin haluttaisiin tietoja em. mittausalustan vuotuisista lämpöoloista esim. 95 % luotettavuudella (keskiarvon vaihteluväli 605 $\pm$ 30.2 yksikköä), vaadittavien havaintopisteiden luku kohoaisi tällöin 23:een.

235. Mittausajankohdat

Mittausajankohdan vaikutus maan lämpöoloihin on ollut pääpiirtein selvillä jo mikroilmastollisen tutkimuksen varhaisista ajoista saakka (esim. HOMÉN 1897). Maan lämpöolojen vuotuinen ja vuorokautinen vaihtelu on maassa tunnetusti paljon säännöllisempää kuin ilmassa, ja tälle on ominaista ns.

lämpötilan jättäytymisilmiö, joka on sitä suurempaa, mitä syvemmälle maahan havainnot ulotetaan (GEIGER 1965). Jos maan lämpötila mitataan esim. säännöllisesti tiettyinä vuorokauden aikoina eri syvyyksiltä, mitatut lämpötilat osuvat eri kohtiin vuorokautisten lämpötilan vaihteluiden kuvaajaa, ja johtopäätösten teko on erittäin vaikeata. Tästä huolimatta erilaisia maan keskilämpötilan laskentakaavoja on esitetty runsaasti (mm. KERÄNEN 1920, PESSI 1956). Nämä vaativat tuekseen vuodenajan mukaan liukuvasti muuttuvia korjauskertomia, ja lämpötiloiltaan toisistaan poikkeavien maiden vertailu (esim. muokattu — muokkaamaton maa) vaatii melko monimutkaisia muuntoja ja kokeellisia esitutkimuksia. Verrattaessa samallekin syvyydelle asetettujen mittarien lukemia toisiinsa, on otettava huomioon, että ääriarvojen jättäytyminen on lämmönjohtokyvyltään paremmassa maassa vähäisempää kuin lämmönjohtokyvyltään huonommassa. Tilannetta on vielä omiaan mutkistamaan se, että maan lämmönjohtokyky muuttuu suuresti sen vesipitoisuuden mukaan. Esim. kostean maan lämmönjohtokyky on aina parempi kuin kuivan (GEIGER 1965).

Vuorokausikohtaisten minimi- ja maksimilämpötilojen avulla on kuitenkin mahdollista laskea maan lämpöoloja kuvaavia indeksejä paljon suuremmalla luotettavuudella kuin esim. ilman lämpöoloille. Paras kuva kuitenkin saadaan, jos maan lämpötilan vaihteluita seurataan jatkuvasti esim. piirturein tai riittävän usein toistetuin mittauksin.

Tässä tutkimuksessa termoelementtimittauksen perusjaksona käytettiin vuorokautta, jonka aikana maan lämpötila mitattiin aina joka toinen (parillinen) tunti. Kivalossa on mittauspäivinä käytetty säännöllisesti kolmea viikonpäivää: maanantaita, keskiviikkoa ja perjantaita. Vaalolehdossa suoritetuissa termoelementtimittauksissa havaintoja on tehty työviikon viitenä päivänä.

24. Lämpösummien koostaminen

Maan lämpöoloja voidaan kuvata usealla tunnuksella, joista vuorokausi- tai kuukausikohtaiset äärilämpötilat ja keskiarvot ovat tunnetuimmat (esim. GEIGER 1965). Kun halutaan ensisijassa vertailla niita olosuhteita, joissa puiden juuristot joutuvat kasvukauden aikana toimimaan, kulloinkin vallitsevan lämpötilan ja sen kestoajan välisen yhteisvaikutuksen kuvaamiseksi on edullista yhdistää em. kaksi tekijää samaksi lämpötila/aika-indeksiksi. Eri aikoina kehitetyt lämpösumman koostamismenettelyt tarjoavat tässä suhteessa ehkä parhaimman ja myös useimmin käytetyn ratkaisun (lämpösumman käytöstä ekologisessa ja fysiologisessa tutkimuksessa esim. SCHNELLE 1955, WENT 1957, SARVAS 1972).

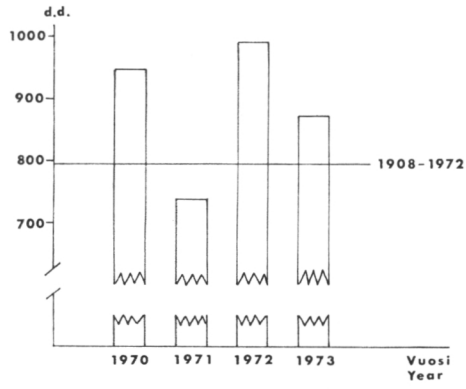
Kasvukauden aikaisten maan lämpöolojen kuvaaminen lämpösumman

avulla on toisaalta yksinkertaisempaa, toisaalta taas huomattavasti vaikeampaa kuin ilman lämpöolojen kuvaaminen. Suurimpana vaikeutena kestävien metsänhoidollisten lähtökohtien luomiselle on puiden juuriston elintoiminnan ja kasvuympäristön lämpötilan välisten riippuvuussuhteiden toistaiseksi vaillinainen tuntemus, sekä epävarmuus juuristoon kasvunperiodisuuden luonteesta (katsaukset esim. LADEFOGED 1939, SHAW 1952, RÖHRIG 1966, LYR ja HOFMANN 1967, KOZLOWSKI 1971, ORLOV ja KOSELKOV 1971).

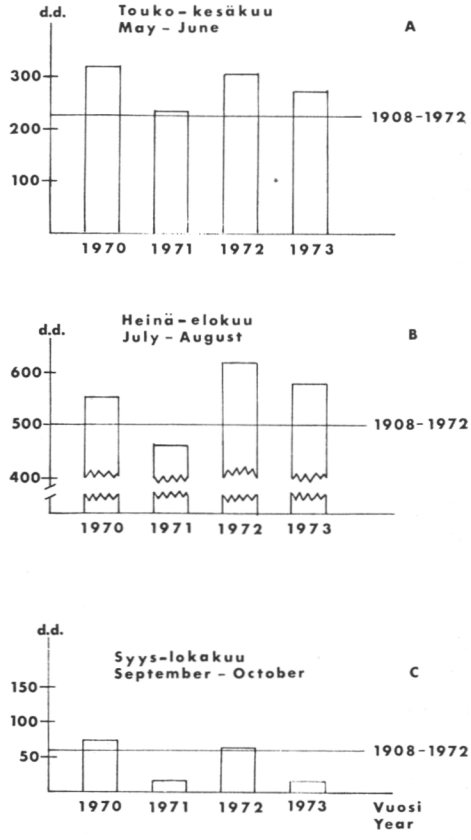
Kun tarkastellaan maan lämpötilan vuotuisia vaihteluita, havaitaan ajallisesti kaksi säännöllistä, aaltoilevaa rytmiä: suurempi vuotuinen ja sen sisällä pienempi vuorokautinen: Vuorokausien rajakohdaksi on lämpösummalaskelmissa usein valittu tavallisen käytännön mukaan klo 24.00, mutta maan lämpöolojen kuvaamisessa tämä menettely ei ole paras mahdollinen. Koska kysymyksessä on perusmalliltaan aaltomainen sinikäyrä, jaksojen rajakohtana on aina mikäli mahdollista käytettävä arvoltaan alhaisinta jakson kohtaa. Kun tämä osuu maan pintakerroksen lämpötilan osalta aikaiseksi aamuksi, on em. vuorokaudenaika, klo 05.00, valittu tässä työssä vuorokausien rajakohdaksi. — On kuitenkin syytä korostaa, että esim. kuukausikohtaisten lämpösummien laskentaan vuorokausijakson rajojen valinta ei sanottavasti vaikuta, ja koko kasvukautta kuvaaviin tuloksiin sillä ei enää ole edes periaatteellistakaan merkitystä.

Tarkasteltaessa jotain biologista ilmiötä olisi parasta, jos lämpösumman laskennassa käytettävä kynnysarvo osuisi mahdollisimman lähelle sitä alinta lämpötilaa, jossa ko. ilmiön tapahtumisintensiteetti osoittaa vielä todettavaa, mutta erittäin vähäistä aktiivisuutta (ns. minimi-kardinaalipiste). Puiden juuriston toiminnan minimilämpötiloina on kirjallisuudessa esitetty yleisimmin +2 - +3° C - +5 - +6° C, mutta on korostettava, että suuri osa juurten kasvunnopeuden määrityksistä perustuu kontrolloiduissa oloissa suoritettuihin lyhytaikaisiin mittauksiin. Maastossa tilanne on ekologisesti tarkastellen aina hyvin monitahoinen, useimmiten kaikista juurten kasvuympäristön ominaisuuksista (kosteus, ilmavaihto, ravinteisuus jne.) samanaikaisesti riippuvainen (SHAW 1952, RÖHRIG 1966, LÄHDE ja SILTANEN 1973 ym.). Luotettavia tietoja pääpuulajiemme juurten kasvun minimilämpötiloista Pohjois-Suomessa ei toistaiseksi ole saatavissa, joten tässä tutkimuksessa valittiin käytettäväksi pääasiassa kirjallisuustietojen pohjalta kynnyslämpötila +5° C (vrt. esim. LEIKOLA 1969).

Lämpösummaa koostettaessa on yleensä käytetty sellaista menettelyä, että valitun aikayksikön keskilämpötilasta vähennetään sovittu kynnyslämpötila, ja näin saadut aikayksikkökohtaiset lämpötilat lasketaan yhteen. Tässä tutkimuksessa lämpösumman koostamisen aikayksiköksi otettiin tunti- (d.h.) periaate. Tuntikohtainen lämpösumma on vielä jaettu 24:llä, jolloin on saatu likimain vuorokausikohtaisen lämpösumman (d.d.) suuruusluokkaa oleva arvo, mutta jälkimmäisessä varsinkin keväällä ja syksyllä tavattava kom-



Kuva 4 (yllä). Havaintovuosien lämpösummat Sodankylässä. Vertailuarvona vv. 1908—1972 lämpösummien keskiarvo.
Fig. 4 (above). The temperature sums for the years under observation in Sodankylä. The mean value of the temperature sums for the years 1908—1972 is given as a comparative value.



Kuva 5 (oikealla). Havaintovuosien lämpösummat alku-, keski- ja loppukesällä Sodankylässä. Vertailuarvo kuten kuvassa 4.
Fig. 5 (on the right). The temperature sums relevant to the early part (A), the mid-part (B), and the end-part (C) of the summers of the years under observation in Sodankylä. Comparative value the same as in Fig. 4.

pensaatiovirhe on eliminoitunut laskennasta (kompensaatiovirheestä esim. SARVAS 1966).

Lämpösumman kelpoisuudesta juuriston kasvuedellytysten kuvaajana maastossa voi vain esittää olettamuksia niin kauan kuin seikkaperäiset selvitykset juurten kasvun ja toiminnan vuotuisesta periodista ja sen riippuvuudesta lämpötilasta ja ajasta puuttuvat. Kuitenkin voidaan päätellä, että paras tulos olisi ilmeisesti saavutettavissa koostamalla lämpösumma ei-lineaarista mallia käyttäen (esim. LADEFOGED 1939), jolloin juuriston kasvua mahdollisimman hyvin selittävä uusi lämpösumma lähenisi muodoltaan hyvin paljon ns. yleisen kasvukäyrän mallia (esim. WHALEY 1961, LYR ym. 1967), ja myös SARVAKSEN (1972) esittämää ja kokeellisesti määrittämää p.u-asteikkoa. Toisaalta on kuitenkin pidettävä mielessä, että yksinkertaisesti koostetut lineaariset lämpösummatkin ovat näennäisestä biologisesta kömpelyydestään huolimatta tarjonneet hyviä palveluksia fenologiselle tutkimukselle, ja ne ovat myös olleet suhteellisen vaivattomia koostaa käytettäessä lähtöaineistona normaaleja lämpötilan mittaussarjoja (esim. MORK 1933, BERGAN 1974).

Tässä tutkimuksessa käytettävät termoelementtimittauksen lämpösummat perustuvat, kuten jo edellä siv. 19 mainittiin, Kivalon koealueen osalta viikottain kolmen, ja Vaalolehdon koealueen osalta viiden vuorokauden aikana joka toinen tunti tehtyihin mittauksiin. Kuukausikohtaisiin lämpösummiin koko kasvukauden aikaisista puhumattakaan, tällaisella systemaattisella näytteenotolla ei kuitenkaan katsottu olevan suurta merkitystä siitäkään huolimatta, että sääolojen vuorokautista vaihtelua ei voida pitää satunnaisena ilmiönä.

25. Mittausvuosien edustavuus

Maan lämpötilan mittaus aloitettiin koemielessä Kivalossa vuonna 1970 ja Vaalolehdossa vuonna 1971. Kun edellisellä koealueella tähän mennessä on seurattu maan lämpötilaa vain neljän ja jälkimmäisellä alueella kolmen vuoden aikana, on kysymys ko. havaintovuosien edustavuudesta varsin ratkaiseva tulosten yleistettävyydelle. Ilmastolliset olosuhteet vaihtelevat Lapissa vuosittain hyvin paljon, ja lämpöoloiltaan suotuisten tai epäsuotuisten vuosien biologinen merkitys korostuu, mitä pohjoisemmaksi Suomessa siirrytään (esim. MIKOLA 1950, POHTILA 1972 ym.).

Kuvassa 4 on esitetty havaintovuosien vuotuiset ilman lämpösummat (d.d.), jotka on laskettu Sodankylän observatorion ilmatieteellisellä asemalla (67° 22′ P, 26° 39′ I, 179 m mpy) mitatuista päivittäisistä keskilämpötiloista (JOKIOISTEN JA ... 1970, 1971, KUUKAUSIKATSAUS ... 1972, 1973). Vertailuna esitetty lämpösumman keskiarvo vuosille 1908—1972 on niinikään laskettu Metsäntutkimuslaitoksessa ilmatieteen laitoksen julkaisemista päivittäisistä keskilämpötiloista.

Yhtenä piirteenä havaintovuosien kesien lämpöoloista (kuva 5) nähdään, että ensimmäinen koemittausvuosi, 1970, on ollut koko ajan keskimääräistä lämpimämpi. Ensimmäinen varsinainen havaintovuosi, 1971, on vuorostaan alkukesällä ollut normaalia hieman lämpimämpi, mutta keski- ja loppukesällä selvästi normaalia kylmempi. Toinen havaintovuosi, 1972, on jälleen ollut koko kasvukauden ajan selvästi keskimääräistä lämpimämpi. Varsinkin keskikesä on tuolloin ollut hyvin lämmintä aikaa. Kolmas havaintovuosi, 1973, on edelleen ollut koko kesän ajan normaalia selvästi lämpimämpi.

Arvosteltaessa eri vuosien lämpöoloja ilman lämpötilan mittausten mukaan on muistettava, että myös vuotuiset kosteussuhteet vaikuttavat suuresti maan pintakerroksen lämpöoloihin (FRANSSILA 1962 ym.). Esimerkkinä lumipeitteen vaikutuksesta voi mainita, että jokaisen lumigramman sulattamiseen kuluu 74 cal. lämpöä, ja sen lisäksi lumipeite heijastaa pois suurimman osan (60—80 %) sille langenneesta säteilystä (esim. GEIGER 1965, PERTTU 1970).

Samoin eroavat esim. kuiva ja märkä kivennäismaa lämpötaloudellisilta ominaisuuksiltaan toisistaan huomattavasti (GEIGER 1965):

Maalaji	Albedo, %	Lämmönjohtokyky, cal/cm/sek/C°	Ominaislämpö, cal/cm³/C°
Märkä hiekka	15—20	2—6	0.2—0.6
Kuiva hiekka	25—30	0.4—0.7	0.1—0.4

Yleisesti ottaen voidaan mm. yllä esitetyistä arvoista päätellä, että kahdesta yhtä lämpimästä vuodesta, jotka eroavat toisistaan kosteusolojensa puolesta, sateisempana vuonna maan pintakerroksen lämpötila on keskimäärin alhaisempi, mutta maan lämpöolot vertikaalisuunnassa tasaisemmat kuin kuivana vuonna. Maassa olevan veden haihtumiseen kuluva lämpömäärä, joka esim. Sodankylän korkeudella voi kosteilla mailla olla huomattava (VIRTA 1966), vaihtelee sekin vuosittain paitsi lämpö- mutta myös ennen kaikkea kosteusolojensa mukaan.

Voidaan esittää, että keskimääräistä lämpimämmät vuodet ovat usein myös kuivempia. Tämä sitoo kosteus- ja lämpötekijät saman malliin, mutta se vaikeuttaa eri vuosien välisten vertailujen tekoa vielä enemmän.

3. TUTKIMUSTULOKSET

31. Käsittelemättömän maan lämpöolot

Kivalon koealueella termoelementtianturit sijoitettiin kahdelle lohkolle käsittelemättömiin kohtiin siten, että yksi tuli maassa olevan pienehkön hakkuutähdekasan alle, kaksi mustikanvarvuston alle, kaksi harvaa mustikkaa ja seinäsammalta kasvavalle kohdalle ja kaksi kenttäkerroksesta vapaalle, n. 2 m^2 suuruiselle kynsisammaleen (*Dicranum sp.*) peittämälle alueelle. Lisäksi asetettiin kolme anturia jyrsittyjen ja aurattujen ruutujen käsittelemättömiin osiin. Vaalolehdon koealueen maata peitti tasainen, noin 5—12 cm vahva karhunsammalkerros, johon seitsemän anturia sijoitettiin kolmelle käsittelyruudulle. Yleensä pyrittiin antureiden sijoittelussa satunnaisuuteen, joskin toisaalta annettiin etusija ns. tyypillisille kohdille ja pyrittiin karttamaan epätavallisia pienalueita.

Taulukossa 4 on esitetty Kivalon ja Vaalolehdon koealueiden maan keskimääräiset vuotuiset lämpösummat. Erilaisen kasvillisuuden peittämän maan lämpöolojen välinen järjestys on Kivalossa hyvin selvä. Keskimäärin kylmintä on ollut maassa hakkuutähdekasan alla. Jonkin verran lämpimämpää on ollut tiheän mustikanvarvuston alla, tätä hiukan lämpimämpää harvan varvuston alla ja kaikkein lämpimintä alalla, josta kenttäkerros on puuttunut kokonaan ja maa on ollut kokonaan kynsisammalen peitossa. Taulukkoon on myös lisätty vastaavien vuosien ilman lämpösummat. Havaitaan, että humuspeitteinen maa oli jo 5 cm syvyydellä huomattavasti kylmempää kuin ilma. Hakkuutähteiden sekä vahvan mustikanvarpukerroksen alla maan pintakerroksen lämpösumma kohosi vain noin kahteen kolmannekseen ilman lämpösummasta.

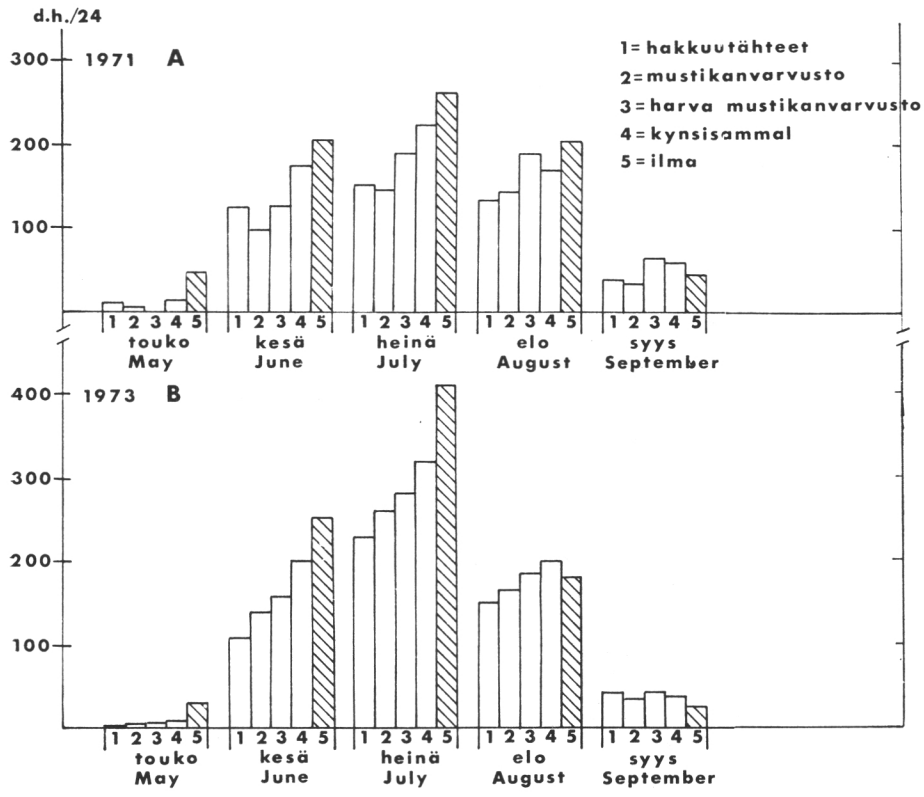
Kuvassa 6 nähdään maan lämpösummien kuukausittainen kehitys Kivalossa kahtena vuonna: 1971, joka edustaa keskitasoa viileämpää vuotta, ja vuonna 1973, joka tarjoaa esimerkin keskimäärää lämpimämmästä vuodesta. Maan pintakerroksen kasvukautisten lämpötilojen jättäytyminen ilman lämpötiloihin nähden on selvästi havaittavissa; toukokuussa ilman lämpösumma on ollut jopa 3—4 kertainen maan lämpösummaan nähden. Varsinkin vuonna 1973 eri lämpösummien järjestys on alkukesällä hyvin selvä. Kylmintä on yleensä hakkuutähdekasan alla ja sitten seuraavat järjestyksessä mittauskoh-

Taulukko 4. Käsittelemättömän maan lämpösummat (d.h./24) Kivalossa ja Vaalolehdossa vv. 1971—1973. Mittaus termoelementillä, syvyys 5 cm. Vertailuna ilman lämpösummat, mittaus termografilla.
Table 4. Temperature sums (d.h./24) pertaining to untreated soil in Kivalo and Vaalolehto in 1971—1973. Measurement with thermocouples at the depth of 5 cm. Air temperatures, measured with thermographs, are given as comparative values.

Koealue, lohko no *Experim. area, Plot No*	Anturit — *Sensors*		Mittausvuosi — *Measurement year*				
	Mittauskohta *Measurement point*	Kpl *Number of sensors*	1971	1972	1973	1971 — 1973	
			Lämpösumma *Temperature sum*			Keskim. *Mean value*	% ilman lämpös. *Temp. sum of the air, %*
Kivalo							
5	Hakkuutähdekasan alla — *Under a pile of logging residue*	1	470	695	533	566	63
5	Tiheä mustikanvarv., seinäsammal — *Dense blueberry shrubry, Hylocomium*	2	438	737	583	586	66
6	Harva mustikanvarvusto, seinäsammal — *Open blueberry shrubberry, Hylocomium*	2	554	837	673	688	77
6	Ei kenttäk., kynsisammal — *No shrub layer Dicranum sp.*	2	669	951	768	796	89
(2	Jyrsityn alan vertailu — *Comparison with tilled soil*	2	772	923	852	869	97)
(5	Auratun alan vertailu — *Comparison with ploughed soil*	1	792	991	808	864	97)
	Ilma, 65 cm — *The air*	1	772	1 012	895	893	100
Vaalolehto						1972—1973	
3,4,13	Karhunsammal, — *Polytrichum sp.*	7	—	602(1	608	605	73
	Ilma 2 m — *The air* ...	2	—	883	776	830	100

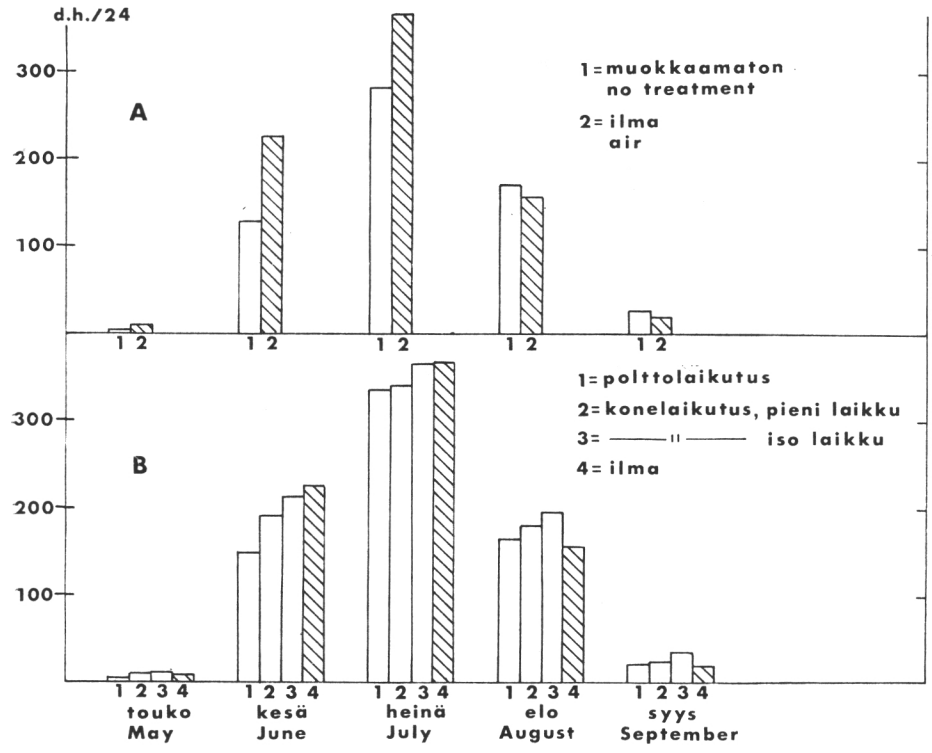
1) Havaintokausi alkoi kahden anturin osalta 06.20. — *In respect of two sensors the observation period began on June 20.*

dat tiheä mustikkavarvusto, harva mustikkavarvusto, kynsisammalen peittämä ala sekä lämpimimpänä ilma. Loppukesällä maan pintakerroksen kuukausikohtainen lämpösumma oli vuorostaan suunnilleen sama kuin ilman lämpösumma. Syyskuussa maa osoittautui ilmaa lämpimämmäksi mittauspaikaksi. Sama kehitys näkyy myös Vaalolehdossa (kuva 7).



Kuva 6. Käsittelemättömän maan lämpösummien kuukausikohtainen kehitys eri mittauspisteissä Kivalossa vuosina 1971 (A) ja 1973 (B).
Fig. 6. Monthly development of the temperature sums relevant to different points of measurement in Kivalo in 1971 (A) and in 1973 (B). Explanation: 1 = pile of logging residue, 2 = blueberry shrubberry, 3 = open blueberry shrubberry, 4 = Dicranum sp., 5 = the air.

Humuspeitteisen maan pintakerroksen vuotuiset lämpöolot ovat mm ilman lämpöoloihin verrattuna hyvin samantapaiset kuin mitä kirjallisuudessa on esitetty (katsaukset esim. GEIGER 1965, VIERECK 1970, MITSCHERLICH 1971). Vertailtuaan risujen peittämän ja hakkuutähteistä vapaan metsämaan pinnan lämpöoloja BJOR (1972) ilmoittaa, että kuumina päivinä humuksen pinnan maksimilämpötila oli hakkuutähteiden alla noin viisitoista astetta alempi kuin alalla jossa hakkuutähteitä ei ollut, ja että maksimilämpötilan esiintymiskerros siirtyi vm. alalla 10—15 cm humuksen pinnasta ylöspäin, ilmaisten näin toimivan pinnan kohoamisen. Yöllä minimilämpötilat olivat paljaalla maalla hieman alemmat kuin hakkuutähteiden peittämällä alalla, mutta ero ei ollut läheskään yhtä suuri kuin maksimilämpötilojen välillä. FRANSSILA (1962) painottaa huonosti lämpöä johtava humuskerroksen paksuuden ratkaisevaa osuutta kivennäismaan lämpöoloille (myös SIRÉN 1955 b).



Kuva 7. Käsittelemättömän (A) ja laikutetun (B) maan lämpösummien kuukausikohtainen kehitys Vaalolehdossa vuonna 1973.
Fig. 7. Monthly development of the temperature sums relevant to unprepared (A) and scalped (B) soil in Vaalolehto in 1973. Explanation (section B): 1 = scalp burning, 2 = machine scalping, small scalp, 3 = machine scalping, large scalp, 4 = the air.

32. Käsittelyn vaikutus maan lämpöoloihin

321. Laikutus

Maan pintakerroksen lämpöoloja seurattiin Kivalon ja Vaalolehdon koealueilla kolmella eri tavalla laikutetulla alueella: käsin ja koneellisesti tehdyissä sekä liekinheittäjällä poltetuissa laikuissa (vrt. ETHOLÉN 1970). Vaalolehdon koealueen konelaikutusruudulla anturit sijoitettiin kahta eri suuruusluokkaa edustavien laikkujen pohjalle.

Taulukossa 5 nähdään laikun keskeltä mitatun maan pintakerroksen vuotuiset lämpösummat. Kivalossa laikku on ollut lämpimämpi kuin ilma, mutta havainto perustuu vain yhden anturin lukemiin. Vaalolehdossa on tarjolla runsaammin tuloksia laikun lämpöoloista. Lämpösummaltaan suurimmaksi osoittautui iso konelaikku, seuraavana oli pieni konelaikku ja polttolaikku oli lämpösummaltaan pienin. Keskimäärin laikku oli kuitenkin ollut selvästi lämpimämpi kuin vastaava käsittelemätön maa.

Taulukko 5. Maan lämpösummat (d.h./24) laikun pohjassa Kivalossa ja Vaalolehdossa vv. 1971—1973. Mittaus kuten taulukossa 4.
Table 5. Temperature sums (d.h./24) of the soil, measured at scalps in Kivalo and Vaalolehto in 1971—1973. Method of measurement according to Table 4.

Koealue, lohko no *Experim. area, Plot No*	Anturit — *Sensors*		Mittausvuosi — *Measurement year*				
	Maan käsittely, mittauskohta *Treatment of soil, Measurement point*	Kpl *No of sensors*	1971	1972	1973	1971 — 1973	
			Lämpösumma *Temperature sum*			Keskim. *Mean value*	% ilman lämpös. *Temp. sum of the air, %*
Kivalo 5	Käsilaikku, 40 × 40 cm *Hand scalp*	1	778	1110	945	944	106
Vaalolehto 3						1972 — 1973	
	Konelaikku, 45 × 65 cm	2		739	740	739	89
	Konelaikku, 60 × 90 cm *Machine scalp*	2		802	817	810	97
	Konelaikku, keskim. *Machine scalp, mean value*	4		770	778	774	93
4	Polttolaikku, 40 × 40 cm *Burnt scalp*	2		625	671	648	78
	Ilma, 2 m ..... *The air*	2		883	776	830	100

Kuvassa 7 on esitetty laikun pohjan maan lämpösumman kuukausikohtainen kehitys Vaalolehdossa vuonna 1973. Polttolaikutettu maa on ollut selvästi kylmin koko kesäkauden ajan, sitten seuraavat mittauspisteet: pieni konelaikku, suuri konelaikku ja kaikkein lämpimimpänä ilma.

Useat tutkijat, jotka ovat vertailleet koskemattoman ja laikutetun maan lämpöoloja, ovat todenneet, että laikutetun maan pintakerroksessa (1—2 cm syvyydessä) lämpöolot eivät ole niin äärevät kuin humuksen pintakerroksessa, mutta että syvemmällä järjestys muuttuu ja laikutetun maan lämpöolot kääntyvät vuorostaan äärevämmäksi (Söderström 1959, Bärring 1967, Shubin ja Popov 1959). Tämä johtuu ennen kaikkea kuivan humuksen huonosta lämmönjohtokyvystä paljastettuun kivennäismaahan verrattuna.

Myös maan kosteusoloilla on suuri merkitys maan lämpöoloille. Suuri vesipitoisuus lisää haihtumiseen kuluvaa lämpöä ja viilentää laikkua. Jonkin verran vaikutusta on myös mikrotopografisilla seikoilla. Mm. Odin (1964, 1969) on todennut, että pienissä kuopissa on ulossäteilytyypin vallitessa keskimäärin hieman suotuisammat lämpöolot kuin aivan tasaisella maalla, sillä kuopan seinät estävät vaihdon ja luovuttavat lämpöä ilmaan.

Eräs selitys polttolaikun lämpösumman alhaisuuteen 5 cm syvyydellä on, että polttamista ei ilmeisesti oltu suoritettu kovinkaan syvältä, vaan laikun

Taulukko 6. Maan lämpösummat (d.h./24) auratulla alalla Kivalossa ja Vaalolehdossa vv. 1970—1973. Mittaus kuten taulukossa 4.

Table 6. Temperature sums (d.h./24) of soil in ploughed plots in Kivalo and Vaalolehto in 1970—1973. Method of measurement according to Table 4.

Koealue, lohko no *Experim. area, Plot No*	Maan käsittely *Soil treatment*	Anturit — *Sensors*		Havaintovuosi — *Observation year*				
		Mittauskohta *Measurement point*	Kpl *No of sensors*	1971	1972	1973	1971 — 1973	
				Lämpösumma *Temperature sum*			Keskim. *Mean value*	% ilman lämpös. *Temp. sum of the air, %*
Kivalo								
5,6	Raskas auraus *Heavy reforestation ploughing*	Aurausvaon pohja ..... *Bottom of the ploughing trace*	2	715	943	831	830	93
5,6	»	Piennar, itäsivu ..... *Shoulder, east side*	5	880	1144	1008	1011	113
	»	» länsisivu ..... » *west side*	2	891	1121	998	1003	112
	»	» keskim. ..... » *mean value*		886	1133	1003	1007	113
5,6	Raskas auraus *Heavy reforestation ploughing*	Palle, itäsivu, länsikylki ..... *Tilt, east side, west shoulder*	2	953	1218	1030	1067	119
6	»	» länsisivu, itäkylki	1	1102	1271	1053	1142	128
	»	» *west side, east shoulder*						
	»	» keskim. ..... » *mean value*		1028	1245	1042	1104	124
	—	Ilma, 0,65 m — *The air*	1	772	1012	895	893	**100**
Vaalolehto							1972 — 1973	
6	Raskas auraus *Heavy reforestation ploughing*	Piennar, eteläsivu ..... *Shoulder, south side*	1		904	828	866	104
6	»	» pohjoissivu	1		1017	913	965	116
	»	» *north side*						
	»	» keskim.			961	871	916	110
	»	» *mean value*						
6	Raskas auraus *Heavy reforestation ploughing*	Palle, eteläsivu, pohjoiskylki *Tilt, south side, north shoulder*	1		1026	924	975	117
6	»	» pohjoissivu, eteläkylki ...	1		1053	928	991	119
	»	» *north side, south shoulder*						
	»	» keskim. — *mean value* ...			1040	926	983	118
5	Kevyt auraus *Light reforestation ploughing*	Piennar, eteläsivu ..... *Shoulder, sout side*	1		872	779	826	100
5	»	» pohjoissivu	1		962	867	914	110
	»	» *north side*						
	»	» keskim.			917	823	870	105
	»	» *mean value*						
5	Kevyt auraus *Light reforestation ploughing*	Palle, eteläsivu, pohjoiskylki *Tilt, south side, north shoulder*	1		1068	927	998	120
5	»	» pohjoissivu, eteläkylki ...	1		1114	983	1049	126
	»	» *north side, south shoulder*						
	»	» keskim.			1091	955	1023	123
	»	» *mean value*						
	—	Ilma, 2 m — *The air*	2		883	776	830	**100**

pintaan oli jäänyt kerros huonosti lämpöä johtavaa, puoliksi palanutta sammalta ja humusta. Polttolaikun tumma pinta absorboi kyllä runsaasti lämpösäteitä; esim. aivan palaneen maan pinnassa on yleensä mitattu erittäin korkeita päivittäisi maksimilämpötiloja (esim. VAARTAJA 1949, 1954). Kulotetun maan onkin yleensä todettu olevan syvemmältäkin lämpimämmän kuin kulottamattoman humuspeitteiden maan (SIRÉN 1955a, b, ÄIKÄS 1969).

322. Vaotus

3221. Metsäauraus

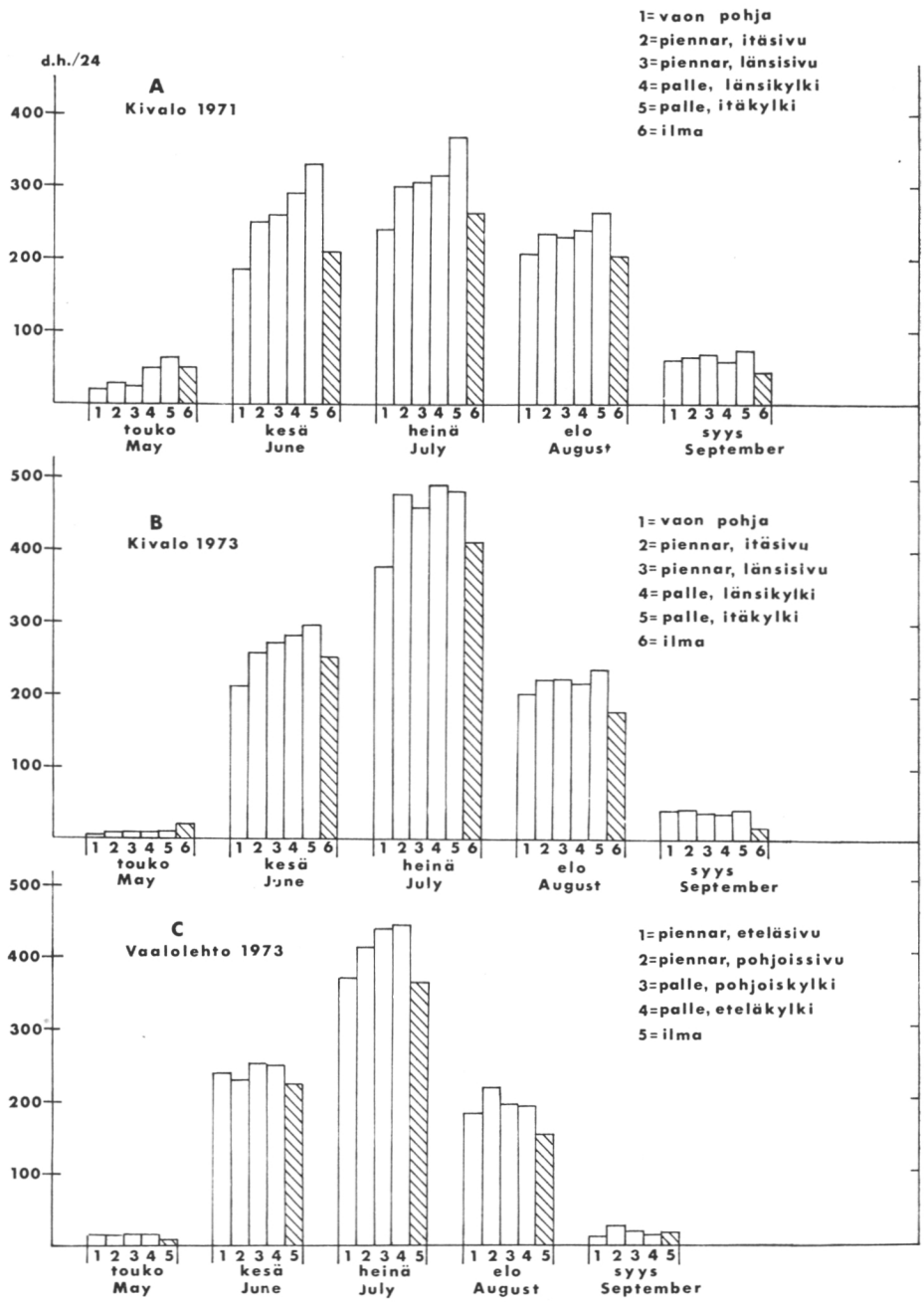
Metsäaurat (tässä tapauksessa ns. piennaurat (OHJEKIRJE 1973) tekevät n. 25 cm syvän vaon kummallekin puolelle noin 60 cm leveän pintareen ja noin 45 cm korkean auranpalteen, jonka mitat ja muoto riippuvat paljon paitsi käytetystä maanmuokkauslaitteesta ja vetokoneesta, myös maan laadusta. kivisyydestä sekä kantojen, hakkuutähteiden ja pintakasvillisuuden määrästä Lisäksi aurapalteet painuvat ja vaot tasoittuvat jonkin verran ajan myötä (KELLOMÄKI 1972).

Kivalossa ja Vaalolehdossa lämpötilan mittausanturit sijoitettiin aurausjäljen kumpaankin pientareeseen ja palteeseen. Seuraavassa kutsutaan auranvaon itä/pohjoispuolella olevaa pientaretta itä/pohjoissivuksi, ja länsi/eteläpuolella olevaa pientaretta länsi/eteläsivuksi. Itä/pohjoispalteen kyljet ovat vastaavasti itä/pohjois- ja länsi/eteläkylkiä (vrt. kuva 3).

Taulukossa 6 on esitetty aurausjäljen (refiefin) eri osien keskimääräiset lämpösummat molemmilla koealueilla. Kivalossa vaon pohja on ollut selvästi kylmin, jopa kylmempi kuin vertailuna ollut ilma. Tätä selvästi lämpimämpiä ovat auran piennar ja palle. Itä- ja länsisivun pintareiden lämpösummilla ei ole kovinkaan suurta eroa, mutta itäpalteen länsikylki, joka on iltapäivän auringolle eniten alttiina, on jonkin verran lämpimämpi kuin iltapäivän auringolta varjoon jäävä länsipalteen itäkylki (vrt. TURTIAINEN ja VALTANEN 1970).

Vaalolehdossa, jossa auranvakojen suunta kulki idästä länteen, on päivällä keskimäärin enemmän varjoon jäävä eteläsivun piennar ollut kylmempi kuin keskimäärin enemmän auringossa oleva pohjoissivun piennar. Sama toistuu myös auranpalteissa, joissa sekä raskaan että kevyen aurauksen palteen eteläkylki on lämpimin. Kummallakin koealueella metsämaan auraus on nostanut maan pintakerroksen lämpösummaa suunnilleen saman määrän. Merkittäessä ilman vuotuista lämpösummaa 100:lla on auran pientareen lämpösumma ollut noin 110—113 ja palteen noin 12—125.

Kuvassa 8 esitetyille aurausjäljen eri osien kuukausikohtaisille lämpösummille on ominaista eri mittauskohtien keskinäisten erojen vähäisyys. Vain



Kuva 8. Metsäauratun maan lämpösummien kuukausikohtainen kehitys eri mittauspisteissä Kivalossa vuosina 1971 (A) ja 1973 (B) sekä Vaalolehdossa vuonna 1973 (C).

Fig. 8. Monthly development of the temperature sums pertaining to soil prepared for reforestation in Kivalo in 1971 (A) and 1973 (B) and in Vaalolehto in 1973 (C). Explanation: Sections A and B: 1 = bottom of the furrow, 2 = shoulder, east side, 3 = shoulder, west side, 4 = tilt, west shoulder, 5 = tilt, east shoulder, 6 = the air. Section C: 1 = shoulder, south side, 2 = shoulder, north side, 3 = tilt, north shoulder, 4 = tilt, south shoulder, 5 = the air.

päivänpuoleisen palteen lämpösumma on kaikkina kuukausina ollut selvästi toisia suurempi. Yleisenä piirteenä näkyy myös refiefin eri osien lämpösummien suurempi keskinäinen vaihtelu alkukesällä ja erojen vähittäinen tasaantuminen loppukesää kohti edettäessä. Merkille pantava on auran palteen ja pientareen lämpösummien suuruus elo-syyskuussa. Onpa Vaalolehdossa eteläsivun piennar kaikkein lämpimin elo- ja syyskuussa, vaikka palteen lämpösumma onkin koko kasvukautta tarkastellen selvästi suurin.

Eräänä syynä lämpösummien eroihin aurausjäljen eri kohdissa on niiden erilainen asema suringon säteilyyn nähden. Kun tiedetään, että esim. 65° leveysasteella kasvukauden aikainen auringon suora säteily esim. 45° etelään suuntautuneella pinnalla on 120 yksikköä, ja vastaavasti 45° pohjoispinnalla vain 30 yksikköä, vaakasuoran pinnan säteilyn ollessa 100 yksikköä (LUNELUND 1927), on ymmärrettävää, että varsinkin aurinkoisina päivinä tulosäteilytyypin vallitessa auranpalle voi lämmitä erittäin voimakkaasti. Auranpaltteen lämpimyyttä pientareeseen ja muokkaamattomaan maahan nähden korostavatkin mm. ÄIKÄS (1969), BÉZDENÉZNYH (1970) ja MÄLKÖNEN (1972). Samalla painotetaan palteen maan lämpöolojen äärevyyttä sekä muistutetaan palteen herkkyydestä kuivumiselle ja routimiselle (mm. POHTILA 1970, 1972).

Usein viitataan auran palteiden lämpöoloja pohdittaessa siihen, että ne ovat aikaisemmin keväällä ja myöhemmin syksyllä lumen pinnan yläpuolella

Taulukko 7. Maan lämpösummat (d.h./24) käsittelemättömällä ja auratulla koealueella Kivalossa v. 1971. Eri syvyystasojen vertailua.

Table 7. Temperature sums (d.h./24) of soil in an unprepared and in a ploughed experimental plot in 1971. Comparison of temperature sums measured at different depths.

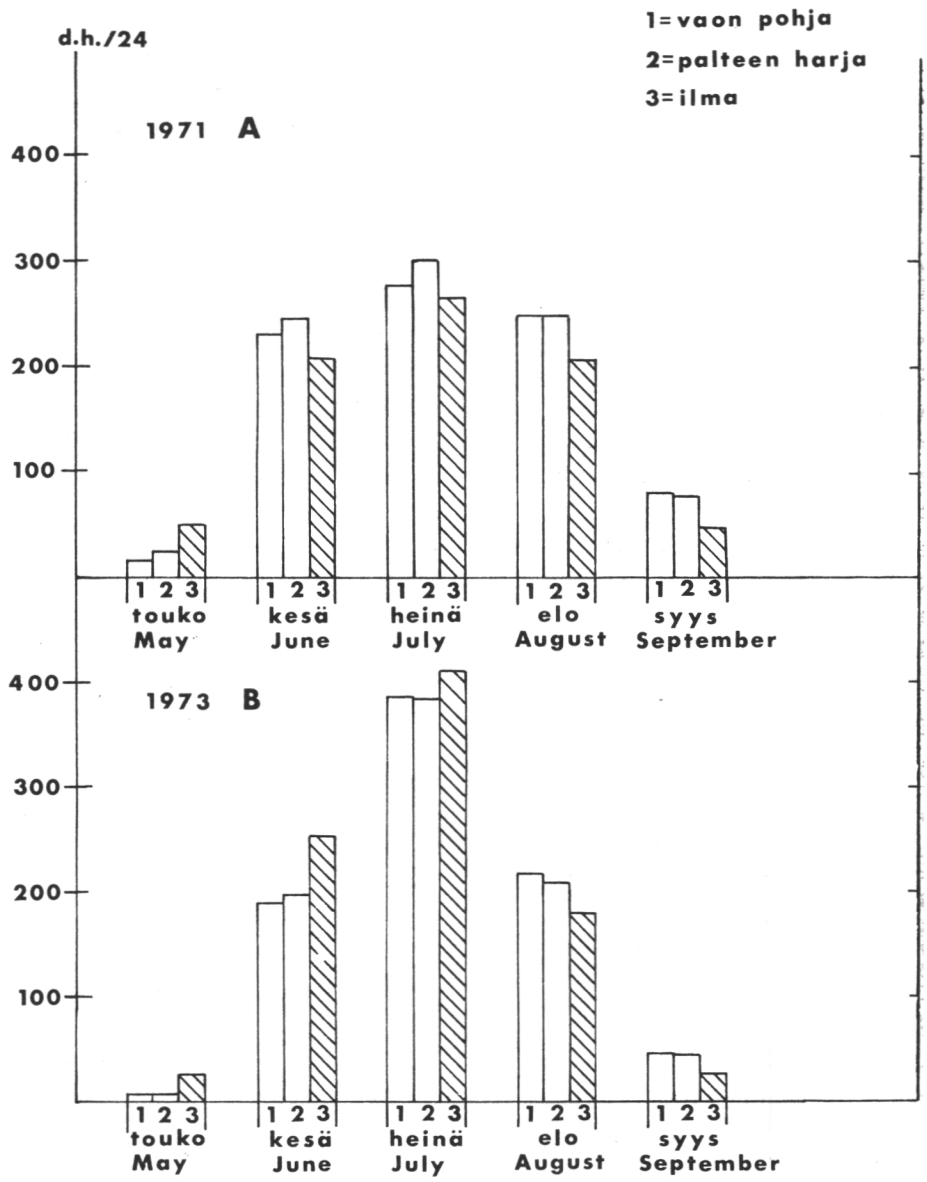
Anturi *Sensor*		Lämpösumma *Temperature sum*						Yhteensä 1971 — *Total 1971*		
Mittauskohta *Measurement point*	Syv., cm *Depth, cm*	Toukok. *May*	Kesäk. *June*	Heinäk. *July*	Elok. *Aug.*	Syysk. *Sept.*	Lokak. *Oct.*	Yht. d.h./24 *Total d.h./24*	% ilman lämpös. % *temp. sum of the air*	% vast. lämpös. 5 cm % *corr. temp. sum of 5 cm.*
Käsittelemätön *Unprepared soil*	1	45.0	307.9	337.0	281.1	74.4	2.2	1047.6	135.7	144.3
»	5	13.6	178.3	216.3	216.6	98.6	2.4	725.8	94.0	**100**
»	10	8.1	150.8	197.1	196.6	83.9	0.2	636.7	82.5	87.7
»	20	7.1	149.7	192.1	196.8	104.4	5.8	655.9	85.0	90.4
Aura, piennar *Shoulder of ploughing trace*	1	36.9	287.6	325.6	261.8	76.9	2.2	991.0	128.4	107.4
»	5	32.9	260.1	304.9	251.1	73.5	0.5	923.0	119.5	**100**
»	10	28.8	254.1	294.9	243.7	69.5	0.7	891.7	115.5	96.6
»	15	25.4	247.2	290.1	242.3	74.4	0.5	879.9	114.0	95.3
Ilma — *The air*	2 m	49.9	208.2	262.9	205.0	46.0	0.0	772.0	100	

kuin pientareet ja käsittelemätön tasamaa. Tällä seikalla ei kuitenkaan kuukausikohtaisten lämpösummien perusteella ole juuri mitään merkitystä. Toukokuu ja syyskuu, jolloin lumipeite sulaa tai toisaalta muodostuu epätasaisesti, ovat lämpösummiltaan reliefin eri osissa melko yhdenmukaiset ja tuolloin kertyneet lämpösummat ovat kaikkiaankin niin vähäisiä, että keskikesällä, s.o. kesä- tai heinäkuussa, kertyvien eri mittauskohtien lämpösummien erot peittävät ne helposti.

Taulukossa 7 on vertailtu Kivalossa vuonna 1971 neljällä eri syvyydellä tehtyjen mittausten perusteella laskettuja kuukausikohtaisia lämpösummia. Koskemattoman, humus- ja pintakasvillisuuspeitteisen maan ja toisaalta aurausjäljen pientareen lämpöolojen suuri ero korostuu verrattaessa toisiinsa lämpösummien kehitystä eri syvyyksillä. Aivan maan pinnassa on koskemattomassa maassa lämpimämpää kuin auran pientareessa, mutta jo hieman syvemmällä maassa auran piennar on vuorostaan selvästi lämpimämpi. Syyskesällä eri mittauskohtien lämpöolot ovat tosin melko yhdenmukaiset. Mielenkiintoisena piirteenä nähdään erityisesti koskemattomassa maassa syksyllä esiintyvä ns. vertikaalinen lämpötilainversio. Syys- ja lokakuussa lämpösumma on 20 cm syvyydessä keskikesän jäljiltä vielä suurin, 10 cm syvyydessä pienempi, mutta pinnan lähellä (5 cm ja 1 cm syvyydessä) auringon suoran säteilyn vaikutuksesta jälleen hieman tätä suurempi.

Taulukko 8. Maan lämpösummat (d.h./24) lautasauratuilla ja täysmuokatuilla aloilla Kivalossa vv. 1970—1973. Mittaus kuten taulukossa 4.
Table 8. Temperature sums (d.h./24) of disk ploughed plots and of fully prepared plots, measured in Kivalo in 1970—1973. Method of measurement according to Table 4.

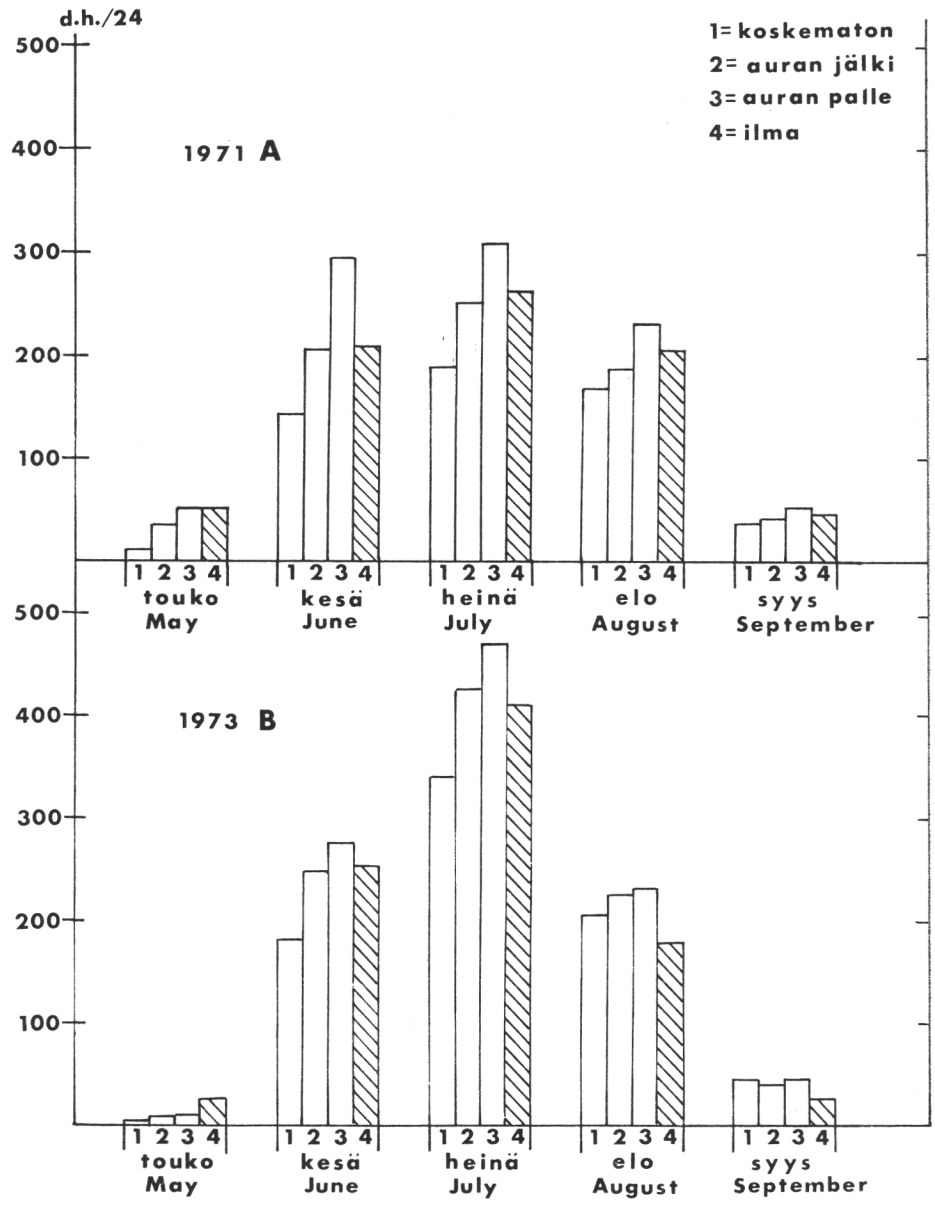
Lohko no *Plot No*	Maan käsittely *Soil preparation*	Anturit — *Sensors*		Havaintovuosi — *Year of observation*				
		Mittauskohta *Measurement point*	Kpl *No of sensors*	1971	1972	1973	1971 — 1973	
				Lämpösumma *Temperature sum*			Keskim. *Mean value*	% ilman lämpös. *% the air*
5	Lautasauraus *Disk ploughing*	Aurausvaon pohja *Bottom of ploughing trace*	1	848	1013	843	901	101
»	»	Palle, itäkylki *Tilt, east shoulder*	1	977	1074	913	988	111
»	»	Palle, länsikylki *Tilt, west shoulder*	1	804	991	766	854	96
		Palle keskimäärin *Tilt, mean value*		876	1026	841	914	102
5	Täysmuokkaus *Full site preparation*	Auranjälki *Ploughing trace*	2	683	1103	944	910	102
»	»	Palle — *Tilt*	1	935	1220	1031	1062	119
	—	Ilma, 65 cm *The air*	1	772	1013	895	893	**100**



Kuva 9. Lautasauratun maan lämpösummien kuukausikohtainen kehitys eri mittauspisteissä Kivalossa vuosina 1971 (A) ja 1973 (B).
Fig. 9. Monthly development of temperature sums of disk ploughed soil in Kivalo in 1971 (A) and 1973 (B). Explanation: 1 = bottom of furrow, 2 = ridge of tilt, 3 = the air.

3222. Lautasauraus

Lautasaurojen siipenä toimii vapaasti pyörivä lautanen, joka repii metsämaahan lähes yhtäjaksoisen uran paljastaen kivennäismaata ja siirtäen hu-



Kuva 10. Lautasauralla täysmuokatun maan lämpösummien kuukausikohtainen kehitys Kivalossa vuosina 1971 (A) ja 1973 (B).
Fig. 10. Monthly development of temperature sums of soil fully prepared with disk plough in Kivalo in 1971 (A) and in 1973 (B). Explanation: 1 = unprepared soil, 2 = ploughing trace, 3 = tilt, 4 = the air.

muksen sivulle palteeksi. Kokeessa käytetyistä laitteista TTS-metsä-äkeen lautanen on varustettu kunttaa repivällä hampailla, mutta Ylö-lautasauran reuna on sileä. Käsittelyteholtaan lautasaurat ovat huomattavasti siipi-

auroja keveämpiä, joten niitä käytetään ennen kaikkea vain pintakasvillisuuden torjumiseen ja haitallisen humuskerroksen poistamiseen maasta ennen uudistamista (lautasauroista esim. SUOMALAISTA ... 1970).

Lautasaurauksen vaikutusta maan lämpöoloihin seurattiin vain Kivalossa, jossa mittauksen kohteena olivat TTS-metsä-äkeen työnjälki sekä maan muokkaus Ylö-lautasauralla (taulukko 8). Aurausjäljen (profiilin) eri osien lämpöolot muistuttavat suuresti varsinaisten metsäaurojen jäljen lämpööloja, mutta palteen harjalta ja vaon pohjalta mitattujen lämpösummien väliset erot ovat paljon pienempiä. Merkille pantavaa on lautasauran vaon pohjan kohtalaisen suuri lämpösumma. Yleisenä istutuspaikkana käytetty lautasauran vako on siten lämpööloiltaan suunnilleen samanlainen kuin laikun pohja, mutta lämpimämpi kuin metsäauran vaon pohja. Täysmuokatuilla (ristiinauratuilla) koeruuduilla suoritetut mittaukset vahvistavat jo edellä esitettyä yleistä johtopäätöstä: paljastetun muokkaamattoman maan lämpösumma on 5 cm syvyydellä karkeasti arvioiden samaa luokkaa tai hieman suurempi kuin vertailukohtana käytetty ilman lämpösumma, ja maan pinnasta koholle käännetyn palteen lämpösumma ylittää ilman lämpösummaa noin 20 %:lla.

Kuukausikohtaisia lämpösummia tarkasteltaessa (kuva 9) toistuu jo aikaisemmin varsinaisen metsäaurauksen yhteydessä esitetty lämpösumman aikakohtainen malli. Palteen aurausjäljen muihin osiin nähden suhteellisen suuri lämpösumma muodostuu melkein yksinomaan keskikesällä. Toisaalta varsinkin loppukesällä lautasauran vaon pohjan lämpösummat ovat kaikkein suurimmat. Täysmuokkauksessa palteen lämpöolojen edullisuus näkyy koko kesän ajan (kuva 10).

323. Jyrsintä

Jyrsinnällä pyritään kuohkeuttamaan metsämaata ja sekoittamaan rikottu humus ja kivennäismaa toisiinsa. Menetelmä soveltuu parhaiten kivettömille tai vähäkivisille maille, joista hakkuutähteet on etukäteen raivattu. Onkin ymmärrettävää, että metsämaan jyrsintä jo tämän vuoksi on meillä ollut vähäistä ja työhön käytetty konekantakin vielä kokeiluasteella. Tässä tutkimuksessa oli käytössä kaksi eri tyyppistä jyrsintä: Kivalossa mitattiin rumpujyrsimen (TTS-metsäjyrsimen) ja Vaalolehdossa LKM-ketjujyrsimen muokkausjäljen lämpööloja. Ketjujyrsintää varten maa valmistettiin auraamalla se ensin KLM 170-metsäauralla. Näin muodostui jyrsintäjäljestä noin 30—50 cm korkea penkki, joka tosin laskeutuu hieman parina ensimmäisenä vuonna (metsämaan jyrsinnästä ja jyrsintäjäljen ominaisuuksista esim. Suomalaista ... 1970, MÄLKÖNEN 1972, SOLISMAA 1973).

Taulukon 9 yläosassa on esitetty Kivalossa mitatut rumpujyrsimen työjäljen vuotuiset lämpösummat. Jyrsintäjälki osoittautuu lämpösumman mukaan arvioiden keskimäärin hieman ilmaa kylmemmäksi, mutta vastaavaa

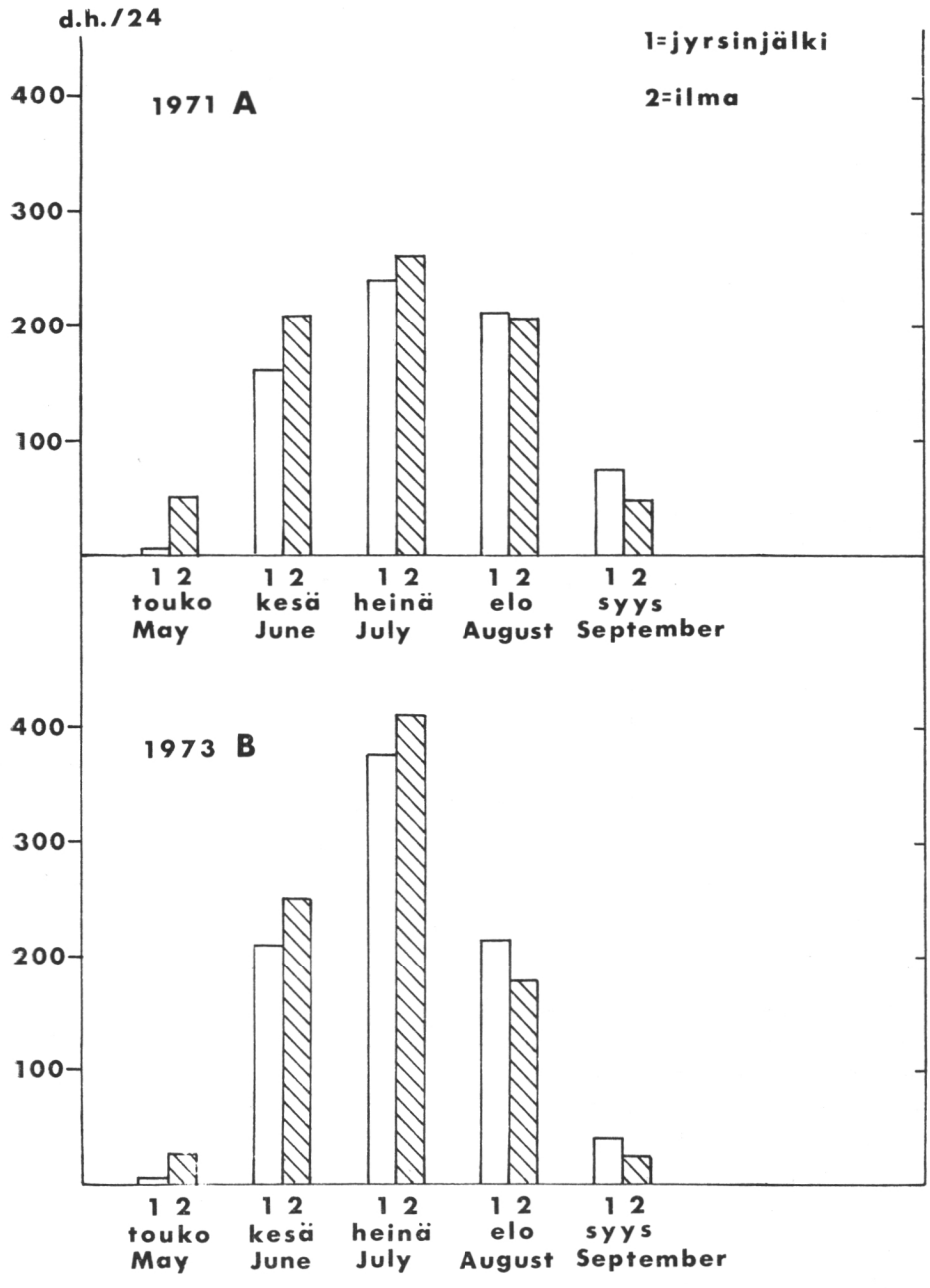
Taulukko 9. Maan lämpösummat (d.h./24) jyrsityillä aloilla Kivalossa ja Vaalolehdossa vv. 1970—1973. Mittaus kuten taulukossa 4.
Table 9. Temperature sums (d.h./24) of soil in tilled areas in Kivalo and Vaalolehto in 1970—1973. Method of measurement according to Table 4.

Koealue, lohko no *Experim. area, Plot No*	Maan käsittely *Soil preparation*	Anturit — *Sensors*		Havaintovuosi — *Year of observation*				
		Mittauskohta *Measurement point*	Kpl *No of sensors*	1971	1972	1973	1971 — 1973	
				Lämpösumma *Temperature sum*			Keskim. *Mean value*	% ilman lämpös. *Temp. sum of the air, %*
Kivalo								
2	Rumpujyrsintä *Drum rotary tilling*	Jyrsinjälki ..... *Tilling trace*	2	687	970	848	893	94
	—	Ilma, 0.65 cm	1	772	1012	895	893	**100**
	—	*The air*						
Vaalolehto							1972 — 1973	
2	Ketjujyrsintä *Chain rotary tilling*	Jyrsinjäljen harja *Tilt*	2	565	1048	984	1016	122
2	»	Jyrsinjäljen etelä-reuna ..... *South side of the tilt*	2	454	870	843	857	103
2	»	Jyrsinjäljen pohjois-reuna ..... *North side of the tilt*	2	462	879	838	859	103
	—	Ilma, 2 m	1	597	883	776	830	**100**
	—	*The air*						

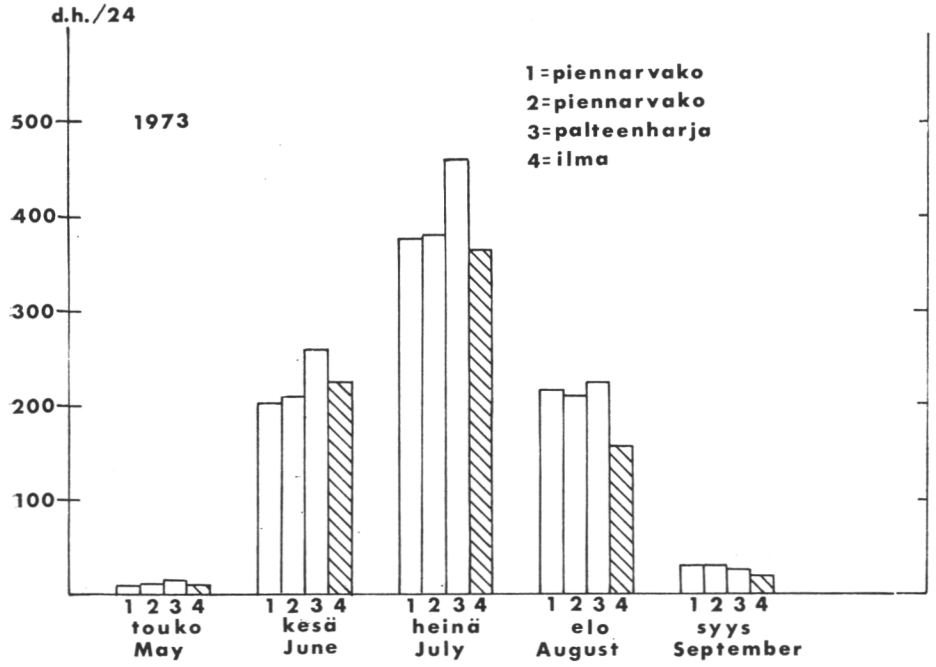
käsittelemätöntä maata selvästi lämpimämmäksi (taulukko 4). Ero on kylmänä ja lämpimänä vuonna suunnilleen saman suuruinen.

Vaalolehdossa (taulukko 9, alaosa) mittauksia suoritettiin KLM-ketjujyrsimen jäljen eri puolilta: jyrsintäjäljen harjalta sekä kummaltakin sivulta. Jyrsimen kokoaman palteen harja osoittautuu nytkin selvästi lämpimimmäksi. Siellä mitattu maan lämpösumma ylittää vertailuna käytetyn ilman lämpösumman, ja on samaa suuruusluokkaa kuin kevyen aurauksen palteen lämpösumma (taulukko 7). Jyrsintäjäljen kummankin reunan lämpösummat ovat jo selvästi pienempiä eikä niiden välillä ole selvää eroa. Tämä johtunee jyrsintäjäljen mataluudesta ja sivujen loivasta kulmasta.

Verrattaessa TTS-rumpujyrsimellä muokatun maan kuukausikohtaisia lämpösummia ilman lämpösummiin (kuva 11), havaitaan jyrsintäjäljen olevan pitkään keväällä ja alkukesällä ilmaa viileämmän, mutta vuorostaan loppukesällä ilmaa lämpimämmän. Tämä ilmiö on samanlainen kuin jo edellä esim.



Kuva 11. Rumpujyrsimellä muokatun maan lämpösummien kuukausikohtainen kehitys Kivalossa vuosina 1971 (A) ja 1973 (B).
Fig. 11. Monthly development of temperature sums of soil tilled with drum rotary tiller in Kivalo in 1971 (A) and in 1973 (B). Explanation: 1 = track of rotary tiller, 2 = the air.



Kuva 12. Ketjujyrsimellä muokatun maan lämpösummien kuukausikohtainen kehitys Vaalolehdossa vuonna 1973. Selitys: 1 = pohjoispuoli, 2 = eteläpuoli.
Fig. 12. Monthly development of the temperature sums of soil tilled with a chain rotary tiller in Vaalolehto in 1973. Explanation: 1 = furrow, north side, 2 = furrow, south side, 3 = ridge of the tilt, 4 = the air.

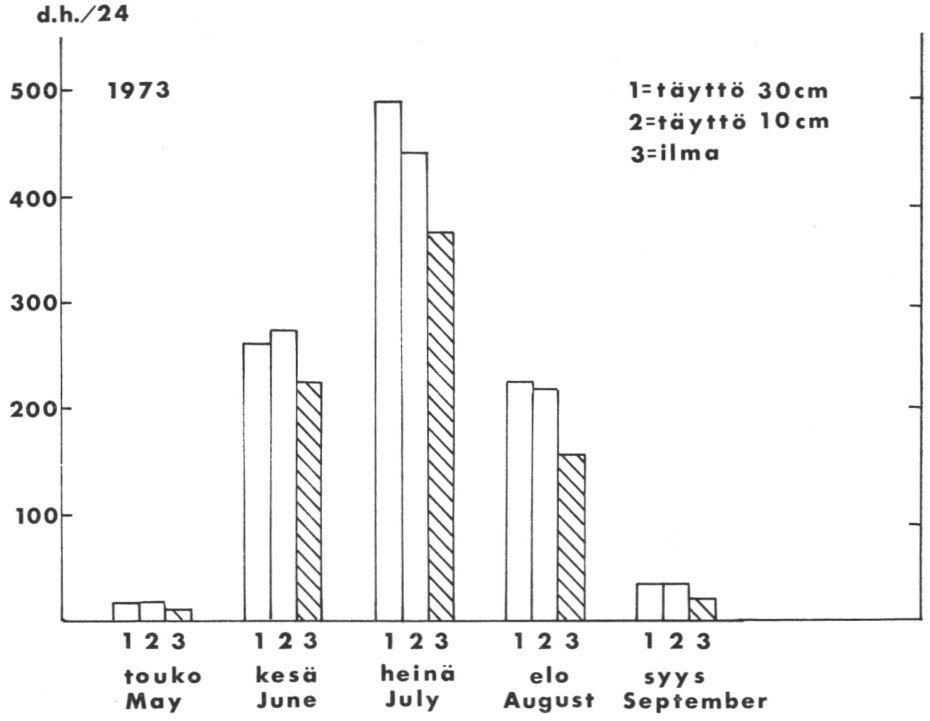
aurauksen yhteydessä on selostettu. Samanlainen on myös ketjujyrsimellä muokatun maan lämpöolojen kuukausikohtainen kehitys (kuva 12). Erityisesti jyrsinpalteen harjan korkea lämpösumma korostuu heinäkuun aikana. Elokuun aikana ovat palteen harjan ja piennarvaon lämpöolot lähes samaa suuruusluokkaa keskenään, ja ilman lämpösumma on edellisiä jo selvästi alempi. Syyskuussa ovat kaikkien mittauskohtien lämpösummat lähes saman suuruiset.

324. Muu maan käsittely

Vaalolehdossa suoritettiin kahdenlaisia maansiirtokokeita, joiden yhteydessä mitattiin maan lämpötilan vaihteluita. Kasvillisuus ja pintamaa kuorittiin noin 30 cm syvyydelle, ja sijalle ajettiin hiekkamoreenia tasaiseksi kerrokseksi. Toisessa maan käsittelyssä alkuperäinen pintamaa ja humuskerros peitettiin niinikään muualta tuodulla 10 cm vahvuisella hiekkamoreenikerroksella (vrt. kuva 3).

Taulukko 10. Paljaan maan lämpösummat (d.h./24) Vaalolehdossa vv. 1971—1973. Mittaus kuten taulukossa 4.
Table 10. Temperature sums of bare soil (d.h./24) in Vaalolehto in 1971—1973. Method of measurement according to Table 4.

Lohko no *Plot No*	Anturit — *Sensors*		Havaintovuosi — *Observation year*			
	Maan käsittely, mittauskohta *Soil treatment, measurement point*	Kpl *No of sensors*	1972	1973	1972 — 1973	
			Lämpösumma *Temperature sum*		Keskim. *Mean value*	% ilman lämpös. *Temp. sum of the air*, %
14	Hiekkaa 30 cm pohjamaan päällä *Sand layer, 30 cm deep, on subsoil*	3	1070	1028	1049	126
15	Hiekkaa 10 cm humuksen päällä *Sand layer, 10 cm deep, on humus*	2	1074	987	1031	124
	Ilma, 2 m — *The air*	2	883	776	830	**100**



Kuva 13. Maan päälle levitetyn kivennäismaan lämpösummien kuukausikohtainen kehitys Vaalolehdossa vuonna 1973.
Fig. 13. Monthly development of the temperature sums of mineral soil spread on the ground in Vaalolehto in 1973. Explanation: 1 = depth of the layer of mineral soil is 30 cm (soil transport 1), 2 = depth of the layer of mineral soil is 10 cm (soil transport 2), 3 = the air.

Kummankin maankäsittelyruudun vuotuiset lämpösummat ovat lähes samansuuruiset (taulukko 10), mikä viittaa niiden lämpöolojen kiinteään riippuvuuteen maanpinnan lämpö- ja säteilyoloista. Vuotuiset lämpösummat kohoavat noin 25 % suuremmiksi kuin vastaavat ilman lämpösummat ja ne ovat yhtä suuret kuin auran palteessa mitatut (taulukko 7). Vertauksen vuoksi voi mainita, että Sodankylän ilmatieteellisen aseman mittausten mukaan paljaan hiekkamaan vuotuiset lämpösummat 5 cm syvyydellä olivat vuosina 1958—1960 keskimäärin 30 % suuremmat kuin samalla paikalla mitatut ilman vastaavat lämpösummat (RESULTS . . . 1969).

Humuksesta ja pintakasvillisuudesta vapaa hiekkamaa lämpiää keväällä nopeammin kuin ilma, ja maan kuukausikohtaiset lämpösummat pysyvät joka kuukausi suurempina kuin vastaavat ilman lämpösummat (kuva 13). Myös Sodankylän ilmatieteellisellä asemalla tehtyjen mittausten mukaan maan pintakerroksen kuukausikohtainen lämpösumma ylitti jatkuvasti vastaavan ilman lämpösumman. Kesäkuussa ero oli jopa 45 %.

4. TULOSTEN TARKASTELUA

Maan käsittelyn vaikutus sen pintaosien lämpöoloihin osoittautui tutkimuksen mukaan hyvin selväksi. Kaikki erilaiset maankäsittelytavat nostivat maan pintakerroksen lämpösummaa, vaikka eri käsittelytapojen välillä oli suuria eroja. Seuraavaan asetelmaan on koottu Kivalon ja Vaalolehdon vv. 1971—73 keskimääräiset mittaustulokset suhteellisina arvoina siten, että kummankin koealueen koskemattoman maan vuotuista lämpösummaa on merkitty sadalla:

Maan käsittely	Kivalo	Vaalolehto
Koskematon maa	**100**	**100**
Laikutus, käsin tai koneella	137	128
Polttolaikutus	—	107
Mv-auraus, palle	160	162
» , piennar	146	151
Lautasauraus, palle	133	—
Rumpujyrsimen jälki	130	—
Ketjujyrsimen jälki	—	168
Maan siirto, keskimäärin	—	172
Ilma	130	137

Jonkinlaisen käsityksen saamiseksi siitä, mitä suuruusluokkaa edellä esitetyt lämpösummat edustavat, on seuraavassa vertailtu PESSIN (1968, taul. 3) esittemiä Etelä-Hämeessä sijaitsevan Leteensuon ja Oulun läänissä sijaitsevan Pelsonsuon mutasuon vuotuisia lämpösummia 20 cm syvyydeltä maan pinnasta. Tulokset ovat keskiarvoja kolmen vuoden havainnoista:

Mittauspaikka	Lämpösumma d.d.	%
Pelsonsuo (64° 31' P; 26° 28' I, 113 m mpy)	702	**100**
Leteensuo (61° 04' P; 24° 15' I, 88 m mpy)	1 314	187

Ilmatieteen laitoksen julkaisemista tiedoista (KUUKAUSIKATSAUS 1972, 1973) on seuraavassa laskettu kolmella paikkakunnalla, Jokioisissa (60° 49' P; 23°

30′ I; 104 m mpy), Maaningalla (63° 09′ P; 27° 19′ I, 88 m mpy) ja Sodankylässä (67° 22′ P; 26° 39′ I, 178 m mpy) tehtyjen kasvipeitteettömän maan lämpötilahavaintojen perusteella vuosien 1972 ja 1973 keskimääräiset vuotuiset lämpösummat 20 cm syvyydeltä:

Mittauspaikka, ilman keskimääräinen lämpösumma, 2 m.	Maalaji	Lämpösumma 20 cm syvyydellä d.d.	%
Sodankylä, 800 d.d.	moreeni	823	100
Maaninka, 1173 d.d.	karkea hieta	1 176	143
Jokioinen, 1253 d.d.	jäykkä savi	1 117	136

Jo näistä ylimalkaisista maan lämpötilan vertailuista voidaan päätellä, että esim. humuspeitteisen metsämaan auraus muuttaa syntyvän palteen pintakerroksen lämpöolot vuotuisella lämpösummalla mitaten samanlaisiksi kuin mitkä vallitsevat koskemattomassa maassa noin 400—600 km etelämpänä sijaitsevilla seuduilla. Saman suuruusluokan maan lämpöolojen muuttamiseen päästään myös ketjujyrsimen käytöllä ja kivennäismaan levittämisellä maan päälle.

Tällaiset karkeat, vain suuntaa antavat luvut ovat hyvin samanlaisia kuin mm. SIRÉNin (1955 a) esittämät laskelmat kulotuksen maan lämpöoloja parantavasta vaikutuksesta. Vm. laskelmissa on käytetty hyväksi yleisesti tunnettua nyrkkisääntöä, jonka mukaan 100 km siirtyminen etelään vastaa kasvukauden keskimääräisen lämpötilan kohoamista 1° C:lla.

Vaaraa käsitellyn maan lämpötilan liiallisesta, istutustaimia vahingoittavasta noususta ei meillä juuri ole, mutta on korostettava siementen ja sirkkataimien arkuutta paahteelle ja meilläkin poutakausina esiintyville huippulämpötiloille (VAARTAJA 1954 ym.). Välillisesti maan lämpöolojen muutos voi sen sijaan aiheuttaa vahinkoa käsitellyn maan liiallisen kuivumisen kautta. Erityisesti viimeisen neljän vuoden (1970—1973) lämpimät ja kuivat kesät ovat Pohjois-Suomessakin nostaneet esiin kysymyksen käsitellyn maan esim. auran palteen haitallisesta kuivumisesta, mikä on tullut selvänä näkyviin viimeaikaisesten kylvö- ja istutuskokeiden tuloksista (esim. POHTILA 1972, 1974, ETHOLÉN 1974).

Vertailevat havainnot käsittelemättömään ja toisaalta eri tavoin käsiteltyyn maahan istutettujen taimien juuriston kehityksestä ovat osoittaneet, että maan valmistus yleensä on edistänyt taimien juuriston kasvua, mikä on näkynyt mm. juurten pituudessa ja kuivapainossa sekä taimien juuri/versosuhteen pienenemisessä, ts. myös juuriston suhteellisen määrän lisääntymisenä (esim. SÖDERSTRÖM 1959, RÖHRIG 1966, HEINSDORF ja SCHULZKE 1969).

Pohjois-Suomessa on toistaiseksi tarjolla vain yksittäisiä havaintoja tai suppeita koetuloksia, mutta näidenkin perusteella voi olettaa maan käsitte-

lyn luomien olojen olevan taimien juurten kasvulle myönteisten (VALTANEN 1973, SOLISMAA 1973, TURTIAINEN ja VALTANEN 1974, MUTKA 1974). On syytä painottaa tehokkaasti muokattuun maahan istutettujen taimien juuristojen kaikesta päättäen parempaa fysiologista kuntoa, mikä taas edistää taimien selviämistä koulimisen, istutuksen tai sopimattoman paakun aiheuttamien juuristodeformaatioiden haitallisista jälkiseurauksista (esim. HUURI 1972, LÄHDE ja SILTANEN 1973, BERGMAN ja HÄGGSTRÖM 1973).

Kokonaiskuvan muodostaminen maan lämpöolojen merkityksestä metsän nuorennoksen menestymiseen vaikuttavana ekologisena tekijänä ei kuitenkaan ole vaivatonta. Kuten edellä todettiin, maan lämpötilan nousun voidaan kyllä katsoa epäilyksettä vaikuttavan edullisesti taimien kehitykseen Pohjois-Suomen oloissa, mutta tällöin edellytetään samalla, että muut kasvutekijät pysyvät joko vakiotasolla tai eivät vuorostaan selvästi rajoita taimien kasvua. Näin ei kuitenkaan aina ole laita, vaan kysymys maan käsittelyn vaikutuksista laajenee välttämättä kaikki eri kasvutekijät huomioon ottavaksi kokonaisongelmaksi.

On hyviä toiveita, että nykyisten maanmuokkausmenetelmien puutteet saadaan vähitellen korjattua ja käsittelymenetelmien valinnassa voidaan antaa entistä paremmat ohjeet metsänviljelyn onnistumisen parantamiseksi. Metsien uudistamiseen kohdistuva tutkimustoiminta ja ennen kaikkea metsämaan käsittelyn vaikutusten kaikinpuolinen selvittäminen säilyy kuitenkin jatkuvasti Pohjois-Suomen metsätalouden menestyksellisen jatkamisen tärkeänä perusedellytyksenä.

5. TIIVISTELMÄ

Julkaisun tarkoituksena on esitellä tuloksia Pohjois-Suomessa kahdella maanmuokkausalueella vv. 1970—1973 suoritetuista maan lämpötilan mittauksista.

Koealueista eteläisempi sijaitsee Rovaniemen maalaiskunnassa Kivalon kokeilualueessa ja pohjoisempi Sodankylän pitäjässä metsähallinnon Sodankylän hoitoalueen Vaalolehdossa. Maan lämpötilaa mitattiin termoelementeillä koko roudasta vapaan kasvukauden ajan säännöllisessti 3—5 päivänä viikossa joka toinen tunti. Mittauksen kohteena olivat seuraavat käsittelyt:

Kivalo:
- koskematon maa
- käsilaikutus
- raskas metsäauraus
- kevyt metsäauraus
- lautasauraus
- täysmuokkaus lautasauralla
- rumpujyrsintä

Vaalolehto:
- koskematon maa
- käsilaikutus
- konelaikutus
- polttolaikutus
- raskas metsäauraus
- kevyt metsäauraus
- ketjujyrsintä
- maan siirto, 2 kpl

Mittaussyvyytenä oli 5 cm, joka määrättiin käyttäen perustasona humuskerroksen yläpintaa tai käsitellyn maan pintaa. Tulokset on laskettu lämpösummina d.h.-periaatteen mukaan käyttäen +5° C kynnyslämpötilana.

Tutkimuksen päätulokset olivat seuraavat:

— Erilainen pintakasvillisuus ja hakkuutähteet vaikuttivat selvästi käsittelemättömän maan lämpösummien suuruuteen. Keskimäärin alhaisin lämpösumma oli hakkuutähdekasan alla, jonkin verran tätä suurempi oli mustikkavarvuston alla ja kaikkein suurin alalla, josta kenttäkerros puuttui kokonaan ja maa oli kynsisammalen peitossa. Maan pintakerroksen lämpöolojen jättäytyminen ilman lämpötilaan nähden oli myös selvää.

— Laikutetuista kohteista alhaisin lämpösumma oli polttolaikussa ja tätä suurempi käsin ja koneella tehdyissä laikuissa. Keskimäärin oli laikku 20—30 % lämpimämpi kuin käsittelemätön, humuksen peittämä maa.

— Metsäauran jäljen eri kohtia vertailtaessa alhaisin lämpösumma mitattiin vaon pohjalla. Tätä selvästi suurempi oli pientareen, ja kaikkein suurin oli

palteen lämpösumma. Itäpuolisen auranpalteen länsikyljestä, joka oli iltapäivän auringolle eniten alttiina, mitattiin kaikkein suurimmat lämpösummat. Aurausjäljen eri osien lämpösummien erot muodostuivat suuriksi ennen kaikkea kesä—heinäkuussa. Keskimäärin oli piennar 50 % ja palle 60 % lämpimämpi kuin käsittelemätön maa.

— Verrattaessa toisiinsa auran palteen ja koskemattoman, humuspeitteisen maan lämpösummia eri syvyyksillä, ilmeni, että aivan maan pinnassa koskemattoman maan lämpösumma oli suurempi kuin auran pientareen, mutta syvemmällä auran piennar oli vuorostaan selvästi lämpimämpi.

— Lautasauran jäljen eri osien lämpösummien suhteet muistuttivat hyvin paljon metsäauran jäljen vastaavia lämpöoloja, mutta erot olivat pienempiä. Lautasauralla täysmuokatun alan mittaustulokset olivat samansuuntaisia kuin normaalisti riveittäin auratun alankin.

— Rumpujyrsimen jäljen lämpösumma osoittautui keskimäärin ilman lämpösummaa hieman pienemmäksi, mutta käsittelemätöntä maata 30 % lämpimämmäksi.

— Paljaan, humuksen päälle levitetyn kivennäismaan lämpösumma oli sama tai hieman korkeampi kuin metsäauran palteen lämpösumma. Vuotuiset lämpösummat kohosivat noin 25 % ilman lämpösummaa ja 70 % käsittelemättömän maan lämpösummaa suuremmiksi.

Tulosten tarkastelussa on mm. arvioitu, millaista siirtymistä etelään erilainen maan käsittely vastaa. Tämän mukaan metsämaan auraus Pohjois-Suomessa muuttaa syntyvän palteen pintaosien lämpöolot lämpösummalla mitaten samanlaisiksi, kuin mitkä vallitsevat koskemattomassa maassa noin 400—600 km etelämpänä sijaitsevilla seuduilla. Saman suuruusluokan lämpöolojen parantamiseen päästään myös ketjujyrsimen käytöllä ja kivennäismaan levittämisellä maan päälle.

Maan lämpötilan lisäksi on syytä kiinnittää huomiota myös muihin taimien menestymiseen vaikuttaviin ekologisiin tekijöihin ja maan käsittelyn vaikutukseen näihin tekijöihin.

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SUMMARY

Introduction

A low soil temperature, which has an immediate weakening effect on the function and growth of the root system and is indirectly harmful to the nutrient economy of seedlings, e.g., by retarding the decomposition of humus and litter, has often been cited as a remarkable ecological factor impairing the development of seedlings in the northern latitudes. Since different soil preparation methods are known to affect temperature conditions in the surface layer of the soil, it has generally been hoped that by utilizing these methods the environmental conditions could be rendered more favourable to the seedlings.

As compared with several other environmental factors, temperature conditions in forest soil have been investigated on a fairly small scale. The lack of satisfactory information in this respect has been felt particularly strongly in the reforestation areas of northern Finland. However, important studies have been published in Finland, for instance, by KERÄNEN and FRANSSILA. The former (1920) reports on the measurement of temperature conditions in snow and soil in Sodankylä in 1915—1917, and the latter (1945, 1960, 1962) deals with the methods of temperature measurement and with the temperature conditions in different types of soil in Lapland. The Finnish Meteorological Institute has also carried out measurements of soil temperature in northern Finland. These measurements cover, amongst others, the years 1957—1960 and since 1962 they have continued regularly (RAPELI 1969, RESULTS ... 1969). SIRÉN (1955 b) has published data on temperature measurements in thick-moss type spruce stands and birch stands.

In Sweden, ODIN (1964) and PERTTU (1970) have published data concerning investigations on microclimate carried out in Norrland. KOHH (1970) has measured the soil temperature in areas ploughed for reforestation in central Sweden, and SÖDERSTRÖM (1959) has studied root growth in seedlings and the physical properties of soil in scalps and virgin soil. BÄRRING's (1967) extensive study of field afforestation also includes data on measurements concerned with temperature conditions in soils prepared in different ways. Relevant Norwegian studies deserving special mention include, above all, the following: MORK's (1933) investigation of the effect of temperature on the germination of seed and his publication (1968) of ecological measurements carried out in Hirkjolen arctic mountain forests in 1932—1967, and BJOR's (1965, 1971, 1972), BRAEKKE's (1972), and BERGAN's (1974) thorough studies dealing with the temperature and water economy of the soil.

In the Soviet Union, too, the effect of different kinds of soil preparation on forest land has been the object of intensive study. Examples of the covering literature are SHUBIN's and POPOV's (1959) investigations on the technique of artificial forest regeneration in southern Karelia as well as the investigations of KURAJEV and SESTAKOV (1970) and BÉZDENÉZNYH (1970) concerned with the changes that the physical properties of soil undergo as a result of ploughing. A comprehensive picture of the thermal and moisture conditions in the soil and their effect on the initial development of coniferous seedlings is given in the textbooks by STRATONOVITS (1966) and ORLOV and KOSELKOV (1971).

When this investigation was planned it was considered very important that the observations should be extended to cover the whole of that part of the year when the ground was thaw. On the basis of literature it is possible to outline, at least, the main features of the pattern of the energy balance of the surface layer of the soil during, e.g., different types of weather (c.f., e.g., ODIN 1969, LAITINEN 1970, BJOR 1972), but as to the kind of environment that soils prepared in different ways provide for the seedlings of forest trees, this question remains open when it is viewed as a problem involving the entire thaw period. Thus, it was necessary to concentrate on the investigation of the temperature conditions in the soil of the regeneration areas during the whole summer season.

The purpose of this investigation is to present data on the measurement of soil temperature in two reforestation areas in northern Finland in 1970—1973. The object of study, soil temperature, is treated, above all, as a factor contributory to successful artificial regeneration of forests.

Material and method

Experimental areas

The measurements of soil temperature were made in two experimental soil preparation areas of which the more southern is located in Kivalo (60° 17′ N; 26° 40′ E; 292 m, above sea level) in the rural commune of Rovaniemi, and the more northern in Vaalolehto (67° 51′ N; 26° 38′ E; 232 m. above sea level) in the parish of Sodankylä.

Kivalo experimental area was established in 1970. The old Norway spruce stand growing on a raw humus site was felled in the winter 1969—1970, and the experiment was established in May-June 1970 using the split-plot method. The area was divided into plots 20 × 45 m. in size. The main treatments consisted of six different soil preparation methods and the subtreatments comprised two fertilization methods at three levels.

Preparation of the soil took place in June, 1970, as follows:

- Scalping was carried out manually with a swamp hoe of Billnäs make.
- Heavy reforestation ploughing was carried out with a KLM—240 reforestation plough using a Caterpillar D—7 crawler tractor as a drawing machine; the furrows were dug at 4 m. intervals.
- Light reforestation ploughing was carried out with a KLM—170 reforestation plough using a Caterpillar D 4/70 crawler tractor as a drawing machine; the furrows were dug at 4 m. intervals.
- Disk ploughing was carried out with a TTS reforestation harrow using a Varmer-Farmet-forest tractor as a drawing machine.
- Site preparation crosswise was carried out with a Ylö-reforestation plough. The experimental plots were ploughed crosswise in two directions; a Fordson farm tractor was used as a drawing machine.
- Drum rototilling was carried out with a TTS forest rotary tiller MJ-1 using a Belarus farm tractor as a drawing machine; the soil was tilled in rows (40 cm wide) at 2 m intervals.

In Kivalo, site preparation in the plots was always carried out longitudinally and thus the tracks of the machines run from south to north.

Vaalolehto experimental area was established in 1969—70. The area, formerly covered by Norway spruce and clear cut in the 1950's, was divided into plots 20 × 60 m. in size. The site preparations involved were randomized (Fig. 2) and they were carried out in spring 1970 except for heavy reforestation ploughing which took place already in autumn 1969. Scalp burning and scalping by herbicides were carried out in autumn 1970.

The methods of soil preparation are described below:

- Hand scalping was carried out manually with a swamp hoe of Billnäs make.
- Machine scalping was carried out with a stub hook using a Ford County farm tractor as a drawing machine.
- Scalp burning was carried out with a portable power spray to which a flame thrower nozzle was attached. The diameter of the burnt area was 50—70 cm.
- Heavy reforestation ploughing was carried out with a PP—1/220 reforestation plough using a Caterpillar D—7 crawler tractor as a drawing machine.
- Light reforestation ploughing was carried out with a KLM—170 reforestation plough using a Caterpillar D 4/70 crawler tractor as a drawing machine.
- Chain rotary tilling was first carried out with a KLM—170 reforestation plough using a Caterpillar D 4/70 crawler tractor as a drawing machine. The ploughing trace was prepared with a KLM chain rotary tiller using a Ford County tractor as a drawing machine.

In Vaalolehto, site preparation in the plots was carried out longitudinally and thus the tracks of the machines run from east to west.

Experiments with soil transfer were made in two plots in Vaalolehto in autumn 1970 and they are described below:

- A surface layer 30 cm. deep was removed from one of the plots and this was replaced with a 30 cm. deep layer of sand (soil transport 1).
- A layer of sand moraine, 10 cm. deep, was spread on the other plot (soil transport 2).

Soil of the experimental areas. The average composition of particles in the soil of Kivalo and Vaalolehto experimental areas is shown in Tables 1 and 2. Both experimental areas were established on morainic soil. In Kivalo the soil mainly consists of fine sand and in Vaalolehto of silt.

When one wishes to compare the composition of particles of the soils of the experimental plots with that of the soils of artificial reforestation areas in northern Finland, the proportion of fine size particles (≦ 0.2 mm.) in the surface layer may be used as a criterion:

	Class of soil particle size ≦ 0.2 mm.
Norway spruce planting sites, on an average[1]	40 %
Natural regeneration of Norway spruce, » [1]	46 %
Scots pine planting sites, » [2]	61 %
Natural regeneration of Scots pine, » [2]	46 %
Kivalo experimental area, »	63 %
Vaalolehto experimental area, »	60 %

On the basis of the above it can be stated that with regard to the proportion of fine size particles in the soil, Kivalo and Vaalolehto experimental areas closely resemble the areas which, on an average, are used in Lapland for planting Scots pine. In the areas chosen for natural regeneration of Scots pine and Norway spruce, the soil is generally of coarser grain.

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[1]) Mutka 1974

[2]) Lähde and Siltanen 1972

Measurement of soil temperature

Measurement periods. Table 3 presents the measurement periods in Kivalo and Vaalolehto experimental areas in 1970—1973. In both areas, trial measurements were made during the first summer (in Kivalo, in 1970 and in Vaalolehto, in 1971) in order to improve the method. Later, measurements were started before there were any signs of thaw in the soil and they were continued till the following autumn when the soil froze again and was permanently covered by snow. This is why the measurement periods slightly vary in length in the different years. However, it can be established that the measurements covered, at least, the entire period of time when the soil was unfrozen.

Measuring equipment. Most of the soil temperature measurements were made using thermocouples. In ecological research this method has long been used and in Finland, too, a great deal of experience of thermocouples has been accumulated (e.g. KERÄNEN 1920, VAARTAJA 1949).

The thermocouple cables used in this investigation consisted of plastic coated copper and constantan wires of the Concord 1W. 2P4. type. The measuring device used was a temperature calibrated manual potentiometer, made by Rubicon Instruments Inc., model No. 2715 B, accuracy 15 μv in 23° C. In practice, the accuracy of measurement varied between 0.5 and 1.0° C, depending on temperature etc.

The thermocouple sensors were constructed by uniting 2 cm. long portions of the copper and constantan wires, with silver solder. However, a sensor of this type proved too small and, therefore, in 1972 all the sensors in both experimental areas were provided with 5 cm. long brass cylinders with a diameter of 7 mm. They were filled with bee wax and tightly sealed with contractive plastic. The sharp-pointed thermocouple sensors were inserted into the soil through the wall of a small hole dug at the desired level beside the measurement point. The cable was led 50 cm. through the soil and was, on top of the ground, anchored to a stick fixed firmly in the ground. After this, the cable was led along the ground surface to the place where the actual measuring took place.

In Kivalo, the measuring was carried out in a fiberglass field shed that could be heated, and in Vaalolehto, a wooden barrack building housing 8 people was used for this purpose. In both places the measurements were made in the same way. The temperature of each sensor was measured in turn with the potentiometer and a record was made of the reading. Since 1972, a 50-point selector switch, model SP2/P/MB, made by Croydon Precision Instruments, was used for switching the sensor channels. The potentiometer was read with the aid of a magnifying glass.

Depth of measurement. During the last few decades, in measuring forest soil temperature, depths of 5, 10, 20, 50, and 100 cm. below the ground surface have generally been used as standard depths in accordance with the recommendation of the World Meteorological Organization. When a bare and even surface, free of humus, is involved, as generally is the case in meteorological investigations, no ambiguity is likely to arise. However, when there is an uneven vegetation cover or an uneven layer of organic matter on the ground, this must be taken into consideration in one way or another. In determining the base level for measurements, one of the following three alternatives may be considered (cf., e.g., FRANSSILA 1960):

1. The boundary between the humus layer and the mineral soil is often regarded as the base level (zero level), because this line is mostly clear-cut, stationary and practically unambiguous.

2. In studies of the energy balance of the earth's surface, the only justifiable base level is the active surface (cf., for instance, KULMALA 1970 and LAITINEN 1970). However, in practice this approach often leads to difficulties, for in forests the moss and dwarf shrub layer is so uneven that the base level may turn out to be a three-dimensional layer.

3. Since vigorous growth of trees and seedlings is often the ultimate goal of forest research workers investigating soil temperature, an appropriate alternative is to use as base level that layer of the soil where the main part of the root system of seedlings and mature trees is located. Choice of the base level would then depend on the geographical location of the experimental area. The tree species involved and the age of the stand should also be considered (cf., for instance, KALELA 1955, PAAVILAINEN 1966, LÄHDE and SILTANEN 1973).

In this investigation, the active surface (alternative 2) was mainly used as the base level (zero level) for the measurement of soil temperature. In areas where the soil had been treated the surface of the revealed mineral soil was used as the base level, and in areas covered by humus, the boundary line between the humus and moss layers, i.e. where there was no more living moss, was used as the base level. The temperature extremes generally occur in the moss layer covering the forest soil, so, in that respect, too, this layer corresponds most closely to the concept of active surface (cf., e.g., BJOR 1972). Since, in Lapland, the major portion of the central root system of planted seedlings is located at a depth of 7—15 cm. below the ground surface (LÄHDE and SILTANEN 1973, MUTKA 1974), a depth of 5 cm. below the base level was chosen as the principal depth of measurements. In Kivalo, a few additional series of measurements were established at the depths of 1, 5, 10, and 15 cm.

The number of measuring instruments required is determined according to the following method generally used in ecological research: The standard deviation of the variation of readings of measuring instruments is estimated by different preliminary experiments, and the number of measuring instruments required to achieve the accuracy of result (standard error of the mean value) prescribed is estimated on the basis of this standard deviation. Hence, it is possible to establish series of measurements the results of which do not, on an average, vary beyond the error limits agreed upon (cf., e.g., HOFFMAN 1965).

Among the publications dealing with this subject, the study made by FRANSSILA (1960) merits special attention. As examples of the data obtained, it can be mentioned that in an EMT(1 Scots pine stand in northern Sodankylä, the standard deviation of the maximum daily temperatures measured with 10 meters at the boundary between the humus layer and the mineral soil was, on an average, 2.9° C. The corresponding value for the minimum daily temperatures was 0.50° C. In an open *Sphagnum*-moss area, at a depth of 10 cm. below the ground surface, the corresponding standard deviations were 1.81° C and 0.84° C respectively. In a similar study conducted at a drained swamp in southern Finland the variation was even greater (HEIKURAINEN and SEPPÄLÄ 1969).

In order to get an idea of the number of thermocouple sensors required to obtain reasonably accurate results, statistical values were calculated for the annual temperature sums of untreated soil in Vaalolehto experimental area in 1972—1973 (cf. Table 4). The mean value of the annual temperature sums measured by seven thermocouple sensors was 605 thermal units, the standard deviation was 73.7 units and the standard error 27.7 units. Thus, the range of variation of the mean value was 605 $\pm$ 54.3 (= 9 %) units.

However, if the aim were to obtain data on the annual thermal conditions in the soil, with a reliability of 95 % (the range of variation of the mean value 605 $\pm$ 30.2 units) the number of thermocouple sensors required would rise to 23.

Time of measurement. Broadly speaking, it has been evident ever since the early phases of microclimatic research that the results of measurements concerned with the thermal conditions of soil depend on the time of measurement (cf., e.g., HOMÉN 1897). As is well

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1) *Empetrum-Myrtillus* type according to the Cajanderian forest site type classification.

known, annual and daily variations in the thermal conditions are much more regular in the ground than in the air.

A so-called lag-effect characterizes this variation and the deeper in the ground the measurements take place the more pronounced is this effect (GEIGER 1965). For instance, if the soil temperature is measured regularly at different depths, at certain times of day, the readings will fall on different points in the sinus curve that illustrates the variations in the daily temperatures, and on account of this it is very difficult to make conclusions. In spite of this, numerous formulae for the calculation of the mean temperature of the soil have been presented (KERÄNEN 1920, PESSI 1956). However, it is necessary to apply to them correction coefficients that change gradually along with the season, and comparison of soils differing in temperature (e.g., prepared and unprepared soils) necessitates fairly complicated transformations and preparatory experimental studies.

In this investigation, a day (24 hours) was used as a base temporal period during which the soil temperature was measured regularly at every other (even) hour. In Kivalo, the measurements were carried out on Mondays, Wednesdays and Fridays, and in Vaalolehto, every day during a 5-day work week.

Calculation of temperature sums

Temperature conditions in the soil can be described by several parameters of which the daily or monthly temperature extremes and mean values are best known (cf., e.g., GEIGER 1965). When the foremost aim is to make comparisons between the conditions under which the root systems of trees function during the growing season, it is beneficial to combine the above two factors into one temperature/time index that describes the joint effect of the temperature prevailing and the period of time involved. The methods of calculation of temperature sums developed at different times perhaps provide the best and most frequently used solution in this respect (cf., e.g., SCHNELLE 1955, WENT 1957, SARVAS 1972, regarding the use of temperature sums in ecological and physiological research).

Description of the temperature conditions of the soil during the growing season by means of temperature sums is on the one hand less difficult and on the other considerably more difficult than the description of temperature conditions of the air. The greatest difficulty met with in attempts to create a firm silvicultural basis for this description is a deficient knowledge of the degree of correlation between the function of the root system and the environmental temperature, and the uncertainty about the nature of periodicity in the growth of the root system (cf., e.g., LADEFOGED 1939, LYR and HOFFMANN 1967, KOZLOWSKI 1971, ORLOV and KOSELKOV 1971).

When a biological phenomenon is investigated it would be best if in the calculation of temperature sums the threshold value to be employed were as near as possible the temperature at which the activity of the phenomenon involved is at its observable minimum (at a so-called minimum cardinal point). In the literature, +2 - +3° C - +5 - +6° C have most frequently been stated as the minimum temperatures for the root systems of trees to function. However, it must be noted that determinations concerning the growth rate of roots are largely based on measurements made in a controlled environment during a short time. In the field, the situation is always very complex from the ecological stand point, depending in most cases simultaneously on all the environmental factors (moisture, aeration, nutrition, and so forth) (cf., e.g., SHAW 1952, RÖHRIG 1966, LÄHDE and SILTANEN 1973). No reliable data are available as yet on the minimum temperatures prevailing in northern Finland during the time of root growth in our leading tree species and, therefore, on

the basis of data contained in the literature (cf., e.g., LEIKOLA 1969) + 5° C was chosen as threshold value in the present study.

Generally, in the calculation of temperature sums the threshold value agreed upon is deducted from the mean temperature of the time unit chosen and the mean temperatures obtained in this way are summed up. In the present study, the degree hour (d.h.) principle was employed in the calculation of temperature sums. Moreover, the hourly temperature sum arrived at in this way was divided by 24 to obtain a value that is of approximately the same order of magnitude as the 24-hour (d.d.) temperature sum but from which the error of compensation found in the latter, particularly in spring and autumn, has been eliminated (cf., e.g., Sarvas 1966).

Representativeness of the years of measurement

Measurement of soil temperature was started on a trial basis in Kivalo in 1970 and in Vaalolehto in 1971. Since in the former locality, temperature has been observed for only four years and in the latter for only three years, it is questionable whether the period of time involved is representative enough for the measuring results to be generally applicable. In Lapland, the climatic conditions vary very much from year to year, and the biological significance of the years that are favourable from the point of view of thermal conditions becomes increasingly accentuated as one moves further north (cf., e.g., MIKOLA 1950).

Fig. 4 presents the annual temperature sums (d.d.) for the observational years, calculated at the Forest Research Institute on the basis of the daily mean temperatures measured at the Sodankylä meteorological station (67° 22 N, 26° 39 E, 179 m a.s.l.) (JOKIOISTEN ja ... 1970, 1971, KUUKAUSIKATSAUS ... 1972, 1973). The mean temperature value for the years 1908—1972, given as a comparative value, has also been calculated at the Forest Research Institute on the basis of the daily mean temperatures published by the Finnish Meteorological Institute.

As to the temperature conditions of the observational years, Fig. 5 shows that the summer of 1970, the trial year, was entirely warmer than average. In 1971, which was the first regular observational year, the beginning of the summer was slightly warmer than average, whereas the middle and the latter part of the summer were distinctly colder than average. The second observational year, 1972, was in turn clearly warmer than average during the entire growing season. Particularly, the midpart of the summer was very warm. Moreover, the summer of the third observational year, 1973, was in its entirety clearly warmer than average.

Results

Temperature conditions in unprepared soil

In the Kivalo experimental area the thermocouple sensors were placed in two unprepared plots as follows: One sensor was placed under a rather small pile of logging residue, two sensors were placed under a dense blueberry shrubbery, two in a spot occupied by an open blueberry shrubbery and *Hylocomium*, and two in a spot that was 2 m² in size, free from the shrub layer of the surface vegetation and was covered by *Dicranum sp.* Moreover, three sensors were placed in untreated spots of tilled and ploughed plots. The experimental area in Vaalolehto was covered by an even *Polytrichum sp.* layer about 5—12 cm deep. In three plots, a total of seven sensors were placed in this layer. The aim was to locate the sensors at random, even if preference was given to so-called typical spots.

Table 4 presents the annual mean temperature sums pertaining to the soil in the Kivalo and Vaalolehto experimental areas. As can be seen, in Kivalo the pattern of soil temperature conditions is clear-cut, depending on the vegetal cover of the ground. On an average, it was coldest under the pile of logging residue; under the dense blueberry shrubbery it was somewhat warmer, and under the open blueberry shrubbery warmer yet and warmest in the spot where the shrub layer of the vegetative cover was missing altogether and the ground was covered by *Dicranum sp.* The table also presents the temperature sums of the air for the corresponding years. It is seen that even at the depth of 5 cm. the soil covered by humus was considerably colder than the air, and under the logging residue and the dense blueberry shrubbery the temperature sum of the surface layer of the soil did not amount to more than 2/3 of the temperature sum of the air.

Fig. 6 shows the monthly development of temperature sums pertaining to the soil in Kivalo in 1971 and 1973. The former year represents a cooler-than-average year and the latter a warmer-than-average year. It is clearly perceivable that during the growing season the temperature of the surface layer of the soil lagged behind the air temperature; in May, the temperature sum of the air was up to 3—4 times as large as that of the soil. Particularly, in the early part of the summer of 1973 the temperature sum pattern was clear-cut. It was coldest under the pile of logging residue and then followed the measurement points dense blueberry shrubbery, open blueberry shrubbery, *Dicranum sp.* and, lastly, the air, the temperature sum of which was the largest. During the latter part of the summer the temperature sum pertaining to the surface layer of the soil was about the same as that of the air. In September the soil proved to be a warmer measurement point than the air.

In Vaalolehto the pattern of development of temperature sums is seen to be similar (Fig. 7).

The effect of treatment on temperature conditions in the soil

Scalping. In Kivalo and Vaalolehto experimental areas the temperature conditions in the surface layer of the soil were observed in three plots scalped manually, mechanically and by a flame thrower respectively (cf. ETHOLÉN 1970). In the Vaalolehto experimental area, the sensors were placed in machine scalps representing two different size classes.

Table 5 gives the annual temperature sums of the surface layer of the soil, measured in the middle of the scalps in 1971—1973. In Kivalo, the scalp was warmer than the air, but this observation is based on the readings of a single sensor only. In Vaalolehto, the data on the temperature conditions in the scalps are more numerous. The temperature sum of the large machine scalp proved the largest, the next in magnitude was that of the small machine scalp and the smallest was the temperature sum of the burnt scalp. On an average, the scalps proved distinctly warmer than the corresponding untreated sites.

Fig. 7 shows the monthly development of the temperature sums of the scalps in 1973. The soil scalped by burning was clearly the coldest throughout the growing season, and next came the small machine scalped plot followed by the large machine scalped plot. The temperature sum of the air was the largest.

Reforestation ploughing. Reforestation ploughs cut furrows abt. 25 cm. deep, with shoulders abt. 60 cm. wide on both sides. Tilts abt. 45 cm. high are formed at the outer edges of the shoulders. The dimensions and shape of the tilts depend not only on the plough and drawing machine employed but also on the quality of the soil, stoniness and the quantity of stubs, logging residue, and ground vegetation. It should also be noted that the tilts settle and the furrows become somewhat levelled with time.

Table 6 shows the annual mean temperature sums of the different parts of the ploughing trace in the Kivalo and Vaalolehto experimental areas in 1970—1973. In Kivalo, the furrow was clearly coldest at the bottom being even colder than the air. The shoulders and the tilts were distinctly warmer. There was not much difference between the temperature sums of the shoulders of the east and west sides, but the west shoulder of the east side tilt, which is the most exposed to the afternoon sun, was somewhat warmer than the east shoulder of the west side tilt which the afternoon sun does not hit.

It is characteristic of the monthly temperature sums of the different parts of the ploughing trace shown in Fig. 8 that there is but little difference between them. Only the temperature sum of the tilt on the sunny side is distinctly larger than the others every month. It is seen that generally the differences between the temperature sums of the various parts of the ploughing trace are greater during the early part of the summer and that towards the end of the summer these differences gradually become evened out. The magnitude of the temperature sums of the tilts and shoulders in August and September should be noted. In fact, in Vaalolehto the southern shoulder of the furrow was the warmest in August and September, even though the temperature sum of the tilt was clearly the largest, if the whole growing season is taken into account.

When the temperature conditions in the ploughing tilt are discussed, it is often pointed out that in the spring the tilt is freed from the snow cover earlier than the shoulders and the untreated even ground, and remains bare longer in the autumn. However, this circumstance does not appreciably affect the monthly temperature sums. The temperature sums for May, when the snow melts, and for September, when the snow cover irregularly forms, are rather similar in the different parts of the ploughing trace and are, all in all, so small that the differences between the temperature sums of the different measurement points, accumulated in midsummer, i.e. in June and July, cover them easily.

Table 7 shows monthly temperature sums calculated on the basis of measurements at four different depths in Kivalo in 1971. The great difference in the temperature conditions between the untreated ground covered by humus and ground vegetation and the shoulder of the ploughing trace is brought out when the development of the temperature sums at the different depths are compared with one another. At the surface of the untreated ground it is warmer than at the surface of the shoulder of the ploughing trace but a little deeper in the shoulder the temperature is distinctly higher. In late summer, the temperature conditions at the different measurement points are rather similar. An interesting feature is a so-called vertical temperature inversion that can be observed particularly in the unprepared soil in autumn. In September and October, the temperature sum is still largest at a depth of 20 cm; at a depth of 10 cm. the figure is smaller, but close to the surface of the ground (at depths of 5 cm. and 1 cm.) it is again, as a result of direct radiation of the sun, a little larger than at the depth of 10 cm.

Disk ploughing. The effect of disk ploughing on the temperature conditions of the soil was observed in Kivalo only. The objects of measurement were the tracks left by a TTS reforestation harrow (disk plough) and a Ylö disk reforestation plough (Table 8). The temperature conditions of the different parts of these tracks greatly resemble those of the tracks left by ordinary reforestation ploughs, but the differences between the temperature sums measured at the ridge of the tilts and at the bottom of the furrows are much smaller. It is to be noted that the temperature sum measured at the bottom of the furrow cut by the disk plough is fairly large. Thus, the temperature measured at the bottom of the furrow cut by the disk plough — the space where seedlings generally are planted — is approximately the same as in a scalp but is, of course, higher than the temperature at the bottom of a furrow cut by an ordinary reforestation plough. Measurements made at experimental plots ploughed crosswise support the general conclusion stated above: The temperature sum

of bared unprepared soil measured at the depth of 5 cm. is roughly the same or slightly larger than the temperature sum of the air used as a criterion, and the temperature sum of the tilt is about 20 % larger than that of the air. In examining the monthly temperature sums presented in Fig. 9, it is seen that the developmental pattern of temperature sums presented in connection with the ordinary reforestation ploughing is repeated here. The temperature sum of the tilt, which is fairly large as compared with those of the other parts of the ploughing trace, has accumulated almost exclusively in midsummer. On the other hand, the temperature sums measured at the bottom of the furrow are the largest, particularly in late summer. In the experimental plots ploughed crosswise the temperature conditions in the tilt are favourable throughout the summer (Fig. 10).

Rotary tilling. In Kivalo, the annual temperature sums for 1971—1973 pertaining to the track left by a drum rotary tiller are shown in the upper section of Table 9. According to these figures, the track of rotary tilling is, on an average, slightly colder than the air but is distinctly warmer than a corresponding unprepared site (Table 4). The difference is of about the same magnitude in warm and cold years.

In Vaalolehto (Table 9, lower section), temperature was measured at the ridge and both sides of the tilt of the track left by a KLM chain rotary tiller. The tilt now, too, proved the warmest. The temperature sum of the tilt was larger than that of the air used as a criterion and was of the same order of magnitude as the temperature sum of the tilt of light reforestation ploughing (Table 7). The temperature sums of both sides of the tilt of the tilling track were distinctly smaller and there was no appreciable difference between them. This was probably due to the tilt being low and the angles of the sides slightly inclined.

On comparison of the monthly temperature sums of the soil tilled with a TTS drum rotary tiller, with the monthly temperature sums of the air (Fig. 11), the tilling track was found to be colder than the air, in spring and early summer, but warmer than the air, in late summer. This phenomenon is similar to that explained in the foregoing, e.g., in connection with reforestation ploughing (Fig. 12).

Other kinds of soil experiment. In Vaalolehto two kinds of soil transfer experiments were carried out and in connection with them measurements were made concerning soil temperature. In one experimental plot the vegetation and surface layer were removed to a depth of about 30 cm. and they were replaced with an even layer of sandy moraine transferred from another location; in the other experimental plot the humus layer was covered with a layer of sandy moraine, 10 cm. deep, which, too, had been transferred from another location (cf. Fig. 3).

The annual temperature sums of the two experimental plots are of almost the same magnitude (Table 10), which suggests that there is a close correlation between the thermal conditions of the experimental plots and the thermal and radial conditions of the air. The annual temperature sums are about 25 % larger than those of the air and they are of the same magnitude as the temperature sums of the ploughing tilt (Table 7). For the sake of comparison it can be mentioned that in 1958—1960 according to the measurements made by the Sodankylä Meteorological Station, the annual temperature sums of bare sandy soil at a depth of 5 cm. were, on an average, 30 % larger than the corresponding temperature sums of the air in the same location (Results . . . 1969).

In the spring, sandy soil with no humus layer or ground vegetation warms up faster than the air, and the monthly temperature sums of the soil are regularly larger than those of the air (Fig. 13). Measurements made at the Sodankylä Meteorological Station showed, too, that the monthly temperature sums of the surface layer of the soil were regularly higher than the corresponding temperature sums of the air. In June the difference was as large as 45 %.

Discussion

The present study clearly showed that soil preparation affects the temperature conditions of the surface layer of the soil. All the different soil preparation methods brought about an increase in the temperature sum. However, the increase varied greatly in magnitude depending on the method of preparation. Below, the mean values of the annual temperature sums measured in Kivalo and Vaalolehto in 1971—1973 are shown as relative values. For the purpose of comparison, the annual temperature sums of unprepared soil in both experimental areas are given as one hundred.

Site preparation	Kivalo	Vaalolehto
Unprepared soil	100	100
Scalping by hand or machine	137	128
Scalp burning	—	107
Reforestation ploughing, tilt	160	162
» » shoulder	146	151
Disk ploughing, tilt	133	—
Track of drum rotarytiller	130	—
Track of chain rotary tiller	—	168
Soil transfer, on an average	—	172
Air	130	137

In Finland, the temperature of prepared soil practically never rises so high as to be detrimental to planted seedlings, but, on the other hand, it must be emphasized that seeds and succulent germlings are very susceptible to blazing sun shine and to top temperatures which occur during sunny periods even in Lapland (cf., e.g., VAARTAJA 1954). Increase in the temperature of prepared soil can, however, have an indirect detrimental effect in that the soil may dry out as a result of it. Results of recent sowing and planting experiments (cf., e.g., POHTILA 1972, 1974, and ETHOLÉN 1974) clearly show that even in northern Finland, particularly during the exceptionally warm and dry summers of the last four years (1970—1973), for instance, the ploughing tilts have dried to a harmful degree.

Observations concerned with the development of the root system of seedlings planted in unprepared soil and in plots prepared in different ways have shown that, in general, soil treatment promotes the growth of the root system. This has manifested itself in the extension growth, dry weight, and in the root/shoot ratio, i.e., the proportion of the root has also increased (c.f., e.g., SÖDERSTRÖM 1959, RÖHRIG 1966, HEINSDORF and SCHULZKE 1969).

The relevant investigative data available concerning northern Finland are based on occasional observations and scanty experiments but, nevertheless, it can be said that the thermal conditions in the soil resulting from site preparation are favourable to the growth of roots of seedlings (VALTANEN 1973, TURTIAINEN and VALTANEN 1974, SOLISMAA 1973, MUTKA 1974). It is well to emphasize here that the root systems of seedlings planted in efficiently prepared soil appear to be in a superior physiological condition, which in turn will help the seedlings to overcome the consequences of root deformations resulting from unsuccessful transplantation or planting, or from an improper containek around the roots (cf., e.g., HUURI 1972, LÄHDE and SILTANEN 1973, BERGMAN and HÄGGSTRÖM 1973).

However, it is not easy to form an exact opinion of the importance of soil temperature as an ecological factor contributory to successful regeneration of forests. As was established above, in northern Finland, an increase in soil temperature can without doubt be regarded as having a favourable effect on seedling development, provided that none of the other developmental factors seriously interfere with this process. However, this condition is not always met and, therefore, in considering the merits of site preparation one should take all the different growth factors into account.

THE EFFECT OF GRAIN SIZE DISTRIBUTION ON THE CONDITION OF NATURAL AND ARTIFICIAL SAPLING STANDS OF SCOTS PINE

ERKKI LÄHDE

Suomenkielinen selostus:

MAAN LAJITEKOOSTUMUKSEN VAIKUTUS MÄNNYN LUONTAISTEN JA VILJELYTAIMISTOJEN KUNTOON

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ABSTRACT

L ä h d e, E r k k i. The effect of grain size distribution on the condition of natural and artificial sapling stands of Scots pine. Suomenkielinen selostus: Maan lajitekoostumuksen vaikutus männyn luontaisten ja viljelytaimistojen kuntoon. (For. Res. Inst., Rovaniemi, Finland). Comm. Inst. For. Fenn. 84.3. 1974.

The study was conducted over 95 regeneration sites in North-Finland, these regenerations differing from one another in the mode of origin and general condition. Natural stands were observed to be located on soils with a lower content of the fine particle-size classes in comparison to artificially established plantations. Sound regenerations established by artificial seeding were located on soils with higher contents of the fine particle-size classes in comparison to those established by planting. In stands exceeding 70 cm in height and of varying condition, a significant difference in the fine particle-size class content of the soil was noted; in stands regarded as failures, very fine sand and finer classes (≤ 0.06 mm) and silt and finer classes (≤ 0.02 mm) occurred in amounts 2—3 times those of sound stands. No failures among natural stands were found.

FOREWORD

The study is part of a project being conducted in North-Finland dealing with the environmental aspect in the development of pine seedlings. The realization of the work was to a major extent made possible by funds received from the firm of Veitsiluoto Osakeyhtiö in 1971. On the behalf of the research station, I wish to express our gratitude. A directive issued by the National Board of Forestry regarding site preparation on mineral soils is based in part on the results of the study.

Amongst others, S e p p o S i l t a n e n, B. Sc. (For.), and T a p a n i P o h j o l a, for. tech. assisted in the gathering of the material. Similarly, numerous members of the staff at the research station contributed towards the realization of the work. In addition, valuable help has been afforded to me by the Perä-Pohjola regional forestry board in the field stage of the work. A h t i N i i n i m a a, B. Sc., has been responsible for the computer processing of the data and E r k k i P e k k i n e n, for.stud., has translated the original text into English. Professors O l a v i H u i k a r i, Y r j ö V u o k i l a and K i m v. W e i s s e n b e r g, Ph.D. have read the manuscript.

My sincere thanks to the afore mentioned persons and to others who have assisted along the way.

Rovaniemi, March 1974.

Erkki Lähde

CONTENTS

	Page
Abstract	3
Foreword	4
1. Introduction	7
2. Research procedure	9
3. Results and discussion	11
4. Summary	18
5. Suomenkielinen selostus	20
6. References	22

1. INTRODUCTION

The structure and particle-size class distribution of a soil are closely linked to both the chemical and physical properties of the soil, and thus have bearing on microbial activity. In site quality classification systems, then, not only soil structure, but also the particle-size class distribution of the soil should be kept in mind (Haig 1929, Coile 1952, Mader & Owen 1961, Holstener-Jørgensen 1967). Subjected to different climatic conditions, soils, which may be the equivalent of one another in terms of structure and particle-size class distribution, can be quite contrasting as habitats for trees. In the case of Finland, to take an example, the climate becomes increasingly humid in the SW—NE direction (Aaltonen 1933). The region north of Saariselkä is an exception, the climate becoming somewhat less humid. Owing to the cold and humid climate of North-Finland, the soil, rich in the fine particle-size classes and thus poorly permeable to water, is oxygen-poor due to excess water (Lähde 1973). The situation is similar in the NW-corner of the Soviet Union; considerable expanses of forest land are water-logged and thus underproductive (Vereteннikov 1964). In a humid climate, such as in Finland, with a flat topography and a soil rich in the fine particle-size classes, the end result is that, as the volume of water builds up and the slowly decomposing humus layer thickens, paludification begins. According to Koposov (1970), a slope of less than 1 : 1 000 in the region of Leningrad, where the soils are plentifully supplied with the fine particle-size classes, hinders runoff considerably and causes paludification. When the slope of the land exceeds 1 : 300, however, paludification does not occur. In a humid climate clear-cutting has the effect of raising the groundwater table (Aaltonen 1948, Pyatetski 1959, Holstener-Jørgensen 1961). If regeneration following clear-cutting is satisfactory, the paludification process comes to an end within 25—28 years in the case of spruce forest of the *Myrtillus*-type, whereas 65—70 years are required in the case of a thick-moss *(Hylocomium-Myrtillus-)* type (Pyatetski 1959).

The vegetation cover on gently sloping fine soils has an added effect on the paludification process following clear-cutting; an example of such is a layer of *Polytrichum*-moss, which hinders the passage of air. In over-mature spruce stands, often growing in such habitats, the vitality and transpiration

capacity of the stands suffer and soil conditions for the satisfactory functioning of roots deteriorate.

In coarse grained, permeable sandy soils, dominated by pine, excess water or lack of oxygen does not come into question even in a humid climate. Neither is there a shortage of water in the root layer, whereas such a shortage may well be the case in less humid climates. In general, it may said that fine grained soils in their virgin state provide in the climatic conditions of South-Finland habitats superior to what they would in North-Finland; conversely, coarse grained soils are relatively more productive in North-Finland than in the south. What is important is to determine the extent to which the production of forests on the fine grained soils of North-Finland may be added to by drainage and site treatment. Be as it may, if the objective is to boost timber production on such sites, then measures are needed to counteract the negative influence of a humid climate and fine grained soils. Such measures include various site preparation methods, shallow ditching, and actual draining of the site to lead away excess water.

A model on which to develop site preparation methods when dealing with such difficult soils, is to be seen displayed by Nature herself; natural seedlings tend to favour mounds/rises as habitats. (Lyford & Mac Lean 1966, Eichrodt 1969). This has also made itself evident in numerous artificial regeneration experiments (Serov 1952, Koshshejev & Lavrov 1953, Preobrazhenski 1955, Stratonovitsh 1958, 1966, Armson 1958, Wilde & Voigt 1959, MacArthur 1964, MacLeod 1964, Provorova 1964, Kulikov 1965, Suvorov 1969, Varfolomeyev *et al.* 1969, Bezdenezhenkh 1970, Kurayev & Shestakova 1970, Pohtila 1970).

According to Lähde and Siltanen (1973), the proportion of the finer, poorly permeable particle-size classes in North-Finland was clearly greater in the locality of dead pine saplings exceeding 100 cm in height than was the case with those as yet alive.

From the point of view of practical forestry, it would be important indeed to know the limits which would reflect in the chosen method of site preparation. In this way, in the application of methods, unnecessarily severe measures would be avoided. Planting of pine, for example, into scarified spots on sites where failure would be inevitable within a few years could likewise be circumvented.

The purpose of the study is to shed more light on the afore mentioned matter by attempting to explain the interdependence between an important soil characteristic, the particle-size class distribution, and the condition of overlying pine stands. To this end, the content of the finer particle-size classes in the soils of sapling stands was compared; the stands differed from one another in height, mode of origin, and in condition.

2. RESEARCH PROCEDURE

The material for the study was gathered during 1971 and 1972. In selecting the regenerations for the study, use was made of the information available from previous studies (Etholén 1972, Lähde & Siltanen 1973), which was supplemented to. As the aim was to compare the condition and the particle-size class distribution of the soil of stands differing in height and in mode of origin, certain conditions were set. Firstly, the objective was to find sapling stands of each mode of origin (natural, artificially seeded and planted). The height classes were the following: < 50, 51—70, 71—100, 101—200, and > 200 cm.

With regard to condition, the division was made between good, poor, and dead. Failures among natural regenerations were not to be found. The region under study delimited by N 66°—68°. The sapling stands were first visually appraised regarding condition. The result was tested by having in each case a sample plot from which height and condition recordings were made, mode of origin was determined, and soil samples were taken.

In the case of stands of only a few hectares in size, the sample plots were located by taking the centre of the stand (visually determined) to serve also as the centre of the sample plot. With stands covering large areas, the sample plots were placed by proceeding for approximately 100 m towards the centre of the stand. Three points (at 10, 20 and 30 m from the centre of the plot) were marked out along each of the four axes of the compass. The saplings nearest to these points were examined more closely; i.e. twelve saplings from each plot. In the case of artificially seeded stands, the dominant individual in each seed-spot was examined. A stand was classified as being in »good» condition, if at least 10 of the sample saplings were in a good condition; »dead» condition meant that at least 3 of the sample saplings were dead and less than a half were in good condition. Only in a few cases was it necessary to make an alteration in the result given by the visual appraisal, the difference then being between »poor» and »good» condition. In height measurement, the growth up to and including 1971 was recorded.

A total of 95 sapling stands were examined. The distribution of these stands in the classification system is shown in Table 1.

Table 1. The number of stands studied; grouped according to height, mode of origin and condition

Taulukko 1. Koetaimistojen lukumäärä taimiston pituuden, syntytavan ja kunnon mukaan ryhmiteltynä

Height of the plantation, cm *Taimiston pituus, cm*	Mode of origin — *Syntytapa*				Class of Condition — *Kuntoluokka*			
	Natural *Luont.*	Artific. seeded *Kylvö*	Planted *Istutus*	Total *Yhteensä*	Dead *Tuhout.*	Poor *Huonok.*	Good *Hyväk.*	Total *Yhteensä*
< 50	5	7	7	19	1	4	14	19
50— 70	5	8	11	24	8	12	4	24
70—100	4	6	7	17	5	8	4	17
100—200	5	5	8	18	5	7	6	18
> 200	6	5	6	17	1	6	10	17
Total — *Yhteensä*	25	31	39	95	20	37	38	95

Soil samples were taken from five points on the sample plot; from the centre of the plot, and from points at 20 m from the centre, along the four axes of the compass. The samples were from the 0—10 cm and 10—20 cm layers. Each sample was approximately 2/3 litre in volume. The particle-size class distribution was determined (by the firm of Viljavuuspalvelu Oy) using the sedimentation method developed by E l o n e n (1971). By setting apart at the calculation stage of the data those saplings in the vicinity of which soil samples were taken, it was possible to determine the amount of the fine particle-size classes present at the habitat of individual saplings and thus to make comparisons between saplings. In order to facilitate analysis of variance, the values expressed as percentages were converted to arc. sin-values.

The intention at the outset of the study had been to deal also with the provenance of the seed used in the artificial regenerations; this, however, was not possible, since for most of the stands reliable information regarding the provenance of the seed was unavailable. It would seem that for most of the stands the seed used originated from regions to the south of the regeneration sites. Considerable difficulties were met in reliably determining the mode of origin and the time of regeneration for the artificially reproduced stands. This was particularly the case with the »dead» stands group; re-seedings or re-plantings to fill gaps were common and in certain cases regeneration as a whole had been renewed several times. As a rule neither of these measures had led to satisfactory results.

3. RESULTS AND DISCUSSION

The proportion of fine sand and of finer particle-size classes in the soil varied between 17—93 %. Disregarding sapling stands in the 51—70 cm height class, the proportion of the fine particle-size classes in the top 10 cm layer of soils of natural stands was generally less than what it was in seeded or planted stands (Table 2). In natural stands of the 51—70 cm class, the proportion of very fine sand and finer classes (i.e. < 0.06 mm), and of silt and finer classes (i.e. < 0.02 mm) was, however, distinctly less than in artificially established stands. Taking the stands as a whole, the difference in the proportion of the fine particle-size classes in the soil of natural and of artificially established stands was significant; the finer the class in question, then so much more significant was the difference. For stands differing in the mode of origin, in comparing the height classes, the differences were significant only in the 100—200 cm class in the proportions of very fine sand and finer classes (i.e. < 0.06 mm) and of silt and finer classes (i.e. < 0.02 mm). The differences were also notable for stands of > 200 cm in height, but were not significant due to the limited nature of the material, and to the wide dispersal among the artificially established stands. The results for the 10—20 cm layer were very similar (Table 3). The differences between the layers were not significant, but as a rule the proportion of the fine particle-size classes in the 10—20 cm layer was slightly less than in the 0—10 cm layer.

The classifying of the stands according to condition made it evident that for the stands less than 70 cm in height the differences were not significant between stands of varying condition. The general trend, however, was the same for the particle-size classes and for both of the soil layers concerned (Tables 2 and 3). Excluding a couple of exceptions, the proportion of the fine particle-size classes in the soils of stands in good condition was less than in those classified as being in poor or dead condition. These exceptions occurred only among stands less than 50 cm in height, between the »good» and »poor» condition classes.

However, in none of the cases among the stands less than 70 cm in height were the differences significant. In the 71—100 cm class, on the

Table 2. The proportion (weight-%) ($\bar{x} \pm s_{\bar{x}}$) of fine particle-size classes in the 0—10 cm layer of sapling stands of various heights, grouped according to mode of origin and condition

Taulukko 2. Maan hienojen lajitteiden osuus (paino-%) ($\bar{x} \pm s_{\bar{x}}$) lajitekoostumuksesta 0—10 cm:n kerroksessa syntytavan ja kuntoluokan mukaan ryhmitellyissä eripituisissa taimistoissa

Height of stand, cm *Taimiston pituus, cm*	Mode of origin — *Syntytapa*				$\bar{X}$	Class of condition — *Kuntoluokka*			
	Natural *Luont.*	Artific. seeded *Kylvö*	Planted *Istutus*	F		Dead *Tuhoutun.*	Poor *Huonok.*	Good *Hyväk.*	F
	Fine sand and finer — (≤ 0.2 mm) — *Hieta ja hienommat*								
< 50	43.8 ± 5.1	67.0 ± 9.3	71.1 ± 6.9	2.85	62.4 ± 2.2	93.0	67.1 ± 11.8	58.9 ± 5.6	1.57
50— 70	61.4 ± 11.4	61.0 ± 3.3	58.2 ± 4.6	0.18	59.8 ± 3.2	60.0 ± 3.2	63.2 ± 5.1	49.2 ± 8.9	1.22
70—100	44.7 ± 9.1	59.0 ± 4.3	48.3 ± 5.6	1.44	51.2 ± 3.6	59.0 ± 6.1	53.3 ± 3.5	37.4 ± 8.6	3.38
100—200	39.7 ± 9.3	64.9 ± 5.5	56.4 ± 7.8	2.14	54.1 ± 4.9	74.2 ± 5.9	50.3 ± 6.7	41.9 ± 7.8	5.31*
> 200	49.1 ± 9.9	76.9 ± 6.6	56.9 ± 14.6	1.18	60.0 ± 6.8	96.6	79.6 ± 7.3	44.7 ± 7.3	6.75*
$\bar{X}$	47.9 ± 4.1	65.2 ± 2.8	58.2 ± 3.4	4.37**	57.8 ± 2.1	66.8 ± 3.5	61.7 ± 3.1	49.2 ± 3.4	6.44***
F									
	Very fine sand and finer — (≤ 0.06 mm) — *Hieno hieta ja hienommat*								
< 50	14.0 ± 2.7	29.4 ± 5.6	31.1 ± 6.1	2.85	26.0 ± 1.5	62.2	21.5 ± 3.0	24.7 ± 3.7	3.35
50— 70	23.4 ± 4.0	31.1 ± 2.4	29.8 ± 4.6	0.77	28.9 ± 2.4	31.4 ± 3.3	30.2 ± 3.8	20.0 ± 4.7	1.66
70—100	14.5 ± 4.0	24.8 ± 3.9	23.5 ± 4.9	1.45	21.8 ± 2.7	29.9 ± 5.5	20.6 ± 2.7	14.1 ± 5.2	3.42
100—200	11.8 ± 3.2	37.3 ± 5.6	27.0 ± 6.2	4.84**	25.6 ± 3.9	47.4 ± 4.8	19.9 ± 2.9	14.2 ± 3.9	17.25***
> 200	17.2 ± 3.0	33.1 ± 14.8	29.7 ± 9.8	0.77	26.3 ± 5.5	92.2	32.8 ± 8.6	15.8 ± 2.1	16.02***
$\bar{X}$	16.3 ± 1.6	30.8 ± 2.9	28.3 ± 2.6	8.69***	26.0 ± 1.6	39.6 ± 4.1	25.7 ± 2.1	19.1 ± 1.8	15.63***
F									
	Silt and finer — (≤ 0.02 mm) — *Hiesu ja hienommat*								
< 50	6.0 ± 1.1	10.9 ± 2.0	14.2 ± 3.2	2.72	10.9 ± 0.7	22.8	9.4 ± 1.6	10.4 ± 1.9	1.59
50— 70	9.9 ± 2.2	14.1 ± 1.4	14.8 ± 2.4	1.02	13.1 ± 1.3	13.6 ± 1.3	14.2 ± 2.3	8.8 ± 1.9	1.35
70—100	7.2 ± 1.4	11.6 ± 1.8	9.4 ± 1.5	1.52	9.7 ± 1.0	12.5 ± 1.7	8.9 ± 1.1	7.5 ± 2.4	2.59
100—200	5.6 ± 1.5	17.2 ± 3.1	12.4 ± 3.0	4.33*	11.8 ± 1.9	22.7 ± 2.3	8.8 ± 1.3	6.3 ± 1.3	20.57***
> 200	7.1 ± 1.2	20.6 ± 12.5	13.9 ± 5.7	0.85	13.5 ± 4.1	70.4	14.9 ± 5.5	6.9 ± 0.8	20.68***
$\bar{X}$	7.2 ± 0.7	14.4 ± 2.1	12.8 ± 1.4	7.13***	11.9 ± 0.9	18.9 ± 3.0	11.6 ± 1.2	8.4 ± 0.8	13.26***
F					0.53				

Table 3. The proportion (weight-%) ($\bar{x} \pm s_{\bar{x}}$) of fine particle-size classes in the 10—20 cm layer of the soil in sapling stands of various heights, grouped according to mode of origin and condition

Taulukko 3. Maan hienojen lajitteiden osuus (paino-%) ($\bar{x} \pm s_{\bar{x}}$) lajitekoostumuksesta 10—20 cm:n kerroksessa pituudeltaan erikokoisissa taimistoissa syntytavan ja kuntoluokan mukaan ryhmiteltynä

Height of stand, cm *Taimiston pituus, cm*	Mode of origin — *Syntytapa*				$\bar{X}$	Class of condition — *Kuntoluokka*			
	Natural *Luont.*	Artific. seeded *Kylvö*	Planted *Istutus*	F		Dead *Tuhoutun.*	Poor *Huonok.*	Good *Hyväk.*	F
	Fine sand and finer — (≤ 0.2 mm) — *Hieta ja hienommat*								
< 50	41.9 ± 6.1	65.4 ± 8.7	67.9 ± 8.2	2.55	61.1 ± 2.5	93.8	66.7 ± 12.2	55.9 ± 5.6	2.10
50— 70	57.4 ± 12.0	55.9 ± 14.4	56.4 ± 4.4	0.09	56.4 ± 3.3	55.8 ± 3.3	59.5 ± 5.6	48.6 ± 8.4	0.73
70—100	38.0 ± 12.3	54.3 ± 5.5	41.7 ± 5.5	1.42	45.3 ± 4.2	54.5 ± 6.7	47.2 ± 5.0	29.8 ± 9.3	3.19
100—200	37.4 ± 10.4	62.8 ± 5.0	56.2 ± 8.0	2.19	52.8 ± 5.1	71.6 ± 5.5	50.8 ± 7.4	39.5 ± 8.7	4.27*
>200	41.1 ± 9.4	73.8 ± 6.2	50.3 ± 15.3	1.78	53.9 ± 7.0	95.8	75.0 ± 6.6	37.1 ± 7.4	8.24**
$\bar{X}$	43.3 ± 4.4	61.7 ± 2.9	54.8 ± 3.6	4.90**	54.0 ± 2.2	63.3 ± 3.7	58.5 ± 3.3	44.8 ± 3.6	7.00***
F									
	Very fine sand and finer — (≤ 0.06 mm) — *Hieno hieta ja hienommat*								
< 50	13.1 ± 2.9	28.1 ± 5.0	29.4 ± 6.4	2.66	21.2 ± 1.5	61.0	21.0 ± 4.8	23.0 ± 3.4	3.45
50— 70	21.5 ± 4.1	28.2 ± 2.8	30.0 ± 4.3	0.98	27.6 ± 2.4	29.5 ± 3.1	29.1 ± 4.0	19.5 ± 3.9	1.35
70—100	11.2 ± 4.6	23.9 ± 3.8	19.6 ± 3.6	2.64	19.2 ± 2.5	26.9 ± 4.3	18.3 ± 2.6	11.2 ± 5.2	4.05
100—200	10.6 ± 3.4	37.4 ± 6.0	29.7 ± 6.7	5.13**	26.5 ± 4.2	48.0 ± 5.4	22.3 ± 4.5	13.5 ± 4.2	11.95***
> 200	15.4 ± 2.9	33.2 ± 14.5	28.5 ± 10.3	0.88	25.2 ± 5.6	90.8	32.4 ± 8.7	14.4 ± 2.5	14.01***
$\bar{X}$	14.5 ± 1.6	29.6 ± 2.8	27.7 ± 2.7	9.88***	24.9 ± 1.6	38.1 ± 4.1	25.1 ± 2.3	17.6 ± 1.8	14.98***
F									
	Silt and finer — (≤ 0.02 mm) — *Hiesu ja hienommat*								
< 50	5.5 ± 1.0	10.4 ± 1.9	13.4 ± 3.0	2.80	10.2 ± 0.6	22.4	9.5 ± 2.1	9.6 ± 1.7	1.80
50— 70	9.7 ± 2.4	12.7 ± 1.9	14.1 ± 2.3	0.91	12.7 ± 1.3	13.0 ± 1.3	13.7 ± 2.4	9.3 ± 2.0	0.75
70—100	5.3 ± 1.8	11.6 ± 1.9	8.3 ± 3.6	3.23	8.8 ± 1.1	11.8 ± 2.1	8.0 ± 1.1	6.4 ± 2.7	2.21
100—200	5.2 ± 1.4	17.9 ± 3.5	13.9 ± 3.3	4.51*	12.6 ± 2.1	23.6 ± 2.9	10.2 ± 2.1	6.2 ± 1.7	13.89***
> 200	6.2 ± 8.9	20.2 ± 12.1	13.7 ± 6.6	0.95	13.0 ± 4.2	68.4	15.3 ± 6.1	6.0 ± 0.9	17.55***
$\bar{X}$	6.4 ± 0.7	14.0 ± 2.1	12.8 ± 1.5	7.99***	11.5 ± 1.0	18.6 ± 3.0	11.6 ± 1.4	7.7 ± 0.8	13.25***
F					0.77				

other hand, the differences were near to being significant ($P < 0.10$). The greater the height of the stand and the finer the particle-size classes in question, the so much more significant were the differences among stands of varying condition. In the height class 101—200 cm, the differences were significant between the condition classes »good» and »dead», and between »poor» and »dead»; in the classes 200 cm, the differences were significant between »good» and »poor» as well with regard to the fine particle-size classes. On a total basis, the proportion of silt and finer classes (i.e. < 0.02 mm) in the soils of stands in poor condition was also significantly less than in those classified as »dead». In both of the soil layers examined the interstand differences were of the same order and magnitude.

In stands differing in the mode of origin and in condition, differences in the content of the fine particle-size classes was observed only among the taller stands. For this reason the data was re-arranged by combining three height classes (71—100, 101—200 and > 200 cm) and by sub-dividing them according to mode of origin into condition classes. The procedure was the same in both stand and sapling based analysis. Altogether 50 stands were included in the so formed group exceeding 70 cm in height. Planted stands had been successful only on sites coarse enough to support natural stands (Table 4). Stands artificially seeded, on the other hand, had flourished on sites richer in the fine particle-size classes than those generally occupied by natural stands; as well, the difference with regard to planted stands was quite notable. Thus, failures of planted stands have occurred on sites coarser than those of failures among artificially seeded stands.

Table 4. The proportion (weight-%) of fine particle-size classes in the 0—10 cm layer of the soil in sapling stands exceeding 70 cm in height, differing in the mode of origin and condition

Taulukko 4. Maan hienojen lajitteiden osuus (paino-%) lajitekoostumuksesta 0—10 cm:n kerroksessa yli 70 cm:n pituisissa syntytavaltaan ja kuntoluokaltaan erilaisissa taimistoissa

Particle-size, mm *Raekoko, mm*	Natural — *Luontainen*			
	Dead *Tuhoutun.*	Poor *Huonok.*	Good *Hyväk.*	F
< 0.2		49.4	42.6	0.24
< 0.06		17.7	14.8	0.33
< 0.02		8.1	6.7	0.54
	Artificially seeded — *Kylvö*			
< 0.2	73.0	64.7	60.3	0.90
< 0.06	49.4	22.6	25.1	4.41*
< 0.02	29.0	10.1	10.9	3.19°
	Planted — *Istutus*			
< 0.2	66.3	59.1	28.5	5.62*
< 0.06	38.6	27.0	11.4	4.41*
< 0.02	16.9	11.7	6.0	2.26°

As was mentioned earlier, no failures among natural stands were found. There was no real difference in the respective contents of the fine particle-size classes in the soils of natural stands in good and poor condition (Table 4). In the case of artificially seeded stands, however, the differences were significant for very fine sand and finer classes (< 0.06 mm) between stands in dead and good condition. The difference between silt and finer classes (< 0.02 mm) contents was close to being significant.

In planted stands the differences between stands in dead and good condition were significant in the groups containing fine sand and finer classes (i.e. < 0.2 mm), and very fine sand and finer classes (i.e. < 0.06 mm). The difference in the content of silt and finer classes (i.e. ≤ 0.02 mm) was also a notable one, but owing to the limited nature of the available material this difference did not rank as significant.

In planted stands exceeding 70 cm in height and classified as dead, fine sand and finer classes (i.e. < 0.2 mm) constituted approximately 2/3 of the particle-size composition of the soil, whereas in stands classified as being in good condition the respective figure was less than 1/3. The content of very fine sand (< 0.06 mm) and of silt and finer classes (< 0.02 mm) in dead plantations was approximately three times that of plantations in good condition. The particle-size class distribution in the soils of plantations in poor condition assumed a halfway position with respect to plantations in good condition and those classified as dead.

The differences were not as great in artificially seeded stands, as in good condition the content of the fine particle-size classes in these was approximately twice that of respective planted stands, and even in dead condition they contained on the average 10 % more of the fine classes. There were no differences between seeded and planted stands in the poor condition class. In natural stands of both good and poor condition the content of the fine particle-size classes was clearly less than in seeded plantations, but particularly with regard to fine sand and finer classes (< 0.2 mm) natural stands exceeded planted stands. For the analysis carried out on individual sapling basis, the material was divided into two groups according to sapling height-i.e. below and above 70 cm (Tables 5 and 6). In addition, the proportions of sand, fine sand and very fine sand were determined. Significant differences were found for the contents of the fine particle-size classes on the habitats of saplings from both height groups and of different modes of origin. The habitats of natural saplings contained the least (significantly), and between seeded and planted saplings the difference lay in the habitat of the former being richer in fine sand and finer classes (< 0.2 mm) but poorer in silt and finer classes (< 0.02 mm). This was due to the habitats of seeded saplings being rich in fine sand; as much as over 50 % in cases. This is to say that artificial seedings on graded soils of the fine sand type (< 0.2 mm)

Table 5. The proportion (weight-%) ($\bar{x} \pm s_{\bar{x}}$) of fine particle-size classes in the 0—10 cm layer of the soil in the immediate vicinity of saplings not exceeding 70 cm in height, grouped according to mode of origin and condition

Taulukko 5. Maan hienojen lajitteiden osuus (paino-%) ($\bar{x} \pm s_{\bar{x}}$) lajitekoostumuksesta 0—10 cm:n kerroksessa syntytavan ja kuntoluokan mukaan ryhmiteltyjen alle 70 cm:n pituisten taimien kasvupaikoilla

Particle-size, mm *Raekoko*	Mode of origin — *Syntytapa*				$\bar{X}$	Class of condition — *Kuntoluokka*			
	Natural *Luont.*	Artific. seeded *Kylvö*	Planted *Istutus*	F		Dead *Tuhoutun.*	Poor *Huonok.*	Good *Hyväk.*	F
⩽ 0.2 ..	53.5 ± 2.7	65.7 ± 2.7	59.2 ± 2.7	5.88**	59.4 ± 1.6	63.7 ± 5.3	57.6 ± 1.9	59.6 ± 1.9	0.36
⩽ 0.06 ..	23.5 ± 1.7	28.6 ± 1.9	29.9 ± 2.1	4.02*	27.0 ± 1.1	31.6 ± 4.4	24.1 ± 2.0	27.6 ± 1.3	1.62
⩽ 0.02 ..	10.4 ± 0.8	11.6 ± 0.8	14.4 ± 1.2	5.23**	11.9 ± 0.5	14.6 ± 2.1	10.4 ± 0.9	12.1 ± 0.7	2.11°
2.0 —0.2 ..	35.9 ± 2.5	27.7 ± 2.5	31.3 ± 2.0		31.7 ± 1.4	31.8 ± 4.9	31.4 ± 2.7	31.9 ± 1.7	
0.2 —0.02 ..	43.0 ± 2.2	54.4 ± 2.5	44.8 ± 1.9		47.6 ± 1.4	49.1 ± 4.6	47.2 ± 3.0	47.5 ± 1.6	
0.2 —0.06 ..	30.1 ± 1.8	37.4 ± 2.3	29.3 ± 1.4		32.5 ± 1.4	32.1 ± 4.1	33.5 ± 2.5	32.2 ± 1.4	
0.06—0.02 ..	13.1 ± 1.0	17.0 ± 1.2	15.3 ± 1.2		15.1 ± 1.2	17.0 ± 2.5	13.7 ± 1.2	15.4 ± 0.8	

Table 6. The proportion (weight-%) ($\bar{x} \pm s_{\bar{x}}$) of fine particle-size classes in the 0—10 cm layer of the soil in the immediate vicinity of saplings exceeding 70 cm in height, grouped according to mode of origin and condition

Taulukko 6. Maan hienojen lajitteiden osuus (paino-%) ($\bar{x} \pm s_{\bar{x}}$) lajitekoostumuksesta 0—10 cm:n kerroksessa syntytavan ja kuntoluokan mukaan ryhmiteltyjen yli 70 cm:n pituisten taimien kasvupaikoilla

Particle-size, mm *Raekoko*	Mode of origin — *Syntytapa*				$\bar{X}$	Class of condition — *Kuntoluokka*			
	Natural *Luont.*	Artific. seeded *Kylvö*	Planted *Istutus*	F		Dead *Tuhoutun.*	Poor *Huonok.*	Good *Hyväk.*	F
⩽ 0.2 ..	49.9 ± 2.4	62.2 ± 2.4	55.8 ± 2.6	5.39**	55.9 ± 1.5	65.1 ± 2.5	55.8 ± 2.6	52.8 ± 2.1	3.58*
⩽ 0.06 ..	17.9 ± 1.1	27.1 ± 2.2	29.1 ± 1.8	11.03***	24.6 ± 1.1	35.1 ± 2.6	24.2 ± 2.0	21.2 ± 1.3	11.86***
⩽ 0.02 ..	8.2 ± 0.6	13.6 ± 1.7	13.4 ± 1.1	7.60***	11.7 ± 0.7	17.2 ± 1.7	11.4 ± 1.4	10.0 ± 0.8	9.72***
2.0 —0.2 ..	45.2 ± 2.5	32.4 ± 2.2	30.7 ± 2.1		36.2 ± 1.4	26.2 ± 2.0	36.2 ± 2.5	39.6 ± 2.0	
0.2 —0.02 ..	41.7 ± 2.2	48.8 ± 2.1	42.5 ± 2.0		44.3 ± 1.2	47.9 ± 1.8	44.3 ± 2.2	42.9 ± 1.9	
0.2 —0.06 ..	32.0 ± 1.9	35.2 ± 2.1	26.8 ± 1.3		31.3 ± 1.1	30.0 ± 1.6	31.5 ± 2.0	31.6 ± 1.6	
0.06—0.02 ..	9.7 ± 0.6	13.5 ± 0.8	15.7 ± 1.0		12.9 ± 0.5	17.9 ± 1.1	12.8 ± 0.9	11.3 ± 0.7	

have been more common than plantings or natural regeneration on such soils. Similarly, sand (2.0—0.2 mm) was most plentiful on the habitats of natural saplings.

On the average, the habitats of saplings over 70 cm in height were somewhat richer in the fine particle-size classes; this would seem to indicate that due to accessibility/location of stands and to prices paid for the various products, the trend in cuttings has been away from pure stands of pine and, via mixed stands, to pure stands of spruce. This has meant that increasingly fine soils have come into the sphere of regeneration.

No significant differences in contents of the fine particle-size classes were noted for habitats of saplings of varying condition less than 70 cm in height (Table 5). For silt and finer classes the difference was nearly significant in so far as the habitats of dead saplings were found to contain more of the fine classes than was the case with saplings in good condition. The trend was similar for very fine sand and finer classes (< 0.06 mm).

With saplings exceeding 70 cm in height differences arising from habitat were quite evident. Between the condition classes »dead» and »good» the differences were very significant. On the habitats of saplings in good condition the decreased amount of the fine particle-size classes is also exemplified by their containing the most sand and the least fine sand and silt. The figure for content of fine sand, silt, and finer classes is 60 % less than that for habitats of dead saplings.

4. SUMMARY

The aim of the study is to explain the relationship between the particle-size class distribution of the soil and the condition of sapling stands of pine. To this end, a comparison of soils was made with regard to the content of the finer particle-size classes. The study was conducted in North-Finland in sapling stands differing in the mode of origin and condition.

The data was gathered in North-Finland within the area delimited by N 66°—68°. Sapling stands in question numbered 95 in all. These were classified in the following manner according to the mean height: < 50 cm, 51—70 cm, 71—100 cm, 101—200 cm and > 200 cm. Further classification was based on the mode of origin (natural, seeded and planted), and on the condition (good, poor and dead).

Employing the above classification and random sampling, twelve saplings from each stand were examined. The particle-size class distribution proved to vary between the stands of different modes of origin and condition. In natural stands the proportion of the fine, less permeable particle-size classes (< 0.06 mm) was smaller than in artificially established plantations. No great difference was observed between seeded and planted plantations, even though the former were located on soils with generally slightly higher contents of the fine particle-size classes. Although the above differences were not significant in the statistical sense, they were emphasized when the data was arranged according to the classification; this was evident on both total and on individual seedling basis. A possible explanation for this may be the following; in the past, only pure stands of pine were cut and regenerated and it is only since the previous decade or so that regeneration of mixed stands of pine-spruce has been carried out in any notable volume. One means of regeneration has been the seed tree method, whereby spruce has been cut down and pine seed trees left standing. In general, pure stands of pine are located on coarser soils than pure stands of spruce.

The above phenomenon was also noted in the case of artificially established plantations of various heights. Plantations less than 70 cm in height were observed to be located on soils with higher contents of the fine particle-size classes than those underlying plantations exceeding 70 cm in height.

The failure of pine plantations, which were believed to have become established, has in North-Finland occurred at the stage where the plantations have reached the height of 1 metre, i.e. the snow-line. The study on hand shows that differences in the particle-size class distribution in soils of plantations of varying condition became significant only after 70 cm in height was exceeded. In plantations less than 70 cm in height and of varying condition, the differences were not significant, although in these cases also the fine particle-size classes were better represented in the soils of failed plantations than in those underlying healthier plantations.

When the stands greater than 70 cm in height were grouped according to the mode of origin and condition, it was observed that healthy plantations established by planting were located on soil in which the content of the fine particle-size classes was of the same order as in natural stands. Healthy seeded plantations, on the other hand, were located on distinctly finer soils. In spite of this, both planted and seeded regenerations regarded as having failed were located on soils having a higher content of the fine particle-size classes than those underlying healthier plantations.

The particle-size limit, which (should the soil be rich in classes finer than it) had the strongest correlation with the condition of the sapling stand, was found to be primarily that existing between fine sand and very fine sand (0.06 mm); of secondary importance was that existing between very fine sand and silt (0.02 mm). No failures were observed among natural stands. Evidently artificial regeneration of pine in North-Finland has been carried out on sites too rich in the fine particle-size classes for it to occur naturally. This is an obvious consequence of attempts to bring about regeneration of pine on sites which formerly had supported over-mature, slow growing stands of spruce. However, the high content of fine, less permeable particle-size classes in the soil of sites typical of spruce habitats has made it quite obvious, that, for pine to flourish on these sites, soil treatment is necessary. Pine does not possess the ability to form a new root system above the old through adventitious roots. Having the ability to form adventitious roots, spruce is able to survive on poorly aerated sites with thick raw-humus layers, where the mineral soil typically is rich in the fine particle-size classes.

The results indicate that, regarding the particle-size class distribution of the soil, good results in establishing pine on scarified sites in North-Finland can be expected on sites where silt and classes finer than it ($\leq$ 0.02 mm) amount to less than 12 % and/or very fine sand and classes finer than it ($\leq$ 0.06 mm) amount to less than 25 %. When planting, these limits may be narrower. It seems that by choosing the correct method of soil treatment and by ridding the site of excess water, artificial regeneration of pine is also feasible on sites with fine particle-size class contents exceeding the limits given above.

5. SUOMENKIELINEN SELOSTUS

Tämän tutkimuksen tarkoituksena on selvittää maan lajitekoostumuksen ja männyn taimiston kunnon välistä riippuvuutta vertaamalla hienoimpien lajitteiden osuutta maan lajitekoostumuksesta erikokoisissa, syntytavaltaan ja kunnoltaan erilaisissa taimistoissa Pohjois-Suomessa.

Tutkimusaineisto kerättiin Pohjois-Suomesta eri puolilta 66°:n ja 68°:n leveyspiirien välistä aluetta. Aineisto sisälsi yhteensä 95 taimistoa. Ne ryhmiteltiin keskipituuden mukaan viiteen luokkaan: < 50 cm, 51—70, 71—100, 101—200 ja > 200 cm. Taimistot luokiteltiin syntytavan mukaan (luontainen, kylvö ja istutus) sekä kuntoluokan mukaan (hyväkuntoinen, huonokuntoinen ja tuhoutunut).

Samaa luokitusta käyttäen kustakin taimistosta tutkittiin erikseen otantaan perustuen 12 tainta. Maan lajitekoostumuksessa oli eroa sekä syntytavaltaan että kunnoltaan erilaisissa taimistoissa. Luontaisissa taimistoissa hienojen, vettä tehokkaasti pidättävien lajitteiden (< 0.06 mm) määrä oli pienempi kuin viljelytaimistoissa. Sen sijaan kylvö- ja istutustaimistojen välillä ero ei ollut selvä, joskin kylvötaimistoissa hienoja lajitteita oli yleensä jonkin verran enemmän kuin istutustaimistoissa. Vaikka edellä esitetyt erot eivät olleetkaan tilastollisesti merkitseviä, silloin kun aineisto jaettiin pituusluokkiin, tulivat erot näkyviin voimakkaina koko aineistossa sekä myös taimikohtaisesti laskettuna. Syynä eroon lienee se, että aiemmin hakattiin ja uudistettiin yleensä vain puhtaita männiköitä ja vasta parina viime vuosikymmenenä on suuremmassa määrin siirrytty uudistamaan mänty-kuusisekametsiä. Eräänä uudistamismuotona on käytetty myös luontaista uudistamista, jolloin männyt on jätetty siemenpuiksi ja kuuset on hakattu pois. Yleensä puhtaat männiköt sijaitsevat karkearakeisemmilla kasvupaikoilla kuin sekametsät tai puhtaat kuusikot.

Edellä kerrottu ilmiö näkyy myös eri pituisissa viljelytaimistoissa. Alle 70 cm:n pituiset taimistot sijaitsevat maalla, jossa on enemmän hienoja lajitteita kuin yli 70 cm:n pituisten taimistojen kasvupaikoilla on.

Jo vakiintuneiksi luultuja männyn taimistoja on tuhoutunut Pohjois-Suomessa siinä vaiheessa, kun taimisto on saavuttanut pituudessaan lumirajan, eli noin 1 m:n koon. Tämä tutkimus osoittaa, että kunnoltaan erilaisten taimistojen maan lajitekoostumus poikkeaa merkitsevästi vasta, kun taimisto on saavuttanut yli 70 cm:n koon. Alle 70 cm:n korkuisissa, kunnoltaan erilaisissa taimistoissa sen sijaan erot eivät olleet merkitseviä, vaikka myös niissä hienoja lajitteita oli enemmän tuhoutuneissa kuin parempikuntoisissa taimistoissa.

Ryhmiteltäessä yli 70 cm:n pituiset taimistot syntytavaltaan ja kuntoluokaltaan voitiin todeta, että hyväkuntoiset istutustaimistot sijaitsivat maalla, jossa hienojen lajitteiden määrä oli samansuuruinen kuin luontaisesti syntyneissä taimistoissa. Hyväkuntoiset kylvötaimistot taas sijaitsivat selvästi hienojakoisemmilla mailla. Kuitenkin myös kylvö- samoin kuin istutustaimistoissa tuhoutuneiksi luokitellut taimistot sijaitsivat merkittävästi enemmän hienoja lajitteita sisältävällä maalla kuin parempi-

kuntoiset taimistot. Raekokoraja, jota hienompien lajitteiden runsaus merkitsi voimakkainta riippuvuutta taimiston kunnon kanssa, näytti olevan ensisijaisesti karkean ja hienon hiedan raja ja toissijaisesti hiedan ja hiesun raja. Tuhoutuneita luontaisesti syntyneitä taimistoja ei etsiskelyistä huolimatta löydetty. On ilmeistä, että mäntyä on Pohjois-Suomessa viljelty sellaisille, runsaasti hienoja lajitteita sisältäville kasvupaikoille, joilla se luontaisena ei esiinny. Tämä on luonnollinen seuraus siitä, että puuntuotannollisesti yli-ikäiset, heikkokasvuiset kuusikot on pyritty uudistamaan männylle. Kuitenkin maan hienojen, vettä tehokkaasti pidättävien lajitteiden runsaus tyypillisillä kuusimailla merkitsee sitä, että mänty ei ainakaan ilman tehokkaita maankäsittelytoimenpiteitä pysty niillä kasvupaikoilla tulemaan toimeen. Männyllä ei ole kuusen kaltaista kykyä muodostaa alkuperäisen juuriston yläpuolelle jälkijuurista uutta juuristoa. Kuusi pystyy jälkijuuriensa avulla tulemaan toimeen paksukunttaisessa ja heikon ilmavaihdon omaavassa maassa, joiden kivennäismaa tyypillisesti sisältää runsaasti hienoja lajitteita.

Tulosten perusteella näyttää siltä, että hyvät edellytykset maan lajitekoostumuksen puolesta hyväkuntoisten männyn taimistojen aikaan saamiselle laikkuihin Pohjois-Suomessa on olemassa kasvupaikoilla, jossa hiesun ja sitä hienompien lajitteiden (< 0.02 mm) osuus on alle 12 % ja/tai hienon hiedan ja sitä hienompien lajitteiden (< 0.06 mm) osuus on alle 25 %. Istutusta käytettäessä raja-arvot lienevät vielä jonkin verran pienemmät. Kivennäismaata oikealla tavalla käsittelemällä ja johtamalla liika vesi pois uudistusalalta voidaan mäntyä viljellä ilmeisen menestyksellisesti myös edellä mainittuja raja-arvoja runsaammin hienoja lajitteita sisältäville kasvupaikoille.

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HAVUPUIDEN LATVAKASVAIMEN JA NEULASTEN VUOTUISEN KASVURYTMIN MÄÄRITTÄMINEN

Esimerkkisovellutus männyn jälkeläiskokeeseen

JARI PARVIAINEN

SUMMARY:

DETERMINATION OF THE ANNUAL GROWTH RHYTHM OF THE TERMINAL LEADER AND NEEDLES OF CONIFERS

Application to a progeny test

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ALKUSANAT

Käsillä oleva julkaisu kuuluu Metsäntutkimuslaitoksen metsänjalostuksen tutkimusosaston varhaistestimenetelmiä käsittelevään tutkimussarjaan, jota johtaa metsänhoitaja, MMK Jouni Mikola. Hän on seurannut kiinteästi tutkimuksen kulkua ja avustanut monissa työn toteuttamiseen liittyvissä ongelmissa sekä lukenut alustavan käsikirjoituksen.

Julkaisu perustuu tekijän laatimaan opinnäytetyöhön maatalous- ja metsätieteiden kandidaatin tutkintoa varten. Julkaisun viimeistelyssä painokuntoon on auttanut vt. professori Matti Leikola. Käsikirjoituksen ovat lukeneet työn eri vaiheissa professorit Risto Sarvas, Max. Hagman ja Paavo Yli-Vakkuri sekä fil. tri, dos. Veikko Koski ja fil. lis. Pertti Hari. Viimeksi mainittu on lisäksi opastanut aineiston matemaattisessa käsittelyssä. Aineiston mittauksessa ovat avustaneet metsänhoitaja Markku Kuusela ja vaimoni Soili Parviainen. Kuvat on piirtänyt Sisko Salminen. Lyhennelmän ja kuvatekstit on kääntänyt englanniksi Ph. D. Kim von Weissenberg. Professori Risto Sarvaksen selvitykset puiden aktiivin periodin etenemisnopeudesta ovat tämän tutkimuksen laskentamenetelmien lähtökohtana.

Tekijä esittää parhaat kiitoksensa kaikille työssä avustaneille.

Suonenjoella, lokakuussa 1974.

Jari Parviainen

SISÄLLYSLUETTELO

Sivu

1. Johdanto 5

2. Tutkimusaineisto ja -menetelmä 6
   21. Koetaimet ja niiden kasvatus 6
   22. Mittaukset 7
   23. Aineiston käsittely 8

3. Tutkimuksen tulokset 12
   31. Kasvainten päivittäinen pituuskasvu 12
   32. Neulasten päivittäinen pituuskasvu 15

4. Tulosten tarkastelua 19

5. Tiivistelmä 23

6. Lähdeluettelo 24

7. Summary 27

1. JOHDANTO

Pituuskasvun ajoittumisen on yleisesti havaittu olevan parhaita osoittajia havupuiden geneettisestä sopeutuneisuudesta tietyn kasvupaikan ilmastoon. Provenienssien jälkeläiskokeissa pituuskasvun ajoittumiseroja onkin selvitetty mm. tarkkailemalla keväistä silmujen puhkeamista tai syksyllä latvasilmun muodostumista (Irgens-Moller 1957, Sweet 1964, Magnesen 1969, 1971). Yleisimmin vuotuisen pituuskasvun eteneminen on kuitenkin määritetty tutkimalla suoraan latvakasvainten tai neulasten pituuskehitystä (Langlet 1959, Dietrichson 1964, 1971), jolloin kasvainten ja neulasten mittaus on tehty kerran tai pari kasvukauden aikana. Havaintopäivien lukuarvot on suhteutettu lopulliseen kasvainten ja neulasten pituuteen, ja näin saatujen suhdelukujen avulla tiedetään, mikä alkuperä on aikainen tai myöhäinen.

Kuitenkin myös puiden vuotuisen pituuskasvun on havaittu selvästi noudattavan ns. yleisen kasvumallin kulkua. Se voidaan jakaa luontevasti nousevan, intensiivisen ja laskevan kasvun vaiheisiin (esim. Mork 1941, Hari, Leikola ja Räsänen 1970). Jotta nämä vaiheet saataisiin mukaan tarkasteluun on tehtävä säännöllisiä, mieluimmin päivittäisiä pituuskasvumittauksia. Vaikeuksia on lisäksi tuottanut tulosten käsittely, sillä päivittäisiä pituuskasvuhavaintoja on ollut vaikea verrata alkuperittäin, koska päivittäinen kasvun taso aina riippuu kasvukautisen pituuskehitysvaiheen lisäksi kulloinkin vallinneista kasvutekijöistä, pohjoismaissa ensi sijassa lämpötilasta.

Käsillä olevan tutkimuksen tarkoituksena on kokeilla, kuinka latvakasvainten ja neulasten päivittäisiä pituuskasvuhavaintoja voitaisiin entistä paremmin käyttää geneettisten kasvurytmierojen toteamisessa. Päivittäisten kasvuhavaintojen käsittely on tässä tehty Harin et. al. (1970) kehittämän pituuskasvumallin avulla soveltaen sitä kotimaisten mäntykantapuiden jälkeläistöjen testaamiseen.

2. TUTKIMUSAINEISTO JA -MENETELMÄ

21. Koetaimet ja niiden kasvatus

Tutkimuksen aineistona oleva jälkeläiskoe (n:o 463) perustettiin metsäntutkimuslaitoksen Ruotsinkylän jalostusasemalle (60°22'P., 24°57'I, korkeus 60 m.p.y.) keväällä 1972 ja taimien kasvattamista jatkettiin samalla paikalla myös vuonna 1973. Kokeessa oli mukana 5 eri pluspuukloonin jälkeläistöä kahdelta Etelä-Suomen kloonikokoelmalta (taulukko 1), joissa kyseiset kloonit olivat saaneet pölyttyä vapaasti joko paikallisella siitepölyllä tai keskenään. Siementen keräys koetta varten tehtiin emopuittain vuosina 1968—1970.

Kasvattamista varten siemenet kylvettiin reikälevyjä käyttäen yksitellen kasvuturpeella täytettyihin muovisiin kasvatuslaatikoihin. Aineiston tilastollista käsittelyä silmällä pitäen jälkeläistöjen paikat arvottiin kunkin toiston (4 kpl) sisällä erikseen. Jokaiseen laatikkoon, joiden koko oli 60 × 40 × 15 cm, kylvettiin kolme jälkeläistöä, ja jokaisesta jälkeläistöstä otettiin kylvökseen mukaan 24 siementä. Myös toisena kasvukautena taimet saivat kehittyä samoissa kasvatuslaatikoissa ja kylvöstä jääneessä tiheydessä.

Taimien kastelu pyrittiin suorittamaan mahdollisimman tasaisesti. Kastelussa käytettiin taimitarhakokeita varten kehitettyä, kiskoilla liikkuvaa kastelulaitetta. Laitteen ydinosan muodosti peltikouru, jonka pohjassa oli veden tasaisen valumisen turvaamiseksi pieniä reikiä ½ cm välein. Kas-

Taulukko 1. Jälkeläistöjen emopuut ja siemenen syntypaikka.
Table 1. Location of plus trees and seed collecting areas for the progenies.

Jälkeläistön n:o *No. of progeny*	Siementunnus *Seed code*	Emopuun klooninumero ja kotipaikkakunta *Clone number of plus tree and its location*	Kokoelmapaikkakunta *Location of gene bank*
1	G-68- 459	E 614 C Suomenniemi	Punkaharju
2	G-69-1 866	E 627 Sulkava	Punkaharju
3	G-69-1 913	E 1101 Punkaharju	Punkaharju
4	G-70- 492	E 1001 Tammela	Ruotsinkylä
5	G-70- 796	P 427 Posio	Punkaharju

vatuspaikan yläpuolella oleviin rakennelmiin kiinnitettiin myös kiskot, joita myöten kasteluvettä tuova muoviletku pääsi liikkumaan. Kastelulaitteen liikkumisnopeus oli n. 28 m/min.

Taimia kasteltiin kuivimpana aikana kolme kertaa päivässä. Yhdellä kastelukerralla kastelulaitetta kuljetettiin taimien yli kerran edestakaisin. Päivittäinen kastelutiheys vastasi noin 5 mm sademäärää. Taimia jouduttiin kastelemaan molempina kasvatuskesinä (1972 ja 1973) lähes päivittäin koko kasvukauden ajan, koska em. kesät olivat poikkeuksellisen kuivia.

Ensimmäisenä kasvukautena taimia ei lannoitettu, sillä kasvatusalustana oli peruslannoitettu turve. Aikaisempien kokemuksien pohjalta (mm. H e m m i l ä 1973) tiedettiin, että peruslannoituksen vaikutus normaalisti ulottuu vain ensimmäiseen kasvukauteen. Tämän vuoksi toisen kasvukauden alussa taimia lannoitettiin kloorivapaalla hivenainepitoisella Super-Y-lannoksella (7 % N, 24 % P_2O_5 ja 15 % K_2O). Jokaiseen taimilaatikkoon levitettiin käsin mahdollisimman tasaisesti 10 g lannoitetta, mikä vastaa n. 400 kg/ha.

22. Mittaukset

Taimien pituuskasvun kulun päivittäistä seuraamista varten jokaisesta alkuperästä valittiin taimilaatikon keskimmäiseltä riviltä 3 valtatainta. Varsinainen pituuskasvumittaus tehtiin viivottimella 0.5 mm tarkkuudella taimien kasvatuslaatikon reunojen varaan asetetun jäykän rautatangon päältä päärangan latvasilmun huippuun. Tällä tavoin pyrittiin välttämään virheitä mittauslähtökohdan suhteen, joita olisi saattanut tapahtua, mikäli mittaukset olisi tehty esim. suoraan turpeen pinnalta. Toisaalta taimet olivat liian pieniä, jotta mittauksen lähtökohdaksi olisi voitu ottaa edellinen vuosikasvain. Neulaa tukena käyttäen mittaukset voidaan suorittaa työntötulkilla (esim. H a r i et. al. 1970), ja mittaustarkkuus on suurempi kuin viivotinta käytettäessä.

Päivittäisiä pituuskasvumittauksia tehtiin toukokuun alusta lähtien kesäkuun loppuun saakka. Mittaukset aloitettiin joka aamu klo 9.30. Näin taimien kasvuvuorokausi määräytyi vuorossa olevan ja tätä edeltäneen mittauspäivän mittausajankohtien erotuksena (pituuskasvun päivittäisestä rytmistä esim. M o r k 1941).

Neulasten kasvumittaukset tehtiin työntötulkilla päivittäin heti kasvainten pituuskasvumittausten jälkeen. Jokaisesta taimesta valittiin silmämääräisesti kaksi neulasta: toinen kasvaimen kärkiosasta läheltä latvasilmua, toinen kasvaimen keskiosasta. Molemmat neulaset valittiin kasvainten etelänpuolelta, ja ne merkittiin vedenkestävällä tussilla. Mittauksen lähtöpisteeksi tuli neulasen ja kasvaimen rajakohta, johon työntötulkin

toinen mittausantura laskettiin hellävaraisesti. Neulasmittaukset aloitettiin, kun neulanen oli pidentynyt riittävästi mittausten järkevää suorittamista ajatellen, yleensä n. 5 mm. Mittaustarkkuus oli 0.1 mm.

Kasvatuspaikalla vallinneen lämpötilan kulkua seurattiin Cu-Ko-termoelementin avulla. Kokeen laitimmaisten taimirivien puoliväliin asetettiin kahteen pisteeseen termoelementtianturit, jotka suojattiin alumiinipellistä taitetulla varjostimella. Keskusyksikkö rekisteröi mittauspisteiden ympärillä vallinneen lämpötilan 20 min välein. Koska piirturin termoelementtianturit olivat vapaana ulkoilmassa suojaimen alla, voitiin niiden antamien lukemien ajatella kuvaavan lämpötilan vaihteluita kasvaimessa melko hyvin (vrt. B j o r 1967, L e i k o l a ja P y l k k ö 1968).

Lämpötilamittauksia kontrolloitiin varjostimella suojatulla elohopealämpömittarilla, jonka lukemat merkittiin muistiin sekä aamulla että illalla. Lisäksi yksi termoelementtianturi oli asetettu termospulloon, jossa oli sulavaa jäätä ($\pm 0°$ C).

Koska termoelementti on herkkä ulkoisille häiriötekijöille (esim. sähkökatkos, ukkonen), käytettiin termoelementin rinnalla jousikäyttöistä termografia. Termografi sijoitettiin säähavaintokojuun, jonne asetettiin lisäksi kontrollilämpömittari. Kasvainten kasvujakson aikana lämpötila rekisteröitiin termoelementin avulla. Neulasten kasvujakson loppupuolella keskusyksikölle sattuneen teknisen häiriön vuoksi kaikki neulasten kasvujakson lämpötilahavainnot saatiin termografinauhoista.

23. Aineiston käsittely

Kootut havainnot käsiteltiin pääosin loppukesän ja alkusyksyn 1973 kuluessa. Laskennassa käytettiin muutamia peruslaskentoja lukuunottamatta yksinomaan tietokonetta (UNIVAC 1108). Tilastolliset analyysit suoritettiin Helsingin yliopiston laskentakeskuksen laatimaa HYLPS-ohjelmistoa hyväksi käyttäen. Aineiston muu laskenta suoritettiin FORTRAN-ohjelmointikielellä.

Päivittäin mitattujen kasvuhavaintojen käsittelyssä käytettiin H a r i n et. al. (1970) esittämää pituuskasvumallia (myös mm. H a r i 1972). Menetelmä perustuu ns. fysiologisen kehitystilan käyttöön päivittäisen pituuskasvuvaihtelun selittämisessä:

Männyn pituuskasvu jonakin päivänä riippuu tietyssä määrin kyseisen päivän pituuskehitysvaiheesta (esim. siitä, onko kasvukautinen pituuskehitys alkamassa vai päättymässä) ja lämpötilaoloista. Jotta kasvukautisen kehitysvaiheen merkitys voitaisiin ottaa huomioon laskennassa, täytyy valita muuttuja, joka kuvaa tätä ns. fysiologista kehitystilaa (vuotuisen periodin vaihetta).

Ympäristöolosuhteet säätelevät kasvien aktiivisia elintoimintoja ja sitä kautta kehityksen kulkua. Esim. viileällä säällä kehitys etenee hitaasti, kun taas lämpimällä säällä kehityksen kulku on nopeampaa. Harin (1972) mukaan merkitään kehityksen etenemistä kirjaimella M (joka kuvaa aktiivista elintoimintaa) ja lämpötilaa kirjaimella X. Oletetaan tämän jälkeen, että kehityksen eteneminen riippuu ainoastaan lämpötilasta, jolloin fysiologinen kehitystila s ajanhetkellä t voidaan määritellä seuraavasti (Hari 1972, Sarvas 1972):

$$s(t) = \int_0^t M(X(t))\, dt \tag{1}$$

Männyllä kehityksen etenemisen (aktiivisen elintoiminnan) kuvaamiseen tietyn lämpötilan X vallitessa Hari et. al. (1970) ovat käyttäneet respiraatiota R ja siten merkinneet M = R. Respiraation määrä puolestaan voidaan ilmaista lämpötilan funktiona. Tässä tutkimuksessa on samoin käytetty hyväksi Dahlin ja Morkin (1959, kuva 1) mittauksia, joiden mukaan kuusen kasvainten respiraatio on eksponentiaalisessa riippuvuussuhteessa lämpötilan kanssa.

Aktiivisten elintoimintojen kuvaamiseen tietyn lämpötilan vallitessa voidaan käyttää myös Sarvaksen (1972, kuva 11) esittämää ns. p.u.-asteikkoa. Tässä muodossa puiden aktiivin periodin etenemisnopeuden ja lämpötilan välinen riippuvuus on sigmoidinen käyrä. Koetteeksi tässä tutkimuksessa sovellettiin myös vm. mallia.

Laskennassa käytettyä menetelmää ovat selostaneet Pohjonen ja Hari (1973) sekä Hari ja Leikola (1974). Seuraavassa esitetään kasvumallin muodostuksen pääpiirteet tähän tutkimukseen sovellettuna:

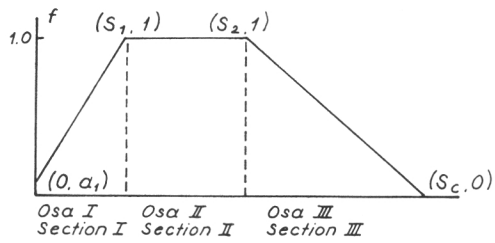
Olkoon t_j hetki, jolloin j:s päivä alkaa ja r_j kyseisen päivän teoreettinen kumulatiivinen respiraatio. Silloin

$$r_j = \int_{t_j}^{t_{j+1}} R(X(t))\, dt \tag{2}$$

Muuttuja r_j on j:n päivän lämpösumman yleistys.

Olkoon s_j fysiologinen kehitystila j:n päivän alussa (s_j on määrätty yhtälön (1) avulla) ja g_j pituuskasvu ko. päivänä. Oletetaan edelleen, että pituuskasvu j:nä päivänä riippuu päivän alkaessa olleesta fysiologisesta kehitystilasta (s_j) sekä myös kumulatiivisesta respiraatiosta (r_j) samana päivänä. Silloin

$$g_j = g(s_j,\ r_j) \tag{3}$$



Kuva 1. Laskennassa käytetyn funktion f muoto (H a r i et. al. 1970)

Fig. 1. The shape of the function f used in the calculations (H a r i et. al. 1970)

Jotta yhtälö (3) tulisi operationaaliseksi oletetaan, että g on r:n lineaarinen funktio.

$$g(s, r) = f(s) \cdot a \cdot (r - b) \tag{4}$$

Funktio f on itseasiassa monimutkainen s:n funktio. Tässä oletetaan edelleen, että funktio f jakaantuu kolmeen lineaariseen osaan seuraavasti (kuva 1):

osa 1: kasvukautisen pituuskehityksen voimistuva vaihe (nousevan kasvun jakso),
osa 2: kasvukautinen pituuskehitys pysyy vakaana (maksimaalisen kasvun jakso), ja
osa 3: kasvukautisen pituuskehityksen heikkenevä vaihe (laskevan kasvun jakso).

Maksimaalisen kasvun jakson aikana kasvainten pitenemisen määrä on yhtälön (4) mukaan lineaarisessa suhteessa ns. kumulatiiviseen respiraatioon (D a h l ja M o r k 1959). Laskentamalliin (yhtälö 4, kuva 3) sisältyvät parametrit voidaan estimoida päivittäin mitattujen pituuskasvuhavaintojen ja lämpötilaan suhteutettujen respiraatioarvojen avulla. Parametrien sisältö voidaan tulkita seuraavasti:

a: määrää päivittäisen pituuskasvun tason,
a_1: määrää päivittäisen pituuskasvun tason havaintojen teon alkamishetkellä,
b: teoreettinen respiraatiotaso, jonka alapuolella kasvua ei tapahdu (tässä tapauksessa b = 200, joka vastaa n. 7° C lämpötilaa),
s_1: (funktio f:ssä) on fysiologinen kehitystila, jossa päivittäisen pituuskasvun nouseva jakso päättyy, ja jossa maksimikasvu alkaa,
s_2: (funktio f:ssä) on fysiologinen kehitystila, jossa päivittäisen pituuskasvun maksimijakso päättyy, ja jossa laskevan kasvun jakso alkaa, ja
s_c: (funktio f:ssä) on fysiologinen kehitystila, jossa päivittäisen pituuskasvun laskeva jakso päättyy.

Jokaisen mittaussarjan parametrit määrättiin tietokoneella valmiiksi laaditulla iterointimenettelyyn perustuvalla ohjelmalla, mikä vaati tietokoneaikaa n. 15 sekuntia/sarja. Maastossa mitatut havaintosarjat merkittiin lomakkeille, joista lävistystyö voitiin tehdä suoraan. Laskentaa varten yksittäisistä taimista tehdyt havaintosarjat yhdistettiin siten, että lopulliset laskelmat tehtiin alkuperien sisällä toistoittain. Käytetyn laskentamallin avulla pyrittiin selvittämään erityisesti funktion f muotoa alkuperittäin.

3. TUTKIMUKSEN TULOKSET

31. Kasvainten päivittäinen pituuskasvu

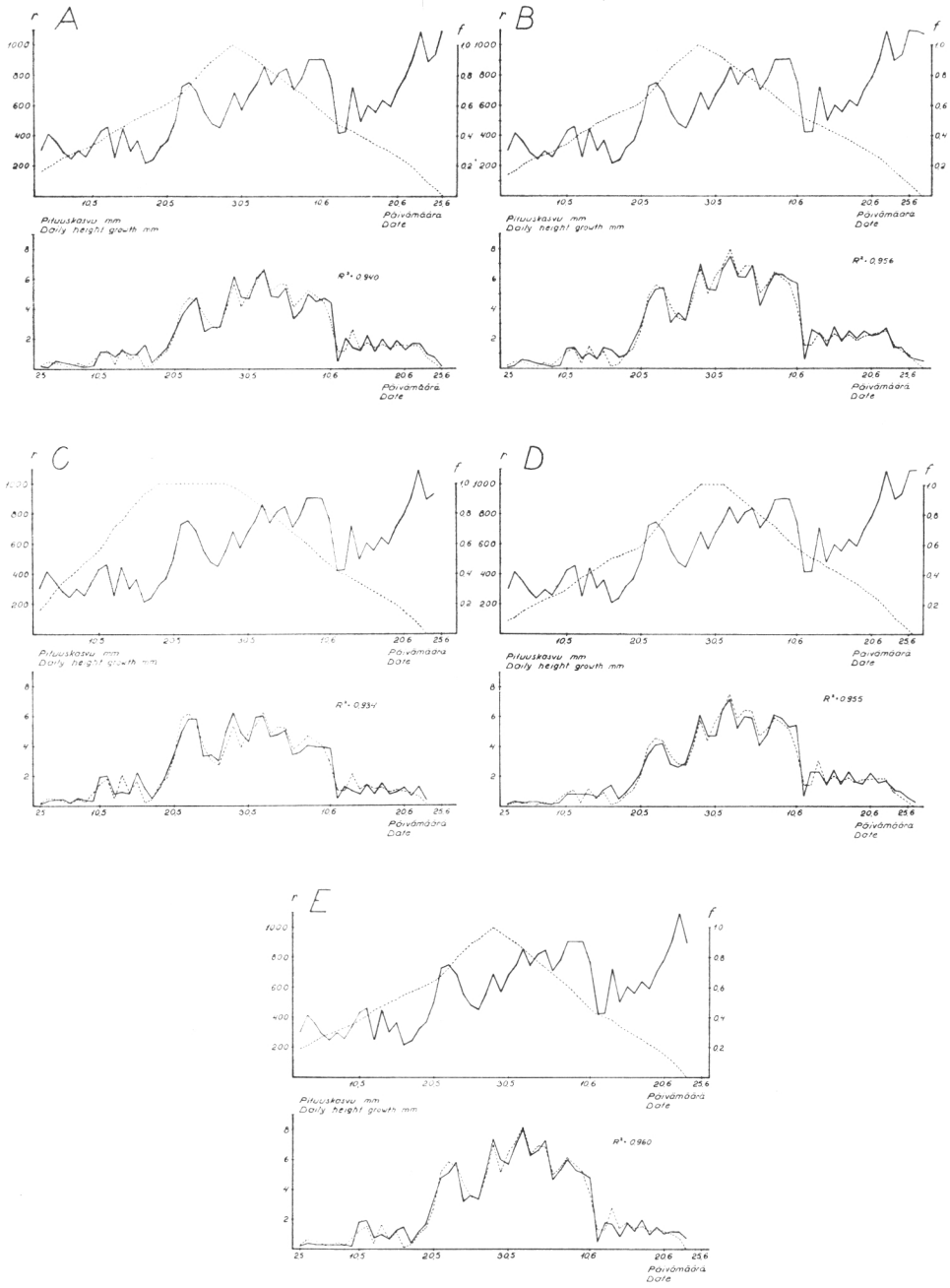
Edellä selostetun pituuskasvumallin avulla suoritetun laskennan tulokset on esitetty alkuperittäin kuvassa 2. Kuvaan 3 on koottu rinnakkain kaikkien jälkeläistöjen mitattu päivittäinen pituuskasvu ja funktion f kulkua esittävät kuvaajat. Kuvassa 2 on näkyvissä myös mitatun ja lasketun pituuskasvun välinen korrelaatiokertoimen neliö (selitysaste saadaan kertomalla korrelaatiokertoimen neliön lukuarvo sadalla). Kun laskennan pohjaksi otettiin respiraation sijasta S a r v a k s e n (1972) esittämä lämpötilan ja aktiivin periodin etenemisnopeuden välinen riippuvuus, saatiin käytännöllisesti katsoen samanlaisia tuloksia, ja selitysasteet olivat jälkeläistöittäin kuvissa esitettyjen lukujen suuruisia.

Jälkeläistöjen välisiä pituuskasvun etenemisen suhteita on mahdollista tarkastella funktion f avulla. Kuvasta 3 voidaan havaita, että jälkeläistön n:o 3 pituuskasvun kulku on ollut muita aikaisempi, kun taas alkuperän n:o 4 pituuskasvu on edennyt alussa hitaimmin.

Laskennassa saatuja funktion f arvoja voidaan sellaisenaan käyttää tilastolliseen testaukseen. Taulukossa 2 on esitetty funktion f arvot kah-

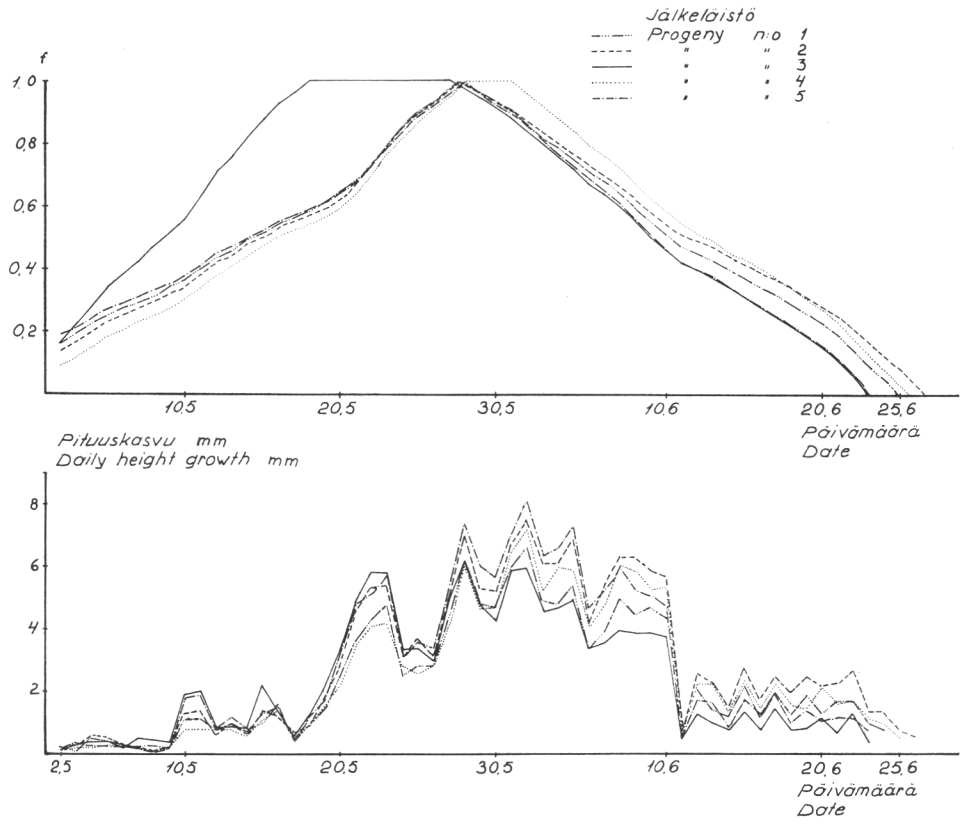
Taulukko 2. Kasvainten päivittäinen pituuskasvu. Kasvumallin avulla lasketut parametrien arvot. Selitys tekstissä.
Table 2. Daily growht of leaders. Values for the parameters calculated on the basis of the growth model. Explanations in the text.

Jälkeläistön n:o ja kotipaikkakunta *No. of progeny and its provenance*	Funktion f kulkua osoittavat lukuarvot. Kaksi esimerkkipäivää *Values giving shape of function f. Examples for two days*		Maksimikasvujakson alkurespiraatio (s_1) *Initial respiration for period of maximum growth (s_1)*	Maksimikasvujakson loppurespiraatio (s_2) *Final respiration for period of maximum growth (s_2)*	Koko pituuskasvujakson loppurespiraatio (sc) *Final respiration for total period of height growth (sc)*	Pituuskasvujakso funktion f avulla määrättynä (taso 0.30) *Period of growth as defined by function f (level 0.30)*	Parametri a *Parameter a*
	18. 05. 73	18. 06. 73					
1 Suomenniemi	0.58	0.26	10 408	10 413	30 280	23 330	0.00117
2 Sulkava	0.57	0.34	10 400	10 403	32 310	34 340	0.00138
3 Punkaharju	1.00	0.22	5 182	10 245	28 290	22 580	0.00112
4 Tammela	0.54	0.34	10 567	12 541	31 220	23 570	0.00118
5 Posio	0.59	0.22	10 573	10 578	29 380	21 680	0.00145
F-arvo	5.05**	2.59	3.55*	1.52	3.65*	1.49	2.41



Kuvat 2 a—e. Kuvan yläosa: päivittäinen kumulatiivinen respiraatio (yhtenäinen viiva) ja funktion f kulku (katkoviiva). Kuvan alaosa: kasvainten mitattu (yhtenäinen viiva) ja laskettu (katkoviiva) päivittäinen pituuskasvu sekä niiden välisen korrelaatiokertoimen neliö. a: jälkeläistö n:o 1, Suomenniemi; b: n:o 2, Sulkava; c: n:o 3, Punkaharju; d: n:o 4, Tammela; e: n:o 5, Posio.

Figs. 2 a—e. Upper part of figure: Daily cumulative respiration (solid line) and shape of function f (broken line). Lower part of figure: Daily height growth of leaders as measured (solid line) and as predicted (broken line) and the square of their correlation. a: Progeny no. 1, Suomenniemi; b: no. 2, Sulkava; c: no. 3, Punkaharju; d: no. 4, Tammela; e: no. 5, Posio.



Kuva 3. Kuvan yläosa: funktion f kulku. Kuvan alaosa: jälkeläistöjen kasvainten mitattu päivittäinen pituuskasvu.

Fig. 3. Upper part of figure: Shape of function f. Lower part of figure: Daily height growth of leaders of progenies.

tena havaintopäivänä sekä funktion f toistoittaisten lukemien perusteella varianssianalyysissä saatu F-arvo. Havaitaan, että pituuskasvun alkuvaiheen aikana eri jälkeläistöt ovat eronneet tilastollisesti hyvin merkitsevästi toisistaan. Sen sijaan pituuskasvun kulun loppuvaiheessa ei niiden välillä ole ollut tilastollisesti merkitseviä eroja.

Muiden laskennassa saatujen parametrien arvot on esitetty samoin taulukossa 2. Pituuskasvumalliin kuuluvaa parametrin a_1 arvoa ei tässä kokeessa voitu luotettavasti määrittää, koska taimien pituuskasvun lähtökohtaa ei oltu erikseen rekisteröity.

Maksimaalisen kasvun päättymishetkessä (s_2) ja maksimaalisen kasvun jakson pituudessa ei jälkeläistöjen välillä todettu tilastollisesti merkitseviä eroja. On kuitenkin huomattava, että jälkeläistöjen sisäinen vaihtelu oli erityisen suuri nimenomaan näiden tunnusten osalta, eivätkä testit tämän

vuoksi osoittaneet merkitseviä eroja. Kuvasta 3 voidaan silti havaita, että jälkeläistöjen n:o 3 ja 4 maksimaalisen kasvun jakso ajoittuu erilleen siten, että jälkeläistön n:o 3 maksimikasvun ajan päättyessä jälkeläistön n:o 4 maksimikasvuvaihe alkaa. Molempien alkuperien maksimaalisen kasvun aika on selvästi todettava kasvuvaihe. Näiden jälkeläistöjen osalta tulokset ovat samanlaisia kuin mitä H a r i et. al. (1970) ja H a r i (1972) ovat esittäneet. Sen sijaan muiden jälkeläistöjen (n:o 1, 2, 5) maksimikasvun aika on hyvin lyhyt muodostaen kuvaajassa vain terävän piikin.

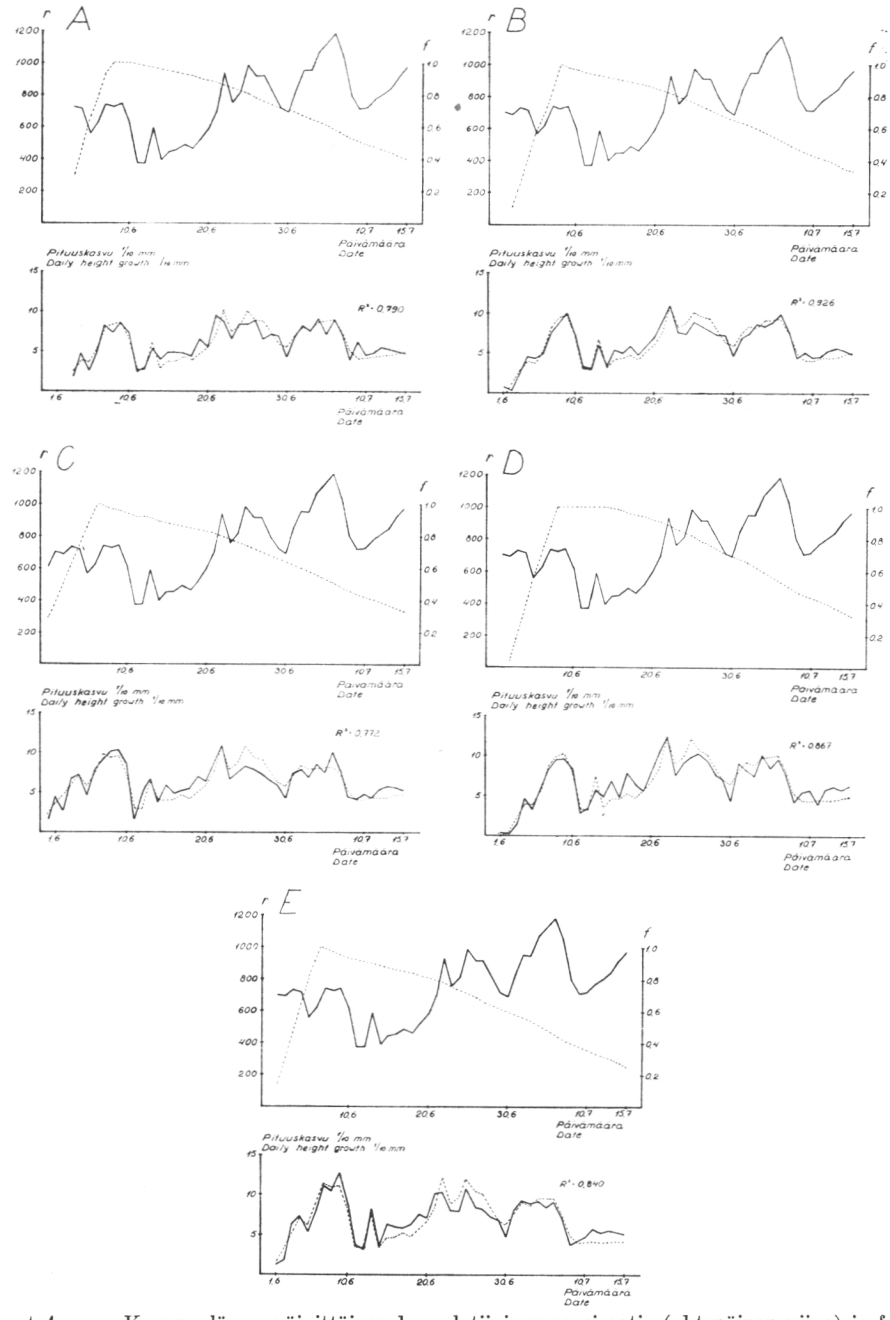
Kokonaiskasvujakson (s_c) ohella osittainen kasvujakso voidaan määrittää käyttämällä hyväksi sovittua funktion f tasoa. Tässä otettiin kasvujaksoerojen tutkimista varten funktion f tasoksi 0.30. Lyhennetty kasvujakso saatiin määrättyä vähentämällä funktion f tason 0.30 kohdalla olevasta nousevan kasvuvaiheen kumulatiivisesta respiraatioarvosta vastaava laskevan kasvuvaiheen kumulatiivinen respiraatioarvo (fysiologinen kehitystila on lausuttu kumulatiivisen respiraation avulla). Näin määritetty kasvujakso on esitetty taulukossa 2 kumulatiivisina respiraatioarvoina.

Kasvuvaiheisiin liittyen taulukossa 2 on myös parametri a:n arvot, jotka kuvaavat kasvun päivittäistä tasoa. Näiden perusteella on pääteltävissä, että jälkeläistön n:o 5 päivittäinen pituuskasvun taso on ollut korkein, ts. tämän alkuperän pituuskasvu on ollut intensiivisintä kasvukauden aikana. Tilastollisesti merkitseviä eroja ei ollut alkuperien välillä.

32. Neulasten päivittäinen pituuskasvu

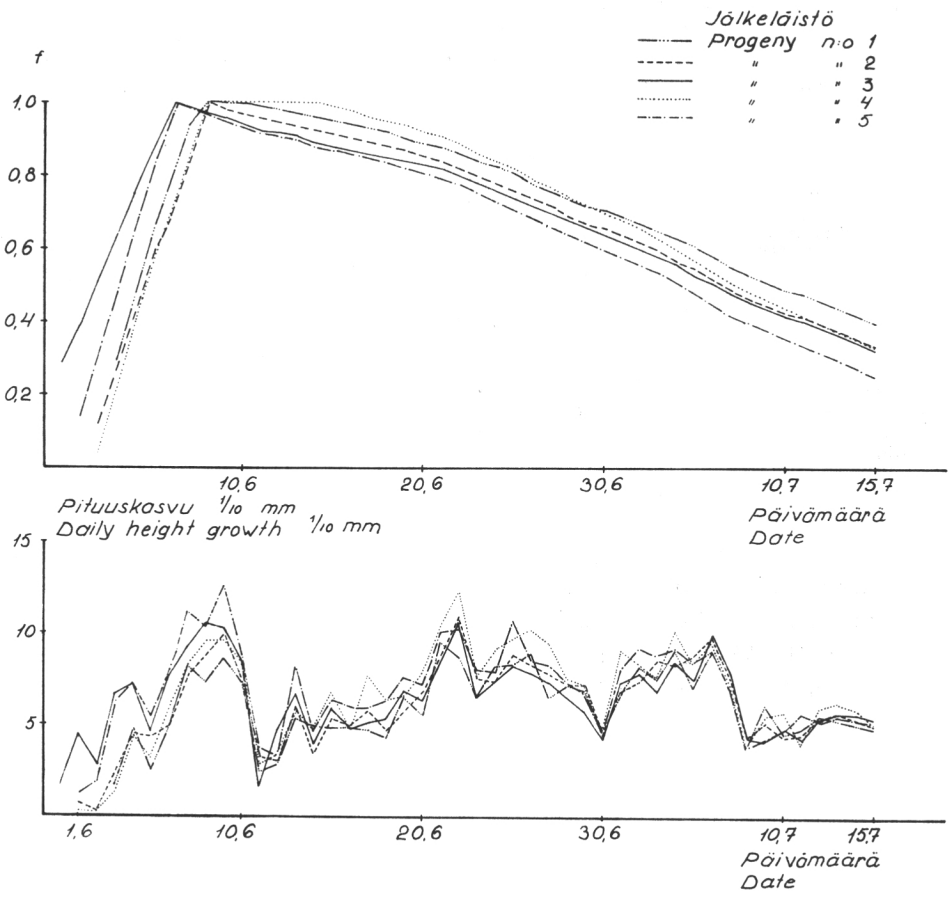
Myös neulasten pituuskasvuhavainnot käsiteltiin edellä kuvatulla laskentamenettelyllä. Neulasten vuotuisen pituuskasvun alkukehitystä ei voitu määrittää tarkasti, koska nyt sovelletun mittausmenetelmän avulla alkuhavaintojen teko oli liian epävarmaa. Laskennan lähtökohdaksi jouduttiin ottamaan rajakohta, jolloin neulasten pituus oli 5 mm. Lisäksi neulasten päivittäiset kasvumittaukset lopetettiin heinäkuun puolivälissä, jonka jälkeen neulasmittaukset tehtiin kolme kertaa viikossa. Näiden rajoitusten vuoksi päivittäisiin mittauksiin pohjautuva laskenta ulottuu toukokuun lopusta heinäkuun 15. päivään saakka.

Laskennan tulokset on esitetty kuvassa 4. Kuvaan 5 on piirretty rinnakkain jälkeläistöjen mitattu neulasten pituuskasvu ja funktion f kulku. Kuvissa on esitetty kasvainten yläosasta läheltä latvasilmua mitattujen neulasten päivittäinen pituuskasvu. Mitatun ja lasketun pituuskasvun välinen korrelaatiokertoimen neliö (selitysaste) oli neulasten osalta kaikissa tapauksissa pienempi kuin kasvainten pituuskasvun laskennassa saatu lukuarvo. Heikompi selitysaste johtunee lähinnä mittausvirheistä.



Kuvat 4 a—e. Kuvan yläosa: päivittäinen kumulatiivinen respiraatio (yhtenäinen viiva) ja funktion f kulku (katkoviiva). Kuvan alaosa: neulasten mitattu (yhtenäinen viiva) ja laskettu (katkoviiva) päivittäinen pituuskasvu sekä niiden välisen korrelaatiokertoimen neliö. a: jälkeläistö n:o 1, Suomenniemi; b: n:o 2, Sulkava; c: n:o 3, Punkaharju; d: n:o 4, Tammela; e: n:o 5, Posio.

Figs. 4 a—e. Upper part of figure: Daily cumulative respiration (solid line) and shape of function f (broken line). Lower part of figure: Daily length increment of needles as measured (solid line) and as predicted (broken line) and the square of their correlation. a: Progeny no. 1, Suomenniemi; b: no. 2, Sulkava; c: no. 3, Punkaharju; d: no. 4, Tammela; e: no. 5, Posio.



Kuva 5. Kuvan yläosa: funktion f kulku. Kuvan alaosa: jälkeläistöjen neulasten mitattu päivittäinen pituuskasvu.

Fig. 5. Upper part of figure: Shape of function f. Lower part of figure: Daily height growth of the needles of the progenies.

Neulasten pituuskasvun yleinen luonne on nähtävissä funktion f muodon avulla. Pituuskasvu nousee hyvin pian maksimivaiheeseen, jonka jälkeen pituuskasvukehitys alkaa hiljalleen vähetä. Samanlaisen neulasten vuotuisen kehitysrytmin on todennut mm. K i e n h o l z (1934). Kasvainten keskiosista mitatut neulaset kehittyivät tässä kokeessa kasvainten kärkiosien neulasia nopeammin. Neulasten kasvun parametrien arvot on esitetty taulukossa 3. Mittausten puutteellisuuden takia ei parametrien a_1 ja s_c arvoja voitu laskea. Myöskään tilastollista testausta ei suoritettu, koska mittaustarkkuus ei ollut riittävä toistoittaisiin vertailuihin.

Neulasten pituuskasvun päättymisen toteamiseksi laskettiin aineistosta, kuinka monta % pituuskasvusta oli tapahtunut tiettyyn mittauspäivään

Taulukko 3. Kasvainten kärkiosan neulasten päivittäinen pituuskasvu. Kasvumallin avulla lasketut parametrien arvot. Selitys tekstissä.

Table 3. Daily growth of needles at the tip of the leader. Values for parameters as calculated on the basis of the growth model. Explanations in text.

Jälkeläistön n:o ja kotipaikkakunta *No. of progeny and its provenance*	Funktion f kulkua osoittavat lukuarvot. Kaksi esimerkkipäivää. *Values giving shape of function f. Examples for two days*		Maksimikasvujakson alkurespiraatio (s_1) *Initial respiration for period of maximum growth (s_1)*	Maksimikasvujakson loppurespiraatio (s_2) *Final respiration for period of maximum growth (s_2)*	Parametri a *Parameter a*	Pituuskasvusta tapahtunut 30. 07. 73 % loppuarvosta *Percentage of final growth as of July 30th, 1973*
	03. 06. 73	05. 07. 73				
1 Suomenniemi	0.40	0.64	2 869	4 830	0.00158	94.0
2 Sulkava	0.37	0.57	5 989	5 991	0.00180	95.8
3 Punkaharju	0.70	0.53	4 205	4 207	0.00183	96.8
4 Tammela	0.28	0.60	5 197	8 791	0.00188	94.0
5 Posio	0.59	0.48	3 594	3 596	0.00214	97.2

mennessä (taulukko 3). Näiden lukujen perusteella neulasten pituuskasvu on jatkunut aina elokuun alkupuolelle saakka. Noin 90 % neulasten kokonaispituuskasvusta on tapahtunut heinäkuun loppuun mennessä. Myös Rutter (1957) on todennut männyn neulasten pituuskasvun jatkuvan ainakin heinäkuun lopulle tai elokuun alkupuolelle.

4. TULOSTEN TARKASTELUA

Tutkimusta tarkasteltaessa on korostettava, että työn painopiste on geneettisen aineiston käsittelyssä. Käytetty laskentamenetelmä vaatii välttämättä tietokonetta. Tämä nostaa tutkimuskustannuksia, mikäli aineisto on kovin laaja, sillä jo yhden havaintosarjan käsittely vie runsaasti keskikokoisen tietokoneen koneaikaa. On kuitenkin todettava, että kasvurytmin osalta on osoitettu korkeita heritabiliteettiarvoja (esim. Stern 1962, Wright 1963, Dietrichson 1967), joka viittaa siihen, että ympäristötekijöiden merkitys puiden kasvurytmissä ei ole kovin dominoiva. Sen tähden luotettavien johtopäätösten tekoon riittää suhteellisen suppea aineisto, vaikka geneettisestä yksilövaihtelusta johtuen aineistot yleensä suositellaan suuriksi (vrt. Tigerstedt 1972). Esim. tässä kokeessa oli neljä toistoa jokaista viittä alkuperää kohti. Vaikka eroja pystyttiin havaitsemaan, vapaapölytteisten jälkeläistöjen yksilövaihtelu oli monien tunnusten kohdalla niin suuri, että aineiston tilastollinen testaus tuotti vaikeuksia.

Laskentamenetelmästä voidaan edelleen todeta, että sen avulla saadaan uusia parametrejä, jotka ovat sellaisenaan käyttökelpoisia tilastolliseen testaukseen. Mikäli laskentamallin antama selitysaste jää heikoksi, parametrien testaus ei kuitenkaan ole tarkoituksenmukaista. Samoin laskentamenettelyn avulla voidaan ottaa huomioon pituuskasvun intensiteetti joko päivittäisen pituuskasvun tason tai maksimaalisen kasvujakson pituuden perusteella. Laskentamalliin kuuluvaa funktiota f käyttäen on lisäksi mahdollista erottaa tietyn pituisia kasvujakson osia.

Kasvujaksoa määrättäessä voidaan ja tulisikin luopua päivien käytöstä ajan kuvaajana. Fysiologiseen kehitystilaan pohjautuvalla laskennalla alkuperien väliset erot saadaan suhteellisesti oikeammin kuin käytettäessä vuorokausia tai päivämääriä kehityksen osoittajina (Hari 1972, Sarvas 1972 ym.). Esim. vuotuisen kehityksen etenemisessä yksi sääsuhteiltaan suotuisa päivä voi vastata kahta tai kolmea epäsuotuisaa päivää. Jos esim. kehityksen etenemisen kuvaamiseen käytetään aikayksikkönä päiviä, oletetaan fenologiassa samalla usein kaikki päivät samanarvoisiksi, mikä sisältää huomattavan virhelähteen. Sen sijaan fysiologinen

kehitystila ajan kuvaajana on ympäristötekijöihin sidottu, vailla rajakohtia oleva kestotapahtuma.

Nyt käytetyn pituuskasvumallin sovellutusmahdollisuuksista voidaan vielä mainita, että kasvumallin selitettäväksi muuttujaksi ei Suomen oloissa tarvita fysiologisen kehitystilan rinnalla muuta kuin lämpötilaan suhteutettu respiraatio tai Sarvaksen (1972) esittämä aktiivin periodin etenemisnopeuden ja lämpötilan välinen riippuvuus. Esim. auringon säteilyn ottaminen mukaan malliin ei ole parantanut sen selitysastetta (Hari ja Leikola 1974). Nyt käytetty menettely on sikäli helppo toteuttaa, koska ympäristöä ei tarvitse yrittää homogenisoida esim. käyttämällä kasvatuskammiota, jotta tuloksia voitaisiin verrata keskenään (Magnesen 1969, 1971). Samoin kokeita on mahdollista verrata mallin avulla keskenään, vaikka ne olisi tehty eri paikoilla tai eri vuosina (Hari ja Leikola 1974).

Mittausten luotettavuuden arviointi voidaan tehdä kasvumallin antaman selitysasteen nojalla (vrt. Hari 1972). Kasvainten osalta tämän työn mittaukset näyttävät onnistuneen hyvin, koska selitysasteet mitatun ja lasketun pituuskasvun välillä olivat kaikissa tapauksissa yli 90 %. Nämä arvot vastaavat Harin et. al. (1970) ja Harin (1972) tutkimuksissa todettuja selitysasteita.

Neulasten kohdalla ei ilmeisesti vältytty mittausvirheiltä. Tähän olivat syynä lähinnä mittauskohteen pienuus ja siitä johtuvat mittaushankaluudet. Silti voidaan osoittaa, että työntötulkilla tehtyjen neulasmittausten todellinen tarkkuus oli $\pm$ 0.3 mm. Virhe tasoittui satunnaisesta luonteestaan johtuen laskennassa verraten hyvin, sillä selitysasteet olivat korkeita, vaikkakin ne vaihtelivat laajoissa rajoissa.

Toisena mahdollisten virheiden aiheuttajana olivat lämpötilan mittaamisesta johtuvat tekijät. Tässä kokeessa lämpötilan mittauksessa käytettiin termoelementtiä, jonka termoelementtilangat mittasivat kasvaimen ympärillä olevan ilman lämpötilan, mikä ei anna kuvaa kasvainten todellisista lämpöarvoista (vrt. Leikola ja Pylkkö 1969, Sarvas 1972). Luotettavin kuva kasvainten todellisista lämpöarvoista olisi saatu, jos piirturin tuntolanka olisi sijoitettu kasvaimen sisään. Mallin selitysasteisiin lämpötilan mittaamisesta johtuvilla tekijöillä ei ole olennaista vaikutusta, mikäli eri ajankohtien suhteelliset lämpötila-arvot tulevat oikein määritettyä.

Aineistona olleiden jälkeläistöjen geneettisten erojen luonnetta tarkasteltaessa lähtökohtana oli tavallaan provenienssin sisäinen yksilövaihtelu, sillä vertailtavat jälkeläistöt olivat yksittäisten eteläsuomalaisten mäntykantapuiden vapaapölytysjälkeläistöjä kahdesta vartekokoelmasta. Etelä-Suomen alueella männyn ominaisuuksissa tapahtuva vaihettuminen on vähittäistä ja portaatonta (klinaalista), minkä vuoksi selviä provenienssi-

rajoja ei pystytä havaitsemaan, eikä sellaisten olemassaoloa voida toisaalta odottaakaan metsäpuiden geenivaihdon tehokkuuden tuntemuksen valossa (K o s k i 1970). Jälkeläistöjen välisten erojen olemassaolo osoittaa, että provenienssin sisällä on nähtävissä samantapaista pituuskasvun vaihtelua kuin provenienssien välillä (vrt. N a m k o o n g 1969).

Kokeessa mukana ollut yksi pohjoista alkuperää edustava jälkeläistö (n:o 5, Posio) ei osoittanut toisista poikkeavaa pituuskehitystä, vaikka monien viitteiden mukaan näin olisi odotettavissa (esim. V i n c e n t 1957, D i e t r i c h s o n 1964, S a r v a s 1967). Ilmeisesti kloonikokoelmassa pohjoiselta alueelta peräisin olevan kloonin emikukat ovat pölyttyneet eteläisen alueen siitepölyllä. Jälkeläistössä pohjoisuutta kuvastavat ominaisuudet eivät ehkä pääse dominanssin tai epistasian takia näkyviin (T i g e r s t e d t 1972). Tosin pieniä viitteitä (päivittäinen pituuskasvun taso oli intensiivisintä, neulasten pituuskasvu päättyi muita aikaisemmin) pohjoisuutta kuvastavista ominaisuuksista on havaittavissa (vrt. O d i n 1972).

Pituuskasvumittausten yhteydessä havaittiin toisena kasvukautena koetaimien pituuskasvussa taimitarhakasvatukselle ominaisia erikoispiirteitä. Normaalisti männyn uuden verson kasvu tapahtuu edellisenä vuonna muodostuneesta silmusta (vrt. esim. K o z l o w s k i 1962). Kesän kuluessa kehittyvä kasvainaihe on jo syksyllä valmis kaikkine kääpiöversoaiheineen, ja seuraavana keväänä (alkukesällä) tapahtuu oikeastaan vain uuden verson purkautuminen silmusta. Tässä kokeessa toisen kasvukauden alussa pituuskasvu ei ollut pelkästään silmusta purkautuvan verson pidentymistä, vaan ensimmäiset pituuskasvun merkit olivat edellisen vuoden alkeisneulasten muodostamien nivelvälien venymistä. Tämä johtui siitä, että ensimmäisenä kasvukautena, jolloin uusien solujen muodostumista tapahtuu koko pituuskasvujakson ajan, latvasilmu on muodostunut tavallaan alkeisneulasten muodostaman latvaruusukkeen sisälle, ja nivelvälisolujen koon suureneminen on jäänyt osittain kesken (vrt. K o z l o w s k i 1971 s. 88). Keväällä tapahtuneen nivelvälien lopullisen pidentymisen johdosta taimien pituuskasvu ja sen ajoittuminen ovat ehkä muuttuneet aikaisemmaksi verrattuna normaaliin männyn vuotuiseen pituuskasvun kulkuun.

Nyt sovellettua pituuskasvumallia voitaneen käyttää paitsi kasvurytmierojen osoittamiseen eri alkuperien välillä myös varhaistestimenetelmiin. Puiden vuotuista pituuskasvurytmiä on pidetty erityisen sopivana juuri tähän tarkoitukseen, koska alkuperien välisten vuotuisten pituuskasvurytmierojen voidaan olettaa pysyvän samanlaisina iän muuttuessa, sillä vuotuinen pituuskasvujakso on tärkeä tekijä puun koko elinikäiselle sopeutuneisuudelle tiettyyn ympäristöön (S c h m i d t 1963, H a g n e r 1970 a, M i k o l a 1973). Tosin yleensä taimien vuotuinen pituuskasvujakso

on pitempi kuin emopuiden, mutta tämä ei muuttane alkuperien välisiä suhteellisia eroja (vrt. Kozlowski 1971, s. 262). Vuotuisen pituuskasvurytmin käyttöä varhaistestitunnuksena tukee myös se seikka, että pituuskasvurytmin erot ovat helpoin mittausmenetelmin todettavissa, ja lisäksi vuotuisen pituuskasvujakson tunnukset ovat kiinteästi yhteydessä pituuskasvun määrään (Schröck ja Stern 1953, Schmidt 1963, Nanson 1968, Sinko 1971). Pyrittäessä arvostelemaan geneettisesti puita jo taimivaiheessa, saattaisi nyt käytetty pituuskasvurytmin tarkastelutapa avata uusia mahdollisuuksia.

5. TIIVISTELMÄ

Tutkimuksessa on tarkasteltu männyn latvakasvainten ja neulasten vuotuista pituuskasvurytmiä pyrkien selvittämään päivittäisten kasvumittausten pohjalla tehdyn kasvumallin avulla jälkeläistöjen välisiä eroja. Aineistona oli 5 männyn pluspuiden vapaapölytysjälkeläistöä kahdelta Etelä-Suomen pluspuiden klooneista koostuvasta vartekokoelmasta. Jälkeläistöjä tarkasteltiin lähinnä provenienssin sisäisen yksilövaihtelun kannalta.

Taimet kasvatettiin taimitarhaolosuhteissa avomaalla turvelaatikoissa. Toisena kasvukautena kasvainten ja neulasten pituuskasvumittaukset suoritettiin joka päivä valtataimista (3 kpl/toisto/jälkeläistö). Kasvainten pituuskasvu mitattiin viivottimella ja neulasten piteneminen työntötulkilla.

Päivittäisiä pituuskasvuhavaintoja hyväkseen käyttävä laskentamenettely (kasvumalli) erotteli sekä kasvainten että neulasten vuotuisessa pituuskasvurytmissä 3 eri vaihetta: nousevan kasvun vaihe, maksimaalisen kasvun vaihe ja laskevan kasvun vaihe. Nämä vaiheet — niiden ajoittuminen ja pituus — olivat alkuperittäin erilaisia. Lisäksi selvitettiin päivittäinen pituuskasvun taso (so. miten intensiivistä pituuskasvu on kasvukauden aikana), joka vaihteli myös alkuperittäin.

Kasvumalli selitti 93.4—96.0 % kasvainten päivittäisen pituuskasvun vaihtelusta ja 77.2—92.6 % neulasten päivittäisen pitenemisen vaihtelusta. Kasvainten ja neulasten vuotuinen pituuskasvun kulku oli yhdenmukainen jälkeläistöjen välisten erojen toteamisen kannalta. Kasvainten keskiosien neulaset kehittyivät kasvainten kärkiosien neulasia nopeammin.

Tulosten tarkastelussa pohditaan nyt sovelletun kasvumallin käyttömahdollisuuksia provenienssikokeissa sekä eri alkuperien geneettisessä varhaistestauksessa.

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7. SUMMARY

The annual growth rhythm of the terminal leaders and needles of pine *(Pinus sylvestris* L.*)* has been studied. The differences between progenies has been elucidated using a growth model constructed on the basis of daily growth measurements.

The material consisted of open-pollinated progeny from 5 pine plus trees growing as grafted clones in two gene banks for southern Finland (Table 1). The intra-provenance variation was studied by means of progenies. The seedlings were raised out of doors in peatfilled boxes at the Ruotsinkylä Tree Breeding Station nursery (N 60°22′, E 24°57′, elev. 60 m), run by the Finnish Forest Research Institute, during the summers of 1972 and 1973. During the second growing season, daily growth measurements were made on the leaders and needles of the dominant seedlings (3 seedling/replication/progeny). The growth measurements of the leaders were made with a ruler to the nearest 0.5 mm and those of the needles with sliding calipers to the nearest 0.1 mm. The temperature was recorded by means of thermocouples.

These data were entered into the dynamic growth model presented by Hari et. al. (1970). The independent variables were the physiological stage of development of the seedling and the theoretical respiration as a function of temperature. Using the model, growth during one growing season can be readily divided into different phases. The method has been described by Pohjonen and Hari (1973) and Hari and Leikola (1974). The growth model as applied to this study is characterized by equations 1, 2, 3, and 4. The dependence of function f on s is shown in Fig. 1.

The growth model indicated that these are three different phases in the annual growth rhythm of both leaders and needles: the phase of increasing growth rate, the phase of maximum growth rate and the phase of decreasing growth rate (Figures 2 a—e and 4 a—e). These phases — their timing and duration — varied from progeny to progeny (Figures 3 and 4). In addition, the daily growth intensity was found to vary between progenies (parameter a, see Tables 2 and 3).

The model explained 93.4—96.0 % of the variation of the daily height growth of the leaders and 77.2—92.6 % of the variation of the daily needle elongations.

The annual growth rhythms of the leaders and needles were so similar that differences between progenies could be detected based on either of these characteristics. The needles at the middle of the leaders developed faster than the needles at the tip. It was inferred that intra-provenance variation occurred between the progeny of plus trees from southern Finland.

The possibilities for applying the presently used growth model in provenance trials and genetic early-tests of progenies is discussed.

ANNUAL PRIMARY PRODUCTION AND NUTRIENT CYCLE IN SOME SCOTS PINE STANDS

EINO MÄLKÖNEN

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PREFACE

The present study has been carried out in the Department of Soil Science, Finnish Forest Research Institute, since 1967. Its subject matter deals with the inherent fertility of forest soil, and at the same time it gives some background information for the Department's research project concerning forest fertilization requirements. At the sample collection stage the present study was included in the Finnish project of the International Biological Programme.

Professor P. J. V i r o, Head of the Department of Soil Science, gave the idea of the study, and he has supported its progression and has guided the preparation of the manuscript. My supervisor at the University of Helsinki, Professor P e i t s a M i k o l a, has shown interest in the progress of the study; he has also checked the manuscript. The discussions with Professor M a t t i L e i k o l a have been of great help in the accomplishment of the study. He has also read the manuscript. Professors Y r j ö V u o k i l a and P e k k a K i l k k i have familiarized themselves with the part of the manuscript concerned with biomass estimate methods and have given much valuable advice. Mr. O l l i H a l o n e n, M. Sc., has advised me in the methods of chemical analysis and checked the relevant part of the manuscript. From my closest colleague Mr. E r k k i L i p a s, Lic. For., I have received valuable advice at different stages of the work.

The laborious work of the nutrient determinations was carried out in the laboratory of the Department of Soil Science by many helpful persons. The computing was carried out with the assistance of Mrs. M a r j a H u o t a r i, B.Sc. The typing and drawing of the figures was done with great skill by Miss H i l l e v i S i n k k o. The preliminary translation of the Finnish manuscript was done by Mr. R. M i l t o n and the English manuscript was checked by Mr. J o h n D e r o m e, B.Sc.

During the main part of this research period I have worked as a research scholarship holder or assistant researcher to the National Research Council

for Agriculture and Forestry. Furthermore the grants from the Foundation for Research of Natural Resources in Finland and from the Research Foundation of Kemira Oy have made it economically possible to carry out the study.

I wish to express my sincere thanks to all the persons and institutions mentioned above.

Helsinki, October 1974

Eino Mälkönen

CONTENTS

Page

1. Introduction 7
   11. Main features of the nutrient cycle 7
   12. Primary production and nutrient requirements of a forest ecosystem ... 9
   13. The biomass estimate methods 11
   14. Aims of the study 12
2. Methods and material 14
   21. Main features of the study 14
   22. Sample plots 15
   23. Sampling procedure 18
   24. Laboratory work 22
      241. Dry weight determinations 22
      242. Methods of chemical analysis 23
   25. Statistical procedure 24
3. Distribution of dry matter in a stand 28
   31. Tree crop 28
      311. The stem 30
      312. The crown 31
      313. Below-ground part 32
   32. Ground vegetation and shrubs 33
   33. Annual biomass production 34
      331. Tree crop 34
      332. Ground vegetation and shrubs 37
   34. Annual litter production 38
      341. Tree crop 38
      342. Ground vegetation and shrubs 40
      343. Decomposition rate of litter 41
   35. Amount of humus in the soil 42
   36. Annual balance of biomass 44
4. Distribution of nutrients in a stand 47
   41. Nutrient stores in soil 47
   42. Nutrient amounts bound by the vegetation 51
      421. Tree crop 51
         4211. Internal nutrient cycle in the tree 53
      422. Ground vegetation and shrubs 54
   43. Nutrient amounts in the litter crop 55
   44. Nutrient amounts leached from the canopy by precipitation 57

Page

5. Nutrient cycle in a stand 60
51. Distribution of nutrients throughout the biological cycle 60
52. Annual nutrient balance of a stand 61

6. Discussion 65
61. Primary production 65
62. Nutrient cycle 67

7. Summary 69

References 71

Selostus 77

Appendices 78

Abbreviations used

d overbark diameter at breast height
h tree height
$\frac{\triangle h}{h}$ crown ratio
v overbark stem volume
o.b. overbark

1. INTRODUCTION

11. Main features of the nutrient cycle

The term »nutrient cycle» is usually used to describe the processes in which nutrients are transferred from the soil to plants, circulated through living organisms and eventually returned to the soil for re-use by plants. The main features of this cycle in a forest ecosystem are generally known, but in fact the nutrient cycle is a complex chain of events comprising several subcycles of varying durations. It should also be remembered that the nutrient cycle does not take place in a closed system; nutrients are constantly being lost while new ones enter the ecosystem.

The principal nutrient sources of vegetation are nutrients liberated by weathering and those which enter the soil from the atmosphere. The biomass production of a plant community could not, however, be very great if it were not for the decomposition of dead organic matter by soil micro-organisms, resulting in the release of nutrients in a form available to plants. Thus, in every independent ecosystem, primary producers and decomposers are the basic agents that sustain the nutrient cycle. In studying the interaction of the components of an ecosystem, three aspects are usually examined: the energy, water, and nutrient cycles. Interest has frequently been focused on the nutrient cycle, since it has often been easy to increase the production of ecosystems by applying nutrients.

It would appear that the nutrient cycle consists of a biological cycle and a geological cycle (R e m e z o v 1958). The biological cycle mainly concerns the transfer of nutrients between the soil and the vegetation. The geological cycle refers to the transfer of nutrients from the sea and atmosphere to the ecosystem, their liberation by weathering, and their loss due to leaching. So in fact the biological cycle represents merely one link in the geological cycle.

From the standpoint of the nutrient cycle, the soil can be regarded as being mainly a chemical system in some respects and a biological one in others (J a n s s o n 1971). Mineral nutrients taken up by plants as cations, such as calcium and potassium, belong almost entirely to the chemical sys-

tem. The supply of these nutrients, available to plants, is almost completely controlled by chemical reactions. On the other hand, nitrogen belongs almost exclusively to the biological system, governed by the activity of heterotrophic soil microflora — the mineralization and immobilization relationships. Phosphorus can probably be regarded as belonging to both the chemical and the biological systems because the soil contains phosphorus compounds in both inorganic and organic forms.

All nutrients bound by organic matter are included in the biological cycle, and therefore make up a great potential store of nutrients. The cycling of such nutrients varies in duration according to the lifetime and rate of decomposition of the different compartments of a plant. In a stand, for instance, it is obvious that the nutrients contained in the annual leaf crop have a shorter cycle than those in wood. Thus, a distinction can be drawn, for instance, between the annual and the lifetime cycle of nutrients (Rodin & Bazilevich 1965, p. 5). Study of forest nutrition has largely been concentrated on the annual cycle, which is usually depicted in terms of the annual amount of nutrients that is bound to the vegetation and the amount that is returned to the soil in the litter crop — *i.e.*, in terms of the annual nutrient balance. In point of fact, the annual nutrient balance of a stand represents the balance between the amounts of nutrients incorporated in the cycles of varying duration.

In the 1950's several researchers began to study the nutrient balance of forests as a whole from the standpoint of Tansley's (1935) ecosystem concept. In the Soviet Union, Remezov *et al.* (1955) studied the nutrient cycle in stands of different tree species in the southern part of the coniferous zone. Ovington (1957, 1959) concentrated on the biomass production and nutrient requirements of Scots pine plantations in the British Isles at different stages of their development. These early investigations soon led to the publishing of a large number of studies on the structure and functioning of the ecosystem, from which Ovington (1962) and Sukachev & Dylis (1964) collated information concerning biomass production and nutrient and energy cycles in different kinds of forest. Similarly, Rodin & Bazilevich (1965) reviewed the literature concerning the dynamics of organic matter and nutrient cycles in different vegetation zones. Research in this field has recently been stimulated by the International Biological Programme (IBP), which was started in the early 1960's in order to elucidate the biological bases of ecosystem production. The programme has already led to a wide variety of preliminary information on the functioning of ecosystems (e.g. Eckardt 1968, Reichle 1970, Ellenberg 1971).

12. Primary production and nutrient requirements of a forest ecosystem

In a stand the trees and the ground vegetation are the primary producers and the ratio between their nutrient requirements depends among other things on the stage of stand development. Obviously the nutrient consumption of the ground vegetation at the seedling stage is many times greater than that of the seedling crop. As the seedlings grow up and eventually form a closed stand, the amount of ground vegetation diminishes. The resulting gradual death and decomposition of ground vegetation releases large quantities of nutrients which can promote the growth of the trees at the very time when their nutrient requirement is at its greatest (O v i n g t o n 1959). The period of the highest total production by trees is approximately simultaneous with the maximum annual current increment of the stemwood (R e m e z o v & P o g r e b n y a k 1965, p. 111). In *Myrtillus-* and *Vaccinium*-type [1]) pine stands established by sowing, this stage of stand development is reached in southern Finland between the ages of 30 and 45 years (K a l l i o 1961). Thus, the highest nutrient requirement of a tree crop occurs at a fairly early stage in its development. Due to self-pruning and natural thinning of the trees, the nutrient consumption of the ground vegetation increases again.

The primary production of an ecosystem can be depicted by L ö n n r o t h's (1929) simple model for the stem volume development of the trees (Fig. 1). It can be seen that, during a given period of measurement, a part of the stand biomass is retained and another removed as litter or standing dead. Both of the parts grow during this period, the retained part grows for the whole period, but the removal grows only until its death or detachment from the plant. This model can be used to describe the biomass production of the trees, the ground vegetation or the entire plant community.

The nutrient consumption of a tree crop per unit of dry matter produced varies widely from one stage of development to another, due mainly to relative changes in the growth of different compartments of the trees with age. The share of needles, rich in nutrients, and roots in the total production of a tree is much larger at the seedling stage than later on. The nutrient content of the wood is lower than that of the other compartments of the tree, and so the stemwood binds a relatively smaller amount of nutrients, although they remain there for a much longer time and can be removed by tree harvesting.

Flowering and seed production call for such large amounts of nutrients that they may even restrict the growth of the stemwood; in fact, good seed years can be detected from the unusual thinness of the annual rings (S i r é n 1961). The decrease in wood production due to an abundant seed crop has

[1]) According to Cajander's classification of forest types (see e.g. C a j a n d e r 1949).

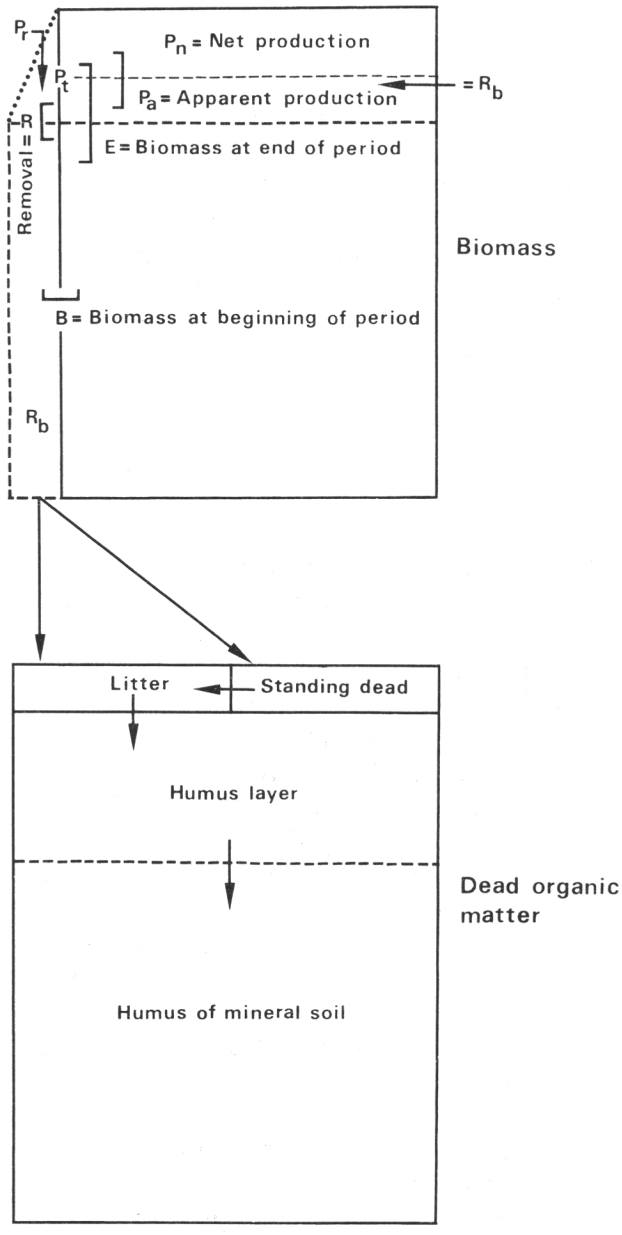

Fig. 1. Model showing the flow of organic matter in an ecosystem (L ö n n r o t h 1929).

P_t = Total production
P_r = Production of removal
R_b = Basic removal

not been studied in detail, but the cone crop of a spruce, for instance, may contain an amount of dry matter almost equal to the annual production of stemwood (M o r k 1942). The effect of seed production on tree growth can thus be considerable.

Biomass production in forests is generally fairly high compared to that in other plant communities growing on sites with an equal level of soil fertility. H a r t m a n n (1959) considers this to be mainly due to the large quantities of nutrients which are involved in the biological cycle between the forest soil and its plant cover.

13. Biomass estimate methods

In general, heartwood and rough bark are included in the biomass in addition to living tissues, but not dead branches (N e w b o u l d 1967). The stemwood production of trees has been the object of extensive study. In a larger sense the biomass production of a stand has been estimated either directly by the harvesting method, or indirectly by measuring gas exchange, leaf area or chlorophyl content (L i e t h 1965). When using the harvesting method, the estimation of biomass can be based on one of the following sampling methods:

1) Mean tree method. The dry weight and biomass production of a tree crop are determined on the basis of one or more trees taken to represent the mean for the biomass (e.g. R e m e z o v *et al.* 1955). Results per unit area are calculated from the dry weight of the mean tree and the total number of stems in the stand. The main drawback of the Mean tree method is the extreme difficulty of finding a tree that really is representative of the mean biomass of different tree compartments (O v i n g t o n & M a d g w i c k 1959).

2) Regression estimate method. This is based on the dependence of the dry weight of randomly selected sample trees on certain tree characteristics. As the dry weight of all trees or tree compartments, also belonging to other tree classes besides the sample trees, can be estimated from these relationships, the method is also called the Allometric method (e.g. S a t o o 1967). It is an application of the conventional Stand volume estimation method, which K i t t r e d g e (1944) found to be equally applicable for estimating the biomass of needles. In order to improve the representativity of the sample trees taken in this method, stratification according to crown class, for instance, has also been used (C r o w 1971).

3) Complete enumeration method. Every individual plant within a fairly small sample area is collected (O v i n g t o n *et al.* 1967). This method is, of course, best suited for determining the biomass of ground vegetation.

Determining the dry weight of roots has proved to be particularly laborious. Most earlier studies on root systems (e.g. Laitakari 1928, Kalela 1954) have concentrated on the morphology and ecology of roots, and so they give very little help in determining their biomass. As it is impossible to measure root production directly by excavating the roots and weighing them, efforts have been made to derive equations which depict the dependence of the dry weight of root systems on some above-ground compartment of the trees (Kira & Ogawa 1968). In several biomass determinations the root system has been completely ignored, and it has been assumed that root biomass remains fairly constant after canopy closure.

Thus, a successful method has not yet been developed for determining the biomass production of every compartment of a plant. Attempts have been made to improve the comparability of research results by suggesting recommendations concerning the measurement of certain basic characteristics (Newbould 1967).

14. Aims of the study

The circulation of nutrients associated with organic matter in a stand is closely linked with many silvicultural questions. Ovington (1960) and Sukachev (1960) both stress the importance of such ecosystem research as a basis for site classification.

With the continual increase in the consumption of wood, several forest improvement measures are being used to increase wood production. Almost without exception these measures also affect the nutrient status of the site. The need for information about the total production of biomass has also become evident in studies on complete tree utilization (Young 1964, Hakkila 1972). Along with the intensification of wood production and tree harvesting, greater effort should be put into the maintenance and improvement of the fertility of the site. Studies on fertilization requirements also call for adequate knowledge of natural nutrient supply and of nutrient circulation.

In view of this lack of broad research into forest nutrition the present study aims at providing an overall picture of the distribution, consumption, and circulation of the macro nutrients — nitrogen, phosphorus, potassium, and calcium — in a stand. Of course, it is not possible in a study of this type to deal with all the questions pertaining to this problem in detail, especially since so much attention had to be paid to the adaptation of biomass estimate methods. Instead, the study is primarily concerned with finding answers to the following questions:

— In what way are the dry matter and annual primary production of a stand distributed between different compartments of the vegetation?

— What are the nutrient requirements of annual primary production?

— In what way is the annual nutrient balance of a stand made up?

As regards research methods, the study can be divided into two parts:

1) Determination of the total biomass of a stand, and study of its annual progression.

2) Study of the distribution of the nutrients and their annual cycle in a stand.

Although these two questions are closely connected with each other, it is more practical to treat dry-matter quantities and nutrients separately.

2. METHODS AND MATERIAL

21. Main features of the study

Information about the distribution of organic matter and measurements of primary production and biomass removal will provide a basis for the study of the biological nutrient cycle. Quantitative investigation of the organic matter in a stand calls for the collection of samples from the trees, shrubs, ground vegetation, litter, and humus; and subsequent determinations of their dry weight. The second phase is to determine their nutrient content. It is possible, on the basis of this information, to outline the annual nutrient balance of a stand.

The dry weight of the tree crop is determined by the Regression estimate method in the following phases:

1) The dry weight of the different compartments of the sample trees is determined using dry-matter samples.

2) Regression equations are derived to express the dependence of the dry weight of the sample tree compartments on fairly easily measurable tree characteristics.

3) The conversion of results to a unit area basis is then accomplished by applying the regression equations to the relevant characteristics of all the trees in the sample plot.

The dry weight of the shrubs and ground vegetation was obtained on the basis of the dry weight of samples collected from sample squares. The organic matter in the humus layer and the surface soil layer of the mineral soil was determined from soil samples.

For a study of the annual nutrient cycle, however, the annual production of the biomass is more important than its total quantity. Since yield studies have been almost exclusively limited to the measurement of stem volume, great difficulties are encountered in determining the production of other tree compartments. Owing to the difficulty of determining the production of the root system no direct study on the biomass production of roots has yet been carried out. For this reason it has had to be assumed that the relative

growth of the below-ground part of a tree equals that of the above-ground part.

In the study of the annual development of a stand the removal of biomass must also be taken into account. The litter crop produced by the above-ground part of the trees can be measured using litter funnels, for example. The dry-matter loss of the root system was assumed to be proportional to that of the above-ground part, as was the case for the annual production, too. As the litter crop of the above-ground part of ground vegetation cannot be measured directly, it had to be assumed that it was equal to the annual biomass production, just as would be the case in a stabilized ecosystem.

Decomposition of litter has been studied intensively with regard to the biological cycle, though not much is yet known about the rate at which nutrients are circulated under natural conditions. In the present study an attempt was made to estimate the decomposition rate of needle litter by observing its dry-matter loss. The release of nitrogen from litter was studied with an isotope trial.

A major factor which affects the annual nutrient requirement of a tree crop is the internal nutrient cycle of trees: the translocation of nutrients from dying tissue to young and growing compartments. The quantities of nutrients translocated from the oldest needles before abscission were estimated by measuring the weight and analysing the nutrient content of needles of different ages from the same trees.

Precipitation carries nutrients into the ecosystem, washes away and extracts nutrients from plants, and finally leaches them away, out of the reach of the plants. The quantities of nutrients reaching the surface of the soil in rain water were studied by measuring the amounts of gross precipitation, throughfall, and stemflow; and then determining their nutrient content. However, the part played by leaching in the nutrient cycle had to be omitted from the study.

22. Sample plots

Three sample plots representing different stages of stand development, ranging from the stage of canopy closure to the stage of maximal annual current increment, were established. All the experimental stands had been established by sowing and were composed exclusively of pine. The soil type of all the stands was podzol and the humus layer was raw humus. Although an effort was made to place the sample plots in the experimental stands on as homogeneous an area as possible regarding the soil and the tree crop, they did not, due to previous cuttings and variable site fertility, form a continuous series representing different stages of stand development.

Table 1. General data concerning the experimental stands.

Characteristic	Sample plot No. 1	Sample plot No. 2	Sample plot No. 3
Location	N 60°31′ E 23°53′	N 61°40′ E 24°19′	N 60°31′ E 23°51′
Height above sea level, m	135	140	125
Climatic data			
Annual			
mean temperature, °C	3.7	2.9	3.7
precipitation, l/m²	545	576	545
total radiation, cal/cm²	79 344	76 622	79 344
Growing season			
length, days	170	161	170
mean temperature, °C	12.2	12.0	12.2
precipitation, l/m²	310	317	310
total radiation, cal/cm²	66 054	57 325	66 054
Soil characteristics			
Thickness of humus layer, cm	2.0	2.0	2.5
Thickness of A horizon, cm	4	9	6
Thickness of B horizon, cm	20	15	23
Soil type	Fine-sand moraine	Coarse sand	Fine-sand moraine
Stoniness (0—30 cm), volume %	32	0	36
Tree crop characteristics			
Age, yrs.	28	47	45
Stem number per ha	2 911	845	1 420
Diameter of median basal area tree (d_{gM}), cm	6.9	14.5	15.7
Height corresponding to median diameter (h_{gM}), m	6.4	12.0	15.4
Dominant diameter, cm	9.7	19.5	20.9
Dominant height, m	7.3	14.0	17.2
Basal area o.b., m²/ha	7.72	12.11	19.94
Volume o.b., m³/ha	30.20	75.45	148.79
Current annual increment o.b., m³/ha/yr.	2.26	4.99	5.86

Sample plot No. 1 was located on fine-sand moraine at Tammela in southern Finland (Table 1). The ground vegetation indicated that it was of the *Vaccinium*-type [1]) (Table 2). The stand had been established after prescribed burning, and so the trees were all approximately of the same age. The area of the sample plot was 30 × 30 m. Although cleaning and thinning of the seedling crop had been carried out, the stand was quite dense for this stage of development.

Sample plot No. 2 was located on coarse sand at Juupajoki. Owing to a forest fire just before the establishment of the stand and to the particle size composition of the surface soil (Table 3), the ground vegetation gave a misleading impression as regards site fertility. Judging by the growth of the trees, the site corresponded in fertility to the *Vaccinium*-type. The area of the sample plot was 30 × 35 m.

[1]) See footnote on page 9.

Table 2. Coverage and frequency of plant species.

Plant species	Sample plot No. 1		Sample plot No. 2		Sample plot No. 3	
	Coverage %	Frequency %	Coverage %	Frequency %	Coverage %	Frequency %
Lichens						
Cladonia rangiferina	1.6	70	10.0	100	0.2	20
Cladonia silvatica	1.3	40	6.5	85	0	0
Mosses						
Dicranum spp.	8.4	60	0	0	16.1	65
Hylocomium splendens	△	10	6.9	90	0.4	20
Pleurozium schreberi	67.8	100	53.5	100	60.8	100
Polytrichum spp.	0	0	△	5	1.0	10
Grasses						
Calamagrostis arundinacea	△	5	0	0	0	0
Calamagrostis epigeios	△	10	0	0	8.4	65
Deschampsia flexuosa	0	0	0	0	2.3	20
Herbs						
Convallaria majalis	0.6	45	0	0	2.6	40
Luzula pilosa	0	0	0	0	△	10
Maianthemum bifolium	0	0	0	0	6.0	70
Melampyrum silvaticum	0.1	10	0	0	0.1	30
Rubus saxatilis	0	0	0	0	0.1	10
Trientalis europaea	0	0	0	0	0.6	30
Dwarf shrubs						
Calluna vulgaris	8.9	95	24.8	100	3.3	55
Linnaea borealis	0	0	0	0	7.7	70
Vaccinium myrtillus	1.5	10	0	0	12.2	75
Vaccinium vitis-idaea	26.5	100	14.0	100	3.9	70

Sample plot No. 3 was located near to Sample plot No. 1 on fine-sand moraine, but its fertility was of the *Myrtillus*-type. Prescribed burning had also been carried out on this area for regeneration, but the burning had been light. The area of the sample plot was 30 × 35 m.

Table 3. Particle size composition of the surface soil (%).

Sample plot No.	Soil layer, cm	20—2 mm	2—0.2 mm	0.2—0.02 mm	0.02—0.002 mm	< 0.002 mm
1	0—10	13.1	25.1	49.5	10.3	2.0
	10—20	20.1	24.8	44.2	9.4	1.5
	20—30	16.6	25.3	47.4	9.4	1.3
2	0—10	0.3	49.7	44.3	3.8	1.9
	10—20	0.3	56.6	39.6	1.9	1.6
	20—30	0.5	65.0	32.9	0.2	1.4
3	0—10	8.0	17.7	54.3	17.1	2.9
	10—20	13.4	16.3	54.3	14.4	1.6
	20—30	12.4	16.5	53.8	16.6	0.7

The mean height and degree of self-pruning of the trees in the sample plots are shown in Fig. 2. The stoniness of the surface soil layer was determined by the Rod testing method (V i r o 1952). The climatic data in Table 1 are based on measurements made by the Finnish Meteorological Institute (Meteorological yearbook. . .). Precipitation and temperature are the averages for the period 1941—70 at Jokioinen (Sample plots No. 1 and 3) and Juupajoki (Sample plot No. 2) synoptic stations. The amounts of total radiation are the averages for the period 1958—70 recorded at Jokioinen (Sample plots No. 1 and 3) and Jyväskylä (Sample plot No. 2) radiation stations. Growing season refers to the average yearly period in which the daily average temperature is above 5 °C.

Ground vegetation cover was studied by analysing all the vegetation in twenty ½ m^2 sample squares located systematically in each sample plot (S a r v a s 1948). Coverage refers to the proportion of the ground area that is covered by above-ground parts of plants. Frequency indicates the percentage of sample squares in each sample plot in which the species appeared. When assessing the coverages, the ground vegetation was divided into two layers: a bottom layer comprising lichens and mosses, and a field layer consisting of grasses, herbs, and dwarf shrubs. Coverage was estimated separately for the two layers. Thus, in an extreme case, the sum of the percentage values for coverage could be 200 (Table 2).

The development of ground vegetation depends on the stand density and the stage of stand development. Especially in Sample plots No. 1 and 2, the plant species composition also reflected the effect of fire: the coverage of lichens and heather was high, as is typical for stands of such an age on sites which have previously been burned (V i r o 1969). Heather very quickly regenerates itself after a fire from seeds which have survived in the soil, and germination is probably promoted by burning (K u j a l a 1926). Thus, on a site that has been burned, the composition of the ground vegetation is apt to give an impression of lower fertility than the growth of the trees would suggest. In Sample plot No. 2 the low stand density, too, promoted the growth of lichens and heather.

Soil fertility of the experimental stands can also be depicted by the dominant height of the trees (Table 1). Comparing these data with the corresponding values for naturally regenerated normal pine stands: 7.6, 14.0, and 16.6 m respectively (I l v e s s a l o 1920), shows that the soil fertility was lowest in Sample plot No. 1 and highest in Sample plot No. 3.

23. Sampling procedure

The stratification of vegetation is necessary in order to obtain representative samples for the determination of dry weight and nutrient content of

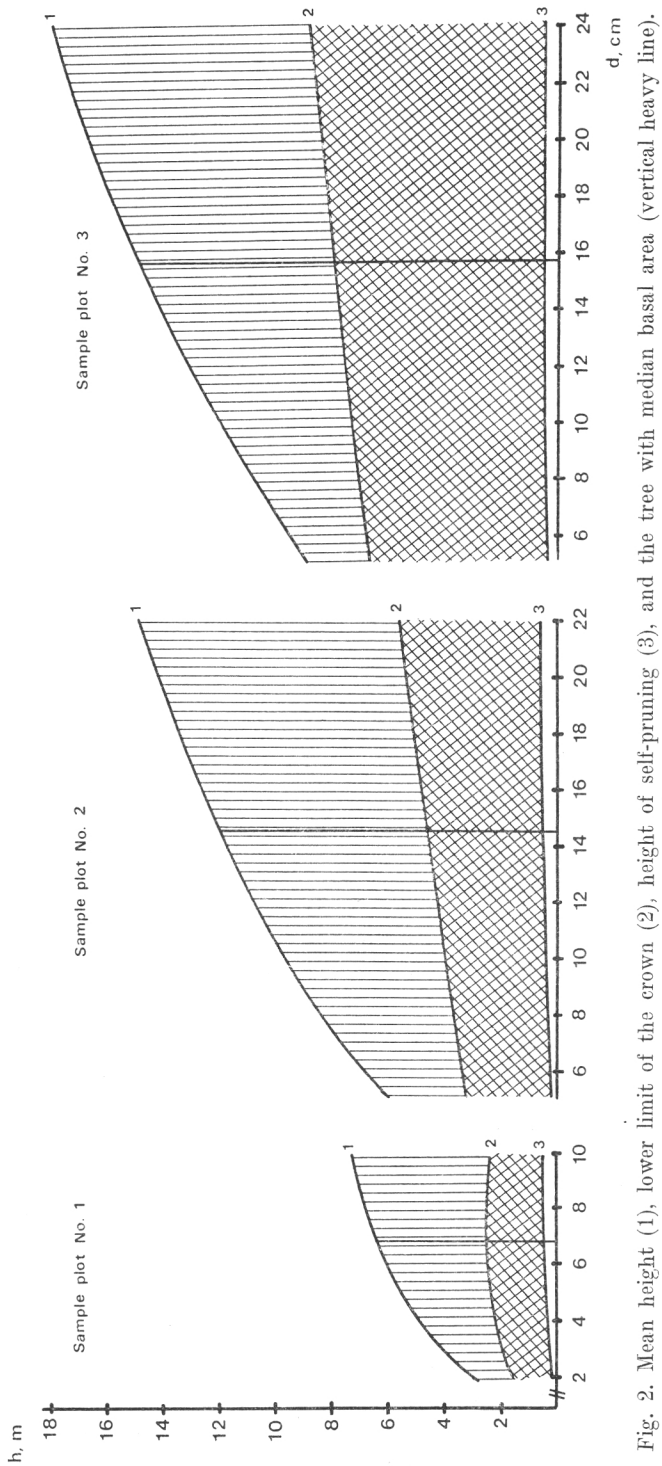

Fig. 2. Mean height (1), lower limit of the crown (2), height of self-pruning (3), and the tree with median basal area (vertical heavy line).

different compartments. The nutrient content of many tissues varies according to their location in the plant; for instance, the nutrient content of bark changes on moving from the butt upwards. Therefore, the vegetation must be stratified in such a way as to ensure sufficient anatomical homogeneity, enable the study to be carried out with a reasonably small number of samples, and finally, the stratification must correspond to the utilization of the different tree compartments.

For dry-matter determination the vegetation was divided into trees, shrubs, and ground vegetation. Twenty sample trees of different diameter classes were chosen from each sample plot by stratified random sampling in such a way that each sample tree represented an almost equal stem volume. The number of sample trees in each diameter class was thus predetermined, but within each diameter class the sampling was random.

The sample trees were felled as carefully as possible on to thick plastic sheeting so as not to lose any of the needles, bark or dead branches. The trees under 12 m in height were cut into 1 m and taller trees into 2 m bolts for stem analysis. The diameters of the bolts with and without bark, and of the heartwood, were recorded at both ends of the bolts.

The branches on each bolt were divided into living and dead, those without living needles being regarded as dead. The branches per bolt were weighed fresh and one living branch from both ends of each bolt was taken as a sample. The parts of the sample branches covered in needles were cut off and the needles removed and sorted according to age. The mass of these compartments from each bolt was weighed seperately. The sample branches were cut up into small pieces, and subsamples weighing about 50 g were taken for dry-matter and nutrient content determinations. Similar subsamples were taken from dead branches.

A 10 cm wide strip of bark was completely removed as a bark sample from both ends of every bolt. A sample disk of stemwood was sawn off for nutrient determination from the butt end of each bolt. The heartwood and sapwood were distinguished on the basis of the colour difference.

The stump and roots were considered to form the below-ground part of a tree. For the purpose of the present study the roots were further subdivided by diameter into roots thicker or thinner than 1 cm. The volume of the stumps and thick roots was measured by water displacement. In order to determine the dry weight of the thin roots, twenty soil samples were taken systematically from each sample plot with a soil sampler 20 cm^2 in cross-sectional area. The samples were divided into those taken from the humus layer and the 0—10, 10—20, and 20—30 cm mineral soil layers. Since pine roots lie close to the surface (K a l e l a 1949), this sampling depth was considered sufficient for dry weight determination.

The quantity and the annual distribution of the litter crop from the trees were measured for two years continually in each sample plot. In Sample plot No. 1, where the level of self-pruning of the trees was still low, twelve litter boxes with a collection area of 1 m^2 were used, being located systematically on the soil surface. Litter funnels with a collection area of ½ m^2 were used in the other sample plots (S a r v a s 1962). Eight funnels were placed in Sample plot No. 2 and twelve in Sample plot No. 3. The upper edge of the funnels was situated one metre above the ground surface. Exchangeable cloth bags, into which the litter fell, were fitted beneath them. The litter boxes and bags were emptied once a week except during winter time.

The ground vegetation was divided into five groups: lichens, mosses, grasses, herbs, and dwarf shrubs. Samples of each plant group were collected from the same sample squares in which the percentage coverage of each species had been estimated. The ground vegetation was cut off close to the humus surface. The dry weight of each plant group, and of *Calluna vulgaris*, *Vaccinium myrtillus*, and *Vaccinium vitis-idaea* in the dwarf shrub group, was determined separately.

To determine the organic matter and the nutrient content of the soil, twenty humus samples were systematically taken with the soil sampler from each sample plot. Mineral soil samples were taken from four holes situated on the diagonals of each sample plot (V i r o 1947).

To determine the nutrient quantities reaching the soil surface in precipitation, the relationship between gross precipitation and throughfall was determined in Sample plot No. 1 during two summers. The location of this sample plot was better than the others because it lay in the middle of a large forest area, the nearest road being a small forest road about 300 metres away. The measurements were planned in cooperation with P ä i v ä n e n (1974), using 214 cm^2 plastic funnels fixed on top of one litre plastic bottles as rain gauges. To prevent litter from entering the gauges, plastic nets were placed in the neck of the funnels, and filters were fitted inside the funnels.

Twenty gauges were located systematically in the sample plot in such a way that 13 gauges lay under the canopy and seven in canopy openings. The grown cover of the sample plot, measured with a Cajanus tube (S a r v a s 1953), was 64 per cent.

Stemflow was measured on three sample trees representing different diameter classes using plastic collars fitted about 30 cm up the stems, and the stemflow conducted by plastic tubes into containers. Gross precipitation was measured with three rain gauges in an open area about a hundred metres from the sample plot.

The water collected in the gauges was measured with measuring cylinders after each period of rainfall. The samples were combined in 12-litre containers, to which had been added 10 ml of toluene to suppress microbial activity.

24. Laboratory work

241. Dry weight determinations

Since the fresh weight of the samples could not be determined with sufficient accuracy in the sample plot, they were put into plastic bags to keep moisture loss to the minimum and later weighed in the laboratory. The sample bags were kept in a refrigerator until weighing except in cases where it was possible to determine the fresh weight on the same day as they were collected.

Apart from the stemwood samples, all the vegetation samples were dried in an oven for 24 hours at 105 °C, after which their dry weight was measured. These weighings gave the dry-matter percentages of the samples, which could be used to convert the fresh weights of the compartments into dry weights.

The dry weight of the stemwood was determined according to basic density values based on its fresh volume (H a k k i l a 1966). As the material from Sample plot No. 1 did not fully satisfy the premises of H a k k i l a's density values in respect to stem volume, the wood density of cores taken by an increment borer from the sample trees at breast height was determined by the Mercury immersion method (E r i c s o n 1959). The average wood density of the sample trees obtained in this way was 5 per cent lower than the average density at breast height (H a k k i l a 1966). This difference, however, was within the confidence limits. Further, as it was obvious that the difference between the materials was smaller in the top part of the stems, due to the juvenile wood zone, it was decided that H a k k i l a's density values could also be used for Sample plot No. 1.

The litter samples were sorted as follows: 1) needles, 2) branches, 3) bark, 4) cones, flowers, and seeds, 5) residual litter. Group 5 included a small amount of litter from epiphytical lichens and fine bark particles.

The roots less than 1 cm in diameter were separated by rinsing the soil samples with water in a 2 mm sieve (K a l e l a 1954). The clean roots were then removed with tweezers and sorted into pine roots and ground vegetation roots. Obviously such a method resulted in some loss of root material. Furthermore, it is difficult to distinguish between living and dead tissue — especially in the case of the thinnest roots — so some dead tissue may have been included in the sorted root material.

242. Methods of chemical analysis

The nutrient analyses were made in the laboratory of the Department of Soil Science, Finnish Forest Research Institute, using normal methods for determining the chemical properties of forest soil (cf. V i r o 1965).

Total analyses

Nitrogen was determined by the Kjeldahl method, using $CuSO_4$ as the catalyst. For total analysis of cations and phosphorus, 4 g of the sample was weighed into a quartz dish, and its dry weight was measured after overnight drying at 105° C. The sample was first charred over a bunsen burner, and then ashed in a muffle furnace at 550° C for two hours. The ash was weighed, dissolved in concentrated HCl, and washed into a beaker with dilute HCl. The solution was evaporated to dryness, and the concentrated HCl treatment repeated twice to precipitate the silica. The residue was dissolved in approximately 50 ml of 0.05-N HCl, left to stand covered on a water bath for two hours, and then filtered and washed with 0.05-N HCl until the filtrate amounted to 200 ml. A 5 or 10 ml aliquot of the filtrate was transferred to a 50 ml volumetric flask and 5 ml of 5 per cent $LaCl_3$ solution added to prevent interference. The volumetric flask was made up to the mark with 0.05-N HCl, and Ca^{2+} and K^+ were measured with a Beckman atomic absorption spectrophotometer.

Phosphorus was determined by the Molybdenum-blue method using metol, $NaHSO_3$, and $SnCl_2$ as reducing agents. A 2—5 ml aliquot of the same filtrate was pipetted into a 100 ml volumetric flask, 3 ml of $NaHSO_3$ solution (10 g $NaHSO_3$/100 ml) added, the flask filled to approximately the 75 ml level with 0.1-N HCl and kept for 3 hours on a water bath to reduce the Fe^{3+}. After cooling 5 ml of molybdenum-reducing solution [1]) was added, made up to the mark with 0.1-N HCl, and 15 minutes later 1 ml of $SnCl_2$ solution [2]) added and mixed immediately. The colour was measured with a Beckman B spectrophotometer 1 hour 30 minutes later.

Exchangeable cations, easily soluble phosphorus, and mineral nitrogen

For these determinations, 10 g humus or 30 g mineral soil was added to 200 ml of ammonium acetate extracting solution (a mixture of 1-M CH_3COOH and 0.5-M NH_4OH) at a pH of 4.65. The suspension was allowed to stabilize overnight, after which it was shaken for one hour and filtered.

Aliquots of the humus filtrate (10 ml) or the mineral soil filtrate (50 ml) were transferred to 50 ml volumetric flasks for the cation determinations. The flasks were made up to the mark with acetate solution, after which 1 ml of 5 per cent $SrCl_2$ solution was added. After mixing, Ca^{2+} and K^+ were measured with a Beckman atomic absorption spectrophotometer.

For determination of easily soluble phosphorus 5—10 ml aliquots of the humus filtrate or 25—50 ml aliquots of the mineral soil filtrate were taken, and 25 ml of 2-N H_2SO_4 was added to each. The same procedure was followed as in the total phosphorus determinations except that acetate solution was used instead of 0.1-N HCl.

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[1]) Molybdate solution: 50 g $(NH_4)_4Mo_7O_{24}$ and 138 ml of concentrated H_2SO_4/1 l.
Reducing agent: 1 g metol, 10 g $Na_2SO_3 \cdot 7H_2O$, and 150 g $NaHSO_3$/500 ml.
Molybdenum-reducing solution obtained by mixing 6 ml of reducing agent and 10 ml of molybdate solution/100 ml.

[2]) 2.5 g $SnCl_2 \cdot 2H_2O$ and 100 ml glycerol dissolved by heating on a water bath. Diluted to 1 000 ml with water.

The mineral nitrogen was extracted from the fresh samples (20 g of humus or 50 g of mineral soil) with 250 ml of 0.5-N KCl solution. Aliquots of the filtrate (50 ml) were made slightly alkaline with MgO, and the ammonia was distilled into a 100 ml volumetric flask containing 1 ml 0.01-N H_2SO_4 and gelatin to prevent coagulation. The determination was carried out with Nessler reagent on a Beckman B spectrophotometer. From another aliquot of the filtrate (100 ml) the humus was precipitated by $Al(OH)_3$. The filtrate was made strongly alkaline and the ammonia was removed by distillation. Nitrate was reduced to ammonia with Dewarda's alloy and the ammonia was then determined as above.

Soil organic matter

The organic matter in the humus layer was calculated from the loss on ignition. The carbon content of the mineral soil was determined by the wet combustion method according to Tyurin as follows. The sample (500 mg) was mixed with 10 ml of 1.0-N $K_2Cr_2O_7$ and 10 ml of concentrated H_2SO_4, boiled for 5 minutes and then diluted with 150 ml of water. After addition of 2.5 ml of concentrated H_3PO_4 the remaining dichromate was titrated with 0.4-N $FeSO_4$. Diphenylamine solution was used as the indicator.

Nitrogen isotope determination

Nitrogen isotope ratio analyses were performed partly in the Biochemical Research Institute in Helsinki and partly in the laboratory of the Royal College of Forestry in Uppsala.

25. Statistical procedure

Statistical analysis began with a study of the correlations between the dry weight of the different compartments and the characteristics of the sample trees (Table 4). The aim was to find the tree characteristics which could best explain the dry weight of the different tree compartments with the aid of a suitable regression model.

In a biological population the standard error of an individual observation appears to be approximately proportional to the magnitude of the observation. In such cases the variation can be reduced by using logarithmic transformation of the original data (Finney 1941). The transformed values often correspond better to other assumptions of the regression analysis, for example, their distribution corresponds better to the normal distribution.

The correlation coefficients showed that stem volume and diameter at breast height, either alone or combined as a suitable transformation with tree height or crown ratio, were very strongly correlated with the dry weight of the various compartments (Table 5). It should be noted that the correlations of the diameter, the square of the diameter, and the basal area with the dependent variables were all identical owing to the logarithmic transformation.

Table 4. The mean, standard deviation, and range of variation of the different tree charasteristics and the dry weight of different tree compartments of the sample trees.

Characteristic	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	$\bar{x}$	s	min.	max.	$\bar{x}$	s	min.	max.	$\bar{x}$	s	min.	max.
Tree characteristic												
Diameter, cm ..	6.8	0.5	2.4	9.7	15.0	0.8	7.0	21.6	14.5	1.1	5.6	23.6
Height, m	6.1	0.3	3.0	7.8	12.0	0.4	7.9	14.8	14.2	0.6	8.0	18.2
Volume, m^3	.0137	.0018	.0013	.0278	.1240	.0158	.0185	.2658	.1407	.0219	.0136	.3531
Crown ratio, % ..	61.1	8.9	42.0	75.0	62.4	4.9	54.0	70.0	43.0	11.2	19.7	63.9
Dry weight, kg												
Stemwood	4.73	0.63	0.44	9.79	42.14	5.48	5.86	91.75	49.06	7.81	4.50	123.83
Bark	0.92	0.10	0.10	1.75	4.92	0.51	1.24	10.02	4.61	0.63	0.79	10.90
Dead branches ..	0.39	0.05	0.05	0.81	1.92	0.31	0.34	5.56	2.99	0.55	0.34	8.31
Living branches	1.71	0.29	0.11	4.65	11.44	1.87	1.01	31.02	6.85	1.35	0.28	18.95
Needles	1.21	0.19	0.09	2.87	5.49	0.65	0.93	11.51	3.91	0.65	0.15	10.30
Cones	n. d.	n. d.	0.00	0.01	0.17	0.08	0.00	1.53	0.05	0.02	0.00	0.26

Apart from ease of measurement, a further premise put on usable independent variables is that the dry weight values calculated from the sample tree data must be reliably convertible to unit area basis. In this respect the use of basal area as an independent variable is justified. However, seeing that stand density affects height growth, it seems necessary to include height among the independent variables in cases where data from stands differing in density are treated together. The inclusion of crown ratio is also justified for explaining the dry weight of the canopy compartments as a variable depicting competition between trees. The dry weights of stumps and roots have the strongest correlation with tree diameter. There is a very close correlation between stemwood volume and the dry weight of the various

Table 5. Coefficients of correlation between the dry weight of different tree compartments and certain tree characteristics.

Dependent variables ($\log_{10}$)	Independent variables ($\log_{10}$)						Significance
	d	h	v	$\frac{\triangle h}{h}$	d^2h	$d^2\frac{\triangle h}{h}$	
Stemwood	0.990	0.962	1.000	0.041	0.998	0.937	n = 60
Bark	0.990	0.936	0.990	0.107	0.990	0.953	0.1 % 0.407
Dead branches	0.940	0.895	0.941	-0.026	0.941	0.872	1 % 0.325
Living branches	0.923	0.792	0.912	0.380	0.913	0.978	5 % 0.250
Needles	0.914	0.763	0.882	0.431	0.884	0.964	
Cones	0.536	0.469	0.525	0.280	0.524	0.571	
Stumps	0.983	0.927	0.979	0.269	0.979	0.972	n = 30
Roots, $\varnothing > 1$ cm	0.985	0.923	0.983	0.309	0.980	0.982	0.1 % 0.554
							1 % 0.449
							5 % 0.349

compartments of the trees. However, volume has no particular advantage over diameter and height, which are far easier to measure.

As the biomass is in most cases examined separately for each compartment, maximum accuracy must be aimed at when calculating the dry weight of the compartments. For this reason log (d^2h), which refers to the volume index, was chosen as the independent variable for the dry weight of stemwood and bark, log $\left(d^2\frac{\triangle h}{h}\right)$ for the dry weight of the crown compartments, and log d for that of the below-ground parts of the trees.

Cones were found on only one sample tree in Sample plot No. 1, the youngest of the experimental stands. In the other sample plots, too, many of the sample trees did not bear cones. Therefore, the dry weight equations for cone crop were calculated from log (y + 0.001). The consequent slight increase in cone dry weight did not greatly affect the results, but the inclusion of this variable made it possible to work out the equations.

Although logarithmic transformation of the data has many advantages, some difficulties arise when the least squares method is used for treating the data. When squared deviations of logarithmic values are minimized, the resulting parameter estimates tend to be underestimates, just as a geometric mean tends to be smaller than the arithmetic mean. The underestimates of regression equations due to the use of logarithmic transformations were corrected by the coefficient (m) based on F i n n e y's (1941) expansion as follows:

$$m = e^{1/2s^2}\left[1 - \frac{s^2(s^2+2)}{4n} + \frac{s^4(3s^4+44s^2+84)}{96n^2} + \ldots\right]$$

where s^2 is the variance of the logarithmic weights and n the number of observations. The size of the correction coefficient depends mainly on the error variance of the regression, and only to a lesser extent on the number of observations.

In the results presented later on, the standard error (s_e) of the regression estimates is given as an absolute unit. As the standard error of an estimate determined from the residual variance of a logarithmic equation cannot be transformed back to an arithmetic scale, the standard errors of estimate were calculated by the following standard formula (S n e d e c o r 1956, p. 125):

$$s_e = \sqrt{\frac{\Sigma(Y-Y_{est})^2}{n-2}}$$

where Y is the weight actually measured and Y_{est} the weight obtained from the dry weight equation.

Regression analysis was used to determine the variation of nutrient content in the longitudinal direction of the stem. The significance of the regression coefficient was tested with the t-test. The residuals from the final equations were examined according to Draper & Smith (1968, p. 86) in order to establish whether the material satisfies the qualifications of the analysis.

3. DISTRIBUTION OF DRY MATTER IN A STAND

31. Tree crop

The dry weight equation of each tree compartment was derived for each sample plot and for the whole material using the sample tree data. The regression equations presented in Table 6 show that it is possible to make reliable estimates of the various compartments of pine from relatively simple tree measurements. The variation coefficient of regression estimate was determined by dividing the standard error of the estimate by the mean value of y so as to express the relative spread of the points from the regression line (see Appendix 1). As could be expected, the relative error was considerably greater for the dry weights of the crown compartments than for those of the stemwood or its bark.

The quantity of dry matter in the tree crop in each sample plot was calculated from these regression equations, using data on the number and height of the stems and crown ratios per diameter class in each sample plot. In order to calculate the dry weight of the stumps and thick roots in Sample plots No. 1 and 3, the equation for the whole material was used because the data for these compartments had been obtained from only five sample trees in each of these sample plots. For other compartments, in which the number of samples was adequate, regression equations based on the sample trees in the sample plots themselves were employed.

The underestimates given by the regression equations, which were due to the logarithmic transformations, were corrected by the method described on page 26. The correction coefficients for all the compartments except the cones varied between 1.02 and 1.20 (Table 7). In most cases, the dry weights obtained from the logarithmic equations were 5—8 per cent less than the actual values obtained by weighing.

According to Table 8 the dry weight of the tree crop in Sample plot No. 2 was about double that in Sample plot No. 1, and the dry weight of the tree crop in Sample plot No. 3 almost double that in Sample plot No. 2. The dry weight of the below-ground part comprised the dry weight of the stumps

Table 6. Equations for the dry weight of different tree compartments.

Dry weight (y)	Sample plot No. 1	2	3	Whole material
I The basic form of equations 1—3 is $\log y = a+b \log (d^2h)$				
1. Stemwood, kg				
a	—1.411	—1.663	—1.730	—1.657
b	0.8316	0.9447	0.9626	0.9403
r^2	0.992	0.991	0.994	0.995
s_e, kg	0.35	2.63	3.19	2.43
% of $\bar{y}$	7.4	6.2	6.5	7.6
2. Bark, kg				
a	—1.827	—1.771	—2.024	—1.828
b	0.7183	0.7106	0.7603	0.7160
r^2	0.964	0.961	0.968	0.980
s_e, kg	0.12	0.56	0.56	0.58
% of $\bar{y}$	13.0	11.4	12.4	16.6
3. Dead branches, kg				
a	—2.130	—2.702	—2.735	—2.358
b	0.6797	0.8486	0.8977	0.7695
r^2	0.742	0.655	0.890	0.884
s_e, kg	0.13	0.88	0.99	0.98
% of $\bar{y}$	33.3	45.8	33.1	55.4
II The basic form of equations 4 and 5 is $\log y = a+b \log \left(d^2\frac{\triangle h}{h}\right)$				
4. Living branches, kg				
a	—3.407	—4.874	—3.953	—3.839
b	1.032	1.411	1.174	1.154
r^2	0.930	0.942	0.941	0.956
s_e, kg	0.55	2.36	2.69	2.75
% of $\bar{y}$	32.2	20.6	39.3	41.2
5. Needles, kg				
a	—3.510	—3.627	—4.338	—3.683
b	1.019	1.043	1.213	1.056
r^2	0.950	0.887	0.889	0.928
s_e, kg	0.23	1.22	1.66	1.06
% of $\bar{y}$	19.0	22.2	42.5	30.2
III The basic form of equation 6 is $\log (y+0.001) = a+b \log \left(d^2\frac{\triangle h}{h}\right)$				
6. Cones, kg				
a	n. d.	—7.341	—7.594	—6.961
b		1.3533	1.3518	1.2140
r^2		0.088	0.363	0.327
s_e, kg		0.40	0.10	0.23
% of $\bar{y}$		235	200	209
IV The basic form of equations 7 and 8 is $\log y = a+b \log d$				
7. Stumps, kg				
a	n. d.	—1.740	n. d.	—2.020
b		0.9247		2.1623
r^2		0.850		0.966
s_e, kg		0.85		0.63
% of $\bar{y}$		23.2		19.6
8. Roots, $\varnothing > 1$ cm, kg				
a	n. d.	—1.967	n. d.	—2.418
b		2.458		2.8242
r^2		0.935		0.970
s_e, kg		1.92		2.50
% of $\bar{y}$		20.3		29.4

Table 7. Correction coefficients for the regression estimates of the dry weight of the tree compartments.

Compartment	Sample plot No.		
	1	2	3
Stemwood	1.06	1.04	1.08
Bark	1.04	1.02	1.05
Dead branches	1.05	1.05	1.07
Living branches	1.08	1.06	1.14
Needles	1.07	1.04	1.16
Cones	n. d.	1.80	1.56
Stumps	1.13	1.03	1.10
Roots, $\varnothing > 1$ cm	1.15	1.04	1.20

Table 8. Dry weight of the tree crop.

Compartment	Sample plot No.					
	1		2		3	
	kg/ha	%	kg/ha	%	kg/ha	%
Stemwood	9 630	38.5	27 100	51.2	55 570	58.4
Bark	1 940	7.8	3 330	6.3	5 320	5.6
Dead branches	780	3.1	1 170	2.2	3 230	3.4
Living branches	3 270	13.1	6 780	12.8	7 360	7.7
Needles	2 320	9.3	3 540	6.7	4 430	4.6
Cones	△	△	20	△	10	△
Above-ground part	17 940	71.8	41 940	79.2	75 920	79.7
Below-ground part	7 040	28.2	11 010	20.8	19 280	20.3
Whole tree crop	24 980	100.0	52 950	100.0	95 200	100.0

and roots over 1 cm in diameter calculated from the equations, and that of the thin roots obtained by rinsing and sorting (Table 10).

The results show that the stage of stand development is indicated by the proportional increase in stem dry weight and by the proportional decrease in the dry weight of other tree compartments, except in some cases the cones.

311. The stem

Stemwood is usually the most valuable part of a tree from the commercial point of view. Since pine produces heartwood, some attention should be paid to the quantity involved. In the two oldest stands, heartwood was generally found in trees with a diameter of 10 cm or more. Its ratio to the total stemwood was 7.9 per cent in Sample plot No. 3, but only 4.1 per cent in Sample plot No. 2. Heartwood formation generally starts at the age of 30—40 years, and it accounts for less than 10 per cent of the total stemwood at the age of 50—60 years (L a p p i - S e p p ä l ä 1952). However, annual rings of sapwood more than 70 years old are seldom found in pine.

Bark consists of dead rough bark and living phloem. The phloem is, of course, the most important part with regard to tree nutrition because it forms the route by which photosynthates move from needles to other compartments.

The proportion of bark, by volume and weight, out of the complete stem was follows:

Sample plot No.	Proportion of bark as percentage of stem		Bark density kg/m³
	Volume	Weight	
1	21.5	16.3	266.0 ± 40.9
2	15.9	10.4	268.7 ± 36.9
3	13.7	8.7	262.9 ± 35.8

The bark density depends on the proportion of phloem and rough bark. T a m m i n e n (1962) states that bark density in pine varies between 250 and 320 kg/m³ according to height, so that the lowest density occurs about half up the stem.

312. The crown

The crown comprises the living branches, needles, and cones. The size of the crown is often expressed as a crown ratio: the length of the crown as a percentage of the height of the tree. This ratio indicates the competition between the trees, their age, and the site conditions.

The proportion of bark in the dry matter of branches is very high. The bark percentage of the branches was not determined in the present study, but according to H a k k i l a (1972) the proportional share of bark could be estimated at 30—35 per cent of the dry matter of the branches.

Pine needles usually remain on the tree for 3—4 years. In the present material, second-year needles accounted for the bulk of the needle dry matter (Table 9). Needles produce photosynthates and also store some of these compounds together with a certain amount of nutrients (T a m m 1955).

Table 9. Distribution of needle dry matter by age class.

Needles	Sample plot No. 1		Sample plot No. 2		Sample plot No. 3	
	kg/ha	%	kg/ha	%	kg/ha	%
1st yr.	730	31.5	1 130	31.9	1 410	31.8
2nd yr.	900	38.8	1 160	32.8	1 570	35.4
3rd yr.	535	23.0	855	24.1	850	19.2
4th yr.	155	6.7	395	11.2	600	13.6
Total	2 320	100.0	3 540	100.0	4 430	100.0

The low photosynthetic capacity of the needles found on lower branches, due mostly to shading, is the main reason for the death of these branches. However, no clear correlation has been found between the dry weight of lower living branches and their needles (M a d g w i c k 1967). Thus, it is obvious that the larger the needle surface area is, the greater is the wood production of the tree. Genetic factors, the age of the tree, and its position in the canopy layer sometimes cause wide variations in the amounts of dry matter produced by similar quantities of needles (B u r g e r 1951).

The wide annual variations in cone production are due to genetic factors, stand age, and climatic fluctuations (S a r v a s 1962). Owing to the relatively young age of the stands, cones accounted for a very small part of the total dry matter in the present material.

313. Below-ground part

The root system of pine already reaches its final depth in soil at the age of 10—20 years (K a l e l a 1949). Probably by the age of 40, the roots of a pine stand have throughly occupied every layer of the soil they will ever extend to, and thereafter their total quantity does not vary much.

Wide seasonal variations have been found in the number of thin roots. The root tips of pine grow rapidly between the start of the growing season and the end of July (K a l e l a 1957). Their number at the height of summer is almost double that at the beginning of the growing season, and it varies within far wider limits in the humus layer than in the mineral soil. The root samples in the present study were taken at the beginning of September, and so the results probably represent an approximate average value for thin roots.

It can be seen in Table 10 that the quantity of thin roots was relatively low in Sample plot No. 2. One reason may have been that roots penetrate deeper into assorted sandy soil than into moraine, so that a higher proportion of the thin roots lay at greater depths in this sample plot. This supposition is confirmed by the following table showing the depth distribution of thin roots.

Soil layer	Sample plot No. 1	Sample plot No. 2	Sample plot No. 3
Humus layer	14.7 %	32.0 %	15.0 %
0—10 cm	66.8 %	35.0 %	63.2 %
10—20 cm	16.2 %	21.3 %	14.4 %
20—30 cm	2.3 %	11.7 %	7.4 %

Table 10. The dry-matter distribution of the below-ground compartments of trees.

Compartment	Sample plot No. 1		Sample plot No. 2		Sample plot No. 3	
	kg/ha	%	kg/ha	%	kg/ha	%
Stumps	1 440	20.4	2 360	21.4	4 120	21.4
Roots, ∅ > 1 cm ..	2 110	30.0	5 910	53.7	11 080	57.5
Roots, ∅ < 1 cm ..	3 490	49.6	2 740	24.9	4 080	21.1
Total	7 040	100.0	11 010	100.0	19 280	100.0

The thin roots in the assorted soil were much more evenly distributed than in the moraine. Pine roots lie very near the soil surface in moraine soil. About 95 per cent of the horizontal roots are to be found in the humus layer and the 0—30 cm mineral soil layer, when calculated according to root length (K a l e l a 1949). The ratio in the surface soil layers is even greater judging from root volume or dry weight. Although roots lie near the surface, they occupy only about 0.5 per cent of the volume of the surface soil layer. Only in the humus and 0—10 cm mineral soil layers do they sometimes occupy more than 1 per cent of the soil volume.

32. Ground vegetation and shrubs

The dry weight of the ground vegetation was estimated with samples from each of the five plant groups collected in the latter half of August (p. 21). A more detailed analysis of individual species would have increased the work many times over without notably improving the accuracy as far as the dry-matter determinations were concerned. The separation of the living and the dead part of mosses was, to some extent, subjective and inaccurate, and thus may have led to errors in the dry-matter quantities of mosses.

The dry weight of the shrubs was also detemined in each of the sample squares. Birch sprouts and pine seedlings under 1.3 m in height were counted as shrubs; but only a very few of them were growing in the sample plots. Since it was not possible to distinguish the roots of pine seedlings from those of taller pines, the estimate for tree roots was increased by a small amount.

Most of the ground vegetation dry matter originated from mosses and dwarf shrubs (Table 11). The dry weight ratios between these two groups varied widely from one sample plot to another. The proportion of root dry weight was on average some 41 per cent of the ground vegetation, which is a much higher figure than that for the trees. The dry weight of dwarf shrub roots generally varies between 35 and 70 per cent, depending on the site (M o r k 1946).

Table 11. Dry weight of ground vegetation and shrubs (kg/ha).

Plant group	Sample plot No.		
	1	2	3
Lichens	5	115	△
Mosses	1 650	1 290	2 510
Grasses	5	0	100
Herbs	10	0	85
Dwarf shrubs			
Calluna vulgaris	470	1 310	145
Vaccinium myrtillus	20	0	145
Vaccinium vitis-idaea	585	350	130
Others	0	0	140
Shrubs	25	35	65
Above-ground part	2 770	3 100	3 320
Below-ground part	1 680	2 680	2 170
Total	4 450	5 780	5 490

The root system of ground vegetation in the present material was distributed between the soil layers as follows: humus layer 37 per cent, 0—10 cm 48 per cent, 10—20 cm 10 per cent, and 20—30 cm 5 per cent. Thus, the roots of the ground vegetation lay closer to the surface than the pine roots (cf. p. 32).

33. Annual biomass production

331. Tree crop

The annual production of biomass is a good basis for the study of the annual nutrient requirements of a stand. In most respects, however, it is more difficult to determine total annual production than to estimate the total quantity of biomass, because the ordinary methods used are only applicable to the estimation of stem increment. In this connection the annual biomass production refers to the apparent production which forms the main part of the annual total production (see Fig. 1). The production of removal is discussed later in the section concerning the annual balance of biomass (p. 44).

The average annual biomass production of stemwood was obtained from the dry weight of the stemwood and the volume increment percentage of the trees. The increment percentage was calculated for a period of three years as the average, weighted with the volumes represented by the sample trees (I l v e s s a l o 1948). The following increment percentages for stemwood were obtained:

Sample plot No. 1 8.1 per cent
2 6.6 » »
3 4.2 » »

The annual biomass production of the stem bark was calculated by subtracting the underbark volume increment from the overbark volume increment, and multiplying by the average density of the bark. The annual volume increment of bark was 0.34 m^3, 0.38 m^3, and 0.47 m^3 in Sample plots No. 1—3 respectively. Ilvessalo (1965, p. 173) states that this method leads to a slight underestimate of the overbark volume increment. The reason for this is that the diameter growth of trees does not include the thickness growth of the bark, since it is difficult to determine that from measurements which are taken only once.

The determination of annual branch production includes a number of complex factors. As the tips of the branches grow, twigs on the older branches die and fall off. Similarly, the lower down the branch is situated, the slower is its growth and the greater the number of twigs that die and fall off.

According to Madgwick (1970) Scots pine branches grow very fast during the first four years, but after this their rate of growth slows down. Their weight between the ages of 7—12 hardly varies at all. As there are no corresponding increment tables for branches as for the stem, general growth models were resoted to (Richards 1969), which revealed that the time-power function was the most suitable for the characteristics available. This simple function defines the growth of branches as follows (Whittaker 1965):

$$\log y = a + k \log t$$

where y is the dry weight of the branch wood with bark, k its growth ratio, and t its age which, in the present study, was taken as an average for each bolt. On the basis of the sample branch data the following equations for the relative growth of the branches were derived using the above formula:

Sample plot No. 1: $\log y = 1.217 + 1.507 \log t$
$r = 0.845 \quad n = 85$

Sample plot No. 2: $\log y = 1.934 + 1.309 \log t$
$r = 0.746 \quad n = 97$

Sample plot No. 3: $\log y = 1.393 + 1.405 \log t$
$r = 0.702 \quad n = 102$

The first derivative of the above-mentioned time-power function indicates the biomass production ($\triangle y$) of sample tree branches as follows:

$$\triangle y = \Sigma \left(y \frac{k}{t} \right).$$

The biomass production was thus estimated by multiplying the branch dry weight (y) of each bolt by k/t and summing the resulting values for a given tree.

The increment percentage for branches weighted with the dry weights represented by the sample tree branches was as follows:

Sample plot No.	1	20.6 per cent
	2	11.4 » »
	3	11.9 » »

Thus, the relative biomass production of the branches in the youngest experimental stand was almost twice that in the others.

As the dry weight of needles increases with age, the needles of the current growing season do not alone indicate the annual production of all the needles. For this reason, it was also necessary to determine the dry weight increase of older needles. Samples taken from various parts of the crowns gave the following data on the development of the dry weight of needles:

Age of needles	Dry weight per 1 000 needles, g	Relative weight
1st yr.	6.041	100
2nd yr.	6.869	114
3rd yr.	7.224	120
4th yr.	8.004	132
Litter	6.668	110

It can be seen that the dry weight of the fourth-year needles was more than 30 per cent greater than that of the current year needles. Therefore, the annual biomass production by needles was calculated from the average annual growth of the relative weight as shown in the above table.

Owing to the difficulties encountered in root studies, it was not possible to produce any reliable estimates of their annual biomass production. There seems to be no correlation in the case of root growth between diameter and length as is the case for above-ground shoots (F a y l e 1968). The annual increase in the diameter of roots follows an irregular pattern. Owing to the eccentric and discontinuous form of their annual sheaths, the production of thick roots cannot be estimated reliably. A still greater problem in estimating the growth of the below-ground part is posed by the life cycle of thin roots.

For instance, roots less than 1 mm in diameter in pine bogs are replaced every third year, and those 2—5 mm thick every tenth year on the average (H e i k u r a i n e n 1957). As no general growth pattern for roots has yet been elucidated, the annual production of the below-ground part of the sample trees had to be estimated from the growth percentage of the above-ground part of the tree crop. This is bound to lead to some error because the growth ratio of roots and above-ground part varies with age. However, in the present material the correlation coefficient between the dry weight of the

Table 12. Annual biomass production of the tree crop.

Compartment	Sample plot No. 1		Sample plot No. 2		Sample plot No. 3	
	kg/ha	%	kg/ha	%	kg/ha	%
Stemwood	780	22.9	1 790	34.9	2 350	36.8
Bark	90	2.6	100	2.0	125	1.9
Branches	675	19.8	775	15.1	875	13.7
Needles	900	26.5	1 380	26.9	1 740	27.3
Cones	△	△	10	0.2	5	0.1
Above-ground part	2 445	71.8	4 055	79.1	5 095	79.8
Below-ground part	960	28.2	1 070	20.9	1 290	20.2
Total	3 405	100.0	5 125	100.0	6 385	100.0

above- and below-ground parts, excluding thin roots, was 0.993, which indicates that biomass was accumulated in both parts at an equal rate.

The values in Table 12, which presents the estimated annual biomass production in the stands, were obtained using the methods described above. The relatively small part played by the stemwood is apparent, especially in the youngest experimental stand. The relative annual production of stemwood increases, of course, with age. The production by the needles accounted for about a quarter of the total production in all three sample plots.

332. Ground vegetation and shrubs

The annual biomass production of the above-ground part of ground vegetation is usually estimated from the dry weight of the shoots that have grown during the last growing season (e.g. R o m e l l 1939, M o r k 1946). In most cases, the annual height growth of shoots can be rather clearly distinguished visually, but the diameter growth of older shoots is not taken into account when using this method. However, the resulting error has been generally regarded as small.

The shoots of *Hylocomium* and *Pleurozium* usually comprise three living segments which each represent one year's growth (R o m e l l 1939, T a m m 1953). The annual production of all mosses was thus assumed to be a third of their total dry matter. The above-ground parts of grasses and herbs represent one-year's growth and are thus equal to one year's production. The annual biomass production of the above-ground part of the dwarf shrubs was estimated according to the growth percentage, which was determined as the proportion of the current year's shoots from the dry weight of the above-ground part. The growth percentage for the different sample plots varied between the limits: *Calluna* 18—24 per cent, *Vaccinium myrtillus* 46—51 per cent, *Vaccinium vitis-idaea* 35—38 per cent.

Table 13. Annual biomass production of ground vegetation and shrubs.

Plant group	Sample plot No. 1		Sample plot No. 2		Sample plot No. 3	
	kg/ha	%	kg/ha	%	kg/ha	%
Lichens	△	△	10	0.7	△	△
Mosses	550	40.2	430	30.8	840	41.4
Grasses	5	0.3	0	0	100	4.9
Herbs	10	0.7	0	0	85	4.2
Dwarf shrubs	310	22.6	360	25.7	190	9.4
Shrubs	5	0.4	10	0.7	15	0.7
Above-ground part	880	64.2	810	57.9	1 230	60.6
Below-ground part	490	35.8	590	42.1	800	39.4
Total	1 370	100.0	1 400	100.0	2 030	100.0

Mosses and dwarf shrubs were the main producers in the ground vegetation (Table 13). Although the ground vegetation in these experimental stands comprised few species (Table 2), the species composition varied throughout the growing season, and so it was not possible to estimate accurately the growth of all species with one sampling. Thus, the dry-matter amounts for herbs, in particular, are underestimates. However, there was so little herb in the ground vegetation that the resulting error was very small. The annual production of the below-ground part of the ground vegetation was estimated from the growth ratio of the above-ground part.

34. Annual litter production

341. Tree crop

Plant residues continually fall to the ground or enter the soil from roots. As the quality of litter has a decisive effect on the properties of humus, much attention has been paid to the role of litter in forest ecosystems. Determination of litter crop supports also the estimates of biomass production by trees and makes possible the study of the dynamics of the ecosystem.

In planning the sampling method, the first step was to decide how many litter funnels would be needed to measure the annual litter crop with satisfactory accuracy. According to S a r v a s (1962) it is possible, even under the most unfavourable conditions, to keep the relative error of seed crop measurement in pine stands down to 10 per cent by using ten funnels of the same type as those employed in the present study. Tree litter, however, falls far less evenly than pine seed, which is conveyed by the wind in a fairly uniform manner. In Sample plot No. 3, where there were 12 funnels, the coefficient of variation was 35 per cent even for the largest litter samples (Fig. 3). The relative error of the estimate was correspondingly about 20

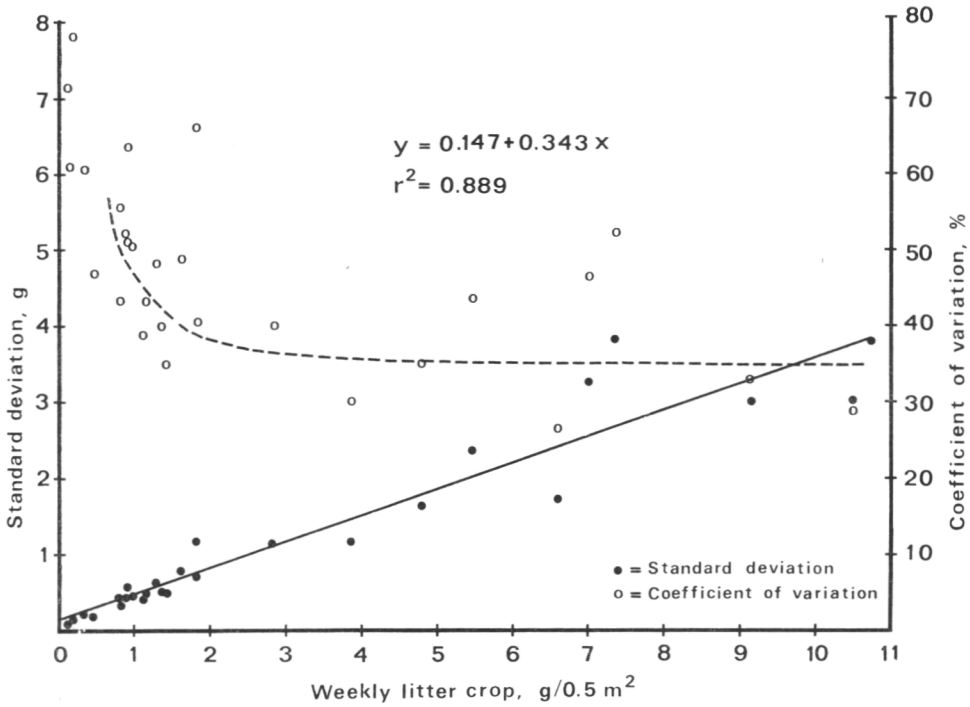

Fig. 3. Relationship between the weekly amount of litter (x), and the standard deviation (y) and coefficient of variation of the mean for Sample plot No. 3. Measurements in 1968.

per cent, even for litter quantities of 10 g per 0.5 m^2. It seems practically difficult to achieve satisfactory accuracy for small litter quantities by this method. The relative error in Sample plot No. 2 with its low stand density and smaller number of funnels was slightly greater. The best estimate for litter crop in this respect was obtained in Sample plot No. 1, where 1 m^2 litter boxes were used instead of 0.5 m^2 funnels. However, it was more difficult to prevent the loss of some finer litter on emptying the boxes than the funnels, and so the results for Sample plot No. 1 were evidently underestimates (Table 14).

Table 14. Annual litter crop of the above-ground part of the trees.

Type of litter	Sample plot No. 1		Sample plot No. 2		Sample plot No. 3	
	kg/ha	%	kg/ha	%	kg/ha	%
Needles	490	85.2	800	75.1	1 110	67.1
Branches	50	8.7	70	6.6	138	8.3
Bark	23	4.0	115	10.8	177	10.7
Cones, seeds, flowers	3	0.5	30	2.8	40	2.4
Residual	9	1.6	50	4.7	190	11.5
Total	575	100.0	1 065	100.0	1 655	100.0

The bark litter data for Sample plots No. 2 and 3 were also underestimates because the upper edge of the funnels was situated one metre above ground and thus the funnels could collect no litter from lower down the boles. In these sample plots roughly a third of the stem bark dry matter was situated less than one metre above the ground surface. However, when branch bark is included in this estimate (Hakkila 1972), this figure falls to about 20 per cent. As fine bark could not be distinguished from other fine litter, a certain amount of bark was also included in the residual litter, which reduced the bark estimate. The branch litter data were only slightly underestimated because 1.9 per cent of the dry matter of dead branches in Sample plot No. 2, and only 0.6 per cent in Sample plot No. 3 was situated lower than the upper edge of the funnels.

Most researchers have found little variation in litter quantities in stands aged 30—100 years (Bray & Gorham 1964, p. 141). Thus, it has been deduced that, after canopy closure, litter quantities depend mainly on environmental factors. However, Bonnevie-Svendsen & Gjems (1957) have found that the amount of needle litter increases with increasing basal area of the stand. In the sample plots used in the present study, the quantity of needle litter varied between 56 and 66 kg per m^2 of basal area.

Clear seasonal differences in litter quantities have been found in addition to annual variations (Viro 1955). Needle fall, in particular, is apt to vary in quantity owing to physiological factors such as temperature and moisture, and mechanical factors such as wind, rain, and frost. It has been found that leaf fall in birch varies mainly with the temperature (Sarvas 1972). The average seasonal distribution of the litter fall calculated from the measurements made in the sample plots showed that the greatest amounts of litter clearly fell in September and October.

Growing trees evidently lose relatively little dry matter from dying main and lateral roots. On the other hand, the tips of thin roots die off frequently. Orlov (1955) estimated that the annual quantity of absorbing roots that die off equals half of the annual needle litter. In the present material the estimated litter amounts of the below-ground part were 170, 230, and 340 kg/ha in Sample plots No. 1—3 respectively.

342. Ground vegetation and shrubs

Ground vegetation produces rather large amounts of litter. All the above-ground parts of grasses and herbs are annual and turn completely into litter. Shedding of leaves and shoots by dwarf shrubs follows roughly the same pattern as for trees. On the other hand, the dead parts of mosses are not so easily detached from the living plants. Their lower litter-producing parts

enter the humus layer while still attached to the living part of the plant, and thus the annual litter quantity produced by mosses cannot be measured by direct methods (A n d r é 1947). It is therefore more difficult to measure the litter crop of ground vegetation than that of trees. It is generally assumed that, in a stabilized plant community, the litter crop equals the annual production of leaves and shoots (M o r k 1946). This assumption had also to be made in the present study, although the experimental stands were not stable plant communities.

343. Decomposition rate of litter

The amount of nutrients available to plants is affected not only by the quality of the mineral soil, but also by the rate at which the litter decomposes and the bound nutrients become available. For this reason the decomposition rate of litter has long been an object of extensive study. However, study of the decomposition rate of forest litter under natural conditions had been rather neglected (M i k o l a 1954, 1959). The main problem lies in the estimation of litter quantities as decomposition progresses, and also in the fact that any method used to isolate the samples alters the experimental conditions. Cellulose has often been used as a test material (e.g. L ä h d e 1966) because 20—30 per cent of the litter is composed of it. The advantage of cellulose is that it is not synthesized by decomposing micro-organisms.

In order to study the decomposition rate of litter, about 3 g of needle litter was put into a nylon net bag. The method was an adaptation of that used earlier by L ä h d e (1966) for studying the biological activity of soil. Half of the litter bags were placed on the bottom layer of the ground vegetation, where litter normally falls. The rest were inserted between the moss and humus layers using special wedges. The sample bags were set out during the first half of May, 1971. Twenty-four bags per sample plot were then removed after 5 months, twelve after 12 months, and twelve after 17 months. The loss of dry matter in the needle litter is presented in Table 15. This was not a very accurate method, and it gave relatively poor results. However, it indicated that the decomposition rate resembled that assessed by M i k o l a (1954).

The composition of the litter, temperature and moisture conditions are, of course, the most important factors affecting decomposition. Pine needles are poor in nitrogen and rich in wax and resin, and so their decomposition is generally considered to be slow. The average 14—22 per cent loss in dry matter, which occured in the litter placed on the ground vegetation during the first summer, was probably due mainly to the loss of water soluble substances (M i k o l a 1954). These can easily be leached out of the litter, and they are also highly susceptible to decomposition by micro-organisms.

Table 15. Relative dry-matter loss from needle litter.

Place of sample bag	During 5 months					During 12 months					During 17 months				
	Sample plot No.			F-value	$HSD_{.05}$	Sample plot No.			F-value	$HSD_{.05}$	Sample plot No.			F-value	$HSD_{.05}$
	1	2	3			1	2	3			1	2	3		
On the bottom layer of ground vegetation	22	14	18	19.71***	3.4	34	26	28	4.67*	7.4	49	44	43	1.17	10.5
On top of the humus layer	34	22	27	23.09***	4.2	38	34	32	2.91	7.0	54	54	50	0.39	12.1
F-value	52.6***	43.0***	23.2***			3.2	8.2*	1.5			0.9	5.3*	2.9		
$HSD_{.05}$	3.2	2.7	3.7			5.2	6.3	6.9			10.9	9.6	8.7		

HSD, honestly significant difference

If litter contains easily decomposable matter, a small amount of nitrogen is enough to accelerate the rate of decomposition because the micro-organisms can re-use this nitrogen (W i t t i c h 1939). About 30 per cent of the dry matter of the litter samples was lost within a year. Initially, decomposition was faster under the moss layer than on top of it — obviously due to the different moisture conditions. As the ground vegetation developed around them, the litter samples placed on the moss were gradually covered. Mere visual inspection can easily give a false impression of the decomposition rate of litter: even the needles that had lost 50 per cent of their dry weight still retained their original shape quite well.

The decomposition rate of the litter of certain ground vegetation species decreases in the following order (M i k o l a 1954):

Maianthemum,
Vaccinium myrtillus, *Trientalis*,
Deschampsia,
Pleurozium.

The dominant ground vegetation species of the stands, *Pleurozium schreberi*, thus produces litter which decomposes at a rate slower than any of the above-mentioned species. If pine needle litter were included, it would be placed between *Vaccinium* and *Deschampsia*.

35. Amount of humus in the soil

The quantity of forest humus, formed mainly of litter derived from vegetation, depends on the rate of litter production and on the rate of

decomposition of the organic matter. In a stable plant community the absolute amount of humus remains fairly constant: annual litter production and humus decomposition are roughly equal. However, if the activity of the litter decomposing micro-organisms is reduced, organic matter begins to accumulate and the nutrient cycle slows down.

Much attention has been paid to the part played by humus in the development of forest ecosystems. As a high proportion of the ion-exchange colloids in the soil consists of organic matter, humus is a major factor affecting plant nutrition. In many cases wood production has been found to be more closely correlated with the microbiological processes of the soil than with any other soil property (T a m m & H o l m e n 1967).

Forest humus can be divided into three principal fractions (W i l d e 1958, p. 77): ectohumus, the partly decomposed organic remains lying on the surface of the mineral soil; endohumus, the fine, dark organic matter mixed with the mineral soil; and cryptohumus, the pale or colourless residues at an advanced stage of decomposition found throughout the different soil layers. The composition and relative quantities of these fractions in the organic matter of the soil depend on the prevailing conditions, which give rise to the different types of humus layers.

Raw humus typically forms a felt-like layer on the surface of mineral soil held together by fungal hyphae and plant roots. However, a lot of fine humus matter is also mixed with the underlying mineral soil. The actual amounts and depth distribution of the humus are given in Table 16.

The data indicate that most of the humus is in the surface layer of the mineral soil, although the subsoil (30—60 cm) sometimes contains large quantities of organic matter (cf. V i r o 1969). The fact remains, however, that humus deeper in the soil decomposes more slowly, and so the rate of turnover in the nutrient cycle becomes slower. For instance, T a m m & H o l m e n (1967) have noticed in central Sweden that part of the humus in the eluvial horizon may have been older than one rotation, while the humus in the illuvial horizon was 460—1 260 years old.

Table 16. Quantity of humus and its distribution along the soil profile (1 000 kg/ha).

Soil layer	Sample plot No. 1	Sample plot No. 2	Sample plot No. 3
Humus layer	18.9	29.9	30.7
0—10 cm	19.7	26.4	23.7
10—20 cm	9.2	10.7	13.6
20—30 cm	5.6	5.0	6.5
Total	53.4	72.0	74.5

36. Annual balance of biomass

The quantity of biomass at the time of measurement forms the basis for determining its annual production. As was noted when discussing the annual biomass production and litter crop, there are many reasons why these characteristics are more difficult to determine accurately than the quantity of biomass at any given time. Determination of the production of removal is the most difficult problem when the total production during a given period is studied.

The proportion of removal out of the biomass generally fades towards the time of death, and so removal increment during an annual period is usually very small. In the present case, the removal did not include stems because none of the trees in the sample plots died during the period of measurement. The production of removal included the loss of dry matter from the trees, for instance, due to destruction of needles by insects during the growing season. However, this loss was very small and could not be measured. There is probably no removal production in older needles because they already start to lose weight at the yellowing stage. The estimation of the removal production of branches was based on the assumption that it equalled the annual branch litter quantity that grew during half of the measurement period, and that its growth ratio corresponded to the average increment of the branches. The removal production of male flowers, for instance, could be estimated from their litter quantities. The root removal production may be important owing to fluctuations in the amounts of thin roots during the growing season, but its dry weight was not possible to determine. The production of ground vegetation removal includes the dry weight of the phenological part of the vegetation that has shrivelled before the moment of measurement, but this was not measured here.

It can be concluded that the annual production of the removal was relatively small compared to the annual total production, and did not constitute major source of error in the estimation of the annual development of the biomass. The annual balance of biomass calculated from the data concerning the distribution of dry matter in the sample plots is shown in the following table:

Biomass changes	Sample plot No.					
	1		2		3	
	kg/ha	%	kg/ha	%	kg/ha	%
Biomass at end of measurement period	28 650	100.0	57 560	100.0	97 460	100.0
Annual total production	4 780	16.7	6 535	11.4	8 450	8.6
Annual removal	2 115	7.4	2 695	4.7	4 025	4.1
Annual net production	2 665	9.3	3 840	6.7	4 425	4.5
Biomass at beginning of measurement period	25 985	90.7	53 720	93.3	93 035	95.5

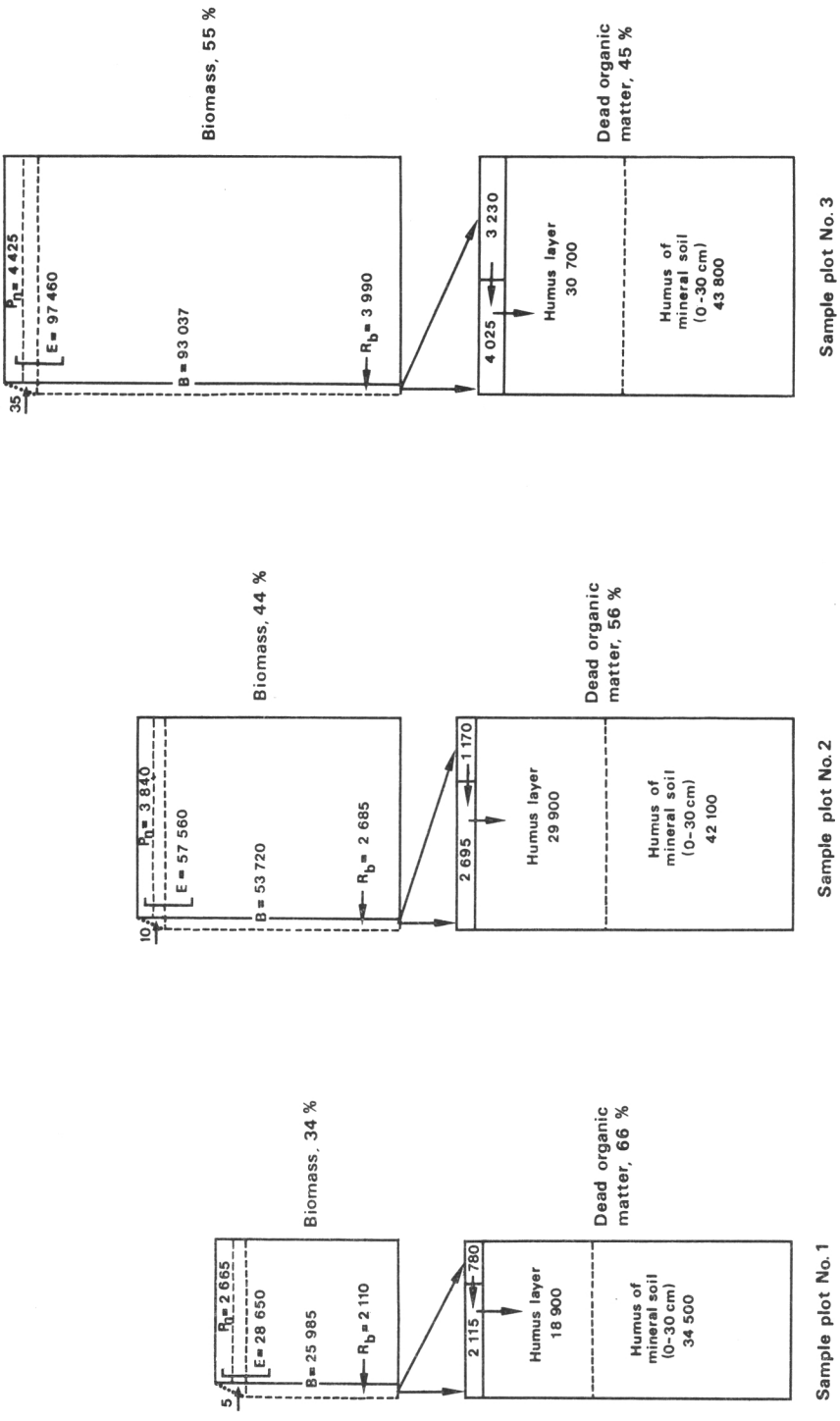

Fig. 4. The annual development of biomass and the distribution of organic matter (kg/ha).

See explanation on page 10.

The table shows that, in all the sample plots, the annual total production was more than twice the removal. The relative net production of biomass, however, decreased sharply according to the stage of stand development.

The annual development of biomass and the distribution of the organic matter in the experimental stands is depicted in Fig. 4. Since standing dead trees were not found in the sample plots, only the dry weight of dead branches was included in the »standing dead» fraction of the organic matter.

4. DISTRIBUTION OF NUTRIENTS IN A STAND

41. Nutrient stores in the soil

The biomass production of a stand depends, among other factors, on the amount of nutrients available to the plants. Finnish mineral soils generally contain adequate amounts of phosphorus and potassium, but the yield capacity of pine stands is dependent upon the amount of calcium in the surface soil (V i r o 1951). Although there is enough calcium to satisfy plant requirements, its beneficial effect on site fertility lies in the promotion of nitrogen mineralization.

I l v e s s a l o (1923) found, using V a l m a r i's (1921) soil analysis data, that the increment of forests is closely correlated with the amounts of total nitrogen and calcium in the surface soil layer. However, only more recently has it been shown that the amount of available nitrogen is, in fact, the commonest growth-limiting factor on podzol soils (A a l t o n e n 1926, V i r o 1967).

The nutrient quantities of the surface soil were determined from the fine soil fractions (< 2 mm). For this reason, the space occupied by gravel, stones, and boulders had to be taken into account when determining the nutrient quantities (Table 17). When the average calcium quantities in the pine stand soils of southern Finland, reported by V i r o (1960), are compared with the quantities obtained in the present study, it seems that the quantity of calcium in Sample plot No. 3 only is in agreement. The amount of exchangeable potassium was generally greater, and that of easily soluble phosphorus lower, than the average for pine stands in southern Finland.

Table 17. The amount of mineral nitrogen, easily soluble phosphorus, and exchangeable potassium and calcium in the surface soil layer.

Soil layer	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	$N_{min.}$	P	K	Ca	$N_{min.}$	P	K	Ca	$N_{min.}$	P	K	Ca
Humus layer	1	3	20	45	1	4	28	48	1	5	31	91
0—10 cm	3	9	32	42	5	7	30	33	5	9	37	113
10—20 cm	3	6	18	44	4	7	14	19	5	3	26	60
20—30 cm	4	6	16	36	5	3	12	19	7	2	17	44
Total	11	24	86	167	15	21	84	119	18	19	111	308

Table 18. The amount of mineral nitrogen, easily soluble phosphorus, and exchangeable potassium and calcium with 95 % confidence limits at different times during the growing season in Sample plot No. 3.

Sampling date	NH_4^+—N	NO_3^-—N	P	K	Ca
	Humus layer, mg/100 g organic matter				
14th May, 1973	7.82± 7.64	0.83±0.20	16.17±7.40	76.4±38.8	279.9± 45.0
29th » »	4.59± 1.65	0.76±0.27	16.84±9.56	56.0±17.2	247.6± 82.1
11th June, »	4.84± 2.33	0.83±0.21	14.85±3.86	53.1±21.1	357.8±108.4
16th July, »	15.80±12.80	1.93±0.53	16.52±9.85	60.3±45.9	306.6±111.2
13th Aug., »	4.26± 1.93	0.91±0.36	13.46±4.66	47.1±19.3	391.5±190.7
15th Oct., »	5.43± 3.58	1.15±0.77	12.25±3.78	43.6±15.6	438.8±197.4
$\bar{x}_{ij}$	7.12± 2.33	1.07±0.19	15.02±2.01	55.9± 8.8	337.0± 44.3
Source of variation:					
replication F-value ..	5.99**	1.38	5.95**	2.89*	3.07*
sampling date F-value	6.78***	8.39***	0.98	1.57	2.99*
	Mineral soil, 0—30 cm, mg/100 g soil				
14th May, 1973	0.86±1.01	0.13±0.02	0.22±0.05	1.68±0.55	4.06±2.31
29th » »	0.40±0.12	0.11±0.03	0.29±0.11	2.00±0.56	4.50±2.38
11th June, »	0.46±0.29	0.25±0.55	0.31±0.32	1.79±0.35	5.63±5.81
16th July, »	0.66±0.52	0.13±0.04	0.28±0.05	1.85±0.49	5.21±3.62
13th Aug., »	1.08±1.27	0.17±0.05	0.29±0.13	1.85±0.37	4.23±2.22
15th Oct., »	0.71±0.50	0.23±0.42	0.16±0.04	1.56±0.50	4.02±3.25
$\bar{x}_{ij}$	0.70±0.22	0.17±0.05	0.26±0.05	1.82±0.14	4.61±0.98
Source of variation:					
replication F-value ..	6.74**	2.71	2.51	6.22**	9.40***
sampling date F-value	1.77	0.96	1.47	1.31	0.67

It is difficult to assess the ability of the soil to satisfy the nutrient requirements of a stand merely on the basis of the available nutrient amounts revealed by soil analysis. From an ecological point of view, the rate of nutrient replacement should be taken into account when the amount of nutrients is being discussed. H o l m e n (1964), for instance, has found a negative correlation between the increment of the trees and the ammonium lactate soluble phosphorus content of the peat, whereas a positive correlation existed between the total phosphorus content of the peat and the increment of the trees. This indicates that a vigorous pine stand growing on peatland may use almost all of the available easily soluble phosphorus in the course of one growing season.

In order to elucidate the changes in the amounts of available nutrients during a growing season, soil samples were taken from Sample plot No. 3 six times between 14th May and 15th October, 1973. Five replicate samples were taken from 1 m^2 sample squares lying about 5 m apart. In morainic soil, nutrient ratios vary widely even within such small sample squares (T r o e d s s o n & T a m m 1969). In the present material the nutrient content of soil also varied widely within the replications (Table 18). Concerning the seasonal variation of nutrient content, it was found that the

content of mineral nitrogen was highest in July in the humus layer. However, it was not possible to explain in more detail the seasonal variation of the soil nutrient content.

Soil acidity affects the availability of nutrients both through the biological activity in the soil and through the solubility of its minerals. The low pH of raw humus limits the activity of micro-organisms. The pH values of the surface soil of the sample plots were as follows:

Soil layer	Sample plot No. 1	Sample plot No. 2	Sample plot No. 3
Humus layer	3.60	3.46	3.70
0—10 cm	4.68	4.42	4.63
10—20 cm	5.12	4.80	5.65
20—30 cm	5.20	4.98	5.77

The humus layer is usually more acid than the mineral soil, and the acidity decreases on moving downwards.

The amount of mineral nitrogen in the soil equals the difference between the net mineralization and the amount taken up by the plants, and consequently, it does not indicate the amount of nitrogen available to the plants. Owing to methodological difficulties it has been impossible to determine the net mineralization directly. Some conclusions, however, have often been drawn about the nitrogen supply in the soil by indirect methods, such as determining the C/N ratio of the humus, which indicates the nitrogen supply in the soil in relation to the potential nitrogen mineralization.

In most cases the lower the C/N ratio is the better the site is for autotrophic plants as regards nitrogen nutrition. Thus, the ratio is one indicator of soil fertility. It usually decreases as organic matter decomposes because carbon is lost as carbon dioxide, whereas nitrogen is bound to decomposing organisms and humus matter. The critical value of the C/N ratio is usually set at 20, at which the organic matter contains carbon and nitrogen in roughly the proportion in which the micro-organisms require them (J e n s e n 1929). In this case there is neither a shortage nor an excess of either element.

The following C/N ratios were obtained for the surface soil of the sample plots:

Soil layer	Sample plot No. 1	Sample plot No. 2	Sample plot No. 3
Humus layer	49.1	48.6	47.7
0—10 cm	29.7	20.7	22.7
10—20 cm	23.4	17.2	17.2
20—30 cm	18.0	16.5	16.2

The decisive factor in the decomposition of organic matter, however, is not the ratio between total carbon and total nitrogen, but rather that between quantities actually available to the micro-organisms. Thus, the C/N ratio by itself does not indicate the rate of decomposition of organic matter (Vartiovaara 1936). Despite the lower C/N ratio of mineral soil, probably as much as 90 per cent of the nitrogen taken up by the trees comes from the raw humus layer (Tamm & Holmen 1967). For this reason the nitrogen amount in the litter is more important for the nutrient status of the site than would seem to be the case judging purely from the nitrogen quantities in the litter and surface soil.

The release of nitrogen from litter was studied by the same method as the litter decomposition except that needle litter, which contained labelled nitrogen, was used. The loss of dry matter and labelled nitrogen from the samples placed on the bottom layer of the ground vegetation was as follows:

	Loss of dry matter, %	Loss of labelled nitrogen, %
During one year	32.4±2.9	25.6±5.7
During two years	60.3±5.5	52.0±7.7

The nitrogenous compounds of the litter appear to be relatively more resistant to decomposition than some non-nitrogenous material. However, the results indicate that initially immobilized labelled nitrogen will first be subjected to mineralization at a relatively high rate.

Plants acquire nutrients also from the atmosphere through precipitation. According to Viro (1953) precipitation carries nutrients in the following amounts (kg/ha/yr.):

N	P	K	Ca
5.87	0.09	2.45	1.99

Apart from quantities lost through tree harvesting, a stand loses nutrients by leaching. This process is so slow in Finland, however, that the fertility of the soil can be considered practically unchanged for a very long time. This is borne out by the following percentages, indicating the ratio between nutrients supplied by precipitation and those leached away (Viro 1953):

	N	P	K	Ca
kg/ha/yr.	+4.00	—0.17	—2.10	—10.00
%	314	44	54	17

There are clear losses of mineral nutrients, but precipitation provides the soil with more than three times as much nitrogen as it leaches away. Losses of mineral nutrients by leaching are compensated for by nutrients released by weathering.

42. Nutrient amounts bound by the vegetation

421. Tree crop

Trees in the same stand may differ in their nutrient content due to local variation in the soil nutrient supply, genetic factors pertaining to the trees, and the position of the trees in the stand. On the other hand, root grafts between trees reduce the effect of soil heterogeneity (Yli-Vakkuri 1953). The variation in nutrient content between trees is usually much smaller than the variation in nutrient content in the soil revealed by soil analysis.

The average nutrient content of the different tree compartments indicated that the nutrient content of the stemwood is lower than that of the other compartments (Appendix 2). The nutrient content of the stemwood also varied according to the amount of heartwood it contained; the content of phosphorus and calcium of the heartwood was notably lower than that of the sapwood. However, the nutrient content of wood is so low that heartwood formation does not have much effect on the internal circulation of nutrients in a tree.

The variation of nutrient content in the longitudinal direction of the stem is depicted in Appendix 3. This examination is based solely on the data collected from Sample plot No. 2 because the variation in nutrient content between the sample plots might have impeded comparability if the entire material had been analysed together.

The calcium content of bark is very high. As much as 80 per cent of the bark ash from certain deciduous trees consists of calcium (Srivastava 1964). The calcium in bark is mostly in the form of calcium pectate in the middle lamellae of the cell walls, and of calcium oxalate crystals. The distribution of cells containing these crystals in the bark is often irregular, as is indicated by the high variation of calcium content in the longitudinal direction of the stem. The calcium content of the bark was highest at a relative height of about 40 per cent along the stem, and the potassium content at about 70 per cent, respectively. The content of nitrogen and phosphorus varied according to the ratio of living to dead bark, and so it increased on moving upwards.

The nutrient content of the living branches and the stem bark were very similar, probably due to the high proportion of bark in the dry matter of the branches. Thus, the variation in the nutrient content of the branches in the longitudinal direction of the stem was due mainly to variation in the bark-to-wood ratio, which itself depends on the diameter of the branches.

The variation of nutrient content of needles with age follows a rather consistent pattern. It has generally been found that the calcium content

Table 19. Amount of various nutrients bound into the tree crop (kg/ha).

Compartment	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Stemwood	5.78	0.58	3.66	5.68	19.51	1.36	8.94	13.55	37.23	2.22	18.34	34.45
Bark	6.54	0.99	3.72	10.67	12.72	1.93	7.33	10.76	19.68	2.93	12.29	26.07
Dead branches .	2.68	0.14	0.34	2.43	3.70	0.20	0.44	1.98	7.53	0.42	0.94	3.94
Living branches	12.75	1.73	7.29	11.28	29.22	3.32	12.00	15.93	30.40	3.61	15.75	19.06
Needles												
1st yr.	8.91	1.13	5.34	1.50	14.32	1.74	6.57	1.82	18.39	2.21	10.62	2.69
2nd yr.	10.06	0.95	3.74	3.83	14.18	1.50	5.41	3.12	20.35	1.98	8.56	6.11
3rd yr.	5.33	0.52	1.95	2.95	10.30	0.99	3.27	2.76	10.21	0.95	4.00	4.10
4th yr.	1.25	0.13	0.49	0.89	4.68	0.47	1.55	1.46	6.46	0.62	2.35	3.08
Cones	△	△	△	△	0.07	0.01	0.04	△	0.04	0.01	0.03	△
Above-ground part	53.30	6.17	26.53	39.23	108.70	11.52	45.55	51.38	150.29	14.95	72.88	99.50
Stumps	1.41	0.24	1.08	0.96	2.12	0.31	1.68	1.39	4.53	0.58	3.25	2.68
Roots, ∅ >1 cm	2.83	0.36	1.67	1.46	5.44	0.83	4.49	3.55	11.86	1.55	8.86	7.20
Roots, ∅ <1 cm	16.86	3.56	9.28	7.54	13.62	2.08	8.22	4.08	19.58	4.04	11.26	13.34
Below-ground part	21.10	4.16	12.03	9.96	21.18	3.22	14.39	9.02	35.97	6.17	23.37	23.22
Total	74.40	10.33	38.56	49.19	129.88	14.74	59.94	60.40	186.26	21.12	96.25	122.72

increases and the content of nitrogen, phosphorus, and potassium decreases as the age of the needles increases. This was also clearly borne out by the data from all the sample plots. The variation of the needle nutrient content in the longitudinal direction of the stem was very small, which indicates, for instance, that the sampling height has very little effect on the results of needle analysis.

As regards the nutrient cycle, absorbing roots can be compared to needles, and lateral roots to the thickest branches and stem. According to the stratification used in the present study, the roots less than 1 cm in diameter resembled to a large extent the living branches as far as their nutrient content was concerned.

The nutrient amounts bound by the tree crop are given in Table 19. The amount of nitrogen was highest, followed in order by calcium, potassium, and phosphorus. The distribution of nitrogen, potassium, and phosphorus between different compartments of the tree was similar: about half of these nutrients contained in the tree crop were found in the canopy, *i.e.*, in living branches and needles. The stems contained 15—20 per cent of the total amounts in the tree crop in Sample plot No. 1 and 25—30 per cent in Sample plot No. 3. The remaining 20—35 per cent was found in the stumps and roots. Calcium was considerably more prominent in the stems, which contained about 35 per cent of the total amount of calcium in the tree crop in Sample plot No. 1 and as much as 50 per cent in Sample plot No. 3.

4211. Internal nutrient cycle in the tree

As the tissues of a plant age and die, some of the nutrients are translocated to the growing parts and are re-used in various biosynthetic processes. In particular, the translocation of nitrogen, phosphorus, and potassium from dying leaves before their abscission is of the greatest importance in satisfying the annual nutrient requirement of the tree (V i r o 1955). On the other hand, calcium is considered to be less mobile, and so it probably plays no role in the internal nutrient cycle of the tree (K r a m e r & K o z l o w s k i 1960, p. 202).

The increase in the dry weight of needles with age makes it difficult to study their nutrient quantities because the content of some nutrients may decrease even when their absolute amounts increase. Accurate determination of the translocation calls for nutrient determinations in absolute amounts of nutrients per needle. The nutrient amounts in the pine needles of different ages collected for this purpose were as follows:

Age of needles	Dry weight per 1000 needles, g	N	P	K	Ca
		mg/1 000 needles			
1st yr.	6.041	90.0	9.5	41.5	14.2
2nd yr.	6.869	91.4	9.5	42.0	20.1
3rd yr.	7.224	95.4	9.7	40.4	22.2
4th yr.	8.004	104.0	10.7	40.4	30.0
Yellowed	6.668	32.7	2.0	8.0	35.4
Change at yellowing, %	—17	—69	—81	—80	+18

The translocation of nitrogen, phosphorus, and potassium from the needles at yellowing was 5—15 percentage units less than in V i r o's (1955) data. In addition, the amount of calcium in the needles even increased at the time of yellowing.

The translocation of nutrients from the fourth-year needles according to the above table corresponds to the following nutrient amounts in the sample plots (kg/ha):

	N	P	K
Sample plot No. 1	0.86	0.11	0.39
2	3.21	0.38	1.23
3	4.47	0.50	1.89

The translocation of nutrients from the oldest needles is probably less important in young stands such as Sample plot No. 1 than in mature stands, owing to the rapid annual increase of needle mass and the nutrient requirement of the young tree crop. In any case, the amount of nutrients translocated from needles to branches are extremely important for the nutrient status

of the tree. For instance, in a 20-year-old *Pinus taeda* stand the trees satisfied some 45 per cent of the annual nitrogen requirement by translocation from yellowing needles (S w i t z e r *et al.* 1968).

Isotope studies were carried out on the translocation of nitrogen from needles. A ^{15}N labelled urea solution was sprayed onto the surface of fourth-year needles in July, and the samples were collected in the middle of September. The results of isotope analysis expressed as atomic percentages are given in the following table:

	1st yr.	2nd yr.	3rd yr.	4th yr.	5th yr.
Needles	0.03	0.01	0.01	0.66 [1])	·
Bark	0.03	0.03	0.02	0.47	0.17
Wood	n. d.	0.02	0.02	0.15	0.08

The data indicated that most of the nitrogen was translocated into the bark and wood corresponding in age to that of the needles, and then into the next oldest part of the shoot. Branch bark, particularly its phloem layer, is obviously the main store of nutrients translocated from needles. At any rate its nitrogen content has been found to vary with the growth rhythm of the tree more than that of the wood (K r a m e r & K o z l o w s k i 1960, p. 121).

422. Ground vegetation and shrubs

In order to determine the amount of nutrients bound by ground vegetation, quadruplicate determinations were made, if possible, on samples from each plant group. Owing to the small number of analyses and the varying species composition of the samples, the variation of the nutrient content was relatively greater than it was in the nutrient determinations on the tree crop. Appendix 4 shows that herbs and grasses generally had a higher content of nitrogen, phosphorus, and potassium than other plants.

The nutrient amounts in the ground vegetation were calculated from the dry weight and nutrient content of the plant groups (Table 20). As the nutrient content of ground vegetation is on the average higher than that of trees, ground vegetation plays a more important role as a consumer of nutrients than would seem to be the case judging from its biomass production. There are also considerable differences in the uptake of nutrients by the different plant groups. Most of the nutrients taken up by mosses are probably absorbed by their growing shoots, owing to the absence of roots (T a m m 1953). Thus, the main sources of nutrients for mosses are the nutrients contained in precipitation, which includes inorganic ions dissolved in rain water from the tree canopy and litter.

[1]) Needles treated with labelled urea.

Table 20. Amount of various nutrients bound into the ground vegetation and shrubs (kg/ha).

Plant group	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Lichens	0.04	△	0.01	△	0.64	0.06	0.17	0.07	△	△	△	△
Mosses	19.52	1.78	9.16	5.76	12.26	1.35	6.50	4.08	33.21	3.46	15.74	10.42
Grasses	0.07	0.01	0.11	0.01	0	0	0	0	2.11	0.15	2.41	0.30
Herbs	0.15	0.03	0.20	0.12	0	0	0	0	1.82	0.22	2.40	0.60
Dwarf shrubs	8.59	0.85	3.76	4.73	14.04	1.20	5.58	7.38	5.86	0.60	4.03	3.03
Shrubs	0.18	0.02	0.08	0.14	0.30	0.04	0.14	0.10	0.44	0.05	0.31	0.89
Above-ground part	28.55	2.69	13.32	10.76	27.24	2.65	12.39	11.63	43.44	4.48	24.89	15.24
Below-ground part	9.91	1.04	3.18	4.49	15.41	2.20	3.22	5.71	15.95	2.76	4.45	7.10
Total	38.46	3.73	16.50	15.25	42.65	4.85	15.61	17.34	59.39	7.24	29.34	22.34

As the nutrient content of the older segments of mosses equals approximately that of the young ones, the translocation of nutrients from dying segments is evidently of minor importance for the nutrient requirement of mosses (T a m m 1953). The above-ground parts of herbs and grasses are annual, and so nutrients are accumulated in them only for a short time. Dwarf shrubs, having woody stems, generally resemble trees in their nutrient requirement.

43. Nutrient amounts in the litter crop

After dry weight determination the majority of the litter samples were combined into monthly groups. However, during the period of maximum litter fall the nutrients were analysed from samples collected weekly. Table 21 shows the average nutrient content of litter as a percentage of dry weight, weighted by the dry weight of litter. The variation of nutrient content between the various types of litter was smaller than that between the corresponding living tissues. The nutrient content of litter from a given tree species does not depend very much on the nutrient content of the soil (V i r o 1955).

Table 21. Average nutrient content of litter as a percentage of dry weight, weighted by the dry weight of litter.

Type of litter	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Needles	0.477	0.036	0.100	0.570	0.445	0.029	0.060	0.435	0.550	0.046	0.121	0.509
Branches	0.508	0.031	0.053	0.310	0.689	0.033	0.054	0.268	0.518	0.033	0.064	0.226
Bark	0.485	0.027	0.060	0.385	0.517	0.029	0.042	0.313	0.458	0.025	0.056	0.425
Cones, seed, flowers	0.602	0.065	0.125	0.107	0.525	0.037	0.054	0.068	0.220	0.020	0.094	0.038
Residual	0.870	0.061	0.104	0.304	1.031	0.074	0.086	0.145	1.422	0.126	0.244	0.332

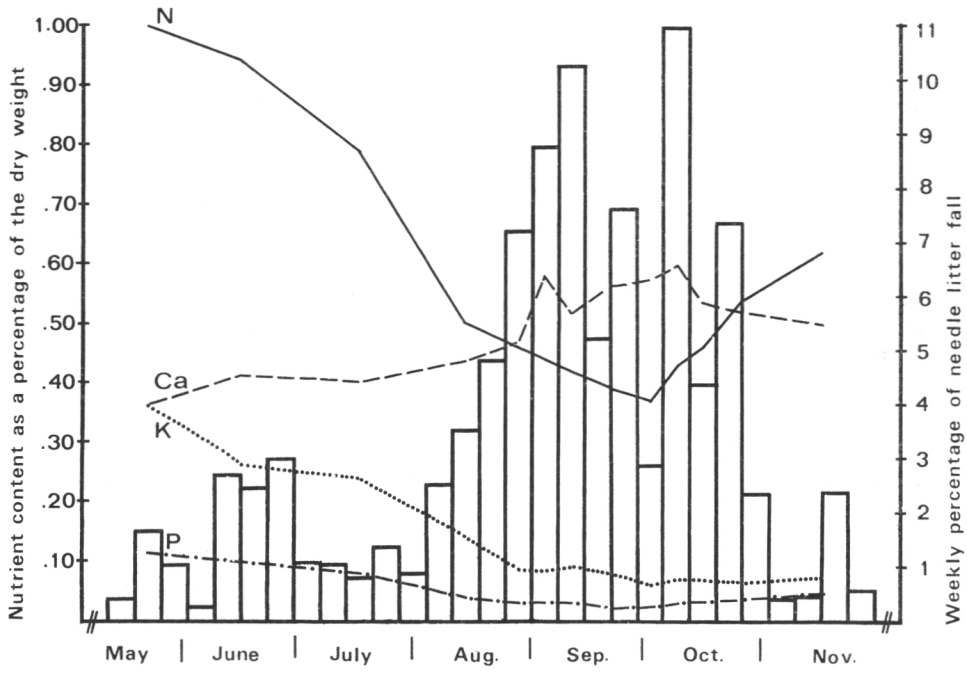

Fig. 5. Seasonal variation in the fall of needle litter and its nutrient content.

During yellowing needles lose weight and their content of nitrogen, phosphorus, and potassium decreases. On comparing the average nutrient content of needle litter with that of the oldest green needles, it was found that the potassium content of the litter was about a quarter of that of the living needles, and the content of nitrogen and phosphorus correspondingly a third and a half, whereas the calcium content remained roughly unaltered. Although some of the needle nutrients had been leached out by precipitation, a major role was played by translocation.

Seasonal variation found in the nutrient content of needle litter was obviously associated with the annual development of the trees (Fig. 5). It can be seen from the analysis data that the content of nitrogen, phosphorus, and potassium of the needle litter decreased towards autumn, being at its lowest during the period of maximum litter fall. The calcium content varied conversely. Obviously the calcium content was mainly increased by the decrease of the other nutrients and organic matter. The time of maximum needle fall and changes in the nutrient content of needle litter may be related, and may be associated with the process that governs the annual development of the tree. However, to study these relationships would call for detailed measurements of litter fall and of certain environmental factors such as temperature.

Table 22. Amount of various nutrients returned to the soil in the litter fall (kg/ha).

Type of litter	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Needles	2.34	0.18	0.49	2.79	3.56	0.23	0.48	3.48	6.11	0.51	1.34	5.65
Branches	0.25	0.02	0.03	0.15	0.48	0.02	0.04	0.19	0.71	0.05	0.09	0.31
Bark	0.11	0.01	0.01	0.09	0.59	0.03	0.05	0.36	0.81	0.04	0.10	0.75
Cones, seed, flowers	0.02	△	△	△	0.16	0.01	0.02	0.02	0.09	0.01	0.04	0.02
Residual	0.08	0.01	0.01	0.03	0.52	0.04	0.04	0.07	2.70	0.24	0.46	0.63
Total	2.80	0.22	0.54	3.06	5.31	0.33	0.63	4.12	10.42	0.85	2.03	7.36

The nutrient amounts returned to the soil in the annual litter fall are given in Table 22. Those in Sample plot No. 3 agree well with V i r o's (1953) data for pine stands at a similar stage of development. In mature pine stands, the annual litter crop usually contains only 3—5 per cent of the total amount of nutrients in the above-ground part of the trees (R o d i n & B a z i l e v i c h 1965, p. 80). According to the present material only 2 per cent of the potassium, but 8 per cent of the calcium in the above-ground part of the trees were returned in litter fall.

44. Nutrient amounts leached from the canopy by precipitation

In studies on the nutrient cycle, increasing attention has been paid to the role of precipitation both as a source of nutrients and as an agent leaching nutrients from the vegetation into the soil. As rain water drips through the canopy, it leaches nutrients out of the needles and bark surface. P o z d n y a k o v (1956) states that water-soluble compounds are formed on the surface of leaves and bark, both as a result of the plants' metabolic processes and of the action of micro-organisms living on their surfaces. On the other hand, it has been shown that leaves are able to absorb nutrients from rain water (T u k e y *et al.* 1952).

Throughfall reaching the ground directly through canopy openings and by dripping from trees was determined using twenty rain gauges. The accuracy of measurement given by fixed collectors varies widely according to the quantity of precipitation (cf. K i m m i n s 1973). Fig. 6 shows the relationship between the amount of throughfall, and the standard deviation and coefficient of variation of the mean for the measurements made in 1971, which comprised 37 measurement periods. As can be seen, the standard deviation showed an approximately linear increase with increasing throughfall, while the coefficient of variation showed a curvilinear increase with decreasing throughfall at values below about 6 mm. With throughfalls greater than this value, the coefficient of variation appeared to decrease

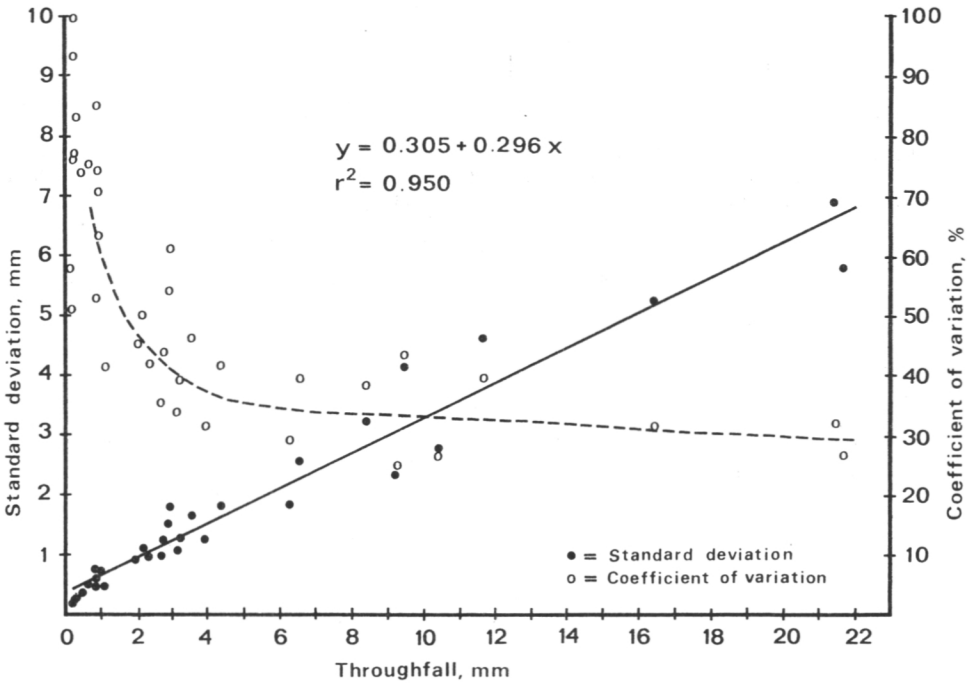

Fig. 6. Relationship between the amount of throughfall (x), and the standard deviation (y) and coefficient of variation of the mean.

almost linearly. The relative error of the estimate, using 20 gauges, was about 15 per cent when the throughfall was 10 mm.

No significant differences were found between the collection periods in the nutrient content of precipitation; obviously the measurement periods were too long to show any such differences. For this reason the nutrient content of the precipitation is given as an arithmetic mean for the entire period of the study (Table 23). The nutrient content of precipitation was generally highest in the stemflow and decreased clearly on moving from under the canopy to the canopy openings. However, there was no difference in mineral nitrogen content between the various types of collection points.

Table 23. The average nutrient content of rainwater, with the 95 % confidence limits, collected at different sampling points.

Sampling point	N	P	K	Ca	$N_{min.}$
	mg/l				
Open area	1.316±0.208	0.025±0.009	0.820±0.168	1.127±0.477	0.734±0.382
Under the canopy	1.689±0.172	0.039±0.011	2.035±0.422	2.835±0.651	0.708±0.243
Canopy opening .	1.355±0.197	0.026±0.008	0.978±0.201	1.365±0.267	0.720±0.245
Stemflow	1.923±0.656	0.055±0.038	4.053±0.866	9.101±4.054	0.775±0.368

The data show that rain water leaches mostly calcium and potassium from the canopy.

The nutrient amounts which reached the soil surface in rain water were calculated on the basis of the precipitation recorded during the different collection periods, and on its nutrient content. The average stemflow per stem was converted into millimetres of precipitation by multiplying it by the total number of stems (Seppänen 1964). Throughfall accounted for 76 per cent of the gross precipitation, stemflow for only 1.3 per cent. These values correspond closely to Päivänen's (1966) data on the distribution of precipitation in pine stands.

Precipitation was collected for about five months each year. The amounts collected were 51 per cent of the annual precipitation during the first year, and 61 per cent the second year. It is obvious that snow leaches less nutrients from the canopy than does rain water. Therefore, the nutrient quantities calculated for throughfall and stemflow were converted into annual means excluding precipitation as snow. However, there are no appreciable differences between the nutrient content of gross precipitation in winter and summer (Viro 1953, Tamm 1958, p. 234). The present nutrient amounts in gross precipitation were found to be slightly greater than Viro's (1953) average data for the whole country. The exception was calcium, the amount of which in the present material was almost two and a half times greater than Viro's.

Table 24 shows that the amounts of potassium and calcium reaching the soil in throughfall were nearly one and a half those in gross precipitation, but owing to interception, less nitrogen and phosphorus reached the soil in the sample plot than in an open area. Thus, the pattern of precipitation causes local differences in the distribution of nutrients in forest soil.

Table 24. Distribution of precipitation and amount of various nutrients reaching the ground in rain water.

Component of precipitation	mm	N	P	K	Ca	$N_{min.}$
		kg/ha/yr.				
Gross precipitation	484	6.63	0.14	3.86	4.88	3.79
Throughfall	325	4.82	0.08	5.78	7.44	1.97
Stemflow	57	0.10	△	0.23	0.44	0.05

5. NUTRIENT CYCLE IN A STAND

51. Distribution of nutrients throughout the biological cycle

The nutrients which are already present in the biological cycle or are likely to be taken up into it form a mobilizable store of nutrients in the ecosystem. In a stand, all the nutrients bound to the vegetation and humus are already included in the cycle, although the mineralization in humus may be very slow. In mineral soil, only exchangeable cations can be counted as mobilizable nutrients.

Both the total and the available amounts of nutrients in the humus layer can be calculated from analysis data, but the quantities of nutrients bound to the humus in the mineral soil can not be analysed directly. The only exception to this is nitrogen, since the nitrogen which is unavailable to the plants is organically bound. The content of phosphorus, potassium, and calcium of the mineral soil humus was estimated from that of the organic matter in the humus layer. Similar differences probably exist in the solubility of the nutrients in the organic matter of the mineral soil as in the humus layer (V i r o 1969). Therefore, it was assumed that the proportion of available nutrients in the mineral soil humus equals that in the humus layer. The distribution of nutrients throughout the biological cycle presented in Table 25 is based on this assumption.

Of the mobilizable nutrient stores, the percentage of potassium bound to the biomass was greatest, followed in order by phosphorus, calcium, and nitrogen. The data clearly show that nitrogen in this respect differs from the other nutrients studied. Only about 10 per cent of the nitrogen store in the sample plots was bound to the biomass; the bulk of it was present in a form unavailable to the plants in the surface layer of the mineral soil. The ratios of available amounts to the total amounts of nutrients in the humus agree fairly well with V i r o's (1969).

The amount of mobilizable nutrients in the ecosystem is subject to constant change. Losses due to leaching and tree harvesting are compensated for by the addition of nutrients entering from the atmosphere and released by weathering. Efforts have been made to calculate the rate of weathering

Table 25. Distribution of nutrients throughout the biological cycle in the experimental stands (kg/ha).

Stage of cycle	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Biomass	110	14	55	62	169	19	75	76	238	28	125	141
Dead braches and litter ...	5		1	6	9	1	1	6	18	1	3	11
Non-available nutrients in humus												
Humus layer	223	10	8	34	358	18	8	29	373	17	7	56
0—30 cm ..	783	17	15	61	1 253	25	11	39	1 282	25	10	80
Total	1 006	27	23	95	1 611	43	19	68	1 655	42	17	136
Available nutrients												
Humus layer	1	3	20	45	1	4	28	48	1	5	31	91
0—30 cm ..	10	20	66	122	14	6	40	71	17	13	80	217
Total	11	23	86	167	15	10	68	119	18	18	111	308
Total	1 132	64	165	330	1 804	73	163	269	1 929	89	256	596
Bound into biomass, % ..	10	22	33	19	9	26	46	28	12	31	49	24
The amounts of available nutrients as percentage of total nutrient amounts in humus of humus layer ...	1.1	23	71	57	0.9	18	78	60	1.1	23	82	62

from the mineral composition of the different horizons of podzol soil (T a m m 1940, p. 122) and by river water analyses (e.g. V i r o 1953). The former method gives very low values for the annual release of metal ions; the latter type of measurement generally results in rather high values.

52. Annual nutrient balance of a stand

The annual nutrient requirement of the vegetation is a major factor which should be taken into account when studying the biological cycle of nutrients. Judging by the nutrient quantities bound annually to the biomass, it can be seen that ground vegetation plays an even greater role in the consumption of nutrients than in the production of biomass (Table 26). The nutrient consumption of the trees and ground vegetation, however, can more easily be compared if the nutrient amounts are expressed per unit of dry matter produced. The differences between the sample plots, as

Table 26. Amount of various nutrients bound to the apparent annual production of biomass (kg/ha).

Compartment	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Stemwood	0.47	0.05	0.30	0.46	1.29	0.09	0.59	0.90	1.57	0.09	0.78	1.46
Bark	0.30	0.05	0.17	0.50	0.38	0.06	0.22	0.32	0.46	0.07	0.29	0.61
Branches	2.63	0.36	1.51	2.33	3.34	0.38	1.37	1.82	3.61	0.43	1.87	2.27
Needles	9.38	1.15	5.40	3.14	15.35	1.80	6.66	3.38	19.67	2.29	10.87	5.68
Cones	△	△	△	△	0.04	0.01	0.02	△	0.02	△	0.02	△
Stumps and roots	2.87	0.56	1.64	1.36	2.05	0.31	1.40	0.88	2.42	0.31	1.56	1.56
Tree crop	15.65	2.17	9.02	7.79	22.45	2.65	10.26	7.30	27.75	3.19	15.39	11.58
Ground vegetation and shrubs	12.19	1.20	5.46	4.93	10.62	1.21	4.11	4.49	23.03	2.76	13.04	8.24
Total	27.84	3.37	14.48	12.72	33.07	3.86	14.37	11.79	50.78	5.95	28.43	19.82
Percentage of various nutrients out of the total annual requirement:												
Tree crop, %	56.2	64.4	62.3	61.2	67.9	68.7	71.4	61.9	54.6	53.6	54.1	58.4
Ground vegetation and shrubs, %	43.8	35.6	37.7	38.8	32.1	31.3	28.6	38.1	45.4	46.4	45.9	41.6
Nutrient consumption per unit of dry matter produced (kg/1 000 kg dry matter):												
Tree crop	4.60	0.64	2.65	2.29	4.38	0.52	2.00	1.42	4.35	0.50	2.41	1.81
Ground vegetation and shrubs	8.90	0.88	3.99	3.60	7.59	0.86	2.94	3.21	11.34	1.36	6.42	4.06
Nutrient consumption per unit of stem volume increment (kg/m^3 stemwood o.b.):												
Tree crop	6.92	0.96	3.99	3.45	4.50	0.53	2.06	1.46	4.74	0.54	2.63	1.98

regards the consumption of nutrients by the trees, are probably due to variations in the nutrient content of the soil and to the stage of stand development — *i.e.*, the structure of the biomass quantity produced. For this reason young trees, for example, take up more nutrients per unit of dry matter produced than old trees. On the other hand, the nutrient consumption of the ground vegetation per unit of dry matter produced in Sample plot No. 2 was generally smaller than that in the other sample plots, owing to the lack of grasses and herbs and to the abundance of heather.

The nutrient consumption of the trees can also be expressed per produced solid cubic metre of overbark stemwood. In this case, of course, the stage of stand development is reflected in the nutrient amounts even more clearly than by comparing the nutrient consumption to the total production of the trees.

The annual requirement of nutrients by trees can be illustrated by the nutrient amounts taken up by trees from the soil, retained by them, and returned to the soil. In the present study, the annual nutrient requirement of the trees was estimated as the sum of the nutrient quantities bound in the annual biomass production and of those returned to the soil in the litter.

Component of balance	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Taken up from soil by trees, kg/ha	19.0	2.5	9.8	11.1	28.2	3.1	11.2	11.6	38.8	4.2	17.9	19.4
Retained by tree crop, kg/ha	15.7	2.2	9.0	7.8	22.5	2.7	10.3	7.3	27.8	3.2	15.4	11.6
Returned in litter, kg/ha	3.3	0.3	0.8	3.3	5.7	0.4	0.9	4.3	11.0	1.0	2.5	7.8
Amount returned as % of amount taken up	17	12	8	30	20	13	8	37	28	24	14	40

In calculating the values shown in this table, the requirement of the below-ground parts was taken into account on the basis of the assumptions presented in the section on biomass production (p. 34). However, the nutrient quantities taken up from the soil are underestimates because they do not include the quantities leached from the canopy by precipitation. Judging by the data in Table 24 it would appear that the uptake of calcium was underestimated by about 20 per cent and that of potassium by 15 per cent due to leaching by precipitation. Nitrogen and phosphorus were not leached from the canopy.

It can be seen from the annual nutrient balance of the trees that the percentage of nutrients returned to the soil in litter grew as the trees developed. Relatively speaking, calcium was returned in the greatest amount in litter as it is not translocated out of the needles.

The annual nutrient balance of the stand is shown in Table 27. The nutrient quantity bound to the annual net production of biomass is of importance because it illustrates the increase in the annual nutrient requirement of the stand. Despite the wide differences in net production between the sample plots (p. 44), the amounts of nutrients bound to the net production were rather similar in all the sample plots.

Nutrient amounts bound to the annual production of biomass should also be compared to the nutrient sources of the forest soil. Potassium,

Table 27. The annual nutrient balance of the stands (kg/ha/yr.).

Component of balance	Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Bound into biomass at end of measurement period	110.2	13.9	54.7	62.0	168.8	19.4	75.1	75.8	238.1	27.9	124.7	141.1
Bound to the annual total production	27.9	3.4	14.5	12.7	33.1	3.9	14.4	11.8	50.9	6.0	28.5	19.9
Removed in litter	15.5	1.5	6.3	8.2	16.3	1.6	5.0	8.8	34.0	3.8	15.5	16.0
Bound to the annual net production	12.4	1.9	8.2	4.5	16.8	2.3	9.4	3.0	16.9	2.2	13.0	3.9
Bound into biomass at beginning of measurement period	97.8	12.0	46.5	57.5	152.0	17.1	65.7	72.8	221.2	25.7	111.7	137.2

calcium, and phosphorus, available to plants in an exchangeable or easily soluble form, were found to be present in amounts corresponding to several years' requirement, but the ratio between mineral nitrogen and its annual requirement is difficult to estimate. From a microbiological point of view, organically bound nitrogen in the soil is extremely stable: the maximum net amount mineralized under similar climatic conditions has been estimated at 1 per cent per annum (N ö m m i k 1968). In the present case this estimate gives a maximum value of 10—17 kg/ha. If the amount of nitrogen in the soil remains more or less constant, the amount liberated through mineralization equals that entering the soil in litter. This would mean that the amount of nitrogen mineralized annually in the present sample plots was roughly double the above estimate. It is obvious, even from these quantities, that nitrogen brought from the atmosphere by precipitation plays a major role in the nitrogen balance of a stand.

The soil is also supplied with nitrogen available to plants by nitrogen binding micro-organisms, although raw humus is not a favourable environment for them. The role of free-living nitrogen binding micro-organisms in the nitrogen balance must be very small as, according to N ö m m i k's (1968) assumption, less than 1.0 kg/ha of nitrogen is annually bound by these micro-organisms. Obviously under these conditions the role played by symbiotic nitrogen binding micro-organisms is equally small.

Nitrogen can also be bound to the rhizosphere by direct absorption from the atmosphere (e.g. M a l o & P u r v i s 1964, R i c h a r d s 1973). However, quantitative measurements have not yet been made of this absorption or of the uptake of the organic nitrogen compounds by plants.

6. DISCUSSION

61. Primary production

With regard to the determination of the primary production of stands, the present study partly aimed at finding suitable methods, since very few of the results of the IBP, for instance, were available when the samples were first collected. Since the material comprised only three sample plots, the results of the study are rather restricted and mainly valid only for each individual stand. On the other hand, the different structure of the experimental stands gave some indication of the effect of stand density and species composition of the ground vegetation on the primary production of the ecosystem.

The determination of biomass production by the harvesting method is laborious and involves destruction of the stand, and so this method can be used for one sampling only. This limits the possibility of studying the biomass development and thus restricts the applicability of the method.

Owing to the close correlation between certain tree characteristics and the dry weight of different tree compartments, the regression estimate method proved to be very suitable for determining the dry weight of different pine compartments. The coefficients of determination of the independent variables formed by the tree diameter, height or the crown ratio were 96 per cent or more for the stem compartments, 86 per cent for the crown compartments, and 85 per cent for the below-ground compartments, when logarithmic regression models were used. It is obvious that valid dry weight equations could thus be derived for wider application.

The errors due to sampling are difficult to estimate in the case of many of the compartments. The only sampling method checked for accuracy was that used for bark. The dry weight of bark determined from the samples was compared to the total measured weight of the bark from ten sample trees. There was no significant difference between the weights of stem bark determined by sampling and those determined by total weighing. The weight of the living branches and needles was determined by weighing them together, but the distribution of dry weight between the branches and needles was

calculated from the sample branches taken from the bolts. However, the distribution thus obtained could not be checked.

A single sampling of the ground vegetation biomass usually leads to an underestimate because different plant species attain their maximum weight at different times. However, it is impossible to take samples of each species at the time when maximum weight is attained without disturbing the surrounding vegetation. The error due to this circumstance was small because the number of different species in the sample plots was very low. The proportion of the ground vegetation in the biomass were 16, 10, and 6 per cent in Sample plots No. 1—3 respectively.

The determination of the annual development of a stand biomass based on single measurements leads to inaccuracies, and this was true also in the present study, although the removal was studied in considerable detail with the aid of litter measurements. As it has not been possible to measure root production, it had to be estimated as a percentage of the above-ground part. Although the data obtained can only be regarded as being rough estimates (cf. Duvigneaud & Denaeyer - De Smet 1970), the use of this procedure can be justified by the close correlation witch exists between the dry weight of the above- and below-ground parts of a tree. Obviously the relative error in the estimation of root production is greater for the ground vegetation than for the tree crop, owing to dissimilarities in over-wintering and regeneration of different species. The annual net production of the root systems can also be estimated from the difference between the maximum and minimum biomass during the growing season, but this method gives only very rough estimates (Dahlman 1968).

According to the growth data the share of the ground vegetation was considerably higher in the annual total production (21—29 per cent) than in the stand biomass. The share of stemwood in the annual total production was only 15 per cent in Sample plot No. 1, 27 per cent in Sample plot No. 2, and 28 per cent in Sample plot No. 3. The annual net assimilation of the needles in the sample plots was 1.4—1.5 kg per kilogramme of needle dry matter. According to Ovington (1957), in a closed Scots pine stand, 1 kg dry weight of needles produces 0.6—1.9 kg of dry matter, but after thinning, when the rate of shading decreases, needle efficiency increases and the average biomass production of the needles reaches a value of 1.2—4.4 kg per kilogramme of needles. As in the case of the other compartments, the annual variation in needle production could not be taken into account either. The ratio of the biomass to the total organic matter of a stand varies, of course, according to the stage of stand development; in this case it was 34, 44, and 55 per cent in Sample plots No. 1—3 respectively. The natural annual biomass removal of the vegetation amounted to 9—13 per cent of the weight of the organic matter in the humus layer.

62. Nutrient cycle

The natural primary production of a stand, from the point of view of nutrition, is determined in the first place by the nutrient balance of the forest soil. As the biomass production of a stand is often limited by the nutrient stores available to the plants, information about the nutrient requirement for optimum growth of the trees is important in research concerning the increase of wood production. Studies on forest nutrition are usually based on the amount of nutrients in the soil, although it is difficult to determine the actual amount of nutrients available to the plants. Furthermore, the nutrient content of the soil varies widely even within small areas, as the results of this study have also shown. Since reliable data on the nutrient status of the soil presuppose large numbers of analyses (Troedsson & Tamm 1969), methods designed to ensure maximum representativity of the samples are generally employed. In that case, however, the reliability of the results has to be checked by means of special empirical studies (Gjems *et al.* 1960).

Scots pine is generally regarded as being modest in its nutrient requirements and efficient in its consumption of nutrients. This is reflected by the barrenness of the sites where it is commonly found and by the relatively low nutrient content of its litter. The data obtained in the present study on the nutrient consumption of pine per unit of dry matter produced (kg per 1 000 kg of dry matter) can be compared to data from other sources, for example, as follows:

	N	P	K	Ca
The present study	4.4—4.6	0.5—0.6	2.0—2.7	1.4—2.3
Ehwald (1957)	4—7	0.3—0.6	1—5	3—9
Holmen (1964)	3.2	0.6	2.3	2.2

Ehwald's values are based on studies with different tree species in central and eastern Europe; Holmen's data refer to a 44-year-old peatland Scots pine stand in central Sweden. Although the amount and structure of the biomass production depend, for instance, on the site fertility and the stage of stand development, all three data are rather similar.

The relatively low annual nutrient requirement of pine is due partly to the internal nutrient cycle of the tree and the re-use of nutrients. In Sample plots No. 2 and 3 the amount of nutrients translocated to the branches from yellowing needles corresponded to about 15 per cent of the annual nitrogen and phosphorus requirements and about 10 per cent of the annual potassium requirement of the trees. In the youngest experimental stand, the amounts translocated from yellowing needles in relation to the annual nutrient requirement were relatively small owing to the rapid annual increase

in the needle biomass. Similarly, the internal nutrient cycle of a tree reduces the amounts returned to the soil with litter. For this reason, the ratio between the amount of nutrients returned to the soil with litter and that annually taken up by the trees was relatively smallest in the case of potassium, followed by phosphorus, nitrogen, and calcium.

The amount of nitrogen, phosphorus, and potassium required by the tree crop depends mainly on the development of the crown, particularly the needles, whereas the amount of calcium is more closely related to the production of stemwood. Consequently, nitrogen, phosphorus, and potassium are usually bound to the biomass of the tree crop for a shorter time than calcium.

The ratio between the nutrient consumption of the trees and that of the ground vegetation are determined mainly by the stage of stand development. During the stages of development represented by the sample plots, the amount of the biomass of ground vegetation is evidently lowest in relation to the total rotation. Even so, the ground vegetation used nearly 40 per cent of the nutrients bound to the annual production of the vegetation. Thus, the ground vegetation plays a much greater role as a consumer of nutrients than as a producer of biomass in a stand.

Obviously, the more completely the cycle of a certain nutrient in the soil can be considered to belong to the biological system, the more restricted is the amount available to the plants on sites such as those included in the present study. The nitrogen isotope experiments carried out showed that the release of organically bound nitrogen from litter may be rapid. This indicates that the amount of the easily mineralizable fraction is rather limited and differs from the great bulk of soil organic nitrogen (O v e r r e i n 1972).

About one quarter of the mobilizable phosphorus was bound to the biomass and approximately an equal ratio of the phosphorus supply in humus was in an easily soluble form. The phosphorus nutrition of plants is not, however, exclusively based on the biological cycle because phosphorus is also released in the weathering of phosphorus containing minerals.

Of the mobilizable nutrient amounts of the stands, potassium was bound into the biomass in relatively the greatest amounts. Owing to its high water-solubility the potassium cycle is very rapid, and according to the present study, more than 70 per cent of the total potassium in the humus layer was in an exchangeable form.

Calcium nutrition was also quite good since only a quarter of the mobilizable amount was bound to the biomass and since most of the calcium in the humus layer was in an exchangeable form. A greater amount of calcium in the soil would evidently promote the biological cycle of nutrients.

7. SUMMARY

The present study is concerned with the distribution of organic matter in a stand, its annual biomass production and the biological nutrient cycle on the basis of material collected in three Scots pine stands. The dry-matter quantity of different tree compartments was estimated by the regression estimate method using 20 sample trees in each sample plot. When a logarithmic regression model was used 96 per cent or more of the variation of the dry weight of stem compartments was explained with the aid of the independent variable formed by the tree diameter and height. The corresponding percentage for the crown compartments was 86, and that for the below-ground parts 85.

The dry-matter quantity of shrubs and ground vegetation was determined by collecting and weighing all plants from 20 sample squares. The share of the biomass of shrubs and ground vegetation was 6—16 per cent of the total biomass of the stands.

The annual biomass production of the above-ground compartments was estimated by the methods used in forest mensuration or by weighing. It was assumed that the percentage annual production of below-ground part was equal to that of the above-ground part. The annual biomass production of the stands varied from 4 780 to 8 450 kg/ha. The ground vegetation represented 21—29 per cent of the total production.

The annual litter crop of the above-ground compartments of the trees was measured by means of litter boxes or funnels, and it was assumed that the litter crop of the ground vegetation was equal to the annual production. Furthermore, it was assumed that the below-ground part of the vegetation produces litter at the same rate as the above-ground part. According to these assumptions, the annual removal of biomass was 4—7 per cent of the stand biomass.

The biological nutrient cycle was mainly depicted in terms of the amounts annually bound into the biomass and those returned to the soil in litter. Scots pine is regarded as being modest in its nutrient requirements and efficient in its consumption of nutrients. It was found that the ground vegetation consumed 1.5—2.5 times as much nutrients per unit of dry matter

produced as the trees. The relatively low annual nutrient requirement of pine is also due to the internal nutrient cycle of the tree and the re-use of nutrients. At the yellowing stage of the needles the amount of nutrients translocated to the branches corresponded to about 15 per cent of the annual nitrogen and phosphorus requirements, and about 10 per cent of the annual potassium requirement of the trees. Thus, the internal nutrient cycle of the tree reduces the amounts returned to the soil in litter. For this reason only 2 per cent of the potassium, but 8 per cent of the calcium in above-ground part of the tree crop was returned in litter fall.

Of the nutrient amounts involved in the biological cycle the percentage of potassium bound to the biomass was greatest, followed by phosphorus, calcium, and nitrogen. Only about 10 per cent of the nitrogen store in the stands was bound to the biomass.

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VUOTUINEN PRIMÄÄRITUOTOS JA RAVINTEIDEN KIERTOKULKU MÄNNIKÖSSÄ

Selostus

Tutkimuksessa tarkastellaan kuiva-aineen jakautumista männiköissä, sen vuotuista primäärituotosta ja ravinteiden biologista kiertokulkua kolmesta metsiköstä kerätyn aineiston perusteella. Puuston kuiva-aine arvioitiin kussakin koemetsikössä 20 koepuun perusteella käyttäen regressioarviointimenetelmää. Logaritmista regressiomallia käytettäessä voitiin läpimitasta, pituudesta ja latvussuhteesta muodostetuilla muuttujilla selvittää vähintäin 96 % rungon, 86 % latvuksen ja 85 % juuriston komponenttien kuivapainon vaihtelusta.

Aluskasvillisuuden kuivapaino määritettiin punnitsemalla 20 näyteruudulta kerätty kasvillisuus. Aluskasvillisuuden biomassan osuus vaihteli 6—16 % metsikön biomassasta. Biomassan osuus metsikön orgaanisesta aineesta oli puolestaan 34—55 %.

Kasvillisuuden maanpäällisten osien vuotuinen tuotos määritettiin kasvunlaskennan menetelmin tai punnitsemalla. Maanalaisten osien kasvu arvioitiin maanpäällisen osan kasvuprosentin mukaiseksi. Koemetsiköiden vuotuinen biomassan kokonaistuotos vaihteli 4 780—8 450 kg/ha, josta aluskasvillisuuden osuus oli 21—29 %.

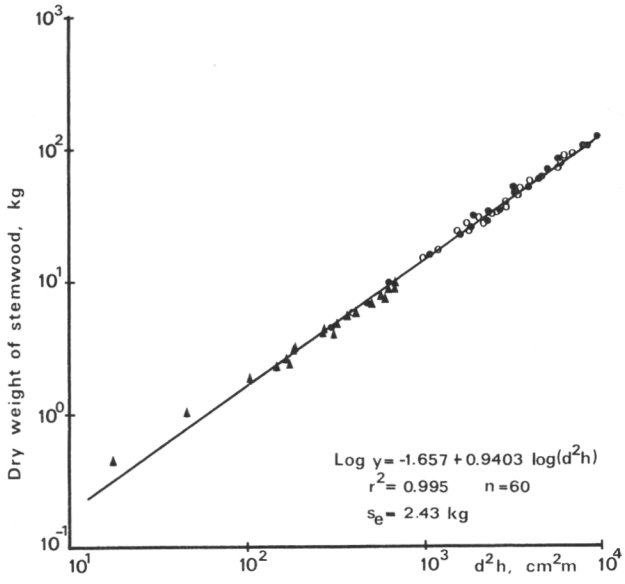
Puuston maanpäällisen osan vuotuinen karikesato määritettiin karikesuppiloiden tai -laatikoiden avulla, mutta aluskasvillisuuden karikesato arvioitiin vuotuisen tuotoksen suuruiseksi. Lisäksi kasvillisuuden maanalaisesta osasta arvioitiin tulevan kariketta samassa suhteessa kuin maanpäällisestä osasta. Näin määriteltynä vuotuinen biomassan poistuma oli 4—7 % metsikön biomassasta.

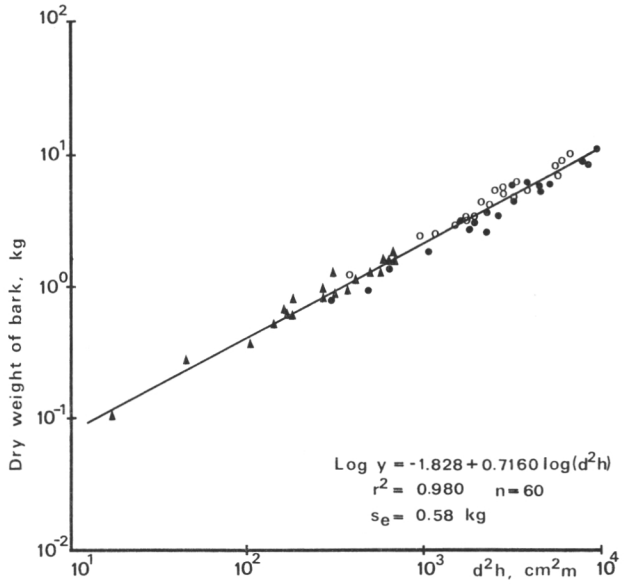
Ravinteiden biologista kiertokulkua metsiköissä tarkastellaan kasvillisuuden vuosittain maasta ottamien, kasvillisuuteen sitoutuvien ja maahan palautuvien ravinnemäärien avulla. Mäntyä on tunnetusti pidetty ravinnetarpeeltaan vaatimattomana ja ravinteiden käytön kannalta säästeliäänä puulajina. Aluskasvillisuus käytti lajikoostumuksesta riippuen 1.5—2.5-kertaisen määrän ravinteita tuotettua kuiva-aineyksikköä kohti puustoon verrattuna. Aluskasvillisuuden osuus metsikön vuotuisesta ravinnetarpeesta oli noin 40 %.

Männyn suhteellisen vähäiseen vuotuiseen ravinnetarpeeseen vaikuttaa myös ravinteiden sisäinen kierto puussa. Neulasten kellastuessa niistä siirtyvä ravinnemäärä vastasi noin 15 % typen ja fosforin sekä 10 % kaliumin vuotuisesta tarpeesta. Puun sisäinen ravinteiden kierto vähentää vastaavasti karikesadossa maahan palautuvia ravinnemääriä. Tästä syystä karikesadossa palautui puuston vuosittain ottamaan ravinnemäärään verrattuna suhteellisesti vähiten kaliumia ja sen jälkeen muita ravinteita järjestyksessä: fosfori, typpi ja kalsium.

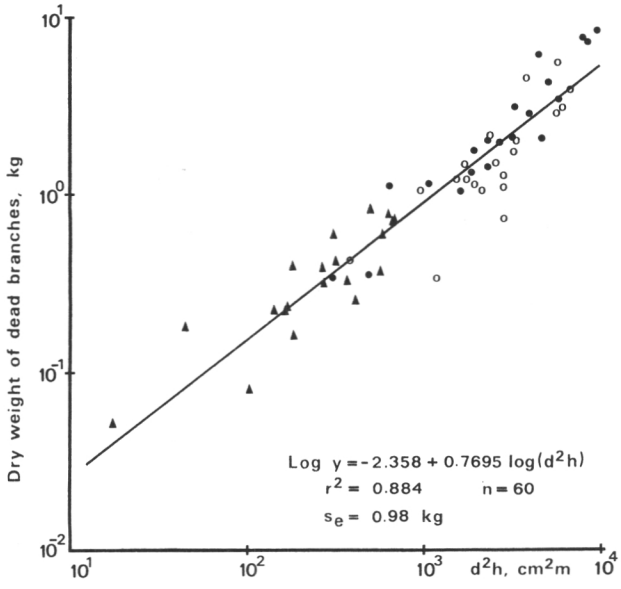
Puuston ravinteiden käytössä typen, fosforin ja kaliumin määrät ovat riippuvaisia lähinnä latvuston ja erityisesti neulaston kehityksestä. Kalsiumin määrä on sen sijaan kiinteämmin yhteydessä runkopuun tuotokseen. Typpi, fosfori ja kalium sitoutuvat näin ollen yleensä lyhyemmäksi ajaksi puuston biomassaan kuin kalsium.

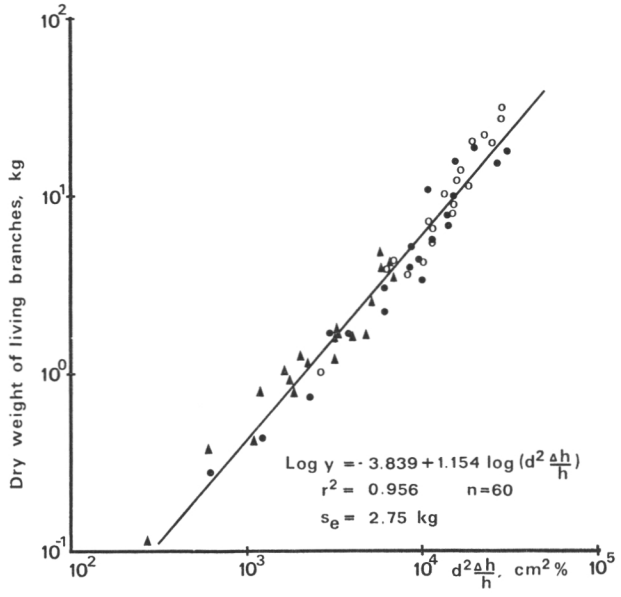
Appendix 1. The relationship between the dry weight of different tree compartments and certain tree characteristics for the whole material (▲ = Sample plot No. 1, o = Sample plot No. 2, • = Sample plot No. 3).



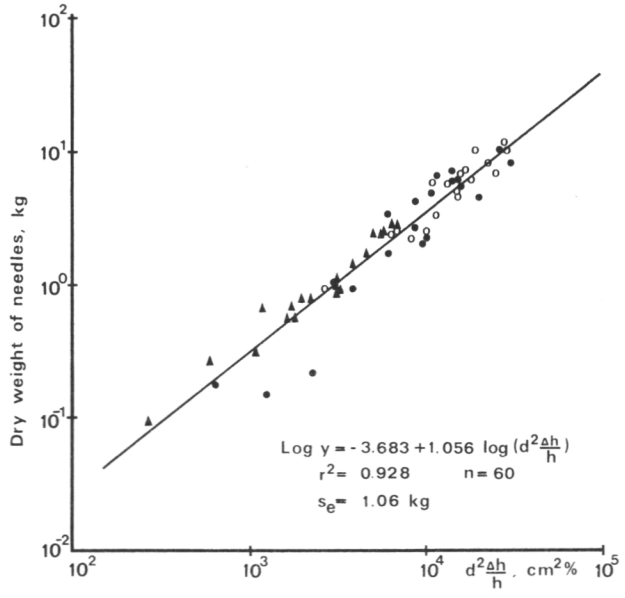


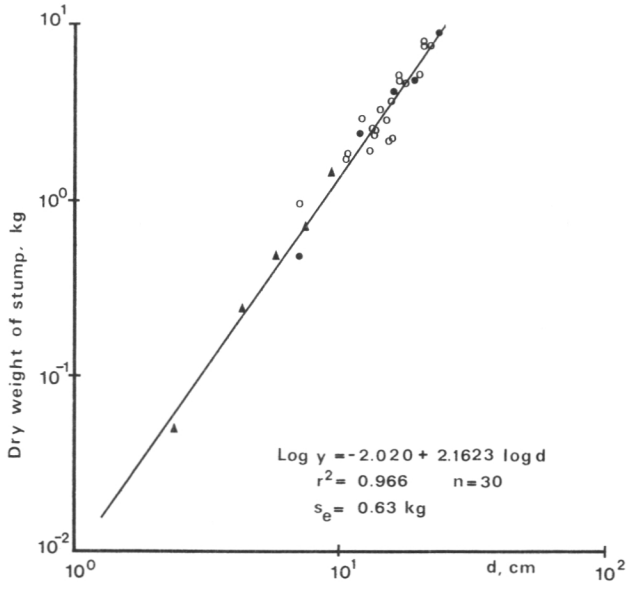
Appendix 1


Dry weight of dead branches, kg
Log y = -2.358 + 0.7695 log(d²h)
r² = 0.884 n = 60
se = 0.98 kg
d²h, cm²m

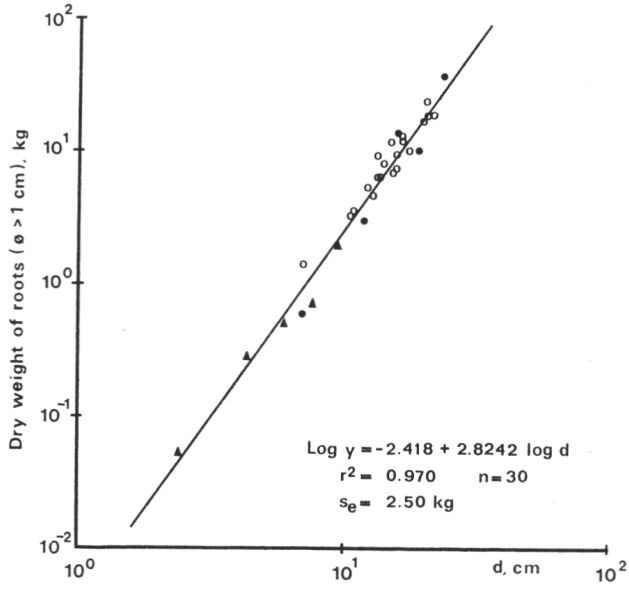

Dry weight of living branches, kg
Log y = -3.839 + 1.154 log (d² Δh/h)
r² = 0.956 n=60
se = 2.75 kg
d² Δh/h, cm² %

Appendix 1


Dry weight of needles, kg
Log y = - 3.683 + 1.056 log (d²Δh/h)
r² = 0.928 n = 60
s_e = 1.06 kg
d²Δh/h, cm²%


Dry weight of stump, kg
Log y = - 2.020 + 2.1623 log d
r² = 0.966 n = 30
s_e = 0.63 kg
d, cm

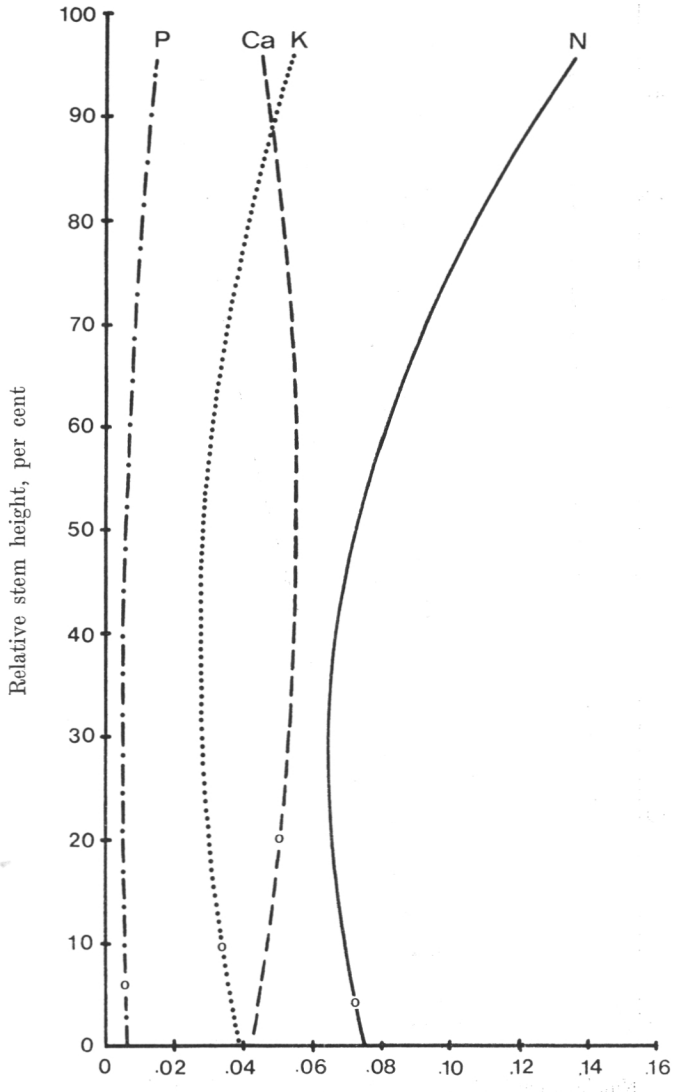
Appendix 1


Dry weight of roots (ø > 1 cm), kg
10^2
10^1
10^0
10^{-1}
10^{-2}
Log y = -2.418 + 2.8242 log d
r^2 = 0.970 n = 30
s_e = 2.50 kg
10^0
10^1
d, cm
10^2

Appendix 2. The average nutrient content of different compartments of the sample trees expressed as a percentage of the dry weight.

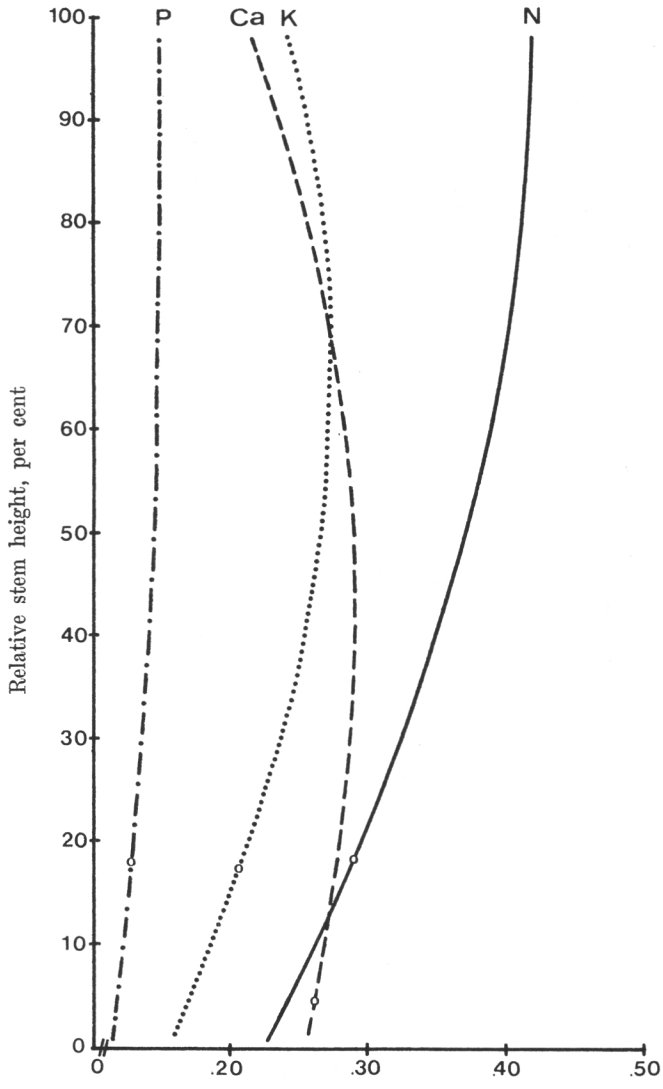
Compartment		Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
		N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Stemwood	$\bar{x}$	.060	.006	.038	.059	.072	.005	.033	.050	.067	.004	.033	.062
	$\pm t_{.05}s_{\bar{x}}$	.004	.0006	.002	.003	.003	.0004	.002	.003	.005	.0005	.001	.002
	$\pm$ % of $\bar{x}$	6.7	10.0	5.3	5.1	4.2	8.0	6.1	6.0	7.5	12.5	3.0	3.5
Bark	$\bar{x}$	.337	.051	.192	.550	.382	.058	.220	.323	.370	.055	.231	.490
	$\pm t_{.05}s_{\bar{x}}$	.021	.004	.019	.062	.018	.005	.024	.050	.022	.006	.035	.049
	$\pm$ % of $\bar{x}$	6.2	7.8	9.9	11.3	4.7	8.6	10.9	15.5	5.9	10.9	15.2	10.0
Dead branches	$\bar{x}$	.342	.018	.043	.311	.316	.017	.038	.169	.233	.013	.029	.122
	$\pm t_{.05}s_{\bar{x}}$	.022	.002	.004	.038	.036	.002	.006	.018	.027	.003	.010	.026
	$\pm$ % of $\bar{x}$	6.4	11.1	9.3	12.2	11.4	11.8	15.8	10.7	11.6	23.1	34.5	21.3
Living branches	$\bar{x}$	.390	.053	.223	.345	.431	.049	.177	.235	.413	.049	.214	.259
	$\pm t_{.05}s_{\bar{x}}$	.016	.003	.015	.035	.014	.002	.008	.018	.030	.005	.015	.025
	$\pm$ % of $\bar{x}$	4.1	5.7	6.7	10.1	3.2	4.1	4.5	7.7	7.3	10.2	7.0	9.7
Needles 1st yr.	$\bar{x}$	1.220	.155	.731	.206	1.267	.154	.581	.161	1.304	.157	.753	.191
	$\pm t_{.05}s_{\bar{x}}$	.032	.008	.043	.017	.046	.005	.026	.012	.035	.010	.070	.018
	$\pm$ % of $\bar{x}$	2.6	5.2	5.9	8.3	3.6	3.2	4.5	7.5	2.7	6.4	9.3	9.4
2nd yr.	$\bar{x}$	1.118	.106	.416	.425	1.222	.129	.466	.269	1.296	.126	.545	.389
	$\pm t_{.05}s_{\bar{x}}$	.032	.004	.027	.043	.052	.006	.022	.029	.066	.008	.049	.038
	$\pm$ % of $\bar{x}$	2.9	3.8	6.5	10.1	4.3	4.7	4.7	10.8	5.1	6.3	9.0	9.8
3rd yr.	$\bar{x}$	.996	.097	.364	.551	1.205	.116	.382	.323	1.201	.112	.470	.482
	$\pm t_{.05}s_{\bar{x}}$	.032	.004	.022	.046	.048	.005	.019	.032	.064	.007	.033	.047
	$\pm$ % of $\bar{x}$	3.2	4.1	6.0	8.3	4.0	4.3	5.0	9.9	5.3	6.3	7.0	9.8
4th yr.	$\bar{x}$	.804	.085	.314	.577	1.185	.120	.393	.369	1.076	.103	.392	.514
	$\pm t_{.05}s_{\bar{x}}$	.033	.004	.022	.058	.044	.005	.020	.036	.070	.008	.033	.052
	$\pm$ % of $\bar{x}$	4.1	4.7	7.0	10.1	3.7	4.2	5.1	9.8	6.5	7.8	8.4	10.1
Cones	$\bar{x}$	.500	.079	.378	.044	.373	.053	.220	.018	.384	.063	.314	.030
	$\pm t_{.05}s_{\bar{x}}$	·	·	·	·	.031	.008	.029	.003	.085	.021	.092	.009
	$\pm$ % of $\bar{x}$					8.3	15.1	13.2	16.7	22.1	33.3	29.3	30.0
Stumps	$\bar{x}$	.098	.017	.075	.067	.090	.013	.071	.059	.110	.014	.079	.065
	$\pm t_{.05}s_{\bar{x}}$	.019	.003	.003	.008	.006	.002	.008	.004	.028	.003	.022	.014
	$\pm$ % of $\bar{x}$	19.4	17.6	4.0	11.9	6.7	15.4	11.3	6.8	25.5	21.4	27.8	21.5
Roots, $\varnothing > 1$ cm ..	$\bar{x}$	.134	.017	.079	.069	.092	.014	.076	.060	.107	.014	.080	.065
	$\pm t_{.05}s_{\bar{x}}$	.023	.003	.017	.010	.006	.003	.008	.004	.025	.003	.019	.011
	$\pm$ % of $\bar{x}$	17.2	17.6	21.5	14.5	6.5	14.3	10.5	6.7	23.4	21.4	23.8	16.9
Roots, $\varnothing < 1$ cm ..	$\bar{x}$	.483	.102	.266	.216	.497	.076	.300	.149	.480	.099	.276	.327
	$\pm t_{.05}s_{\bar{x}}$	.096	.030	.050	.030	.108	.035	.064	.016	.090	.022	.053	.061
	$\pm$ % of $\bar{x}$	19.9	29.4	18.8	13.9	21.7	46.0	21.3	10.7	18.9	22.2	19.2	18.7

Appendix 3. The variation of nutrient content in the longitudinal direction of the stem (○ = the average nutrient content weighted by the dry weight).



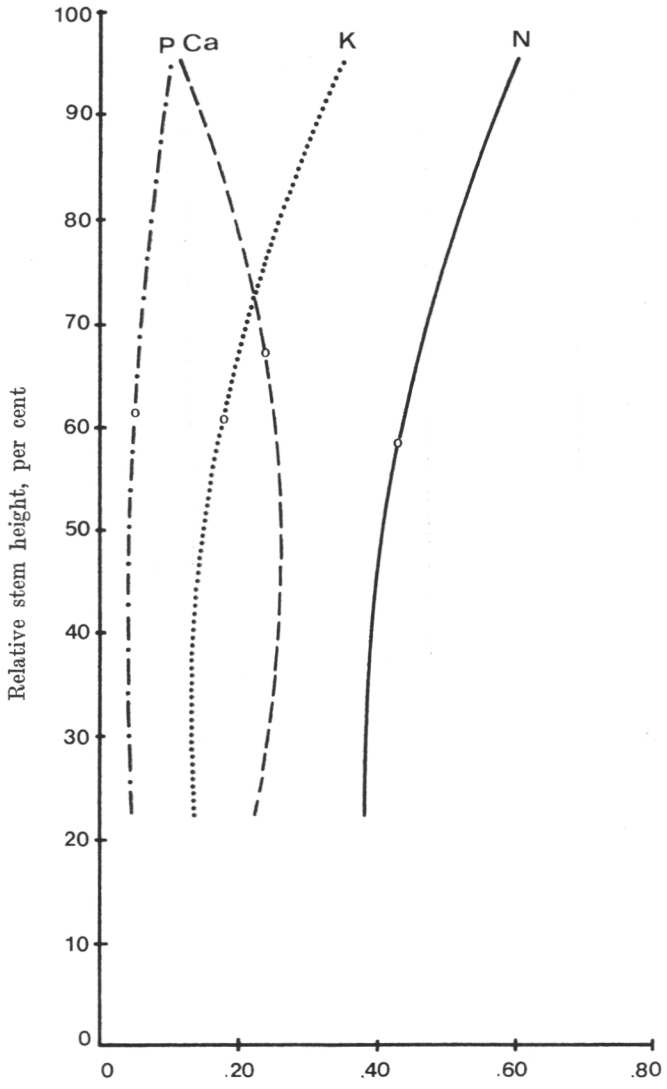
Stemwood: $N = 0.0748 - 0.0008\ y + 0.000015\ y^2 \quad r^2 = 0.672$
$P = 0.0055 - 0.0001\ y + 0.000002\ y^2 \quad r^2 = 0.583$
$K = 0.0381 - 0.0006\ y + 0.000008\ y^2 \quad r^2 = 0.566$
$Ca = 0.0420 + 0.0005\ y - 0.000005\ y^2 \quad r^2 = 0.304$
$n = 72$

Appendix 3



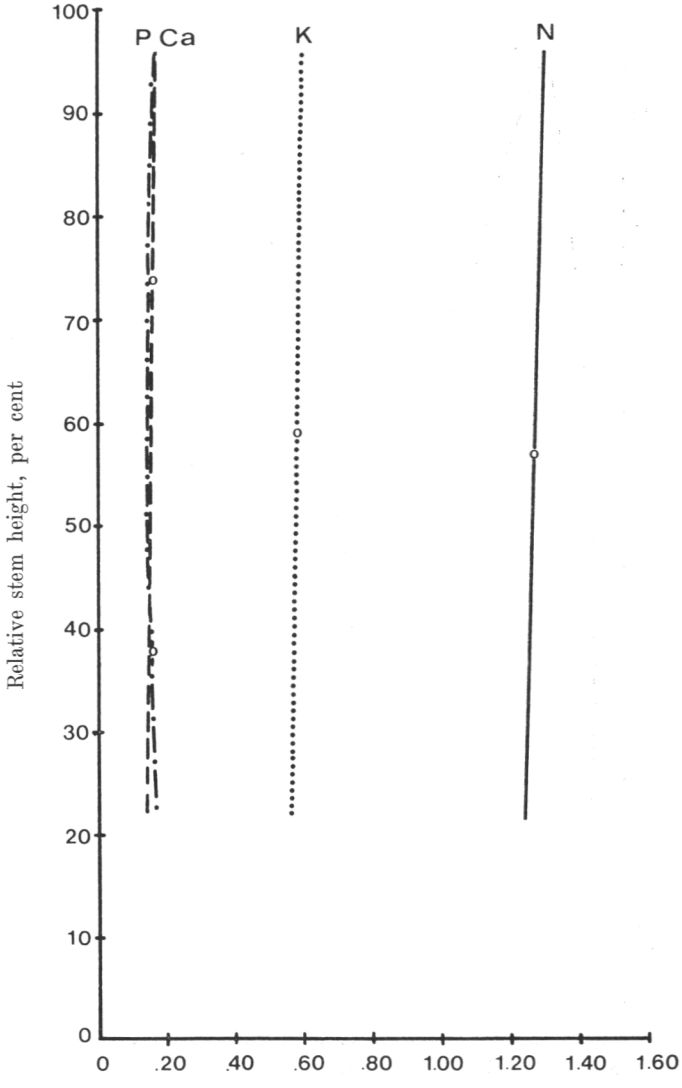
Stem bark: $N = 0.2484+0.0080\ y-0.000041\ y^2 \quad r^2 = 0.772$
$P = 0.0293+0.0018\ y-0.000012\ y^2 \quad r^2 = 0.664$
$K = 0.1048+0.0076\ y-0.000059\ y^2 \quad r^2 = 0.567$
$Ca = 0.3077+0.0038\ y-0.000047\ y^2 \quad r^2 = 0.094$
$n = 155$

Appendix 3



Living branches: $N = 0.4057 - 0.0022\ y + 0.000045\ y^2$ $r^2 = 0.623$
$P = 0.0633 - 0.0014\ y + 0.000019\ y^2$ $r^2 = 0.810$
$K = 0.1785 - 0.0033\ y + 0.000054\ y^2$ $r^2 = 0.697$
$Ca = 0.1231 + 0.0059\ y - 0.000063\ y^2$ $r^2 = 0.658$
$n = 70$

Appendix 3



1st year needles: $N = 1.2218+0.000795\ y$ $r^2 = 0.022$

$P = 0.2077-0.0021\ y+0.000018\ y^2$ $r^2 = 0.309$

$K = 0.5560+0.000423\ y$ $r^2 = 0.013$

$Ca = 0.1335+0.000373\ y$ $r^2 = 0.061$

$n = 102$

Appendix 4. Average nutrient content of the ground vegetation and shrubs expressed as a percentage of the dry weight.

Plant group		Sample plot No. 1				Sample plot No. 2				Sample plot No. 3			
		N	P	K	Ca	N	P	K	Ca	N	P	K	Ca
Lichens	$\bar{x}$	.738	.061	.170	.097	.555	.049	.145	.059	·	·	·	·
	$\pm t_{.05}s_{\bar{x}}$	.064	.006	.022	.019	.105	.006	.019	.019				
	$\pm$ % of $\bar{x}$	8.7	9.8	12.9	19.6	18.9	12.2	13.1	32.2				
Mosses	$\bar{x}$	1.183	.108	.555	.349	.950	.105	.504	.316	1.323	.138	.627	.415
	$\pm t_{.05}s_{\bar{x}}$	.098	.021	.064	.049	.073	.016	.032	.038	.226	.019	.032	.060
	$\pm$ % of $\bar{x}$	8.3	19.4	11.5	14.0	7.7	15.2	6.3	12.0	17.1	13.8	5.1	14.5
Grasses	$\bar{x}$	1.385	.168	2.210	.250	·	·	·	·	2.105	.152	2.405	.304
	$\pm t_{.05}s_{\bar{x}}$	.102	.045	.429	.016					.461	.022	.429	.130
	$\pm$ % of $\bar{x}$	7.4	26.8	19.4	6.4					21.9	14.5	17.8	42.8
Herbs	$\bar{x}$	1.510	.305	2.180	1.165	·	·	·	·	2.410	.253	2.818	.703
	$\pm t_{.05}s_{\bar{x}}$	·	·	·	·					.671	.099	.655	.283
	$\pm$ % of $\bar{x}$									31.4	39.1	23.2	40.3
Dwarf shrubs													
Calluna vulgaris	$\bar{x}$	.738	.059	.288	.250	.863	.071	.346	.346	.903	.065	.407	.252
	$\pm t_{.05}s_{\bar{x}}$	.044	.003	.033	.018	.099	.004	.077	.039	.273	.019	.153	.051
	$\pm$ % of $\bar{x}$	6.0	5.1	11.5	7.2	11.5	5.6	22.3	11.3	30.2	29.2	37.6	20.2
Vaccinium myrtillus	$\bar{x}$	1.250	.113	.577	.608	·	·	·	·	1.130	.109	.578	.529
	$\pm t_{.05}s_{\bar{x}}$	.490	.043	.249	.026					.137	.013	.025	.127
	$\pm$ % of $\bar{x}$	39.2	38.1	44.7	4.3					12.1	11.9	4.3	24.0
Vaccinium vitis-idaea	$\bar{x}$	.832	.094	.390	.586	.780	.077	.299	.813	.995	.088	.390	.579
	$\pm t_{.05}s_{\bar{x}}$	.021	.010	.041	.033	.029	.006	.005	.016	.204	.010	.095	.140
	$\pm$ % of $\bar{x}$	2.5	10.6	10.5	5.6	3.7	7.8	1.0	2.0	20.5	11.4	24.4	24.2
Other dwarf shrubs	$\bar{x}$	·	·	·	·	·	·	·	·	1.158	.174	1.496	.815
	$\pm t_{.05}s_{\bar{x}}$									.080	.022	.178	.108
	$\pm$ % of $\bar{x}$									6.9	12.6	11.9	13.3
Shrubs	$\bar{x}$	.716	.081	.300	.597	.857	.103	.390	.293	.675	.079	.477	1.369
	$\pm t_{.05}s_{\bar{x}}$	.297	.052	.056	.155	.168	.026	.103	.047	.452	.056	.241	.968
	$\pm$ % of $\bar{x}$	41.5	64.2	18.7	26.0	19.6	25.2	26.4	16.0	67.0	70.9	50.5	70.7
Below-ground part	$\bar{x}$	.590	.062	.189	.267	.575	.082	.120	.213	.735	.127	.205	.327
	$\pm t_{.05}s_{\bar{x}}$	.089	.011	.021	.027	.020	.016	.019	.019	.091	.020	.025	.035
	$\pm$ % of $\bar{x}$	15.1	17.7	1.11	10.1	3.5	19.5	15.8	8.9	12.4	15.7	12.2	10.7

MÄNNYN KÄPYSADON ENNUSTAMISESTA

UKKO RUMMUKAINEN

Summary

ON FORECASTING THE CONE CROP OF SCOTS PINE

HELSINKI 1975

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ALKUSANAT

Oheinen tutkielma oli uuden käpysadonarviointimenetelmän osalta periaatteessa valmis ja kirjoitettukin jo 1950-luvulla. Käsikirjoitusluonnoksen lukivat silloin professori Risto Sarvas, ylijohtaja V. K. Ahola ja metsänhoitaja Jaakko Simolinna. Sen jälkeen 1950-luvun lopulla järjestettiin kuitenkin vielä menetelmän lisäkokeiluja. Kun käpysadon arvioinnin hoitaminen Metsäntutkimuslaitoksessa siirtyi samoihin aikoihin allekirjoittaneelta toisiin käsiin, julkaisun lopullinen laatiminen jäi odottamaan.

Asian tultua äskettäin uudelleen esille on alunperin vain uutta arviointimenetelmää koskenut selostus muokattu uudelleen ja esitetty pääasiassa vain edellä mainittujen lisäkokeilujen antamien tulosten pohjalta. Lisäksi on nyt mukana männyn 1- ja 2-vuotisten käpyjen silmävaraisten arviointien antamia tuloksia vertailevia lukuja.

Julkaiseminen tuli uudelleen puheeksi jo vähän ennen professori Sarvaksen kuolemaa. Hän luki alkuperäisen käsikirjoituksen toiseen kertaan, tutustui uuteen suunnitelmaan ja suositteli julkaisemista nyt esillä olevassa muodossa. Tämän käsikirjoituksen on lukenut metsänhoitaja Olavi Helenius, joka 1960-luvun alusta lähtien on Metsäntutkimuslaitoksessa hoitanut käpysadon arviointia, sekä MMT Matti Leikola. Tekijä tuntee kiitollisuutta mainituilta henkilöiltä saamastaan avusta. Erityisesti professori Sarvaksen kanssa käydyt monet puiden siemensatoja ja niiden määrittämistä koskeneet keskustelut ovat paljon antaneet. Kiitos lankeaa myös niille noin 200 kenttämiehelle, jotka vuosien varrella olivat vapaaehtoisesti mukana käpyjen laskentakokeissa sekä B.Sc. John Deromelle, jonka käsialaa ovat englanninkieliset käännökset.

Ukko Rummukainen

SISÄLTÖ

Sivu

1. Johdanto 5

2. Silmävaraisesta käpysadon arvioinnista 7
   2.1. Käpysatoluokituksen käytännöllisestä merkityksestä 7
   2.2. Pikku- ja isokäpyarviointitulosten vertailua 8
   2.3. Käpyjen keräämisen kannattavuus suuruudeltaan erilaisista käpysadoista 12

3. Uusi käpysadon ennustamismenetelmä 15
   3.1. Käpysadon arvioimiskokeita 1- ja 2-vuotisten käpyjen määriä laskemalla 15
   3.2. Käpyjen laskennan suorittamisesta käytännössä 19

4. Tiivistelmä 22

5. Lähdeluettelo 23

6. Summary 25

1. JOHDANTO

Metsätalouden tarpeita varten suoritetaan vuosittain koko maan käsittävä puiden siemensatojen arviointi. Arviointitulosten perusteella suunnitellaan ja järjestetään männyn- ja kuusenkäpyjen keruita. Arviointeja on mahdollista käyttää hyväksi myös muulla tavalla, esim. keskittämällä maanpinnan laikutustöitä odotettavissa olevien käpysatojen mukaisesti.

Satoarvioinnit tapahtuvat siten, että Metsäntutkimuslaitoksen toimesta kysellään syksyisin metsäammattimiehiltä männyn ja kuusen käpysadon ja koivun siemensadon runsautta miesten toimialueilla.

Samalla tiedustellaan arvioijien käsitystä kävynkeruun kannattavuudesta arvioinnin kohteena olevasta männyn ja kuusen käpysadosta (»kannattaa kerätä»—»ei kannata kerätä»).

Männyllä arvioidaan erikseen 1-vuotisten pikkukäpyjen ja 2-vuotisten tuleentuneiden isojen käpyjen runsaus.

Sadot arvioidaan silmävaraisesti ennalta sovitun satoluokituksen mukaisesti. Vuosina 1951—1969, jonka kauden mäntyä koskevat satoarvioinnit ovat tässä tutkielmassa tarkastelun kohteina, piti arvioijien määrittää, mitä seuraavista käpysatoluokista sadot heidän mielestään näyttivät lähinnä vastaavan:

0 = ei yhtään käpyjä
1 = hyvin vähän
2 = vähänlaisesti
3 = keskinkertaisesti
4 = paljonlaisesti
5 = runsaasti

Tämä luokitus oli ollut käytössä 1930-luvun alusta lähtien (H e i k i n h e i m o 1931).

Silmävaraisen arvioinnin antama kuva käpysadosta on epämääräinen ja enemmän tai vähemmän subjektiivinen. S a r v a k s e n (1944, 1946) mukaan se tuo selvästi näkyviin ainoastaan kato- ja hyvin runsaat käpyvuodet. Runsaidenkaan käpysatojen tarjoamia mahdollisuuksia arviointitulos ei tuo esille konkreettisesti. Saman suuruiseksikin arvioitu sato saattaa käytän-

nössä tarkoittaa erilaista absoluuttista käpysatoa riippuen esim. siitä, missä osassa maata arviointi on suoritettu. Pohjois-Suomessa käpyjen määrä puuta kohden näyttää olevan huomattavasti pienempi kuin Etelä- ja Keski-Suomessa arvioitaessa sadot silmävaraisesti yhtä suuriksi (Rummukainen 1956).

Itse arvioinnin suoritusta haittaa varsinkin männyllä sekä 2-vuotisten että etenkin 1-vuotisten käpyjen huono näkyvyys puissa. Kiikarin käyttökään ei näytä riittävästi auttavan arvioitaessa satoja yleiseen tapaan pystypuista.

Kun käpysatoja arvioidaan käytännön metsänhoidon tarpeita varten, olisi hyvä saada sadoista kuva mahdollisimman aikaisessa vaiheessa, jotta kävynkeruiden ja muiden toimenpiteiden suunnitteluun, varojen hankkimiseen niitä varten yms. jäisi riittävästi aikaa. Se olisi ilmeisen tärkeää nimenomaan männyn siemensadon hyväksikäyttöä ajatellen, koska männyn siementä tarvitaan enemmän kuin kuusen siementä ja käpyjen keräämistä siten joudutaan suorittamaan useammin. Metsätilastollisen vuosikirjan (1974) mukaan vuonna 1972 istutettiin noin 143 milj. männyn- ja noin 61 milj. kuusentainta. Samana vuonna käytettiin kylvöihin männyn siementä noin 13 000 kg ja kuusen siementä noin 300 kg.

Männynkäpyjen kehittymiseen kuluva pitkä aika, kaksi kesäkautta, tarjoaa teoriassa mahdollisuuden saada selville käpysadon suuruus jo 1-vuotisten käpyjen arvioinnin perusteella eli vuotta ennen käpyjen tuleentumista. Tähän käpysadon arvioinneissa on pyrittykin arvioimalla, kuten edellä jo todettiin, myös 1-vuotisten käpyjen määriä tuleentuneiden 2-vuotisten käpyjen runsauden lisäksi.

Oheisessa tutkielmassa pyritään selvittämään, miten käpysato 1-vuotisten käpyjen perusteella voitaisiin määrittää entistä luotettavammin. Sitä varten tarkastellaan aluksi, mitä silmävaraiset arviointitulokset käytännössä merkitsevät arvioinnin konkreettisuuden ja käpyjen keruun kannattavuuden kannalta. Toiseksi tarkastellaan 1-vuotisten käpyjen arviointituloksia verrattuna luotettavampina pidettäviin 2-vuotisten käpyjen arviointituloksiin. Lopuksi esitellään uusi arviointimenetelmä, jota soveltaen ilmeisesti olisi mahdollista ennustaa männyn käpysato 1-vuotisten käpyjen mukaan nykyistä varmemmin.

2. SILMÄVARAISESTA KÄPYSADON ARVIOINNISTA

2.1. Käpysatoluokituksen käytännöllisestä merkityksestä

Silmävaraisten käpysatoarviointien antama kuva satojen käytännöllisestä merkityksestä on epämääräinen, koska jokainen arvioija on itse vaistonvaraisesti päättänyt, milloin sato on vaikuttanut »hyvin vähäiseltä», »vähänlaiselta» jne.

Tällainen arviointi on kuitenkin vuosikymmenestä toiseen katsottu riittäväksi ilman että menetelmän tarkentamiseen käytännössä olisi ryhdytty. Karkeakin kuva tietysti riittää niin kauan kun siementarve on vain murto-osa männiköiden siementuotosta ja kun käpyjä kerätään vain hakkuiden yhteydessä.

Tarvetta arviointitulosten konkretisoimiseen on alkanut ilmetä vasta metsänviljelyn lisääntymisen eli siementarpeen kasvamisen myötä ja siitä syystä, että käpyjen keruuta niin pitkälle kuin mahdollista on alettu kohdistaa hyvälaatuisiin männiköihin ja suorittaa jopa kalleina pystykeräyksinä.

Sitä, mitä eri käpysatoluokkia vastaava sato käytännössä tarkoittaa, on selvitetty eräiden satoarviointien yhteydessä (R u m m u k a i n e n 1954, 1956, 1956 b). Yhdistelmä tuloksista on taulukossa 1.

Luvuista ilmenee mm. että käpysatoluokkien väliset käpymäärät eivät lisäänny tasaisesti luokasta toiseen siirryttäessä. Huonojen satojen puolella käpymäärät kasvavat suhteellisesti nopeammin kuin hyvien satojen puolella. Esim. »hyvin vähäisen» (1) sadon muuttuminen »vähänlaiseksi» (2) merkitsee keskimääräisen käpymäärän noin 5-kertaistumista puuta kohden. »Paljonlaisesta» (4) »runsaaseen» (5) satoon siirryttäessä sato enää puolitoistakertaistuu. »Hyvin vähäisen» sadon muuttumiseen »runsaaksi» tarvitaan käpymäärän lisääntyminen noin 40-kertaiseksi, mutta »keskikertaisen» (3) sadon muuttumiseen »runsaaksi» enää sen 7.5-kertaistuminen.—Todettakoon että Ruotsissa on käpysatoluokkien välisiä suhteita määritettäessä päädytty aivan samoihin tuloksiin (H a g n e r 1958).

Kun esillä olevassa tutkielmassa tarkastellaan käpysadon määrittämismahdollisuutta yksittäisten oksien käpyisyyden perusteella (s. 15), kiinnostavat tässä yhteydessä erityisesti käpymäärien suhteelliset erot.

Taulukko 1. Käpysatoluokituksen merkityksestä käytännössä.
Table 1. The practical significance of the cone crop classes.

Käpysatoluokka *Cone crop class*	Käpyjä, kpl/puu *N:o of cones/tree*	Keskim. *Average*	Sato = × edellisen luokan keskim. sato *Crop = number of times greater than average crop of previous class*
0	0	0	—
1	1— 25	12	—
2	26—100	63	4.8 (n. 5)
3	101—200	150	2.4 (n. 2.5)
4	201—400	300	2.0
5	401—	500	1.6 (n. 1.5)

Käpysatoluokkien välisiä absoluuttisia eroja voidaan havainnollistaa taulukon lukuihin pohjaten esim. seuraavan esimerkin avulla.

Oletetaan hehtaarin alalla kasvavan 500 hakkuukypsyyttä lähentelevää eli käpysadon arviointikohteeksi soveltuvaa mäntyä. Oletetaan myös jokaisen kävyn tuottavan 20 siementä. Tällöin alan käpy- ja siementuotto erilaisia käpysatoluokkia vastaavan käpysadon vallitessa on seuraavanlainen:

Käpysatoluokka:	Käpyjä, kpl/ha:	Siemeniä, kpl/ha:
0	0	0
1	6 000	120 000
2	31 500	630 000
3	75 000	1 500 000
4	150 000	3 000 000
5	225 000	4 500 000

Olettaen kiloon mahtuvan noin 220 000 siementä (C a j a n d e r 1917, s. 307) »hyvin vähäinen» (1) sato tuottaisi siten hehtaarille siementä runsaan 0.5 kg ja »runsas» (5) käpysato noin 20 kg.

S a r v a k s e n (1964, s. 377) mukaan suurin Suomessa mitattu hehtaarisato täysiä siemeniä on 10.1 kg, Keski-Euroopassa noin 40 kg.

2.2. Pikku- ja isokäpyarviointitulosten vertailua

Taulukossa 2 ja kuvassa 1 on esitetty tulokset vuosien 1951—1969 käpysatoarvioinneista sekä 1-vuotisten pikkukäpyjen että 2-vuotisten isojen käpyjen mukaan arvioituina. Aikaisemmilta vuosilta ei ole käytettävissä molempien arviointien tuloksia ja vuodesta 1970 alkaen taas arvioinneissa on sovellettu käpysatoluokitusta, jossa on vain 4 luokkaa vuosien 1951—1969 aikana käytetyn 6 luokan asemesta (H e l e n i u s 1970).

Taulukko 2. Männyn käpysadot vuosina 1951—1969 arvioituna erikseen 1-vuotisten (ylärivit) ja 2-vuotisten (alarivit) käpyjen mukaan.

Table 2. Cone crop for the period 1951—1969, estimated separately from the number of 1 year-old cones (upper row) and from the number of 2 year-old cones (lower row).

Vuosi *Year*	Arviointeja *N:o of estimates*							Käpysatolk. keskim. *Average cone crop class*
	eri käpysatoluokissa (0—5), kpl *Placed in different cone crop classes, (0—5)*						yht. *Total*	
	0	1	2	3	4	5		
1951 (—50)	18	172	201	100	10	0	501	1.82
1951	1	42	94	73	3	—	213	2.16
1952 (—51)	3	53	91	61	9	1	218	2.11
1952	1	10	58	113	56	22	260	3.07
1953 (—52)	14	76	200	140	13	—	443	2.14
1953	1	17	78	121	29	6	252	2.71
1954	8	74	123	66	4	2	277	1.96
1954	7	94	93	45	1	0	240	1.75
1955 (—54)	9	74	102	50	4	1	240	1.87
1955	—	64	117	111	23	—	315	2.30
1956 (—55)	10	97	132	61	7	1	308	1.87
1956	3	64	118	83	13	1	282	2.15
1957 (—56)	3	12	146	79	13	0	253	2.34
1957	—	17	71	118	65	15	286	2.97
1958 (—57)	2	63	119	82	12	1	279	2.15
1958	6	54	118	53	9	1	241	2.03
1959 (—58)	4	43	95	68	17	4	231	2.27
1959	1	6	29	68	79	35	218	3.48
1960 (—59)	2	45	94	74	13	6	234	2.29
1960	—	18	63	88	17	1	187	2.57
1961 (—60)	—	30	82	57	12	3	184	2.33
1961	—	26	74	119	59	22	300	2.92
1962 (—61)	0	34	118	94	24	1	271	2.41
1962	1	88	165	116	18	2	390	2.17
1963 (—62)	11	172	247	89	8	0	527	1.83
1963	14	270	254	50	6	0	594	1.60
1964 (—63)	17	226	237	104	7	0	591	1.76
1964	15	150	174	53	11	—	403	1.74
1965 (—64)	7	72	97	212	126	58	572	2.97
1965	0	20	28	104	222	119	493	3.80
1966 (—65)	0	72	157	134	18	1	382	2.26
1966	6	34	169	286	61	10	566	2.69
1967 (—66)	4	136	283	68	2	5	498	1.88
1967	17	143	215	59	4	0	438	1.75
1968 (—67)	4	138	223	57	11	0	433	1.85
1968	2	179	189	57	10	0	437	1.76
1969 (—68)	2	96	162	122	42	3	427	2.28
1969	—	12	37	203	149	—	401	3.22

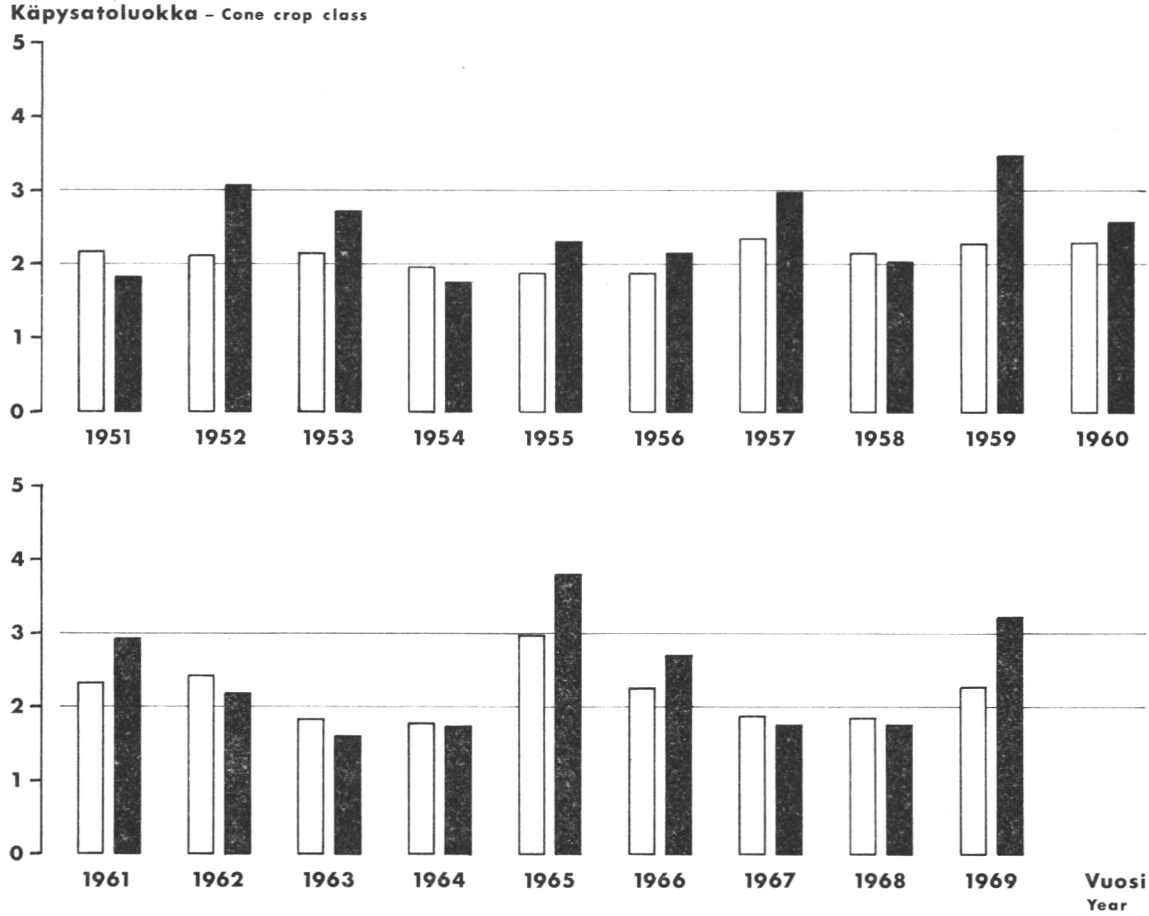
Tuloksista ilmenee mm:

— 1-vuotisten käpyjen mukaan suoritettu arviointi on yleensä ennustanut sadon huonommaksi kuin saman sadon arviointi 2-vuotisina käpyinä.

— Arviointitulosten ero on ollut sitä suurempi, mitä paremmaksi sato on osoittautunut 2-vuotisten käpyjen mukaan arvioituna.

— Jos sadot molemmissa arvioinneissa ovat osoittautuneet heikoiksi, ovat tulokset olleet lähellä toisiaan.

— Muutamissa tapauksissa 1-vuotisten käpyjen arviointi on ennustanut sadon paremmaksi kuin miksi se 2-vuotisten käpyjen mukaan on osoittautunut. Tällöin on säännöllisesti ollut kysymys sadosta, joka 2-vuotisten käpyjen mukaan arvioituna on jäänyt pienemmäksi kuin edellisen vuoden sato niinikään 2-vuotisten käpyjen mukaan arvioituna.



Kuva 1. Vuosien 1951—1969 käpysadot 1-vuotisten (valkeat pylväät) ja 2-vuotisten (mustat pylväät) käpyjen mukaan arvioituna.

Fig. 1. Cone crops for the period 1951—1969, estimated from the number of 1 year-old cones (unshaded columns) and 2 year-old cones (shaded columns).

— 1-vuotisten käpyjen arviointi ei ole kertaakaan ennustanut koko maan käpysatoa keskinkertaiseksi (luokka 3) tai paremmaksi (vuoden 1965 sato lähinnä keskinkertaista, 2.97). 2-vuotisten käpyjen mukaan arvioituna on tällaisia satoja esiintynyt 19 vuoden aikana 5 kertaa.

Käytännön kannalta suurin merkitys ja suorastaan ratkaiseva haitta käpyjen keruun organisointia ajatellen on sillä, että 1-vuotisten käpyjen arviointi ilmeisestikään »ei näe» luotettavasti odotettavissa olevaa, käpyjen keruun kannalta tärkeää hyvää käpyvuotta vaan saattaa antaa siitä jopa aivan väärän kuvan (ks. s. 13). On jokseenkin samantekevää osuvatko vai ei arvioinnit yksiin lopullisesti huonoksi osoittautuvan käpysadon kohdalla, koska siitä ei keräystä kuitenkaan järjestetä.

Jo kauan on ollut tiedossa, että hyvän käpyvuoden edellä 1-vuotisten käpyjen arviointien joukkoon saattaa syystä tai toisesta tulla mukaan muutama yleisestä satokuvasta poikkeava, tavallista parempaa lopullista satoa lupaava arviointi. Näitä poikkeuksia on koetettu käyttää hyväksi tulkittaessa pikkukäpyarviointien tuloksia. Joskus tulkinnassa on osuttu oikeaan, kuten esim. vuoden 1952 satoa ennustettaessa (R u m m u k a i n e n 1952). Lopullinen käpysato osoittautui näiden poikkeusten eikä 1-vuotisten käpyjen arvioinnin antaman yleiskuvan mukaiseksi. Toisinaan on tulkinta kuitenkin mennyt jopa pahasti vikaan, kuten vuoden 1958 sadon kohdalla (R u m m u k a i n e n 1957). Poikkeusten perusteella arveltiin sadosta tulevan ai-

Taulukko 3. Vuoden 1959 käpysadon arviointitulokset 1- ja 2-vuotisten käpyjen mukaan lääneittäin.

Table 3. The estimated results for the 1959 cone crop based on the number of 1 year- and 2 year-old cones, distributed by province.

Lääni: *Province:*	1-vuotiset kävyt: *1 year-old cones*		2-vuotiset kävyt: *2 year-old cones*		Erotus, käpysatolk. *Difference, cone crop class*
	Arvioinnit, kpl *N:o of estimates*	Käpysatolk. *Cone crop class*	Arvioinnit, kpl *N:o of estimates*	Käpysatolk. *Cone crop class*	
A. Uudenmaan	5	3.00	10	4.00	1.00
B. Turun ja Porin	19	2.32	15	4.07	1.75
C. Hämeen	23	2.09	16	4.06	1.97
D. Mikkelin	21	2.43	18	4.44	2.01
E. Kymen	17	2.53	10	4.20	1.67
F. Pohjois-Karjalan	30	2.37	18	4.11	1.74
G. Kuopion	3	1.00	11	3.45	2.45
H. Keski-Suomen	20	2.70	10	3.60	0.90
I. Vaasan	24	2.42	24	3.52	1.10
J. Oulun	49	2.16	51	2.96	0.80
K. Lapin	30	1.73	48	2.79	1.06
Yhteensä — *Total*	241		231		
Keskim. — *Average*		2.26		3.49	1.50

nakin yhtä hyvän kuin 1957 vaikka se jäi huomattavasti heikommaksi. Poikkeusten tulkinnankaan varaan ei siis ilmeisesti voida luotettavasti kävynkeruusuunnitelmia rakentaa.

Edellä on vertailtu arviointituloksia koko maan puitteissa. Kun käpysadot maan eri osien välillä yleensä vaihtelevat, on kiintoisaa tarkastella arviointien antamaa kuvaa myös alueittain. Taulukossa 3 on se vuoden 1959 osalta tehty lääneittäin. Voidaan todeta tulosten suunnan olevan saman kuin koko maan käsittäneessä tarkastelussakin mutta vieläkin kärjistetymmin: tulosten arviointien välinen ero on yleensä ollut sitä suurempi mitä paremmaksi käpysato on lopullisesti muodostunut.

2.3. Käpyjen keräämisen kannattavuus suuruudeltaan erilaisista käpysadoista

Siihen, ryhdytäänkö käpyjä keräämään, vaikuttavat männyillä lähinnä seuraavat seikat: siementarve, siementen tuleentumisaste, käpysadon suuruus sekä käpytuhot.

Tässä yhteydessä tarkastellaan pääasiassa käpysadon suuruuden vaikutusta. Sitä on Suomessa selvitetty käpysadon arviointien yhteydessä tiedustelemalla arvioijilta paitsi sadon runsautta arviointipaikkakunnillaan, myös keruun kannattavuutta ko. sadosta (»kannattaa kerätä»—»ei kannata kerätä»). Vaikka kannattavuustiedustelu muodollisesti on koskenut vain käpysadon runsauden vaikutusta, on ilmeistä että arvioijien ratkaisuun on usein vaikuttanut jonkin verran myös siementarve arviointihetkellä, ja se, miten paljon käpysadosta ja sen hyväksikäytön tarpeellisuudesta arvioinnin aikoihin on tiedotusvälineissä tai muuten puhuttu (Rummukainen 1954, 1956 b). Näillä seikoilla ei kuitenkaan ole ollut ratkaisevaa vaikutusta sadon käyttökelpoisuuden määrittämisessä.

Taulukossa 4 on esitetty tulokset keruun kannattavuudesta vuosien 1950—53 käpysadonarviointien yhteydessä. Mainittuna ajanjaksona saatiin vuonna 1952 keskimäärin hieman keskinkertaista parempi käpysato, muina vuosina sitä huonompi (taulukko 2, kuva 1). Koko ajan oli pulaa männyn siemenestä.

Lukujen mukaan käsitys keruun kannattavuudesta muuttuu jyrkästi siirryttäessä »hyvin vähäisestä» (1) käpysadosta »vähänlaiseen» (2) sekä »vähänlaisesta» sadosta »keskinkertaiseen» (3). Käytännön kannalta näillä muutoksilla on ratkaisevaa laatua oleva ero siinä, että kun edellisessä tapauksessa (1→2) keruun kannattavuus muuttui 3 %:sta lähes 39 %:tiin se jälkimmäisessä (2←3) tapauksessa muuttui 39 %:sta lähes 86 %:ttiin. Edellisen muutoksen jälkeen siis vielä suurin osa arvioijista piti keruuta kannattamattomana, kun sen sijaan jälkimmäisen muutoksen jälkeen ylivoimaisesti suurin

Taulukko 4. Männynkäpyjen keruun kannattavuus suuruudeltaan erilaisista käpysadoista arvioijien käsityksen mukaan vuosina 1950—53.

Table 4. Profitableness of collecting pine cones based on the estimates of the size of the cone crop made by fieldworkers during the period 1950—53.

Käpysatoluokka *Cone crop class*	Arviointeja, kpl *N:o of estimates*	»Kannattaa kerätä»—arviointeja *N:o of »worth collecting» estimates*	
		kpl	%
0	24	0	0.0
1	175	5	2.8
2	424	166	39.1
3	416	357	85.8
4	99	99	100.0
5	27	27	100.0
Yhteensä — *Total*	1 165		

osa heistä oli jo keruun kannalla. Siten jäljempi muutos on kriittinen myös käpysadon arviointeja ajatellen. Mikäli 1- ja 2-vuotisten käpyjen mukaan suoritetut arvioinnit tällä satoluokkavälillä eivät anna suunnilleen samanlaista kuvaa käpysadosta, se saattaa ratkaisevasti vaikuttaa joko käpyjen keräämisen organisointiin tai keräyksen tulokseen. Kuten s. 11 on todettu, pikkukäpyarviointi juuri mainitulla välillä pyrkii antamaan odotettavissa olevasta käpysadosta liian huonon kuvan. Siten käpyjen keruuta ilmeisestikään yleensä ei sen perusteella ole helppoa suunnitella todellisen sadon ansaitsemalla teholla.

Esim. vuodeksi 1958 saatiin 1-vuotisten käpyjen mukaan koko maan sadolle käpysatoluokkaa 2.15 vastaava arvo. Kun sama sato vuotta myöhemmin arvioitiin 2-vuotisten käpyjen mukaan, saatiin arvoksi 2.03. Pikkukäpyarviointi ennusti siis sadon paremmaksi kuin isokäpyarviointi. Kysymyksessä oli tyypillinen sellainen tapaus jolloin näin näyttää käyvän (s. 10).

Vuodeksi 1959 ennusti 1-vuotisten käpyjen arviointi sadon luokkaa 2.27 vastaavaksi eli 0.12 luokkaa paremmaksi kuin edellisen vuoden sadon. Ero oli niin pieni, että sen pohjalta ei ollut mielekästä ryhtyä suunnittelemaan käpyjen keräämistä sen enempää kuin vuotta aikaisemminkaan. Kuitenkin 2-vuotisten käpyjen arviointi osoitti vuoden 1959 sadon käpysatoluokkaa 3.48 vastaavaksi eli 1.21 käpysatoluokkaa paremmaksi kuin pikkukäpyarviointi. Pikkukäpyarvioinnit ennustivat siis sekä vuoden 1958 että vuoden 1959 sadot käpyjen keräämisen kannalta suunnilleen yhtä hyviksi eli sellaisiksi, että niistä keruuta kannatti noin 40 % käpysatojen arvioijista. Isokäpyarvioinnin mukaan vuoden 1958 sadosta kerääminen oli todella mainitulla tavalla kannattavaa. Sitävastoin vuoden 1959 sato muuttui isokäpyarvioinnissa niin paljon paremmaksi, että siitä keräämistä kannattivat käytännöllisesti katsoen kaikki arvioijat.

Todettakoon jo tässä, että kun kevättalvella 1959 tätä tutkielmaa varten järjestettiin eri puolilla maata 1- ja 2-vuotisten käpyjen vertailevia laskemisia samoista oksanäytteistä, saatiin 2-vuotisten käpyjen määräksi (vuoden 1958 sato) yhteensä 6 734 kpl ja 1-vuotisten käpyjen määräksi (vuoden 1959 sato) 42 794 kpl eli runsaasti 6 kertaa enemmän (taulukko 5). Laskelmat tukivat siis käsitystä, että 1-vuotisten käpyjen silmävaraisen arvioinnin antama kuva vuoden 1959 sadosta oli harhauttava.

Vuoden 1965 satoa koskevat arvioinnit, joka sato oli paras koko kaudella 1951—1969, antoivat toisella tavalla kiintoisat tulokset. Tällöin 1-vuotisten käpyjen mukaan suoritettu arviointi ennusti sadon arvon käpysatoluokkaa 2.97 vastaavaksi. 2-vuotisten käpyjen arviointi antoi sille arvon 3.80. Ero oli siten 0.83 käpysatoluokkaa eli varsin huomattava nytkin. Pikkukäpyjenkin mukaan ennuste kuitenkin oli niin hyvä, että sellaisesta sadosta olisi jo noin 85 % arvioijista ollut valmis käpyjä keräämään. Siten arviointitulosten numeerisella erolla ei sen näennäisestä suuruudesta huolimatta olisi ollut kovinkaan ratkaisevaa vaikutusta keräämisen suunnitteluun. Lisäksi 1-vuotisten käpyjen arvioinneissa esiintyi niin runsaasti yleiskuvasta poikkeavia hyvän sadon arviointeja, joiden merkityksestä on puhuttu s. 11, että niidenkin perusteella varsin hyvää satoa voitiin odottaa.

K ä p y t u h o i s t a, joita esiintyy 1-vuotisten ja 2-vuotisten käpyarviointien välisenä aikana ja jotka siis saattavat vaikuttaa 1-vuotisten käpyjen mukaan suoritetun arvioinnin tuloksen tulkintaan, lienee ennen muuta mainittava siemenaiheiden puutteellisen pölyttymisen seurauksena tapahtuva 1-vuotisten käpyjen variseminen toisen kasvukauden alussa. Ilmiötä on tutkinut perusteellisesti S a r v a s (1962). Jos noin 20 siemenaihetta kävyssä jää pölyttymättä, seuraa pikkukävyn variseminen. Ilmiö on siten riippuvainen hedekukkimisen runsaudesta ja voi pienentää 1- ja 2-vuotisten käpyjen satoarviointien välillä erityisesti huonojen käpyvuosien satoa. Toistaiseksi on vaikeata päätellä, miten varisemismahdollisuus olisi syytä ottaa huomioon arvioinneissa, koska juuri huonoina käpyvuosina 1-vuotisten ja 2-vuotisten käpyjen mukaan suoritetut satoennusteet ovat parhaiten osuneet yksiin.

Elollisen luonnon piiriin kuuluvista tekijöistä saattavat pikku- ja isokäpyarviointien välisenä aikana satoa verottaa orava (V a r t i o 1946), käpylinnut (J u u t i n e n 1952, 1953) ja tikat (P y n n ö n e n 1939, 1943). Millään niistä ei kuitenkaan ilmeisesti ole niin suurta vaikutusta männyn käpysatoihin, että ne ainakaan suurissa puitteissa arviointeja häritsisivät. Pääosa tuhoista myös tapahtunee vasta isokäpyarvioinnin jälkeen ja erityisesti hyviä käpyvuosia seuraavina huonoina vuosina, jolloin mielenkiinto käpyjen keruuta kohtaan on yleensä tavallista vähäisempi.

3. UUSI KÄPYSADON ENNUSTAMISMENETELMÄ

3.1. Käpysadon arvioimiskokeita 1- ja 2-vuotisten käpyjen määriä laskemalla

Pikkukäpyjen silmävarainen arviointi antaa siis kokemusten mukaan niin epävarmoja tuloksia, että sen varaan on vaikea suunnitella käytännön toimenpiteitä.

Kun 1-vuotiset kävyt joka tapauksessa tarjoavat potentiaalisen mahdollisuuden saada käpysadosta kuva jo vuotta ennen sadon tuleentumista eli metsätalouden tarpeita ajatellen hyvissä ajoin, ryhdyttiin 1950-luvun puolivälissä tutkimaan niiden määrän arvioimisen kehittämistä.

Tällöin päädyttiin menetelmään, jossa hakkuualoilla laskettiin kaadettujen mäntyjen latvuksista sekä 1- että 2-vuotiset kävyt samoista oksista. Vertailemalla laskentatuloksia pääteltiin seuraavana syksynä tuleentuvan sadon suuruus verrattuna käsillä olevaan satoon. Kun satojen määritys täten perustui pelkästään varmasti läheltä nähtyihin käpyihin jotka yksin kappalein pantiin muistiin, voi menetelmän johdonmukaisesti sovellettuna odottaa poistavan arvioinnista subjektiivisuuden. Jos laskentaa suoritetaan riittävän monella paikalla, ei hyvän käpyvuoden tulo ilmeisestikään jää huomaamatta. Laskentakokeiluja suoritettiin pienessä mitassa jo talvikautena 1955—56, mutta laajemmissa puitteissa seuraavina kolmena vuonna eli ennustettaessa vuosien 1957, 1958 ja 1959 käpysatoja.

Vuoden 1957 satoa ennustettaessa kevättalvella 1957 pyydettiin kenttämiehiä laskemaan molempia käpylajeja hakkuualoilla latvuksista samoista oksista, kuitenkin lähemmin määrittelemättä miten monella hakkuualalla, miten monesta latvuksesta ja oksasta. Laskentatuloksia ei pyydetty ilmoittamaan sellaisinaan, vaan ainoastaan niiden perusteella saatu yhteenveto siitä, kuinka monta prosenttia enemmän tai vähemmän 1-vuotisia käpyjä oli verrattuna 2-vuotisten määrään.

Lisäksi kyseltiin seuraavia asioita:

— Onko 1-vuotisia käpyjä jokaisessa latvuksessa vaiko vain osassa niitä?
— Onko 1-vuotisia käpyjä koko latvuksen alalla vaiko vain jossain sen osassa?
— Onko 1-vuotisia käpyjä esiintymisalueella latvuksessa joka oksassa vaiko vain osassa oksia?
— Onko 1-vuotisia käpyjä paikassaan yksi vaiko useampia kappaleita?
— Mitä puutavaraa oli tehty hakkuualan männyistä?

Näin saatiin monenlaisia tietoja, joista suurimmalla osalla ei kuitenkaan ollut käyttöarvoa. Pikkukäpyjen määrän suhde 2-vuotisten käpyjen määrään verrattuna oli käyttökelpoista tietoa, samoin selvitys siitä oliko kysymyksessä tukki- vaiko kuitupuuhakkuuala. Todettakoon että laskelmia suoritettiin vain kahdella kuitupuuhakkuualalla muiden ollessa tukkialoja.

Laskelmia suoritti 67 miestä. Heidän mukaansa syksyksi 1957 voitiin odottaa keskim. 50 % parempi käpysato kuin oli saatu syksyksi 1956.

Tulos kuvasti huomattavasti paremmin vuoden 1957 käpysatoa kuin syksyllä 1956 suoritettu silmänvarainen pikkukäpyarviointi (taulukko 2, kuva 1). Näin siitä huolimatta että arvioinnit eivät jakautuneet tasaisesti maan eri osien kesken ja vaikka käpysatojen suuruus eri puolilla maata muuttui eri tavoin vuodesta 1956 vuoteen 1957. Muutosten paikallinen erilaisuus näkyi myös laskelmissa, sillä ne jakautuivat seuraavasti:

1-vuot.	käpyjä	enemmän	kuin	2-vuotisia	= 41	arvioijaa
»	»	yhtä paljon	»	»	= 11	»
»	»	vähemmän	»	»	= 15	»
					Yht. 67	arvioijaa

Järjestettäessä uusi laskentakokeilu kevättalvella 1958 saatiin vapaaehtoista työtä suorittamaan 30 miestä.

Tällä kerralla pyydettiin laskelmat suorittamaan vain tukkihakkuualoilla. Työtä yksinkertaistettiin edellisestä vuodesta, sillä ohjeet olivat seuraavanlaiset:

> Latvusten kaikkia käpyjä ei tarvitse yrittää etsiä, vaan riittää kun mielivaltaisesti valituista oksista tai oksan osista sieltä täältä hakkuualan eri puolilta lasketaan molemmat käpylajit. ... Vastaukseksi tähän tiedusteluun tulisi näihin havaintoihin perustuva ilmoitus käpymäärien suhteesta (esim. »Pikkukäpyjä 80 % tul. käp. määrästä», »Pikkukäpyjä 120 % tul. käp. määrästä» jne.). ... Käynti yhdellä hakkuualalla ja muutaman kymmenen oksan tutkiminen riittää ... Mikäli on nähtävissä merkkejä siitä, että oravat ovat syöneet tuleentuneita käpyjä, pyydetään siitä mainitsemaan.

Laskelmien mukaan vuodeksi 1958 oli odotettavissa keskim. 30 % pienempi käpysato kuin mikä oli saatu 1957. Kuten aikaisemmin (s. 11) on todettu, silmävaraisesti suoritettu pikkukäpyarviointi johti arviointituloksen tulkitsijat päättelemään sadot yhtä suuriksi.

Sadon muutoksen alueittaiseen erilaisuuteen viittaa jälleen arviointien jakautuminen:

1-vuotisia	käpyjä	enemmän kuin	2-vuotisia	= 5	arvioijaa
»	»	yhtä paljon kuin	»	= 1	»
»	»	vähemmän kuin	»	= 24	»
				Yht. 30	arvioijaa

Huolimatta havaintojen niukkuudesta ja sattumanvaraisesta jakautumisesta maan eri osien välille laskelmat tälläkin kerralla ennustivat käpysadon luotettavammin kuin silmävarainen arviointi, sillä vuoden 1958 sato osoittautui 2-vuotisten käpyjen mukaan arvioituna selvästi huonommaksi kuin vuoden 1957 sato (taulukko 2, kuva 1).

Lähes joka neljäs eli 7 käpyjen laskijaa ilmoitti oravien syöneen tuleentuneita käpyjä talven aikana. Vaikka oravilla ei olisikaan ratkaisevaa merkitystä käpysadon alentajana (ks. s. 14) ja vaikka kysymyksessä oli suhteellisen hyvän käpyvuoden jälkeisen sadon ennustaminen, jolloin oravia voi esiintyä tavallista runsaammin ja jolloin käpyjen keruuta kohtaan mielenkiinto yleensä on tavallista laimeampaa, viittaavat runsaat syöntihavainnot siihen, että eri vuosien satojen todellisen suhteen selvittämiseksi laskelmat ilmeisesti olisi aiheellista suorittaa syksyllä.

Kevättalvella 1959 vuoden 1959 käpysatoa ennustettaessa laskentaohjeita muutettiin vain vähän edellisestä vuodesta. Nytkin laskennat piti keskittää tukkihakkuualoille. Jokaisella alalla toivottiin laskettavan käpyjä 10 kaadetun männyn latvuksesta, jokaisesta latvuksesta 10 oksasta latvuksen yläosasta. Laskentatulokset piti lähettää sellaisinaan Metsäntutkimuslaitokseen, mutta laskijoita pyydettiin sen lisäksi esittämään myös omia käsityksiään tulevan sadon suuruudesta.

Mikäli näkyi merkkejä oravan, käpylintujen tai muiden syiden 2-vuotisille kävyille aiheuttamista tuhoista, kehotettiin siitä mainitsemaan.

Käpyjä laski tällä kerralla 48 miestä yhteensä yli 60 hakkuualalla (taulukko 5). Alat sijaitsivat verraten tasaisesti maan eri puolilla.

Jokaisen laskelman mukaan oli vuodeksi 1959 odotettavissa parempi käpysato kuin mikä oli saatu vuonna 1958. Pikkukäpyjen määrä oli keskim. 6.35 kertaa niin suuri kuin tuleentuneiden.

Käpyjen määrän kuusinkertaistuminen merkitsee käpysatoluokkina ainakin noin 1.5 käpysatoluokkaa lähdettäessä vuoden 1958 tasosta (ks. taulukot 1 ja 2). Lähes niin suuri, 1.45 lk, olikin muutos 2-vuotisten käpyjen silmävaraisten arviointien mukaan (1958 sato = 2.03, 1959 sato = 3.48).

Käpyjen laskenta ja tuleentuneiden käpyjen silmävaraiset arvioinnit antoivat siten varsin tarkasti samanlaisen kuvan sadon muutoksesta. 1-vuotisten käpyjen silmävaraisen avioinnin antama kuva sitävastoin poikkesi edellisistä suuresti. Niiden mukaan vuoden 1958 sadon arvoksi saatiin 2.15 ja vuoden 1959 sadon arvoksi 2.27. Nekin siis ennustivat sadon paranevan, mutta muutokseksi saatiin vain 0.12 käpysatoluokkaa. Kun tälläinen käytännössä merkityksetön lisäys oli tulossa huonoon satoon, ei ennuste tarjonnut edellytyksiä ryhtyä suunnittelemaan käpyjen keräämistä. Kun vuoden 1959 käpysato osoittautui koko tutkimuskauden 1951—1969 toiseksi parhaaksi (paras oli vuoden 1965 sato, arvo 3.80, ks. taulukko 2 ja kuva 1), voidaan pikkukäpyjen silmävaraisten arviointien antamaa kuvaa pitää käy-

Taulukko 5. Käpyjen laskentatulokset talvella 1958—59. 1-vuotiset kävyt = vuoden 1959 sato. 2-vuotiset kävyt = vuoden 1958 sato.

Table 5. Results of counting the cones in the winter 1958—59. 1 year-old cones = 1959 crop. 2-year-old cones = 1958 crop.

Läänit ja kunnat *Provinces and communes*	Hakkuualoja, kpl *N:o of cutting areas*	1-vuotisia käpyjä, kpl *N:o of 1 year old cones*	2-vuotisia käpyjä kpl *N:o of 2 year old cones*	1959 sato = × niin suuri kuin 1958 sato *1959 crop = number of times as large as the 1958 crop*
Lapin lääni:				
Rovaniemi	1	839	378	+ 2.20
»	1	1 292	203	+ 6.40
»	2	2 150	414	+ 5.20
Salla	1	364	80	+ 4.50
Oulun lääni:				
Hyrynsalmi	?	?	?	+ 4.00
Kuhmo	?	?	?	+15.00
Muhos	2	984	166	+ 5.90
Oulujoki	1	910	386	+ 2.30
Vaala	1	561	44	+12.70
Vaasan lääni:				
Alajärvi	1	587	194	+ 3.00
Perho	2	174	68	+ 2.50
Seinäjoki	1	1 260	244	+ 5.20
»	1	734	241	+ 3.00
Ähtäri	1	259	7	+37.00
Keski-Suomen lääni:				
Pihtipudas	1	608	62	+ 9.80
Pylkönmäki	1	774	279	+ 2.80
Toivakka	1	393	9	+43.00
Viitasaari	1	995	95	+10.50
Kuopion lääni:				
Iisalmi	1	314	12	+26.10
Rautalampi	1	891	37	+24.00
Rautavaara	1	228	88	+ 2.60
Pohjois-Karjalan lääni:				
Ilomantsi	1	78	11	+ 7.00
Liperi	1	454	35	+13.00
Pielisjärvi	1	2 766	366	+ 7.50
»	3	1 686	150	+11.40
»	1	1 128	45	+25.00
Turun ja Porin lääni:				
Harjavalta	1	344	57	+ 6.00
Kankaanpää	?	?	?	+ 5.00
Mynämäki	1	790	119	+ 6.60
Parkano	1	?	?	+ 4.00
Hämeen lääni:				
Forssa	1	550	124	+ 4.40
Kuru	2	1 550	466	+ 3.30
Lempäälä	1	295	66	+ 4.50
Orivesi	2	1 876	222	+ 8.40
»	1	388	56	+ 6.90
Padasjoki	2	896	770	+ 1.20
Vilppula	1	855	225	+ 3.80
Virrat	1	375	216	+ 1.70

Taulukko 5 jatk. — *Table 6 cont.*

Mikkelin lääni:				
Punkaharju	1	296	12	+12.00
Savitaipale	2	2 416	322	+ 7.50
Sulkava	3	459	57	+ 8.20
Kymen lääni:				
Miehikkälä	1	1 900	34	+34.00
Parikkala	1	2 149	69	+31.00
Sippola	3	2 757	75	+36.00
Uudenmaan lääni:				
Bromarv	1	707	76	+ 9.3
Lapinjärvi	3	2 397	99	+24.4
Lohja	1	272	24	+11.3
Tuusula	1	1 102	208	+ 5.3
Yhteensä — *Total*	60+?	42 794	6 734	
Keskim. — *Avarage*				+ 6.35

tännön kannalta aivan virheellisenä. Jälleen kerran ne eivät »nähneet» sellaisen sadon tuloa, josta käpyjen kerääminen oli hyvin kannattavaa.

Käpyjen laskijoista vain kaksi ilmoitti nähneensä merkkejä siitä, että oravat olivat syöneet 2-vuotisia käpyjä. Joku laskija epäili lisäksi 2-vuotisia käpyjä karisseen jäätyneistä puista niitä kaadettaessa ja siten haitanneen laskutoimituksia.

Yhteenvetona kolmen vuoden aikana suoritetuista käpyjen laskemisista voidaan siis todeta, että laskennat antoivat joka kerralla oikean kuvan käpysadon muutoksen suunnasta. Muutokset osoittautuivat lisäksi varsin samansuuruisiksi 2-vuotisten käpyjen silmävaraisten arviointien tulosten kanssa. Siten käpyjä laskemalla näyttäisi olevan mahdollista saada jokseenkin luotettava kuva sadosta jo vuotta ennen sen tuleentumista.

3.2. Käpyjen laskennan suorittamisesta käytännössä

Käpyjen laskennat olisi ilmeisesti syytä keskittää pelkästään tukkihakkuualoille, joilta männyn siemen edelleen suurimmaksi osaksi hankitaan. Hakkuualojen pitäisi mieluimmin sijaita suurilla yhtenäisillä männikköalueilla. Kuten on huomautettu (S i m c l i n n a, kirje U. R:lle 21. 3. 1957), sellaisilla alueilla hakkuita todennäköisesti suoritetaan vuodesta toiseen, joten laskennat antavat kuvan kävynkeruumahdollisuuksista sellaisilla paikoilla missä keräämiselle on parhaat luontaiset tekniset edellytykset. Jos laskentoja tehdään kooltaan rajoitetuissa männiköissä sijaitsevilla hakkuualoilla, ne helpommin osuvat tavalla tai toisella, esim. maan viljavuuden tai puuston iän puolesta poikkeuksellisiin metsiköihin, jonkalaisia ei ole käytettävissä keräyksen kohteina käpysadon tuleennuttua. Kun mainitunlaiset poikkea-

vuudet vaikuttavat käpysadon muodostumiseen, voi tällaisesta metsiköstä saatu ennuste antaa joko liian hyvän tai huonon kuvan kävynkeruumahdollisuuksista paikkakunnalla.

Tukkihakkuualojen lisäksi käpyjen laskentaa voitaisiin suorittaa myös pystykeräysten yhteydessä, josta jäljempänä enemmän.

Hakkuualalla saadaan ilmeisesti riittävän hyvä kuva käpytilanteesta jos käpyjä lasketaan esim. 10 latvuksesta ja kustakin latvuksesta 5 oksasta. Kun käpyjä muodostuu eniten latvuksen yläosassa, on laskennat kaikkialla suoritettava samalla tavalla valituista oksista jotta eri arviointien tulokset olisivat vertailukelpoisia. Laskentakohteiksi voisi valita esim. maassa makaavan latvuksen ylöspäin olevia oksia, ylimmän aivan latvuksen yläpäästä, alimman latvuksen puolivälistä ja muut 3 oksaa suunnilleen samalta linjalta ja yhtä pitkien välimatkojen päästä niiden väliltä.

Jokaisesta latvuksesta merkittäisiin muistiin kaikissa 5 oksassa havaittujen 2-vuotisten käpyjen yhteinen määrä sekä erikseen samoissa oksissa havaittujen 1-vuotisten käpyjen yhteinen määrä eli kaksi lukua latvusta kohden. Jokaisesta 10 latvuksesta saadut luvut lähetettäisiin sellaisinaan, siis 10 lukua 2-vuotisten käpyjen ja 10 lukua 1-vuotisten käpyjen laskennoista Metsäntutkimuslaitokseen yhdistelmän ja päätelmien tekoa varten.

Paras laskenta-ajankohta olisi ilmeisesti syksy ennen lumen ja pakkasten tuloa. Tällöin laskentatoimitukset olisivat helpot tehdä maan ja oksien ollessa lumettomia. Tällöin myös 2-vuotisten käpyjen karisemisvaara puita kaadettaessa olisi mahdollisimman vähäinen puiden ollessa sulia. Samoin oravat ym. käpyjen tuhoojat eivät ehdi verottaa 2-vuotisia käpyjä yhtä paljon kuin suoritettaessa laskennat vasta seuraavana kevättalvena, kuten kokeiluissa tehtiin. Vaikka tällaiset laskentatuloksia sekoittavat tekijät olisivatkin merkitykseltään vähäisiä, on ne syytä eliminoida.

Lisäksi tietysti syksyllä laskettaessa jää mahdollisimman pitkä aika varautua käpy- ja siemensadon hyväksikäyttöön, mikäli se osoittautuu aiheelliseksi.

Kuten taulukosta 5 ilmenee, ei näytä olevan suurta merkitystä sillä laskeeko sama mies samalla paikkakunnalla käpyjä yhdeltä vaiko useammalta hakkuualalta. Usealla alalla laskeminen ei tietenkään ole haitaksi, mutta se lisää työtä. Sitävastoin olisi ilmeisesti hyvä jos esim. läänin sisällä laskelmia suorittaisi riittävän moni mies. Laajimpien eli vuoden 1959 kokeilujen mukaan samassa läänissä sadon muutos yleensä näköjään ennustetaan eri miesten laskelmien pohjalta varsin yhteneväisesti, mutta joukkoon voi kuitenkin osua myös joku jopa suuresti poikkeava ennuste. Jotta tällaiset poikkeavuudet, joiden syyt saattanevat olla monet, eivät pääsisi suhteettoman paljon vaikuttamaan alueen käpysadosta saatavaan yleiskuvaan, on laskelmia suoritettava riittävän monen miehen toimesta. Kenties 5 laskijaa lääniä kohden olisi sopiva perusmäärä. Kun läänejä mantereella on 11, tarvittaisiin silloin

55 laskijaa selvittämään koko maan satokuvaa. Kaksinkertainen määrä olisi 110 miestä. Silmävaraisia arviointeja suorittaa nykyisin vuosittain 400—500 miestä (O. Helenius, suullisesti).

Laskentatulosten luotettavuuden kannalta olisi varmaan eduksi jos työtä vuodesta toiseen suorittaisivat samat miehet. Heitä voitaisiin opastaa siihen. Opastaminen koskisi ilmeisesti lähinnä yhteisen linjan löytämistä laskentakohteiden valinnassa.

Käpyjen laskenta antaa kuvan vain 1- ja 2-vuotisten käpyjen määrien suhteesta. Hyvissä ajoin saatu luotettava kuva pelkästään siitä on jo hyödyllinen. Kuvan käytännöllinen arvo tietysti suurenisi jos suhdeluku voitaisiin muuntaa konkreettiseksi eli odotettavissa oleva sato kiloiksi hehtaaria kohden verrattuna parhaillaan käytettävänä olevan sadon edustamaan kilomäärään. Se vaatisi jatkuvia, vuodesta toiseen suoritettavia kävynkeruita. Jatkuvaa keräystä ei toistaiseksi kuitenkaan suoriteta kuin korkeintaan siemenviljelmillä. Ne taas ovat tukkimänniköihin verrattuna vielä varsin nuoria ja muutenkin erilaisia. Kenties niistä saatuja käpysaantoja silti voitaisiin jotenkin käyttää hyväksi konkretisoitaessa koko maan satokuvaa laskentatulosten pohjalta.

4. TIIVISTELMÄ

Käytännön metsätalouden tarpeita varten on suoritettu vuosittain puiden siemensatojen arviointeja määrittämällä satojen suuruudet niiden tuleentumissyksynä 0—5-luokituksen mukaisesti (s. 5). Männyn käpysadot arvioidaan myös 1-vuotisten pikkukäpyjen mukaan, jolloin arvioinnilla pyritään voittamaan vuosi lisäaikaa satojen hyväksikäytön valmisteluille.

Männyllä käpysatoluokkien käytännöllistä merkitystä selvitettäessä on mm. havaittu (taulukot 1 ja 4) käsityksen kävynkeruun kannattavuudesta muuttuvan merkitsevästi siirryttäessä käpysatoluokasta 2 (keruuta kannattaa noin 39 % sadon arvioijista) luokkaan 3 (keruuta kannattaa noin 86 % arvioijista).

Tutkittaessa 1- ja 2-vuotisten käpyjen mukaan suoritettuja samojen satojen arviointeja vuosilta 1951—1969 havaitaan (taulukot 2 ja 3, kuva 1) 1-vuotisten käpyjen arvioinnin antaneen sadoista huonomman kuvan kuin miksi ne ovat lopullisesti osoittautuneet silloin kun on saatu niin hyviä satoja että keruu on kannattanut. Koko tutkimuskautena 1-vuotisten käpyjen arviointi ei kertaakaan ennustanut koko maan sadon arvoa käpysatoluokkaa 3 vastaavaksi, mutta 2-vuotisten käpyjen mukaan suoritettu arviointi osoitti sellaisia tai parempia satoja saadun 5 kertaa. Siten 1-vuotisten käpyjen arviointitulokset ovat olleet epäluotettavia eivätkä ole tarjonneet pohjaa käpysatojen hyväksikäytön suunnittelulle.

Epäkohdan korjaamiseksi on kehitetty arviointimenetelmä, joka perustuu hakkuualoilla suoritettavaan 1- ja 2-vuotisten käpyjen laskentaan kaadettujen puiden latvuksista. Vuosina 1957—59 suoritetuissa kokeiluissa laskennat antoivat varsin hyvän kuvan odotettavissa olleista käpysadoista. Samojen satojen silmävaraisia arviointeja haittasivat edellä mainitut puutteet.

Käpyjen laskentaa esitetään suoritettavaksi syksyisin tukkihakkuualoilla, kullakin hakkuualalla 10 latvuksesta ja jokaisesta latvuksesta tietyllä tavalla valituista 5 oksasta. Jokaisessa latvuksessa havaittujen 1- ja 2-vuotisten käpyjen lukumäärät merkitään erikseen muistiin ja tiedot lähetetään Metsäntutkimuslaitokselle yhteenvetojen ja päätelmien tekoa varten.

Laskenta antaa ilmeisen luotettavan kuvan käsillä olevan ja seuraavaksi syksyksi tuleentuvan käpysadon suuruuden suhteesta. Suhdeluvun konretisoimiseksi esitetään tutkittavaksi mahdollisuutta sen kytkemiseksi männyn siemenviljelmiltä vuosittain saataviin käpysaantoihin.

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6. SUMMARY

On forecasting the cone crop of Scots pine

In order to be able to satisfy the seed requirements of practical forestry, estimates of the cone crop of pine are taken in Finland every autumn. Field workers stationed in different parts of the country make estimates of the cone abundancy in their locality by eye. They estimated using the following classification how closely the number of cones corresponded to the following cone crop classes during the years 1951—1969:

0 = no cones
1 = very few cones
2 = a few cones
3 = a moderate number of cones
4 = rather a lot of cones
5 = very many cones

What these classes actually signify in practical terms (Tables 1 and 4) has been investigated in some studies. For instance, it has been found that the opinion of the people carrying out the estimations as far as the profitableness of collecting the cones is concerned, undergoes a significant change when moving from a crop classified as cone crop class 2 to that of class 3.

Information about the size of the cone crop should be obtained as early as possible so that the cone collection operations can be properly organised. For this reason, the abundance of 1 year-old cones, which will be ripe the following year, is estimated seperately from that of ripened 2 year-old cones. The results estimated according to the number of 1 year-old cones may deviate from the estimation results for the same cones when they are 2 year-old cones (Tables 2 and 3, Fig. 1). From the practical point of view, the greatest significant fact about this is that the 1 year-old cone estimation does not reveal the arrival of a good cone year; on the contrary, it regularly gives a poor picture of it. Thus it is difficult to plan cone collection operations on the basis of 1 year-old cone estimations carried out by eye.

At the end of the 1950's, a new method for the estimation of the cone crop of pine was tried out which had been designed to overcome this difficulty. The number of both 2 year- and 1 year-old cones was counted in the crowns of felled trees, in conjunction with felling operations. Thus by comparing the absolute numbers obtained, the size of the mature crop for the following year was predicted. During the study period 1957—59, the best cone occurred in 1959 (Table 2, Fig. 1). The estimation of 1 year-old cones which was carried out by eye predicted a cone crop which was approximately the same size as the actual one in the year 1958. Approximately a six times greater crop (Table 5) was expected after the number of cones had been counted, which in fact it proved to be when the 2 year-old crop was estimated.

The counting of cones, as well as the collecting of them, can nowadays only be carried out on areas where felling operations are taking place. It would appear, that if counting took place on a sufficient number of cutting areas (e.g. 10 crowns and from each crown for example 5 branches from a certain part of the crown), then a relatively true picture of the cone situation would be obtained.

By counting the number of cones, the relationship between the abundancy of 2 year-old and 1 year-old cones only is indicated. In order to obtain a concrete forecast, the value of this relationship should be coupled to the size of the cone collection yield. However, this is not easy to do as cones are not collected every year. Only by using seed orchards, which in Finland are still rather young, can cone collection be carried out continuously. Perhaps seed orchards could be used for converting the relative crop picture given by counting into concrete terms.

ERILAISTEN RAUDUSKOIVU-JÄLKELÄISTÖJEN PITUUSKASVU ETELÄ- JA KESKI-SUOMESSA

JYRKI RAULO JA VEIKKO KOSKI

SUMMARY

HEIGHT GROWTH OF DIFFERENT PROGENIES OF BETULA VERRUCOSA EHRH. IN SOUTH AND MIDDLE FINLAND

HELSINKI 1975

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ALKUSANAT

Tässä julkaisussa esitetään ensimmäiset koko laajaan aineistoon perustuvat tulokset niistä rauduskoivun jälkeläiskokeista, jotka vuosina 1965—1969 perustettiin Metsäntutkimuslaitoksen toimesta. Työt tehtiin yhteistyössä metsähallituksen, Keskusmetsälautakunta Tapion, Metsänjalostussäätiön, A. Ahlström Osakeyhtiön, Enso-Gutzeit Osakeyhtiön, Rauma-Repola Oy:n, Oy Kaukas Ab:n ja Oy Wilh. Schauman Ab:n kanssa. Kokeiden perustamiseen, hoitoon, mittauksiin, tulosten käsittelyyn ym. tutkimukseen liittyviin toimenpiteisiin on osallistunut yli sata edellä mainittujen sekä Metsäntutkimuslaitoksen metsänhoidon- ja metsänjalostuksen tutkimusosaston työntekijää. Lausumme parhaat kiitokset heille kaikille. Erityisesti kohdistamme kiitoksemme Koivukeskukselle ja Suomen Vaneriyhdistykselle, joiden aloitteesta ja rahoituksen turvin tehokas rauduskoivun jalostustyö 1960-luvulla voitiin Metsäntutkimuslaitoksessa aloittaa. Työn ohjaajaa ja voimakasta innoittajaa, professori R i s t o S a r v a s t a ei kiitoksemme enää tavoita.

Professori M a x. H a g m a n, apulaisprofessori A r n e R o u s i ja maat. metsät. tri M a t t i L e i k o l a ovat tarkastaneet käsikirjoituksen ja tehneet siihen huomioonotettuja korjauksia. Käännöstyön englannin kieleen on suorittanut B.Sc. J o h n D e r o m e. Heille esitämme parhaat kiitoksemme. Työnjako tutkijoiden välillä on ollut seuraava: R a u l o on vastannut kokeiden suunnittelusta, perustamisesta, hoidosta ja mittauksista. Tulosten käsittely, päätelmien teko ja työn julkaisukuntoon saattaminen on kirjoittajien yhteistyötä.

Helsinki 1974-11-11

Jyrki Raulo *Veikko Koski*

SISÄLLYSLUETTELO

Sivu

1. Johdanto 5
2. Aineisto 6
   21. Koemateriaalin valinta ja kasvatus 6
   22. Kenttäkokeet 8
3. Aineiston käsittely ja tulokset 16
   31. Yleistä 16
   32. Erilaiset koejärjestelyt 20
   33. Vapaapölytys- ja risteytysjälkeläistöt 21
   34. Kaukoristeytys ja heteroosi 23
   35. Maantieteellisten siirtojen vaikutus 23
4. Tulosten tarkastelu ja päätelmät 25
5. Kirjallisuus 28
6. Summary 29

1. JOHDANTO

Monet koivun biologiset ominaisuudet, kuten nopea alkukehitys, nuorella iällä saavutettu sukukypsyys ja nopea siemenen valmistuminen tekevät koivun metsänjalostajalle havupuita paljon mieluisammaksi kohteeksi. Tästä huolimatta havupuiden valta-asema metsätaloudessa piti koivun jalostuksen Suomessa pitkään taka-alalla. Ulkomaisen rahoituksen turvin tosin voitiin 1960-luvun alussa aloittaa monet koivun jalostamiseen liittyvät teoreettiset tutkimukset, jotka koskivat koivun kukintaa, risteytysjalostuksen perusteita ja mutaatiojalostuksen mahdollisuuksia (mm. Vaarama ja Valanne 1968 ja 1969, Hagman 1971, Sarvas 1972, Valanne 1972).

Ruotsissa oli jo 1940-luvulla perustettu eräitä koivun provenienssikysymystä ja hybridijalostusta selvittäviä kokeita (Johnsson 1951 ja 1967, Erkén 1972). Myös Länsi-Saksassa on koivu ollut jossakin määrin jalostajien objektina (Stern 1963 ja König 1971). Edellä mainitut koivun jalostamista koskevat tutkimukset eivät kuitenkaan ole olleet riittäviä rauduskoivun jalostuksen perustaksi Suomessa. Nämä ulkomailla tehdyt, jokseenkin pieniin aineistoihin nojautuvat kokeet eivät myöskään ole voineet tuoda esiin Suomessa käytäntöön suositeltavia alkuperiä.

Rauduskoivun (*Betula verrucosa Ehrh.*) jalostamiseen liittyvää käytännön toimintaa voitiin voimakkaasti tehostaa Metsäntutkimuslaitoksessa vuodesta 1961 lähtien. Tällöin Suomen Vaneriyhdistys teki Koivukeskuksen aloitteesta huomattavan lahjoituksen käytettäväksi tähän tarkoitukseen. Näillä varoilla suoritettavissa tutkimuksissa asetettiin päätavoitteeksi suomalaisten pluspuiksi valittujen rauduskoivujen jalostusarvon määrittäminen. Testausohjelma laadittiin sellaiseksi, että perustettavien jälkeläiskokeiden avulla saataisiin tietoja myös pluspuiden vapaapölytysjälkeläistöjen ja pluspuiden välisten risteytysjälkeläistöjen kehityksestä, metsikön sisäisten ja metsiköiden välisten risteytysjälkeläistöjen kehityksestä sekä kaukoristeytysten jalostukselle mahdollisesti tarjoamista eduista. Ohjelmaan sisällytettiin myös maantieteellisten siirtojen vaikutuksen tutkiminen ja eräitä jälkeläiskoetekniikkaan liittyviä erillisselvittelyjä. Vuosina 1965—1969 perustettiin Suomen eri osiin laajoja edellä mainittuja kysymyksiä selvittäviä koesarjoja. Esillä olevassa tutkimuksessa rajoitutaan tarkastelemaan erilaisten vapaapölytys- ja risteytysjälkeläistöjen pituuskehitystä Etelä- ja Keski-Suomeen perustettujen jälkeläiskokeiden antamien tulosten perusteella. Esituloksia eräistä tähän tutkimukseen sisältyvistä jälkeläiskokeista ovat julkaisseet Koski ja Raulo (1972), Koski (1974) ja Raulo (1974).

2. AINEISTO

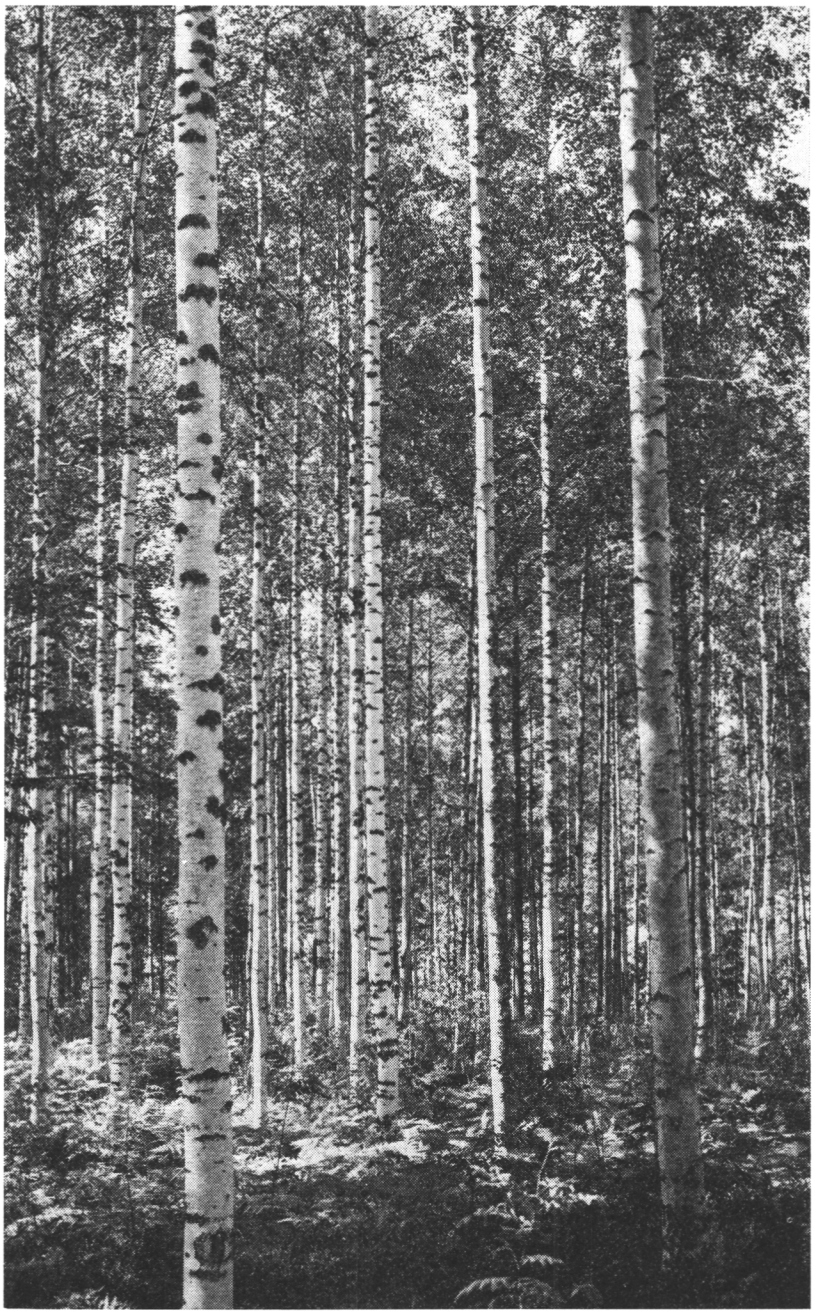
21. Koemateriaalin valinta ja kasvatus

Aina vuoteen 1964 asti noudatettiin rauduskoivun jalostuksen perusmateriaalin valinnassa samoja periaatteita kuin havupuilla (S a r v a s 1947 ja 1953). Pluspuuksi valittavan puuyksilön tuli erottua selvästi naapureistaan sekä hyvän kasvun että hyvän laadun perusteella. Metsikköön, jossa puu kasvoi, ei tällöin kiinnitetty erityistä huomiota. Vuonna 1964 siirryttiin rauduskoivun pluspuiden valinnassa keskitettyyn valintaan Koivukeskuksen tähän tarkoitukseen myöntämän erillisrahoituksen turvin ja Koivukeskuksen, Metsänjalostussäätiön, metsähallituksen ja Keskusmetsälautakunta Tapion aktiivisella tuella. Tällöin jalostuksen lähtökohdaksi valittiin kokonaisuudessaan hyvälaatuisia metsiköitä (Kuva 1), joista merkittiin pluspuiksi hyvälaatuiset valtapuut (R a u l o 1969). Keskitettyä pluspuiden valintaa alettiin noudattaa myös muiden puulajien pluspuiden valinnassa 1960-luvun loppupuoliskolla (O s k a r s s o n 1970 ja 1972).

Käsilläolevan tutkimuksen lähtömateriaaliin sisältyy kaikkiaan 163 pluspuuta. Nämä edustavat sekä hajanaisesti että keskitetysti valittuja pluspuita jälkimmäisten osuuden ollessa kuitenkin yli 80 %. Emopuiden jakaantuminen eri paikkakunnille on esitetty kuvassa 2.

Vuonna 1962 tehtiin valvottuja risteytyksiä Rautalammilla sekä kerättiin vapaasti pölyttynyttä siementä Rautalammilta, Punkaharjulta ja Keuruulta. Tällöin tehdyt risteytykset olivat miltei kaikki metsikön sisäisiä risteytyksiä. Vuonna 1964, jolloin rauduskoivu kukki runsaasti sekä Etelä- että Keski-Suomessa, toteutettiin laaja ristetysohjelma Tuusulassa, Punkaharjulla ja Rautalammilla. Tällöin kerättiin myös vapaapölytyssiementä useilla paikkakunnilla kasvavista pluspuista. Kaikissa risteytyskohteissa pyrittiin jokainen emopuu pölyttämään isäpuilla, jotka edustivat samaa metsikköä, läheistä saman alueen metsikköä ja eri maantieteellisellä alueella sijaitsevaa metsikköä (kaukoristeytys). Seuraavana vuonna keskitettiin risteytystyöt ja vapaapölytyssiemenen keruu Sulkavan ja Rautalammin metsiköihin, joissa tehtiin sekä metsiköiden sisäisiä että eri metsiköissä olevien puuyksilöiden välisiä risteytyksiä. Vuonna 1966 Punkaharjulla ja Sulkavalla tehdyt risteytykset edustivat pelkästään näiden metsiköiden puuyksilöiden välisiä risteytyksiä.

Huolimatta siitä, että rauduskoivun risteytystekniikka on jokseenkin



Kuva 1. Hyvälaatuinen rauduskoivikko Metsäntutkimuslaitoksen Punkaharjun kokeilualueessa. Pääosa tutkimuksen lähtömateriaalista on peräisin tämänkaltaisista koivikoista (Kuvannut M. Mannelin).

Figure 1. High quality stand of Betula verrucosa at the Finnish Forest Research Institute's experimental area in Punkaharju. Most of the starting material used in the study has originated from such stands (Photo M. Mannelin).

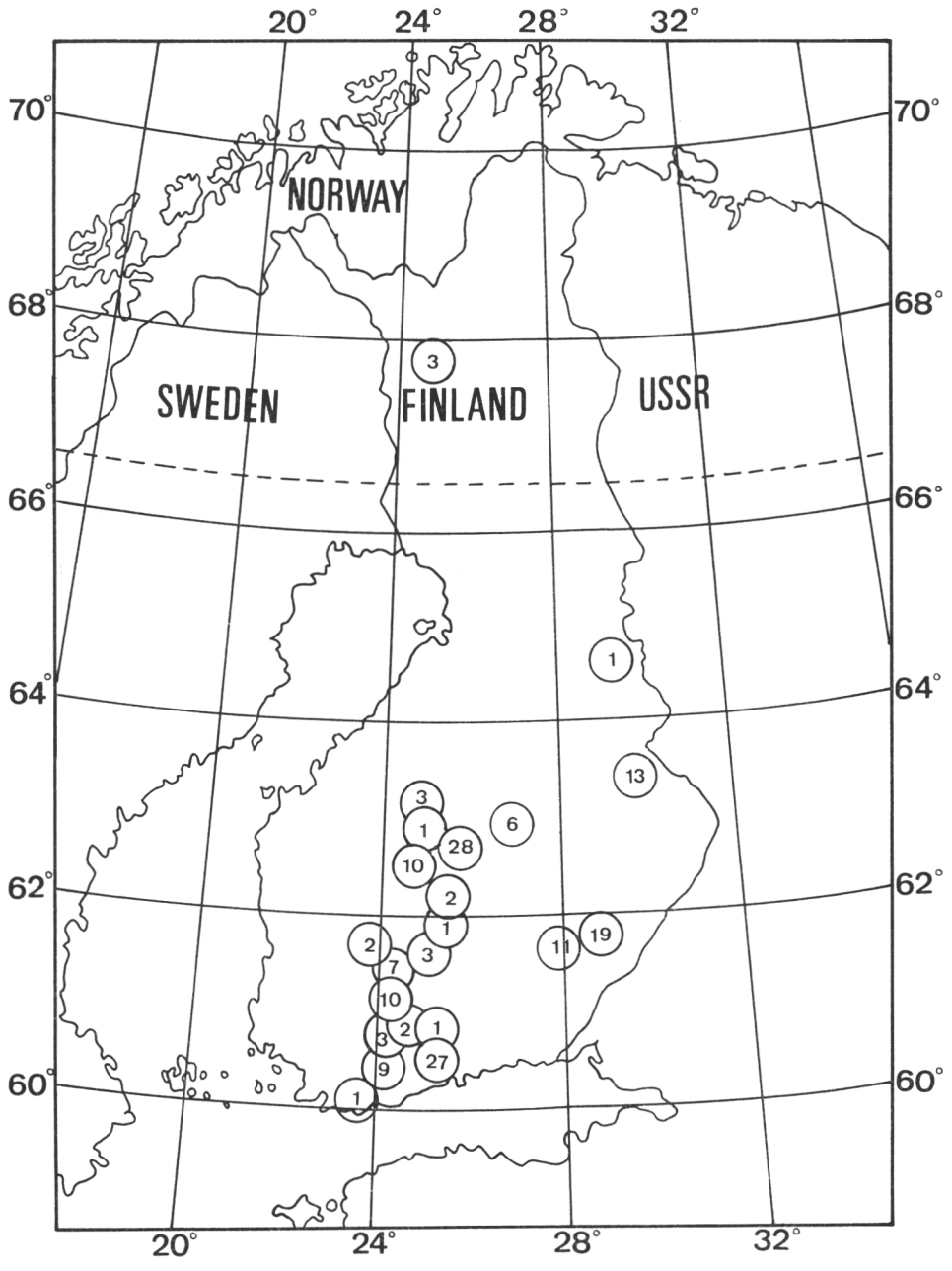
yksinkertainen saatiin käyttökelpoista siementä ainoastaan osasta tehdyistä risteytysyhdistelmistä. Tähän vaikuttivat eristyspussien rikkoutumiset ennen niiden poistamisajankohtaa ja oksien katkeilemiset. Mikäli pölyttämättömistä kontrollipusseista kerätyn siemenen itävyys ylitti 5 % hylättiin kaikki kyseisessä emopuussa tehdyt yhdistelmät. Tehtäessä risteytyksiä Rautalammilla v. 1964 pölytettiin erehdyksessä myös kontrollipussit. Näin ollen ei näistä risteytyksistä saatu kontrolli-itävyyttä. Varsinaiset risteytyssiemenet käytettiin kuitenkin koetaimien kasvattamiseen.

Kunakin vuonna käytettävissä olleiden siementen itävyys määritettiin kylvövuoden kevättalvella. Tämän jälkeen siemenet annosteltiin kylvöjä varten siten, että itävien siementen määrä neliömetriä kohden tuli kaikissa kylvöerissä teoreettisesti saman suuruiseksi.

Vuosina 1962 ja 1964 hankituista siemenistä kasvatettiin taimet Metsänjalostussäätiön Haapastensyrjän, Pieksämäen ja Vanajan taimitarhoilla. Kylvöt tehtiin varhain keväällä alkuperittäin ilman toistoja muovihuoneisiin turvealustalle. Seuraavana keväänä valittiin kylvöksistä koulintamateriaaliksi tanakat ja hyvin kehittyneet taimet. Nämä koulittiin lauta- ja eräissä tapauksissa myös puikkokoulintaa käyttäen alkuperittäin avomaalle. Koulitut kaksivuotiaat koetaimet nostettiin, lajiteltiin ja lähetettiin jälkeläiskokeisiin joko seuraavana syksynä tai vasta seuraavana keväänä. Koulittujen taimien lajittelussa poistettiin kaikki mekaanisesti vaurioituneet, selvästi kaksihaaraiset ja kasvussaan muista selvästi jälkeenjääneet taimet. Lajittelu oli näin ollen taimitarhoilla silloin käytetyn yleisen tavan mukainen. Kokeeseen 17 taimia nostettaessa noudatettiin jonkin verran ankarampaa lajittelua kuin muiden kokeiden taimien valinnassa. Tähän kokeeseen valittiin vain kunkin kasvatuserän valtataimia. Vuonna 1965 hankitusta siemenestä kasvatettiin taimet metsähallituksen Pataman taimitarhalla. Täällä kasvatus toteutettiin lähes samoin kuin Metsänjalostussäätiönkin taimitarhoilla. Eri alkuperiä edustaneet taimet koulittiin kuitenkin jo taimitarhaan toistoittain. Koulintamateriaalia ja kokeisiin lähetettäviä taimia lajiteltaessa noudatettiin samoja periaatteita kuin yleensä aikaisemminkin.

22. Kenttäkokeet

Kokeita perustettaessa ei ollut käytettävissä tietoa siitä, miten erilaiset koejärjestelyt poikkeavat toisistaan erotuskyvyn suhteen. Tästä syystä käytettiin aluksi tuohon aikaan Suomessa yleisesti omaksuttua tapaa, jossa koeyksikön suuruus oli 10×10 m ja taimimäärä koeyksikössä 25 kpl. Vuodesta 1966 lähtien kokeissa pyrittiin käyttämään pinta-alaltaan ja taimimäärältään eri suuruisia koeyksikköjä, jotta saataisiin tietoja suuruudeltaan erilaisten koeyksiköiden käyttökelpoisuudesta jälkeläiskokeita perustettaessa. Nyt käsiteltäviin kokeisiin sisältyy sellaisia, joissa koeyksikkö on yksi



Kuva 2. Emopuiden jakaantuminen eri paikkakunnille. Ympyrän sisässä oleva numero ilmaisee emopuiden lukumäärän kullakin paikkakunnalla.

Figure 2. The map indicates the location of plus trees whose offspring have been used in the progeny tests. The circled numbers indicate the number of trees in each locality.



Kuva 3. Risteytyssiemenen keruuta Punkaharjun pluskoivikosta elokuussa 1964. Kaikki risteytykset tehtiin kasvavissa pluspuissa (Kuvannut M. Mannelin).

Figure 3. Collecting controlled crossing seeds from plus trees at Punkaharju in august 1964. All the controlled crossings were carried out on plus trees (Photo M. Mannelin).

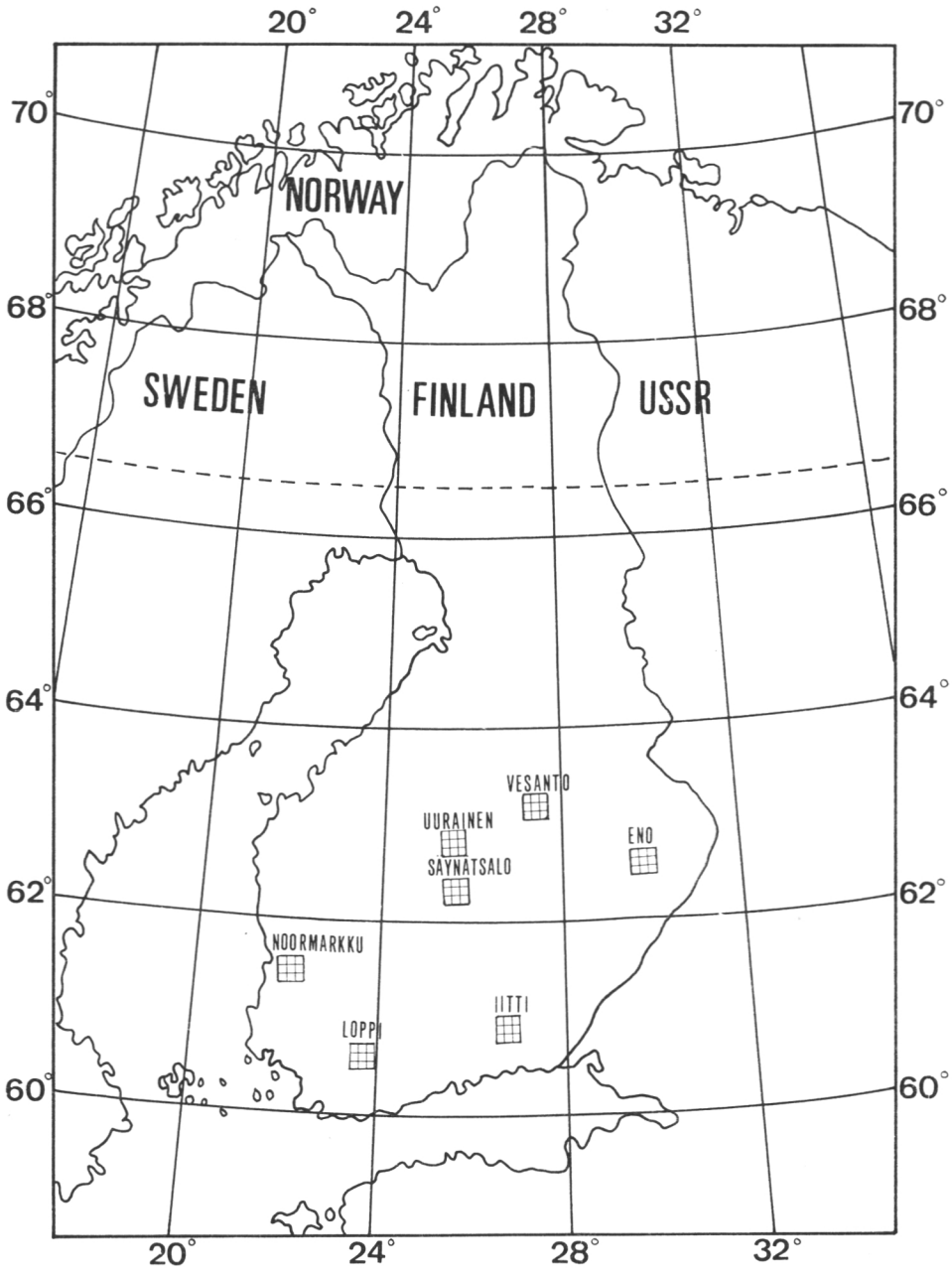
taimi tai 9, 25, 49, 100 tai 400 taimen muodostama ruutu. Tutkimusaineistoon sisältyvien kokeiden sijainti, kokeen haltija, perustamisvuosi ja yksityiskohtainen rakenne on esitetty taulukossa 1. Koealueet on merkitty myös kuvaan 4. Taulukossa 1 on kokeet numeroitu juoksevasti 1—19. Tämän lisäksi on kunkin kokeen kohdalla mainittu sen numero Metsäntutkimuslaitoksen metsägeneettisessä rekisterissä. Tämän esityksen tekstissä käytetään yksinkertaisuuden vuoksi taulukossa 1 esitettyä kokeiden juoksevaa numerointia.

Tutkimuksen aineistoon sisältyvien kokeiden lisäksi perustettiin parikymmentä muuta jälkeläiskoetta ja n. 200 jälkeläisviljelystä. Osa näistä on tuhoutunut eri syistä ja osasta ei ole ollut käytettävissä mittaustuloksia. Näin ollen ne on jätetty nyt tehtävän tarkastelun ulkopuolelle. Suurimpana syynä kokeiden ja jälkeläisviljelysten epäonnistumiseen oli väärä viljelyalan valinta ja usein pienten taimien jälkihoidon puute (R a u l o 1973). Myyrät aiheuttivat merkittäviä tuhoja kymmenessä jälkeläiskokeessa.

Perustettaessa kokeita v. 1965 paalutettiin koeruudut maastoon edellisenä syksynä ja kokeissa tarvittavat taimet tilattiin taimitarhoilta koealu-

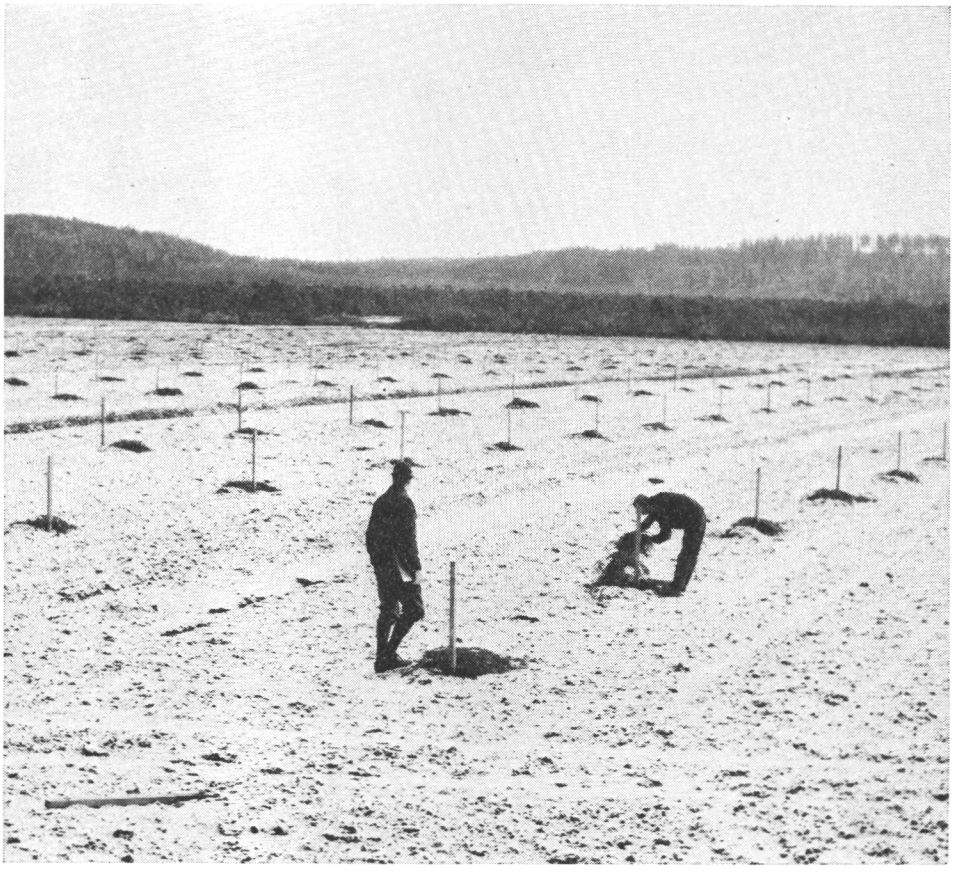
Taulukko 1. Kokeiden numerointi, sijainti, haltija ja yksityiskohtainen rakenne.
Table 1. General information about the progeny tests included in this investigation.

Koe n:o *Code number used in the present paper*	Kokeen rekisteri n:o *The number in the register of forest genetical experiments*	Kunta *Locality*	Haltija *Owner*	Perustamisvuosi *Year of planting*	Perheitä, kpl *Number of families*	Lohkoja, kpl *Number of blocks*	Taimia, kpl/koeyksikkö *Number of plants per plot*	Kokeen taimimäärä, kpl *Total number of young trees*
1	542/1	Säynätsalo	Enso-Gutzeit Osakeyhtiö ...	1965	18	4	25	1 800
2	542/5	»	» » ...	1965	7	4	25	700
3	542/6	»	» » ...	1965	16	2	25	800
4	542/7	»	» » ...	1967	20	4	25	2 000
5	542/4	»	» » ...	1967	9	4	100	3 600
6	543/1	Eno	Oy Kaukas Ab	1965	11	4	25	1 100
7	543/2	»	» » »	1965	7	5	25	875
8	543/3	»	» » »	1967	38	7	25	6 650
9	544/2	Uurainen	Oy Wilh. Schauman Ab ..	1966	14	4	25	1 400
10	544/1	»	» » » » ..	1966	5	2	400	4 000
11	544/3	»	» » » » ..	1966	5	3	400	6 000
12	476/1	Iitti	Kml Tapio	1967	34	5	49	8 330
13	476/2	»	» »	1967	134	9	9	10 854
14	476/3	»	» »	1967	200	22	1	4 400
15	476/4	Vesanto	Rauma Repola Oy	1967	180	20	1	3 600
16	476/5	»	» » »	1967	174	10	1	1 740
17	476/6	Loppi	Metsänjalostussäätiö	1967	100	40	1	4 000
18	280/1	Noormarkku	A. Ahlström Osakeyhtiö ...	1967	19	3	100	5 700
19	280/2	»	» » » ...	1969	106	8	9	7 632
			Kaikkien kokeiden yhteinen taimimäärä — *Total*					75 381



Kuva 4. Koealueiden jakaantuminen eri paikkakunnille.
Figure 4. The map indicates the location of the progeny tests.

eille istutuskeväänä 25 taimen nipuissa. Taimien saavuttua alueille ne jaettiin ennalta arvottuihin koeruutuihin ja valeistutettiin näiden keskipaalujen viereen. Tämän jälkeen taimet istutettiin 2 × 2 m:n välein 40 × 40 cm:n suuruisen laikun keskelle tehdyn kuopan laitaan. Tätä ennen oli taimien istutuspaikat merkitty koeruutuihin. Myöhemmin kokeita perustettaessa koealueet paalutettiin, taimien paikat merkittiin koeruutuihin ja taimet kuljetettiin istutusalueille jo istutusta edeltäneenä syksynä (Kuva 5). Siellä ne valeistutettiin koeruutujen keskelle keväällä tapahtuvaa istutusta odottamaan. Koetta 19 perustettaessa taimia ei valeistutettu syksyllä koeruutuihin, vaan niille varatulle pellolle koealueen läheisyyteen. Sieltä ne siirrettiin valeistutukseen koeruutujen keskelle varhain keväällä ja istutus aloitettiin välittö-



Kuva 5. Koe n:o 13 syksyllä 1966, jolloin taimet valeistutettiin koeruutujen keskelle keväällä 1967 tapahtuvaa varsinaista istutusta odottamaan (Kuvannut P. Leinonen).

Figure 5. Plot n:o 13 in autumn 1966. The seedlings have been planted temporarily in the center of the sample plots ready for proper planting in spring 1967 (Photo P. Leinonen).

mästi. Koetaimien asianmukaisesta nostosta, lajittelusta ja niputuksesta vastasivat taimitarhojen hoitajat ja työnjohtajat heille annettujen ohjeiden mukaisesti tai Metsäntutkimuslaitoksen toimitusmiehen ohjatessa edellä mainittuja töitä. Kokeiden varsinaiseen perustamiseen liittyvät työt tehtiin kokeiden haltijoiden ammattimiesten johdolla ja Metsäntutkimuslaitoksen toimitusmiesten ohjaamina. Kokeen 17 perustamisen hoiti Metsänjalostussäätiö Metsäntutkimuslaitoksessa laadittujen perustamisohjeiden mukaisesti. Kokeet 10 ja 11 perustettiin muokkaamattomalle mustikkatyypin metsämaalle, kokeet 18 ja 19 ojitetulle ja muokatulle vesijättömaalle ja kokeet 1, 2 ja 3 muokkaamattomalle, aiemmin heinää kasvaneelle pellolle. Muut kokeet perustettiin muokatulle, maanviljelyksestä hylätylle pellolle.

Kaikkien kokeiden kehitystä seurattiin vuosittain tehdyin tarkastuksin ja taimet vapautettiin tarvittaessa pintakasvillisuuden aiheuttamasta haitallisesta kilpailusta. Entisille heinäpelloille perustetuissa kokeissa työ jou-



Kuva 6. Koe n:o 1 Säynätsalossa kevättalvella 1972 (Kuvannut L. Tervo).
Figure 6. Test n:o 1 at Säynätsalo in early spring 1972 (Photo L. Tervo).

duttiin tekemään 4—5 kertaa. Sänkipelloilla selvittiin 1—2 kerralla ja kynnetyillä ja äestetyillä alueilla ei heinimistä yleensä tarvinnut tehdä. Säynätsalossa, Iitissä ja Noormarkussa sijaitsevilla koealoilla taimet lannoitettiin 2 vuoden kuluttua istutuksesta. Taimistojen myöhemmässä kehitysvaiheessa koealueilta poistettiin niille syntyneet luontaiset taimet sekä lehtipuiden vesat ennen kuin ne haittasivat koetaimien kehittymistä.

Kaikki mittaukset tehtiin Metsäntutkimuslaitoksen työryhmien toimesta lukuunottamatta koetta 17, jonka mittauksesta huolehti Metsänjalostussäätiö. Suuri osa kokeista on mitattu 2—4 kertaa. Tässä tutkimuksessa käytetään eri kokeiden viimeisten mittausten tuloksia. Kunakin mittauskertana merkittiin muistiin koealakartoille kuolleitten taimien määrä ja mitattiin kokeen kaikkien taimien pituus yhden, viiden tai kymmenen cm:n tasaavaa luokitusta käyttäen.

3. AINEISTON KÄSITTELY JA TULOKSET

31. Yleistä

Kunkin kokeen mittaustuloksista laskettiin kaikkien perheiden keskipituudet ja keskipituuksien variaatiokerroin. Tämän jälkeen tarkasteltiin graafisesti perhekeskiarvojen jakautuman ja variaatiokertoimen avulla piirretyn normaalijakautuman yhteensopivuutta. Tämä todettiin kaikissa tapauksissa hyväksi. Kuvassa 7 esitetään tällaisen tarkastelun tulos kokeista 13, 15, 17 ja 19. Tämän jälkeen laskettiin montako prosenttia paras perhe kussakin kokeessa ylitti kokeen kaikkien perheiden keskiarvon. Nämä tulokset on esitetty taulukossa 2. Taulukossa 3 on esitetty kokeittain kaikki ne perheet, joiden pituus t-testissä merkitsevästi poikkesi ko. kokeen keskipituudesta.

Taulukko 2. Yhdistelmä kokeiden pituusmittauksista.
Table 2. Height data of all the families used in the progeny tests.

Koe n:o *Code number*	Mittausvuosi *Year measured*	Kokeen ikä, v *Number of growing seasons between planting and measuring*	Perheitä, kpl *Number of families included in the calculations*	Kokeen keskipit., cm *Mean height of all families, cm*	Variaatiokerroin, % *Variation coefficient of the family means, %*	Parhaan perheen keskip., cm *The mean height of the tallest family, cm*	Parhaan perheen ja kokeen keski-arvon ero, % *Difference between the tallest family and the experiment mean, %*
1	1972	8	18	697	5.2	750	8
2	1972	8	7	647	3.2	680	5
3	1972	8	16	707	5.8	810	15
4	1972	6	20	375	6.6	415	8
5	1972	6	9	341	7.6	387	13
6	1974	10	11	728	5.8	797	9
7	1974	10	6	648	5.7	706	9
8	1974	8	38	527	8.0	607	15
9	1973	8	16	507	12.0	604	13
10	1973	8	5	463	16.3	595	28
11	1973	8	5	456	7.4	496	9
12	1972	6	34	401	5.8	448	12
13	1972	6	129	421	6.9	501	19
14	1972	6	191	380	6.6	448	18
15	1973	7	162	408	11.0	512	25
16	1973	7	158	507	7.9	618	22
17	1973	7	98	497	5.6	565	14
18	1972	6	16	438	4.4	481	10
19	1973	4	106	376	9.9	482	28

Taulukko 3. Luettelo niistä perheistä, joiden keskipituus oli kokeen keskiarvoa merkitsevästi suurempi.

Table 3. Description of those families which had a mean height significantly greater than the mean value of the experiment.

Koe n:o *Code number*	Emopuu ♀		Isäpuu ♂		Koe n:o *Code number*	Emopuu ♀		Isäpuu ♂	
	N:o *No*	Kunta *Locality*	N:o *No*	Kunta *Locality*		N:o *No*	Kunta *Locality*	N:o *No*	Kunta *Locality*
1	K251	Rautalampi	K256B	Rautalampi	12	K336	Rautalampi	E2359	Renko
»	K251	Rautalampi	K964	Rautalampi	»	K337	Rautalampi	E2356	Viljakkala
»	K961	Rautalampi	K258	Rautalampi	»	K338	Rautalampi	E2363	Kangasala
»	E1599	Keuruu		0 [1])					
»	E1600	Keuruu		0	13	E1982	Punkaharju	E398	Bromarv
					»	E1987	Punkaharju	E2378	Punkaharju
2	E1987	Punkaharju	E1980	Punkaharju	»	E1989	Punkaharju	E3006	Tuusula
					»	E2374	Punkaharju	E2378	Punkaharju
3	E1972	Punkaharju	E1980	Punkaharju	»	E2376	Punkaharju	E1500	Tuusula
»	E1972	Punkaharju	E2101	Punkaharju	»	E2376	Punkaharju	E2378	Punkaharju
					»	E3012	Tuusula	E3004	Tuusula
4	E3021	Tuusula	E3003	Tuusula	»	E3012	Tuusula	E3006	Tuusula
»	K970	Pielisjärvi	E3017	Tuusula	»	E3012	Tuusula	E3017	Tuusula
»	K961	Rautalampi		0	»	E3013	Tuusula	E1500	Tuusula
					»	E3013	Tuusula	E3004	Tuusula
5	K337	Rautalampi	E2356	Viljakkala	»	E3013	Tuusula	E3017	Tuusula
»	K257	Rautalampi		0	»	E3018	Tuusula	E2359	Renko
					»	E3021	Tuusula	K379	Pielisjärvi
6	K251	Rautalampi	K256B	Rautalampi	»	K249	Rautalampi	E210	Janakkala
»	K251	Rautalampi	K963	Rautalampi	»	K249	Rautalampi	E2361	Kangasala
					»	K250	Rautalampi	E2101	Pusula
7	E1981	Punkaharju		0	»	K339	Rautalampi	E2297	Lohja
					»	K961	Rautalampi	K378	Pielisjärvi
8	E1982	Punkaharju		0	»	E2812	Sääksmäki		0
»	E1986	Punkaharju		0	»	K251	Rautalampi		0
»	E2366	Punkaharju		0	»	K335	Rautalampi		0
»	E2371	Punkaharju		0	»	K339	Rautalampi		0
»	E3013	Tuusula		0	»	K341	Rautalampi		0
»	K234	Viitasaari		0	»	K970	Pielisjärvi		0
»	K235	Viitasaari		0					
»	K248	Rautalampi		0	14	E1987	Punkaharju	E2378	Punkaharju
»	K257	Rautalampi		0	»	E2369	Punkaharju	E2378	Punkaharju
»	K277	Karttula		0	»	E3008	Tuusula	E3004	Tuusula
»	K340	Rautalampi		0	»	E3008	Tuusula	E3017	Tuusula
»	K969	Rautalampi		0	»	E3018	Tuusula	E1500	Tuusula
»	K980	Pielisjärvi		0					
					15	E2372	Punkaharju	E1984	Punkaharju
9	E184	Keuruu		0	»	E3010	Tuusula	E3006	Tuusula
»	E1598	Keuruu		0	»	E3017	Tuusula	E2359	Renko
»	E1981	Punkaharju	E1984	Punkaharju	»	E3019	Tuusula	E1500	Tuusula
»	E1987	Punkaharju	E1980	Pusula	»	E3020	Tuusula	E3003	Tuusula
»	E1987	Punkaharju	E1986	Punkaharju	»	E3020	Tuusula	E3006	Tuusula
					»	E3028	Tuusula	E3003	Tuusula
10	K251	Rautalampi	K963	Rautalampi	»	K248	Rautalampi	E2355	Viljakkala
					»	K961	Rautalampi	E2359	Renko
11	K251	Rautalampi	K963	Rautalampi	»	K961	Rautalampi	K378	Pielisjärvi
					»	K341	Rautalampi		0
12	E2369	Punkaharju	E3006	Tuusula	16	K336	Rautalampi	E210	Janakkala
»	E2376	Punkaharju	E1500	Tuusula	»	K338	Rautalampi	E2296	Lohja
»	K248	Rautalampi	E2102	Pusula					
»	K249	Rautalampi	E2294	Lohja	17	E2369	Punkaharju	E1500	Tuusula
»	K336	Rautalampi	E210	Janakkala	»	E2369	Punkaharju	E2378	Punkaharju

jatkoa — *cont.*

Koe n:o *Code number*	Emopuu ♀ N:o *No*	Emopuu ♀ Kunta *Locality*	Isäpuu ♂ N:o *No*	Isäpuu ♂ Kunta *Locality*	Koe n:o *Code number*	Emopuu ♀ N:o *No*	Emopuu ♀ Kunta *Locality*	Isäpuu ♂ N:o *No*	Isäpuu ♂ Kunta *Locality*
17	E3012	Tuusula	E1500	Tuusula	19	E3662	Sulkava	K964	Rautalampi
»	E3013	Tuusula	E3006	Tuusula	»	E3663	Sulkava	K342	Rautalampi
»	E3021	Tuusula	E3003	Tuusula	»	K250	Rautalampi	K342	Rautalampi
»	E3021	Tuusula	E3003	Tuusula	»	K340	Rautalampi	E3662	Sulkava
					»	K340	Rautalampi	K335	Rautalampi
18	K247	Rautalampi		0	»	K341	Rautalampi	E2394	Sulkava
»	K338	Rautalampi		0	»	K342	Rautalampi	E1599	Keuruu
»	K969	Rautalampi		0	»	K343	Rautalampi	E370	Keuruu
					»	K343	Rautalampi	K342	Rautalampi
19	E2380	Sulkava	E370	Keuruu	»	K968	Rautalampi	K342	Rautalampi
»	E3002	Sulkava	E2380	Sulkava	»	K969	Rautalampi	E370	Keuruu
»	E3002	Sulkava	E2396	Sulkava	»	K969	Rautalampi	E2394	Sulkava

[1]) 0 = Vapaapölytys — *Open-pollinated*

Taulukko 4. Kokeen 13 varianssianalyysin tulos.
Table 4. Experiment no 13, analysis of variance.

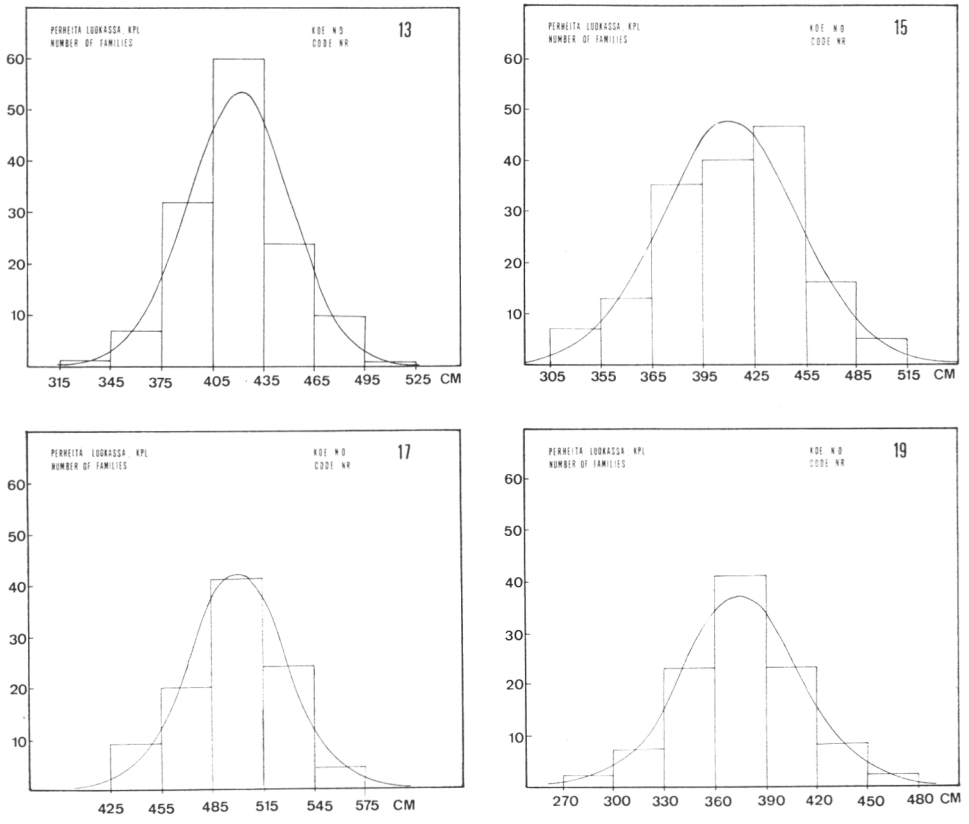
Vaihtelun lähde *Source of variance*	Vapausasteet *df*	Neliösumma SS_x	Keskineliö s^2	F
Perheiden välinen — *Between the families*	130	87 625	674.04	3.16 ***
Lohkojen välinen — *Between the blocks*	8	109 979	13 747.34	64.5 ***
Perhe × lohko — *Family × block*	1 040	221 737	213.21	8.79 ***
Jäännös — *Error variance*	3 537	85 801	24.26	
Kokonais — *Total*	4 715	505 141		

Taulukko 5. Kokeen 19 varianssianalyysin tulos.
Table 5. Experiment no 19, analysis of variance.

Vaihtelun lähde *Source of variance*	Vapausasteet *df*	Neliösumma SS_x	Keskineliö s^2	F
Perheiden välinen — *Between the families*	105	270 445	2 575.7	1.34 *
Lohkojen välinen — *Between the blocks*	7	123 946	17 706.6	9.21 ***
Perhe × lohko — *Family × block*	735	1 412 018	1 921.1	17.01 ***
Jäännös — *Error variance*	6 784	765 881	112.9	
Kokonais — *Total*	7 631	2 572 291		

* = merkitsevyys — significance 95 %
** = » — » 99 %
*** = » — » 99.9 %

Eräissä kokeissa on mukana hyvin pohjoisia perheitä ja lajiristeytymiä. Nämä esiintyvät taulukon 1 luvuissa, mutta ne on jätetty pois tuloksia käsiteltäessä. Suurten kokeiden mittaustulosten käsittelyssä käytettiin tietokonetta, koska analyysit haluttiin tehdä yksittäisten taimien eikä ruutukeskiarvojen perusteella. Tarkoituksena oli myös soveltaa kaksisuuntaista varianssianalyysiä yksilötasolla. Tätä vaikeuttivat puuttuvat arvot, joita isoissa kokeissa miltei aina esiintyy. Taimia kuolee tai vahingoittuu eri syistä hyvinkin hoidetuissa kokeissa. Täydelliseen havaintoaineistoon pääsemiseksi voidaan mittaustuloksista jättää laskennan ulkopuolelle sellaiset perheet, joista puuttuu monta havaintoa, tai sellainen lohko, josta puuttuu monta perhettä. Eräissä tapauksissa on tarkoituksenmukaista ottaa mukaan vain osa kunkin ruudun taimista. Kokeessa 13 oli vuoden 1972 mittauksissa yht. 1 817 puut-



Kuva 7. Perhekeskiarvojen jakautuminen pituusluokkiin sekä kokeen keskipituuden ja standardipoikkeaman perusteella piirretty normaalijakautuma kokeissa 13, 15, 17 ja 19.

Figure 7. The frequency distribution of family means as a histogram, and the normal distribution drawn on the basis of the mean value and standard deviation, in experiments 13, 15, 17, and 19.

tuvaa havaintoa. Jättämällä pois kaksi perhettä ja ottamalla laskentaan joka ruudusta vain neljä suurinta tainta jäi puuttuvia arvoja vain 121. Nämä korvattiin kokeen keskiarvolla. Täten saatiin täydellinen aineisto yksilötasolla tehtävää kaksisuuntaista varianssianalyysiä varten. Vastaava analyysi tehtiin myös kokeen 19 tuloksista. Tulokset on esitetty taulukoissa 4 ja 5.

Molemmissa tapauksissa osoittautui perhe × lohko -yhdysvaikutus tilastollisesti erittäin merkitseväksi. Tällaisessa tapauksessa ei varianssianalyysiä voida jatkaa normaalilla tavalla (S c h e f f e 1959). Testisuureet perheiden ja lohkojen välisen vaihtelun merkitsevyyden testaamiseksi muodostettiin käyttämällä jakajana yhteisvaikutuksen keskineliötä jäännösvaihtelun keskineliön sijasta. Tällöin edellytettiin, että interaktio on satunnaista.

32. Erilaiset koejärjestelyt

Erilaisten koejärjestelyjen tehokkuutta tutkittaessa määritettiin kokeista tehtyjen varianssianalyysien ja t-testien jälkeen kuinka suuri ero kussakin kokeessa voitiin 99 %:n luotettavuudella todeta merkitseväksi. Eri kokeiden vertaamista varten laskettiin tämän jälkeen kuinka monta prosenttia pienin merkitsevä ero oli kokeen keskiarvosta. Taulukossa 6 on esitetty kuinka suuret erot erilaisilla koejärjestelyillä voitiin näin osoittaa merkitseviksi. Tästä voidaan todeta, että »one-tree-plot» -järjestelmä 10, 20 tai 22 lohkolla on ollut erotuskyvyltään selvästi heikoin. Käyttämällä 9 taimen ruutuja ja 8—9 lohkoa on n. 10 %:n erot saatu tilastollisesti merkitseviksi. Tärkeä tulos on, että

Taulukko 6. Merkitsevän (99 %) eron suuruus erilaisissa koejärjestelyissä.
Table 6. The relative size of the statistically significant (99 %) differences within different experimental layouts.

Kokeen n:o *Code number*	Koejärjestely *Layout*			Kaikki taimet *All young trees*	Valtataimet *Dominant trees*
	Perheitä, kpl *Number of families*	Lohkoja, kpl *Number of blocks*	Taimia ruudussa, kpl *Number of plants per plot*	Todettavan eron suuruus, % *Least significant difference, %*	
14	200	22	1	16.0	.
15	180	20	1	16.0	.
16	174	10	1	22.0	.
17	98	40	1	8.0	.
13	134	9	9	7.2	7.4
19	106	8	9	10.0	4.5
4	20	4	25	5.2	.
12	34	5	49	4.7	7.5
5	9	4	100	6.8	.
10	5	2	100	8.8	.
11	5	3	100	6.0	.

ottamalla 9 taimen ruudusta 3 tai 4 valtatainta mukaan laskentaan, saadaan miltei sama erotuskyky kuin käytettäessä kaikkia taimia.

Yleisesti voidaan todeta, että käytetyllä koetekniikalla voidaan taimiston tässä ikävaiheessa luotettavasti erottaa omaksi osajoukoksi ne perheet, jotka ruutukokeissa eroavat kokeen keskiarvosta yli 10 % ja »one-tree-plot» -kokeissa yli 16 %. Vertaamalla näitä lukuja taulukon 2 variaatiokertoimiin voidaan todeta, että tällaisia perheitä voi olla vain muutama kappale kussakin kokeessa.

33. Vapaapölytys- ja risteytysjälkeläistöt

Kaikissa kokeissa vapaapölytys- ja risteytysjälkeläistöjen keskipituudet olivat hyvin lähellä toisiaan. Tarkempaa tilastollista tarkastelua varten jaettiin kokeiden 13, 14, 15, 16 ja 19 perheet kolmeen luokkaan sen perusteella, miten niiden keskipituudet suhtautuivat ko. kokeen keskipituuteen. Muut kokeet on tässä tarkastelussa jätetty pois perheiden pienen lukumäärän vuoksi. Jakautumat on esitetty kokeittain taulukossa 7.

Eri kokeiden jakautumat on yhdistetty kahdella tavalla. Taulukossa 8

Taulukko 7. Vapaapölytys- ja risteytysperheiden jakautumat ja keskipituudet eri kokeissa.

Table 7. The distribution of families originating from open- pollination and controlled crosses into categories —, 0, and +, and the pooled mean heights.

Kokeen n:o *Code number*	Pölytyslaji *Type of pollination*	[1]) Luokka *Category* —	0	+	Perheitä yht., kpl *Total number of families*	Keskipituus, cm *Mean height, cm*
		Perheitä, kpl *Number of families*				
13	Vapaa — *Open*	1	5	5	11	445
	Risteytys — *Cross*	19	80	19	118	419
14	Vapaa — *Open*	1	10	0	11	374
	Risteytys — *Cross*	1	174	5	180	355
15	Vapaa — *Open*	1	119	6	126	421
	Risteytys — *Cross*	5	30	1	36	373
16	Vapaa — *Open*	0	124	2	126	514
	Risteytys — *Cross*	1	32	0	32	480
19	Vapaa — *Open*	2	11	0	13	372
	Risteytys — *Cross*	10	66	17	93	377

[1]) — = Keskiarvoa merkitsevästi huonompi — *Mean significantly lower*
0 = Ei eroa keskiarvosta merkitsevästi — *No significant differences between the means*
\+ = Keskiarvoa merkitsevästi parempi — *Mean significantly higher*

Taulukko 8. Yhdistelmä vapaapölytys- ja risteytysperheiden jakautumisesta luokkiin.
Table 8. The distribution of open -pollinated and crossed families into classes.

Pölytyslaji *Type of pollination*	[1]) Luokka *Category*			Perheitä yht., kpl *Total number of families*
	—	0	+	
Vapaa — *Open*	5	263	13	287
Risteytys — *Cross*	36	382	42	460
Yhteensä — *Total*	41	651	55	747

$\chi^2 = 3.26$ $20\ \% < P < 30\ \%$

Taulukko 9. Luokkien jakautumat vapaapölytys- ja risteytysperheisiin.
Table 9. The distribution of categories in open- pollinated and crossed families.

[1]) Luokka *Category*	Pölytyslaji *Type of pollination*		Perheitä yht., kpl *Total number of families*
	Vapaa *Open*	Risteytys *Cross*	
—	5	36	41
0	269	382	651
+	13	42	55
Yhteensä — *Total*	287	460	747

$\chi^2 = 19.27$ $P < 0.001\ \%$

[1]) — = Keskiarvoa merkitsevästi huonompi — *Mean significantly lower*
0 = Ei eroa keskiarvosta merkitsevästi — *No significant differences between the means*
\+ = Keskiarvoa merkitsevästi parempi — *Mean significantly higher*

ovat riveinä vapaapölytys ja risteytys ja sarakkeina luokat —, 0 ja +. Tässä asetelmassa tarkastellaan sitä, jakautuvatko eri luokat samalla tavalla sekä risteytysjälkeläistöissä että vapaapölytysjälkeläistöissä. Asetelmasta laskettu χ^2 saa arvon 3.26. Vapausasteiden lukumäärän ollessa 2 tämä merkitsee, että jakautumat ovat yli 20 %:n todennäköisyydellä samanlaiset.

Taulukossa 9 ovat riveinä luokat —, 0 ja + sekä sarakkeina vapaapölytys ja risteytys. Tässä asetelmassa tarkastellaan sitä, esiintyykö vapaapölytys- ja risteytysperheitä eri luokissa samoissa suhteissa kuin niitä on kokeissa mukana. Laskettu χ^2 on 19.3. Tämä osoittaa, että jakautumat ovat ainoastaan 0.1 %:n todennäköisyydellä samanlaiset.

Vaikka risteytys- ja vapaapölytysjälkeläistöjen yhdistetyt keskiarvot olivat kokeissa lähes samat, osoitti suoritettu χ^2-testi eroja eri pölytystyyppien jakautumisessa luokkiin —, 0 ja +. Vapaapölytysperheiden joukossa

on keskiarvoa merkitsevästi parempien perheiden lukumäärä odotusarvoa suurempi ja lisäksi erot jakautumisessa selittyvät sillä, että risteytysperheiden keskinäinen hajonta on jonkin verran suurempi kuin vapaapölytysperheiden.

34. Kaukoristeytys ja heteroosi

Eri paikkakuntien puiden välisistä risteytyksistä syntyneet perheet eivät missään kokeessa erottuneet selvästi muista perheistä. Kaukoristeytyksistä ja paikkakunnan sisäisistä risteytyksistä syntyneitä perheitä vertailtiin erityisesti kokeessa 19, jossa esiintyy jälkeläistöjä kolmen paikkakunnan puiden erilaisista risteytysyhdistelmistä (Taulukko 10). Tästä voidaan todeta, että sisäisistä ja kaukoristeytyksistä syntyneet jälkeläistöt ovat keskenään hyvin samanpituisia. Varianssianalyysi osoitti, etteivät erot ole merkitseviä, $F = 1.812$.

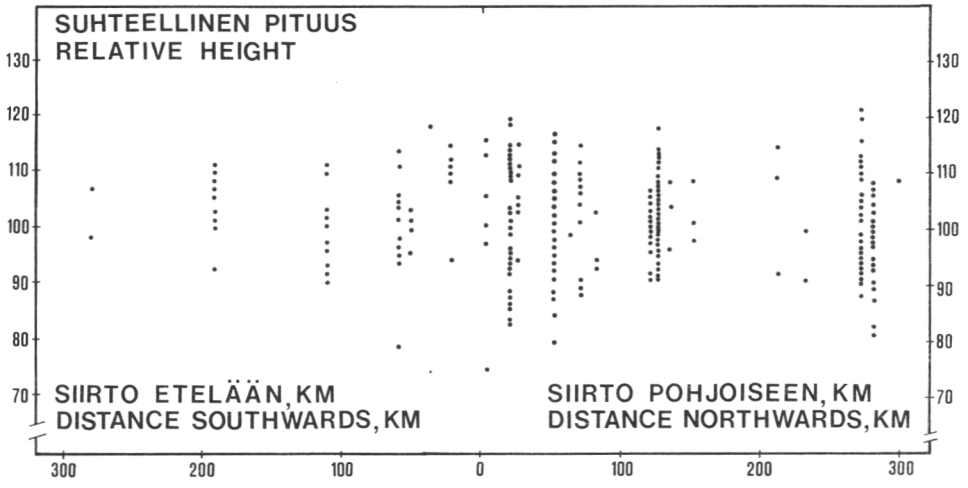
Taulukko 10. Kokeessa 19 esiintyvien metsikön sisäisistä ja kaukoristeytyksistä syntyneiden perheiden keskipituudet v. 1973.
Table 10. The mean heights of families originating from pollinations within the same stand and long-distance-crossings.

Risteytyslaji *Type of crossing*		Perheitä, kpl *Number of families*	Taimia, kpl *Number of plants*	Keskipituus, cm *Mean height, cm*	SD, cm
Metsikön sisäinen *Within stand*	Rautalampi × Rautalampi	24	580	388	79
	Sulkava × Sulkava	10	204	394	92
Kaukoristeytys *Long-distance*	Rautalampi × Sulkava ...	20	472	378	85
	Sulkava × Rautalampi ...	11	312	382	89
	Rautalampi × Keuruu	22	500	386	73

35. Maantieteellisten siirtojen vaikutus

Maantieteellisten siirtojen pituuskasvua lisäävä tai vähentävä vaikutus ei missään kokeessa tullut selvästi näkyviin. Pohjois—etelä -suunnassa tapahtuneiden siirtojen vaikutusta pituuskasvuun tarkasteltiin lähemmin kokeiden 8, 14 ja 15 vapaapölytysjälkeläistöjen ja metsiköiden sisäisten risteytysjälkeläistöjen tulosten perusteella. Siirron pituus mitattiin kilometreinä emopuiden kotipaikan ja koepaikan välillä. Eri kokeiden tulosten yhdistämiseksi merkittiin kunkin kokeen keskiarvo 100:lla ja laskettiin kullekin perheelle (217 kpl) suhteellinen pituus. Maantieteellisen siirron pituutta ja perheiden

suhteellista pituutta on tarkasteltu graafisesti kuvassa 8. Vaikka pisimmät siirrot sekä pohjoiseen että etelään ovat lähes 300 km, minkäänlaisilla siirroilla kumpaankaan suuntaan ei ole vaikutusta pituuskasvuun. Näissä kokeissa oli kaikkien perheiden eloonjäämisprosentti alkuperästä riippumatta varsin korkea.



Kuva 8. Maantieteellisten siirtojen vaikutus alkuperien suhteelliseen pituuskasvuun.
Figure 8. The influence of geographic transfers on the relative height growth.

4. TULOSTEN TARKASTELU JA PÄÄTELMÄT

Jälkeläiskokeet, joiden tuloksia pituuskasvun osalta on edellä esitelty ovat sekä lähtömateriaalin että koeviljelyiden osalta mittavia ja viljelyteknisesti hyvin onnistuneita. Tuloksia on edellä käsitelty monelta eri kannalta. Kaikissa kohdissa ne eivät vastaa niitä odotuksia, jotka kokeita perustettaessa asetettiin.

Tulosten tulkinnan kannalta perhe × lohko -yhdysvaikutus, joka säännönmukaisesti osoittautui erittäin merkitseväksi, on hankala ilmiö. Selityksenä tähän voidaan pitää maaperän vaihtelua lohkojen sisällä, satunnaisia eroja istutuksessa ja usein laikuttain esiintyneitä tuhoja. Näillä perusteilla yhdysvaikutuksia on pidetty sattumanvaraisina eikä todellisina. Perhe × lohko -yhdysvaikutuksen suuruuden vuoksi ei pidetty aiheellisena jatkaa varianssianalyysin tulkintaa esimerkiksi heritabiliteettiestimaattien laskemiseen.

Edellä mainittuja virhelähteitä ei voida oleellisesti pienentää silloin, kun kokeessa on paljon perheitä. Näin ollen saadaan tällaisissa kokeissa vain suuret erot osoitetuiksi, eli heikoimmat ja parhaat perheet erilleen muista. Mikäli vertailtavina on vain muutamia harvoja perheitä, voidaan pienetkin erot saada esiin, kuten taulukosta 4 voidaan todeta (J o h n s s o n 1967).

Erilaisten ruutukokojen vertailussa »one-tree-plot» ei tässä tapauksessa osoittautunut hyväksi. Yhdeksän taimen ruutu, josta neljä suurinta tainta otettiin mukaan laskentaan, osoittautui huomattavasti tehokkaammaksi. Viisi »varatainta» ruudussa merkitsee sitä, että yksittäiset kuolleet taimet eivät aiheuta puuttuvia arvoja mittaussarjaan. Tuhoista kärsineet taimet jäävät näin myös yleensä laskennan ulkopuolelle.

Periytyvien erojen suuruutta voidaan arvioida yhdessä kokeessa ilmenevän perhekeskiarvojen jakautuman perusteella, jonka todettiin sopivan hyvin normaalijakautuman puitteisiin. Tällöin muuntelun laajuus voidaan esittää variaatiokertoimen avulla. Kaikkien kokeiden painotettuna keskiarvona perhepituuksien keskiarvojen variaatiokertoimelle saadaan arvo CV = 8.0 %. Tämän avulla voidaan tarkastella perhevalinnan yleisiä edellytyksiä. Seuraavaan asetelmaan on poimittu eräitä esimerkkejä siitä, kuinka suurella todennäköisyydellä aineistossa esiintyy perheitä, jotka ylittävät kokeen keskiarvon 10, 20 ja 30 prosenttia.

Vaadittu paremmuus *Expected height increase*	Todennäköisyys *Probability*
10 %	10:100 eli 10 %
20 %	6:1 000 eli 0.6 %
30 %	1:10 000 eli 0.001 %

Asetelmasta voidaan nähdä, että vaatimustasoa nostettaessa todennäköisyys pienenee hyvin nopeasti. Nyt käsillä olevat kokeet sisältävät suurimmillaan n. 200 perhettä. Voidaan laskea, että tällaisessa kokeessa on odotettavissa yksi perhe, jonka paremmuus keskiarvoon verrattuna on 20 %. Samalla tavalla voidaan kustakin kokeesta siinä mukana olevien perheiden lukumäärän perusteella arvioida, kuinka paljon keskiarvoa parempi paras perhe todennäköisesti on. Vertailemalla yllä olevassa asetelmassa ja taulukossa 2 annettuja lukuja voidaan todeta kokeissa esiintyvien erojen olevan normaalijakautumaan perustuvien odotusten mukaisia.

E r k é n'in (1972) julkaisemista tuloksista voidaan poimia eräitä lukuja, joiden avulla on mahdollista verrata Ruotsissa 24 ja 26 vuoden ikäisistä koivukokeista saatuja tuloksia tässä esitettyihin tuloksiin. Erkén'in taulukoista 3, 4 ja 5 on poimittu ne rauduskoivujälkeläistöt, jotka ovat peräisin suunnilleen samoilta leveysasteilta (60°00′—64°30′) kuin tässä työssä tutkitut alkuperät. Vertailun kohteeksi otettiin valtapituus, jonka lähinnä voidaan katsoa vastaavan tässä työssä käytettyä ruudun suurimpien taimien keskipituutta. Aineisto jää tosin pieneksi, kuten seuraavasta asetelmasta ilmenee.

Koe n:o (Erkén 1972) *Code number (Erkén 1972)*	Perheitä, kpl *Number of families*	Valtapituus, m *Dominant height, m*	Variaatiokerroin, % *Variation coefficient %*
66	9	13.9	4.3
128	6	17.7	5.0

Edellä selostetulla tavalla Erkén'in julkaisemasta aineistosta lasketut perhekeskiarvojen variaatiokertoimet ovat samaa kertalukua kuin nyt esitellyissä kokeissa (Taulukko 2).

Geneettiseltä kannalta on selvää, ettei risteyttäminen sinänsä heikennä tai paranna jälkeläistön kasvunopeutta. Ei kuitenkaan ole mahdotonta, että valvottuun risteyttämiseen liittyvät toimenpiteet aiheuttaisivat fysiologisia muutoksia siemenissä. Nämä muutokset voivat vaikuttaa siemenistä syntyneiden taimien kehitykseen. Koska nyt esitellyissä kokeissa risteytys- ja vapaapölytysjälkeläistöt olivat keskimäärin täysin samanvertaisia, voidaan todeta, että kasvavissa puissa suoritettu risteyttäminen ei vaikuta siementen laatuun.

Kokeita suunniteltaessa odotettiin näkyvää tulosta siemensiirroista (J o h n s s o n 1967, E r k é n 1972, C l a u s e n 1973). Samoin odotettiin heteroosia kaukoristeytysten seurauksena. Saadut tulokset eivät olleet odo-

tusten mukaisia. Jos tulokset perustuisivat vain yhteen kokeeseen, jouduttaisiin vakavasti epäilemään jossain vaiheessa sattunutta koe-erien sekaantumista tms. syytä tulosten selitykseksi. Kokeita on kuitenkin monta ja ne on perustettu ja mitattu eri vuosina ja eri henkilöiden toimesta. Koska kaikkien kokeiden tulokset ovat toisiaan tukevia, ei odottamatonta lopputulosta voida pitää erheellisenä. Itse asiassa tulos ei ole ristiriidassa sen kuvan kanssa, joka muiden tutkimusten perusteella on saatu rauduskoivun populaatiorakenteesta Suomessa. Rauduskoivu on yleinen puulaji kaikkialla Etelä- ja Keski-Suomessa. Siitepölyn leviämisen kautta tapahtuva geenivirtaus metsiköiden ja alueiden välillä on tällaisessa tilanteessa tehokas. Tästä seuraa, että puiden heterotsygotia-aste pysyy korkeana ja populaation sisäinen geneettinen vaihtelu suurena. Olosuhteiltaan yhtenäisellä alueella jäävät eri populaatioiden väliset erot pieniksi (K o s k i 1970). Tältä pohjalta voidaan käsittää, ettei eri paikkakuntien puiden risteyttäminen lisää rauduskoivulla merkittävästi heterotsygotiaa. Siirroista saatu tulos ei tietenkään ole tulkittavissa siten, ettei kaukaisimpienkaan aineistoon sisältyvien populaatioiden välillä olisi geneettisiä eroja. Pituuskasvuun vaikuttavien perintötekijäin yhdistelmissä olevat erot ovat kuitenkin niin pieniä, ettei niitä nyt käytetyllä koetekniikalla ole saatu esiin Etelä- ja Keski-Suomen olosuhteissa.

Maantieteellisten siirtojen vaikutusta muihin ominaisuuksiin, kuten vuosirytmiin tai taudinalttiuteen, ei rauduskoivulla ole selvitetty. Siksi esitettyjen koetulosten perusteella ei voida suositella pitkiä siirtoja. Siirtäminen ei toisaalta tunnu millään tavoin tarkoituksenmukaiselta, koska aivan ilmeisesti samalla alueella esiintyvä periytyvä muuntelu tarjoaa hyvän lähtökohdan jalostukselle.

Eri perheiden keskipituuksien välillä todettiin suuri additiivisiin geenivaikutuksiin perustuva periytyvä muuntelu. Tämän perusteella voidaan arvioida, että jälkeläiskokeisiin perustuvan siemenpuiden valinnan avulla voidaan nykyään perustettavien viljelykoivikoiden nuoruusiän pituuskasvua parantaa 10—20 %.

Kokeiden sisältämässä aineistossa ei ole yhtään sellaista risteytysperhettä, joka erityisen nopeakasvuisena erottuisi muiden perheiden muodostaman normaalijakautuman ulkopuolelle. Tämä viittaa siihen, ettei erityinen kombinaatiokyky näyttele sanottavaa osaa rauduskoivulla pituuskasvun kohdalla kokeissa käytetyissä olosuhteissa. Tästä syystä ei erityiseen kombinaatiokykyyn perustuvaa rauduskoivun pituuskasvun risteytysjalostusta voida pitää lupaavana linjana.

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6. SUMMARY

Activities connected with the breeding of *Betula verrucosa Ehrh.* have been intensified at the Finnish Forest Research Institute since 1961 with the aid of funds provided by the Association of Finnish Plywood Industry. The determination of the breeding value of Betula verrucosa selected for Finnish plus trees has been the main goal. The test programme has been planned such that the progeny tests which have been set up would provide information about the development of progeny obtained from controlled crossings within stands and between stands and about the possible advantages for breeding of long-distance crossings, in addition to information about the development of open-pollinated progeny of plus trees and the progeny of controlled crossings between plus trees. Study of the effect of geographical transfer and some independent investigations connected with progeny test technique have also been included in the programme.

Altogether 163 plus trees from southern and central Finland are included in the starting material used in the study (Figure 2). Various controlled crossings were carried out between these trees during 1962—66. Open-pollinated seed was collected from several parent trees at the same time. Two year-old nursery seedlings which had spent their first growing season in plastic greenhouses and their second in the open were used in the progeny tests. The tests were established at seven different localities in southern Finland, the test units comprising altogether 75 000 seedlings (Figure 4, Table 1). The tests received intensive silvicultural treatment and were measured for several years. The mean heights and variation coefficients of the mean heights of all familes of each test have been calculated from the results of the latest measurements. The percentage by which the best families exceeded the mean of each test has been calculated as well as which families were statistically significant in different tests from the mean for the test (Tables 2 and 3). Variance analysis and the t-test (Table 4) were used to determine which differences within each test were significantly different at the 99 % level when studying the efficiency of different types of test lay-out. The relationships between open-pollinated and crossing progeny were examined using the results of tests 13—16 and test 19 (Tables 5 and 7). Comparison between the crossings within stands and between stands was done on the results of test 19 (Table 8), and the effect of geographical transfer was clarified using the results of tests 8, 14, and 15 (Figure 8).

The magnitude of the inherited differences can be estimated from the distribution of the family means occurring in one test, the distribution being found to fit well with the normal distribution (Figure 7). The spread of the variation can thus be described using the variation coefficient. The value CV = 8.0 % was obtained for the variation coefficient of the height as the weighted mean of all the tests.

When the tests were planned, it was expected that there would be a visible result for seed transfer. Similarly, heterosis was expected to be the result of long-distance crossings. The results did not come up to these expectations. If the results had been based on only one test, then there would be real reason to suspect that some mixing of

the test origins would have taken place. However, several tests have been carried out, which have been set up and measured during different years by different people. Since the results of all tests are in agreement, the unexpected final result cannot be regarded as an erratic one. It does not prove, howewer, that there are no genetical differences between the populations included in this material which are situated furthest from each other. The differences in the genetic factor combinations which affect the height growth are, however, so small that they have not become apparent in the testing methods used under the conditions prevailing in southern and central Finland.

As the effect of geographical transfer on other properties of Betula verrucosa such as the annual cycle or susceptability to disease has not been clarified, long distance transfer cannot be recommended on the basis of the results of these tests. In additions, transfers do not at all seem neccessary since the inherited variation occurring in the same area obviously provides good starting material for breeding.

A large amount of inherited variation based on the additive gene effects was demonstrated between the average heights of different families. It can thus be estimated that the height growth of young cultivated birch stands can be improved in the near future by 10—20 % if seed trees chosen on the basis of progeny tests are used.

All the families tested fell within the normal distribution formed by the other families without exception. This indicates that growth rate of Betula verrucosa is not characterised by special combination ability. For this reason, cross breeding based on special combination ability cannot be regarded as a promising line for improving of growth rate of Betula verrucosa.