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VEGETATION SUCCESSION OF ABANDONED HAY FIELDS IN CENTRAL FINLAND
A quantitative approach

EEVA-LIISA JUKOLA-SULONEN

SELOSTE

KASVILLISUUDEN SUKKESSIO VILJELEMÄTTÄ JÄTETYILLÄ HEINÄPELLOILLA KESKI-SUOMESSA KVANTITATIIVISIN MENETELMIN TARKASTELTUNA

HELSINKI 1983

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Cover (front & back): Scots pine (*Pinus sylvestris* L.) is the most important tree species in Finland. Pine dominated forest covers about 60 per cent of forest land and its total volume is nearly 700 mill. cu.m. The front cover shows a young Scots pine and the back cover a 30-metre-high, 140-year-old tree.

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Vegetation succession on 3 to 26-year-old abandoned fields was studied during the period 1971—1979 at Suonenjoki, Central Finland. Both seasonal and annual dynamic changes were examined at the species and the community level using biomass, shoot density and frequency values. A number of methods were used for classifying and ordinating the material. The minimum variance clustering method, which was based on the biomass values, gave results which were in agreement with those obtained using reciprocal averaging species and sample plot ordinations, and factor analysis species groupings. The succession and moisture-fertility gradients were interpreted from the ordination. The results of the ordination were applied to a larger samplesize of abandoned fields. Three succession stages, so-called successional sub-associations: *Phleum pratense* L. (3—5 years stage), *Agrostis tenuis* Sibth. (6—14) and *Alchemilla vulgaris* coll. (15—24) sub-associations, being named according to the dominant species, were obtained on the basis of classification and ordination methods.

The species were grouped into succession classes using factor analysis and reciprocal averaging ordination. This grouping was then used to develop a number of matrix models for estimating the progression of succession. The best models gave parallel results with those of the ordination and classification methods.

Inter- and intraspecific competition was studied using ratio of biomass/shoot density and shoot weight. A competition relationship was found between *Agrostis tenuis* and *Phleum pratense*. Populations of single species growing in mixed stands did not obey the -3/2 power law, but the law regulated the ratio between the mean shoot density and mean shoot weight in the whole field layer community at the meadow stage.

Field voles (*Microtus agrestis* L.) were found to have a strong effect on the production of their food species and of the whole plant community.

While species dominance, primary production and the ecological efficiency of the plant community decreased, the diversity and the stability increased throughout the studied succession stages. The dominance-diversity functions became increasingly logarithmical as the effect of the trees and shrubs, several planted, gradually increased.

Although the plots and species studied can be classified using different methods, it was not possible to find any objective stages. The succession trends on all of the field plots differed to some extent from each other. The structural and even the functional features of the changes were continuous. The rate of change was greatest at the onset of field succession, but slow on the older fields.

Kasvillisuuden sukkessiota tutkittiin Suonenjoella, Keski-Suomessa, vuosina 1971—1979 sukkessioiältään 3—26 vuotta vanhoilla viljelemättä jätetyillä heinäpelloilla. Biomassojen, versotiheyksien ja frekvenssien avulla seurattiin vuodenaikaisia ja vuotuisia dynaamisia muutoksia sekä kasvilaji- että yhteisötasolla. Aineiston luokitteluun ja ordinointiin käytettiin useita menetelmiä, joista biomassapohjainen minimivarianssiklusterimenetelmä antoi reciprocal averaging -laji- ja -näytealaordinaation sekä faktorianalyysin lajiryhmittelyn kanssa yhteneväisen tuloksen. Ordinaatiosta tulkittiin sukkessio- ja kosteusravinteisuusakselit. Ordinaatiotulokset suhteutettiin suurempaan vanhojen peltojen aineistoon. Luokittelun tuloksena erotettiin kolme sukkessio-osakasvustoa: *Phleum pratense* (3—5 v.)-, *Agrostis tenuis* (6—14 v.)- ja *Alchemilla vulgaris* (15—24 v.)-vaihe dominanssin mukaan nimettyinä.

Faktorianalyysin ja reciprocal averaging -analyysin avulla luotiin lajien sukkessioluokitus ja sen avulla useita matriisimalleja sukkession kulun estimoimiseksi. Parhailla malleilla saatiin samansuuntainen tulos kuin ordinaatioja luokittelumenetelmillä.

Lajienvälistä kilpailua tutkittiin satojen/tiheyksien ja versokokojen avulla. Todettiin kilpailusuhde *Agrostis tenuiksen* ja *Phleum pratensen* välillä. Yksittäisten lajien populaatiot eivät sekakasvustoina toteuttaneet -3/2 -potenssilakia, mutta koko kasviyhteisössä niittyvaiheessa laki sääteli keskimääräisen tiheyden ja yksilöpainon suhdetta.

Peltomyyrän (*Microtus agrestis* L.) todettiin vaikuttavan ravintokasviensa kautta koko kasviyhteisön tuotokseen voimakkaasti.

Tutkitussa sukkessiovaiheessa kasviyhteisön lajidominanssi, perustuotos ja ekologinen tehokkuus laskivat, mutta diversiteetti ja vakaus kasvoivat. Dominanssi-diversiteetti funktiot muuttuivat yhä logaritmisempaan suuntaan samalla kun vähitellen puiden ja pensaiden (osaksi istutettuja) vaikutus kasvoi ja muutti koko kasviyhteisön.

Vaikka tutkittuja aloja ja lajeja voitiin luokitella halutulla tavalla, mitään portaittaisia muutoksia ei voitu havaita eikä objektiivisia vaiheita määrittää. Kullakin pellolla oli jossain määrin muista poikkeava sukkessiosuuntansa. Muutokset niin rakenteellisissa kuin toiminnallisissakin piirteissä olivat jatkuvia ja vähittäisiä. Muutosnopeudet olivat suurimpia pellon sukkession alussa, mutta hyvin hitaita vanhoilla pelloilla.

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1. INTRODUCTION

11. Background and aims of the study

This study was carried out in the Department of Forest Protection at the Finnish Forest Research Institute, during the period 1971—1983. The study was included in the research programme on the theme of ''Changes in the vegetation of abandoned fields and clear-cut areas and their effect on the qualitative and quantitative relationships of vole populations'', which was started in the Department in 1971 under the leadership of Dr. Terttu Teivainen. Since 1979, the study has evolved into the author's research project titled: ''Succession of the vegetation on forestation areas and its effect on seedling survival during the first few years after regeneration'' and was financed by the Academy of Finland. The results of vegetation studies on areas damaged by the water vole (*Arvicola terrestris* L.) (Teivainen, Jukola et al. 1979), and on the suitability of short rotation areas as vole biotopes (Teivainen & Jukola-Sulonen 1983) have been published earlier.

The aims of the study:

1. To determine the structural and functional changes in hay fields of four different ages over a period of nine years, and to relate part of the results to a more extensive material concerning abandoned fields.
2. To determine whether the fields develop a uniform succession series and whether the changes which take place can be used to predict the future course of succession.
3. To test the applicability of the most recent methods of plant ecology and sociology in succession studies.
4. To make an ecological survey of the habitat of the field vole (*Microtus agrestis* L.) for the subsequent classification of vole damage areas.

12. Previous research

Following the cessation of shifting agriculture at the beginning of this century in Finland and the development of the forest site type theory by Cajander (1909), considerable attention was given to the study of the secondary succession of forest vegetation (Linkola 1916, 1921). This subject has again arisen during the last few years for a number of reasons. These are: 1) Since the end of the 1960's a large area of agricultural land has been left uncultivated as a result of the Field Reservation Act (Act restricting the use of fields 216/1969). It was passed in order to control agricultural over-production. 2) The introduction of clear-cutting and associated forestation activities in the 1950's. 3) The applicability of the Finnish forest site type system in practical work has had to be reconsidered because the climax stage of tree stands, on which the classification is based upon, are fast disappearing.

Rather few succession studies have been carried out in Finland following this most recent wave of intrest in plant succession. Kalela (1961), Tujulin (1967), Kosonen (1969), Raatikainen & Raatikainen (1975), Törmälä & Raatikainen (1976) and Hokkanen & Raatikainen (1977a) have dealt with the changes in field succession. In addition, a number of theses have been written on this subject at the Department of Botany, the University of Helsinki (Jukola 1974, 1977, Hintsanen 1979, Silfverberg 1980). Forest succession has been studied by Kellomäki (1972), Mannerkoski (1976), Ferm & Pohtila (1977), Kellomäki et al. (1977), Ferm & Sepponen (1981), Raulo & Rikala (1981), Kuusipalo & Vuorinen (1981), Kanninen et al. (1982), Hari et al. (1982) and Kananen (1983). Vegetation studies in primary succession have been recently made in Finland, for instance on land uplift areas along the Gulf of Bothnia (Vartiainen 1980).

The peak amount of agricultural land removed from production under the field reservation agreement, which was enforced in 1969, was 240 000 ha. By 1983, about 80 000 ha of this area had been taken back into production. About 100 000 ha were still frozen under the agreement, and about 26 000 ha had been afforested (Monthly re-

view of agricultural statistics 1983). Under the agreement, a land-owner has to prevent the development of weeds and promote reforestation. The success of these management measures and factors which should be considered when the fields are used for agriculture, have been studied at the University of Jyväskylä (Hokkanen & Raatikainen 1977a, Hokkanen 1979).

A number of problems have arisen in converting unused fields into a productive state through afforestation (Leikola & Raulo 1973, Metsämuuronen et al. 1978, Teivainen 1979, Teivainen et al. 1979). After agriculture use ceases, a thick field layer vegetation develops on the fields. This layer competes with tree seedlings for water, nutrients and light. In addition to this, the vegetation fells the seedlings with snow. A field layer has an indirect effect on the seedling by providing shelter and food to damagers of the seedlings, such as voles, insects and fungi. This study is also concerned with this problem. As continuous and rather fast changes occur in the field layer on abandoned fields, it is obvious that voles react rather sensitively to these seasonal and annual changes in the vegetation. The choice of habitat, survival and the dynamics of the vole population are largely dependent on the amount and quality of the food provided by the vegetation. The regular changes in the vegetation can also be used to elucidate the relationships between the vole populations and the possibilities for survival offered by the vegetation.

The effect of harvesting and ploughing on cultivated fields is to inhibit the natural succession of the vegetation. When active cultivation ceases, changes occur in the relationships between the species growing on the field towards a more or less state of equilibrium. These changes, however, occur within the limits determined by environmental conditions. In the case of abandoned fields, such a series of changes follow an order with respect to time, beginning with an open cultivation stage. An open-cultivated field is first colonized by annual species, which subsequently give way to perennial herbs and grasses. This meadow stage ceases as the development of shrubs and trees continues (Beckwith 1954, Odum 1960, Kalela 1961, Koponen 1967, Tujulin 1967, Bazzaz 1968, Hansson 1971, Jansson 1974, Hæggström 1983).

Hay fields are in a special position when compared to other cultivated fields. After their cultivation ceases, the perennial species sown continue to grow. Succession has, even in this case, started from ploughing but the annual stage has been almost completely suppressed due to the sowing of grasses. The sown species affect the course of succession for a long time after the hay harvesting activities have ceased (Beckwith 1954). The origin, and the competition situation, are thus entirely different in the initial stage of hay field succession than that after other cultivated plants, although other cultivated plants do affect the initial stages of succession after cultivation ceases (Ellenberg 1950, Poranen 1971).

Only a few studies have been carried out in Finland concerning hay field succession. However, Linkola (1916, 1935), Teräsvuori (1920), Poranen (1971) and Berg et al. (1978) have treated the subject to some extent. Paatela (1953) and Raatikainen & Raatikainen (1975) have studied the changes occurring during the five year period following the seeding of hay fields throughout Finland. Hokkanen & Raatikainen (1977a) have studied the changes during the first six years, and Silfverberg (1980) has studied abandoned hay fields in the Åland Islands until the reforestation stage.

A large number of studies on the succession of abandoned fields have been conducted in the USA (Keever 1950, 1979, Beckwith 1954, Quarterman 1957, Bazzaz 1968, Tramer 1975, Whitford & Whitford 1978, Foster et al. 1980, Pickett 1982, Reichhardt 1982), Czechoslovakia (Lepš & Prach 1981, Prach 1981, Lepš et al. 1982), Switzerland (Ellenberg 1950), Poland (Faliński 1980), Sweden (Tamm 1956, Bråkenhielm 1977, Steen 1980) and West Germany (Schmidt 1975).

The succession of a plant community occurs on two levels. They are seasonal and annual changes. Owing to the relative simplicity of the plant communities growing on old fields, they represent a convenient point for elucidating the dynamics of plant communities (Evans & Cain 1952). Changes in succession have been studied using a variety of methods: through the examination of permanent sample plots yearly, simultaneous examination of different-aged plots or combinations of both methods (Klapp 1958, Tramer 1975). Most studies on the succession of abandoned fields

have been done by simultaneously studying fields of different age (e.g. Paatela 1953, Beckwith 1954, Bazzaz 1968, Raatikainen & Raatikainen 1975, Hokkanen & Raatikainen 1977a). The most accurate results are obtained by following permanent sample plots yearly. This method is slow, but is the only method which provides reliable results about the structural and functional changes in the plant community (Tramer 1975). The sample plots were followed on a yearly basis, although it was not possible to follow the same sample quadrats because the plant analyses were done by the harvesting method. This method was chosen because it gives the most accurate species abundances. Other plant analysis methods give less accurate estimates of these parameters. Furthermore, the fact that the study is part of the basic study into the feeding and habitat ecology of the field vole (*Microtus agrestis* L.) meant that the harvesting method had to be used.

The materials in succession studies are collected in such a way that there appears a more or less clear time trend. For this reason, the newest multivariate methods, developed for analysing vegetation materials, are particularly useful. These methods permit one or more environmental gradients to be obtained from the material (Austin 1977, van der Maarel & Werger 1978). The methods can be divided into three groups: direct gradient analyses, the classification methods and the ordination methods (Gauch 1982).

Direct gradient analysis was used for slope vegetation analysis (Whittaker 1956, Kärenlampi & Kauhanen 1972). The classification methods, such as the Braun-Blanquet (1928) method and association and cluster analyses (Williams & Lambert 1959, Sneath & Sokal 1973), were used to divide the material, on the basis of similarities in the vegetation, into groups at different similarity levels. The most commonly used of the ordination methods are polar ordination (Bray & Curtis 1957), principal component analysis and factor analysis (Goodall 1954, Ivimey-Cook et al. 1969), and reciprocal averaging analysis (Hill 1973). Most of the ordination methods define the location of both samples and species in the space defined by the gradients. These methods have been used in Finland by Hinneri (1972), Sepponen et al. (1982), Oksanen & Ahti (1982) for the ordination of forest vegetation, Kosonen (1976) for meadow vegetation, Pakarinen (1976, 1979, 1982), Pakarinen & Ruuhijärvi (1978) for peatland vegetation, Kärenlampi (1972) and Oksanen (1978) for subarctic vegetation, Oksanen (1981) for rock vegetation and Jukola (1977), Silfverberg (1980) and Hintsanen (1979) for the vegetation of abandoned fields.

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2. THE STUDY AREA

21. General

The study area is situated on Heikkilä Farm (62°36'N, 27°5'E) in the village of Jauhomäki, approximately 4 km south of Suonenjoki. The farm buildings are sited on the top of a moraine while the fields are located on the surrounding slopes. The gradient of the slope is about 6°. The area is characterized by NW-SE moraines. Lakes or peatland hollows fill low-lying areas while the raised ground forms eskers (Aario 1966).

The study farm on the moraine is bordered on its south-west slope by an *Oxalis-Vaccinium myrtillus* type (OMT) spruce forest and an alder (*Alnus incana* (L.) Moench) stand, in the north by the abandoned fields of another farm, in the east by the Kuopio-Jyväskylä highway and in the south-east by the old almost unused stretch running over the moraine (Fig. 1). The farm's 9 ha field area came under the field reservation agreement in 1969. However, part of the fields on the farm were abandoned earlier. Four fields having a total area of 3.4 ha were ploughed and sown with grasses (*Phleum pratense* L. and *Trifolium pratense* L.) in 1953, 1958, 1965 and 1968. Up to 1968 their grass was harvested and they were not used for grazing. The code name used for the fields is the last year when tillage was carried out. The succession age of the plant communities that have developed on the fields up until the time when samples are harvested is counted from this year.

22. Study sites

The field ploughed and sown in 1968, named Field Plot 68 (P68) is situated, in contrast to the other fields, on the eastern slope of the moraine (Fig. 1). The field is bordered by an old afforested field in the north, the highway in the east, and both the southern and western edges by a field which had been ploughed every summer until 1973 when the field was abandoned.

The parts surrounding the field area have become densely overgrown with *Alnus incana* and *Rubus idaeus*

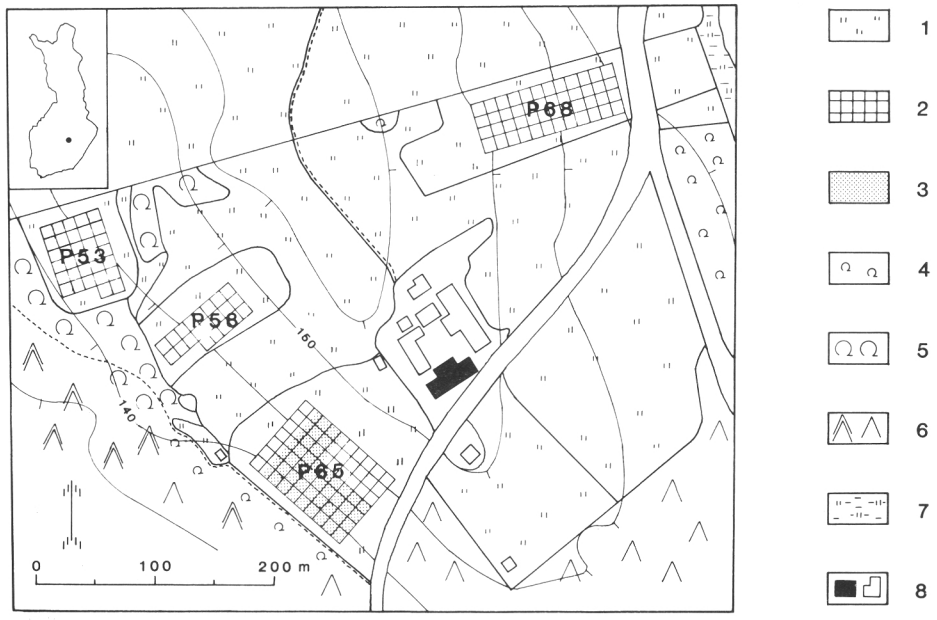


Fig. 1. Map showing the location of the fields studied at Suonenjoki, Central Finland, and the surrounding vegetation cover. The numbers of the fields refer to the year when ploughing and seeding were last done. Legend of the map symbols: 1 = abandoned field, 2 = field plot with 10 x 10 m subplots, 3 = planted area in 1972, 4 = thicket, 5 = deciduous forest, 6 = coniferous forest, 7 = lake shoreline march, 8 = farm buildings.

Kuva 1. Tutkimuskohteen sijainti ja ympäröivä kasvillisuus Suonenjoella Keski-Suomessa. Peltojen symbolit ovat viimeisiä muokkaus- ja kylvövuosia. Merkkien selitykset: 1 = viljelemättä jätettyä peltoa, 2 = tutkitut peltolohkot (10 x 10 metrin ruudukko), 3 = vuoden 1972 istutusala, 4 = pensaikkoa, 5 = lehtimetsää, 6 = havumetsää, 7 = järvenrantasuo, 8 = tilan rakennukset.

L. thickets. In addition, *Festuca rubra* L., *Epilobium angustifolium* L. and *Anthriscus sylvestris* (L.) Hoffm. are growing along the edge of the field. No grass crops had been harvested on the field since the establishment of the field reservation agreement and the vegetation had developed undisturbed after sowing.

In 1971, when the study was started, the vegetation had been developing for three years. Samples were collected in 1971, 1973, 1975, 1976 and 1977. They were from different succession stages of P68 and are called here 3, 5, 7, 8 and 9-year sample plots. In 1980, the owner of the farm again cultivated this field. It was tilled and sown with oats the following year. *Elymus repens* (L.) Gould and *Epilobium angustifolium*, which grew abundantly on the field, spread even more as a result of tilling. In 1981 the weeds on the field were destroyed with herbicides.

The field ploughed and sown in 1965, Field Plot 65 (P65), is on the south-western slope of the moraine (Fig. 1). The field is bordered on the southern edge by the highway and a spruce (*Picea abies* (L.) Karsten) stand (OMT). Along the roadside edge there is a narrow meadow, the plant species growing on which include *Rubus arcticus* L., *Dactylorhiza maculata* (L.) Sob, *Geranium sylvaticum* L., *Trollius europaeus* L., *Filipendula ulmaria* (L.) Maxim., *Rubus idaeus* and *Anthriscus sylvestris*. The other field edges are bordered by a field last ploughed in 1971. There are no ditches around P65, apart from those at the road's edge. Three hay crops were harvested from the field after sowing, the last in 1968. In 1971, when the study began, the vegetation was 6 years old. Samples were then collected from the field at intervals of two years between 1971 and 1979. This gave a succession series of 6, 8, 10, 12 and 14-year sample plots. The sample plots are named according to their age or, in uncertain cases, according to the field plot (65) and age (8) P65-8.

Approximately 37 % of the area of the field plot was allowed to develop undisturbed during the course of the experiment. The rest of the field (63 %, Fig. 1) was planted in 1972 with a total of 1 305 seedlings of different tree species. The planting experiment was done to test the susceptibility of the seedlings of different tree species to vole damage under field conditions. Therefore it was possible to follow the effect of human activities on afforestation and succession of the entire plant community. Alternate rows of one and two-year-old Scots pine (*Pinus sylvestris* L.) seedlings (300), four-year-old Norway spruce (*Picea abies*) seedlings (140), one-year-old birch (*Betula pendula* Roth) seedlings (500) and one-year-old hybrid aspen (*Populus tremula* x *P. tremuloides* Michx.) seedlings (140) were planted on the field plot. The seedlings were planted 2 m apart in the centre of patches, 40 x 40 cm in size. In addition, 15 rows of *Betula pendula* seedlings (225) were planted in the upper part of the field plot.

The field ploughed and sown in 1958, Field Plot 58 (P58), is situated on the south-western slope of the moraine (Fig. 1). It is bordered on its southern edge by an *Alnus incana* stand which has developed after the reforestation of an old meadow, and on the other edges by the same abandoned field, last ploughed in 1971, as the previously described field. Ditches following the direction of the slope, whose sides are overgrown with *Filipendula ulmaria* and *Salix* spp. shrubs, run across the bottom part of the field. *Gagea minima* (L.) Ker-Gawler grows in abundance on the field in early spring (May). However, there were no indications of this species on the ground when the samples were collected.

Snow melt water flows over the slope until the month of June. Altogether 10 hay crops were harvested. In 1971, when the experiment was started, the vegetation on the field had been developing for 13 years. Samples were taken in 1971, 1973, 1975 and 1977. The samples taken from the studied succession stages are referred to as 13, 15, 17 and 19-year-old sample plots. In 1971 several half-meter-tall *Alnus incana* saplings were already growing on the lower part of the field. The thicket at the southern edge of the field was cleared in 1976.

The field ploughed and sown in 1953, Field Plot 53 (P53), is situated further from the farm's center on the same slope as the two previously described fields (Fig. 1). The field is bordered on its southern edge by the OMT type forest and an alder stand. The forest edge was clear cut in 1975. P53 is bordered along its northern edge by the neighbouring farm's old fields and in the east by a field last tilled in 1971 and a strip of forest consisting of birch and alder. The field is surrounded by ditches. *Filipendula ulmaria*, *Epilobium angustifolium*, *Rubus idaeus* and *Salix* species were growing along the field edges. *Alnus incana* and *Salix* stands also grew along the southern edge of the field during the course of the study, but part of them were cleared away in 1976. These species were rapidly replaced, however, by sprouts. By 1968, a total of 15 hay crops had been harvested on the field. In 1971 when the study was commenced the field vegetation was already 18 years old. Samples were taken in 1971, 1973, 1975, 1976 and 1977. Those from the various succession stages of the field are called 18, 20, 22, 23 and 24-year-old sample plots.

23. Climatic conditions

During the study period (1971—1979) the summers in 1972 and 1973 were warmer and in 1976 and 1977 cooler than the average (Fig. 2, Kolkki 1969). The winters in 1972—73, 1973—74 and 1974—75 were mild and the successive winters colder than the average. 1974 was wetter and 1975, 1976 and 1978 were drier than normal.

The mean length of the growing season at Suonenjoki was 160 days during 1931—1960 (Kolkki 1969). The growing season was longer than this in 1972, but in the other years it was either normal (1971, 1974 and 1975) or appreciably shorter (1973, 1976, 1977, 1978 and 1979). The effective temperature sums, mean daily temperature above 5°C (average value for Suonenjoki 1 150 d.d., Kolkki 1969) were greatest in 1972, 1973, 1975 and 1979, and smallest in 1976 and 1977 (Fig. 3). The growing season normally starts during the first few days of May and finishes at the beginning of October. In 1973, 1975 and 1977 the growing season had started already in April, but in 1974, 1978 and 1979 it did not begin until mid-May. The growing season continued later into autumn in 1971, 1972 and 1975, but stopped early in September in 1973, 1977 and 1978. In 1975 and 1976 there was a long cold spell at the end of May and in the beginning of June night frost was recorded. The cold spell preceded a period when the temperature was considerably warmer than normal.

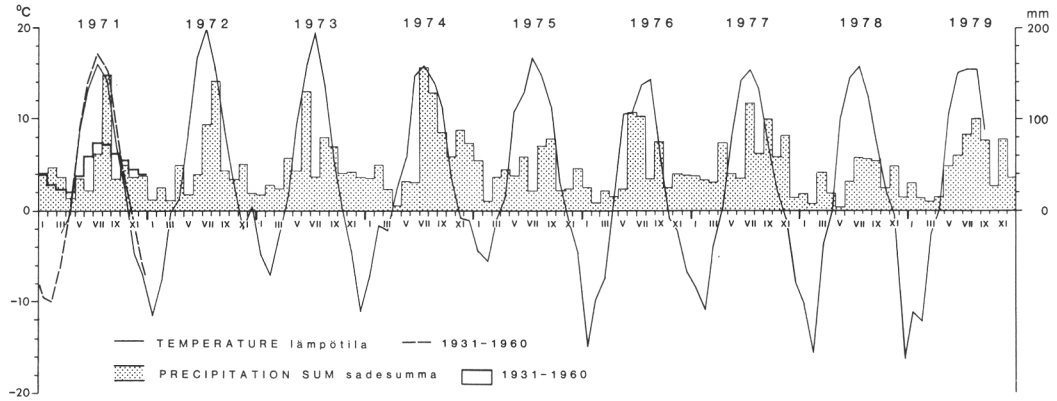


Fig. 2. Mean monthly temperatures and monthly precipitation sums during the duration of the study, 1971—1979 at Suonenjoki Research Station, and their long-term normal values in Kuopio (Kolkki 1966, Helimäki 1967).

Kuva 2. Lämpötilan kuukausikeskiarvot ja kuukausisadesummat tutkimuskaudella 1971—1979 Suonenjoen tutkimusasemalla sekä näiden pitkän ajan normaaliarvot Kuopiossa (Kolkki 1966, Helimäki 1967).

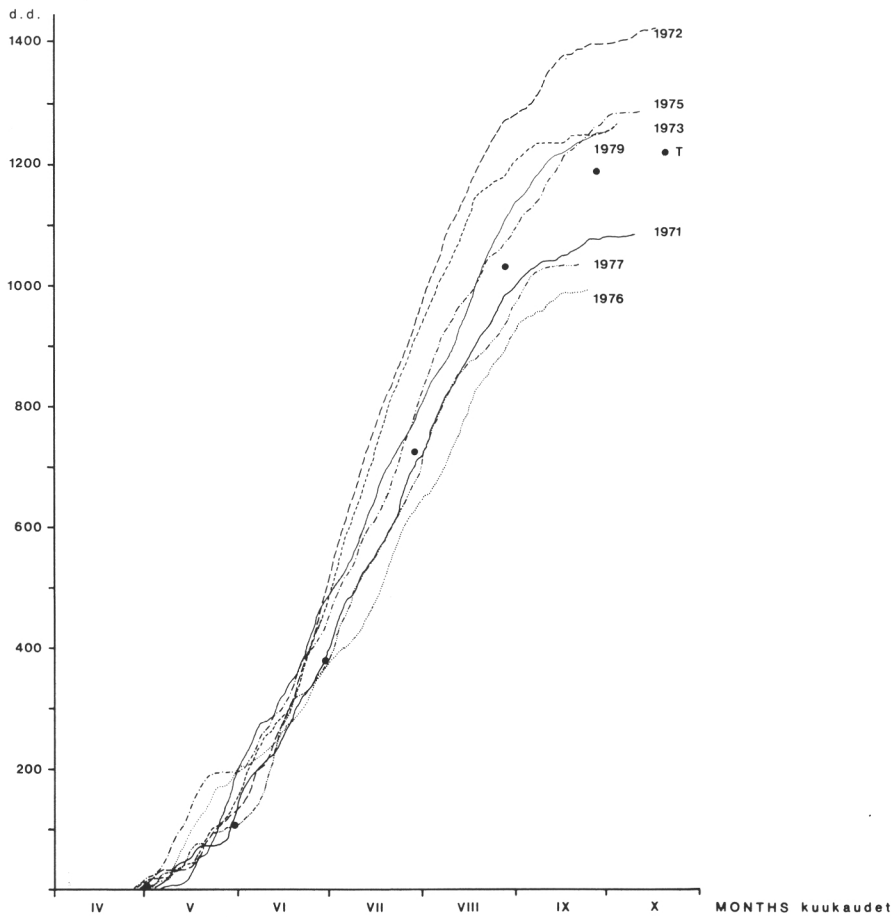


Fig. 3. Daily course of the temperature sum (d.d. = $\Sigma > 5$ °C) in different years (1971—1979) at Suonenjoki Research Station and the long-term normal values for each month (T 1931—1960) (Kolkki 1969).

Kuva 3. Lämpösumman (d.d. = $\Sigma > 5$ °C) päivittäinen kehittyminen eri tutkimusvuosina (1971—1979) Suonenjoen tutkimusasemalla sekä pitkän ajan normaaliarvot kuukausittain (T 1931—1960) (Kolkki 1969).

3. RESEARCH METHODS

31. Sampling methods

311. The field and ground layers

The plant analyses were carried out using the harvesting method. Field plots were set up in the fields, apart from the borders of the fields and the sides of the ditches. The field plots were divided up into 10 x 10 m subplots. There were 48 subplots in P68, 70 in P65, 21 in P58 and 32 in P53, making a total of 1.71 ha. Vegetation samples were taken from randomly sited posts in the field plots during 1971—1975, and from the centre of the 10 x 10 m subplots in 1976—1979. Samples were not taken from the same point twice. A frame was used to mark the edges of the sample quadrats. All the living and dead above-ground plant biomass was cut off level with the ground surface. The samples were sealed in plastic bags and immediately sent for analysis or to be frozen. The samples were analysed immediately after being harvested in 1971 and 1973. When this was done, collecting and treating the samples lasted over a month. In 1975, 1976, 1977 and 1979 all the samples were harvested in a couple of days and then frozen ready to be analysed later.

The living and dead plant biomass were separated when the samples were analysed. The plant species were identified (1971—79) and the separate shoots on each base counted (1971, 1973 and 1975). The samples were dried for 24 hours at 105 °C and weighed to an accuracy of 0.01 g.

The size of the sample quadrats used in 1971—1975 was 50 x 50 cm (0.25 m^2), but in subsequent years 25 x 25 cm (0.0625 m^2). This enabled the number of samples to be increased while the work and the costs to be decreased.

In 1979 samples were collected from P65 only. The purpose was to determine the effect of planted and natural trees and shrubs on the field and ground layers. 30 sample quadrats were collected from the planted area, at one meter from the tree stems, and 30 samples from outside the planted area. The samples were analysed in the same way as earlier.

The above-described plant analysis, which was done once a growing season, is designed to determine yearly vegetation changes (succession samples).

Harvesting dates, the temperature sums (d.d. = $\Sigma > 5$ °C) in the mid-date of the harvesting period and the number of sample quadrats collected in the study years were:

Field plot	Sample plot	Study year	Study date	Temp. sum	Quadrats
P68	3	1971	1.— 6.7.	432	10
	5	1973	5.— 8.7.	567	10
	7	1975	2.7.	462	10
	8	1976	5.7.	390	12
	9	1977	25.7.	650	24
P65	6	1971	16.6.— 8.7.	347	17
	8	1973	19.6.— 3.7.	411	17
	10	1975	2.7.	462	17
	12	1977	25.7.	650	30
	14	1979	9.8.	860	60
P58	13	1971	30.6.— 6.7.	404	10
	15	1973	9.7.—17.7.	667	10
	17	1975	2.7.	462	10
	19	1977	25.7.	650	21
P53	18	1971	12.—15.7.	529	10
	20	1973	18.—20.7.	765	10
	22	1975	2.7.	462	10
	23	1976	5.7.	390	32
	24	1977	25.7.	650	32

The phenological studies of seasonal vegetation changes were made for two consecutive years - 1972 and 1973. Two to three samples (0.25 m^2) were taken each month (5—6 times during the growing season) from all the fields: in 1972—25.5, 24.6, 22.7, 25.8, 14.9 and 13.10 and in 1973—25.5, 27.6, 23.7, 22.8 and 29.9. The samples were collected from within the same 10 x 10 m subplots using the harvesting method described earlier. A 10-cm-wide strip was left between each sample quadrat. The samples were handled immediately after harvesting. The living and dead parts were separated, dried and weighed in the same way as before. The aim was to determine the dynamics of the production of the above-ground parts of the plants.

The phenological changes in the different plant species were followed also in 1972 and

1973. Biomass samples of the 20 most abundant species (5—100 ind./species) were collected systematically each year from the same subplots at the same dates as the other phenology samples. Sample handling was also the same. The method is described in more detail by Jukola (1977).

Herbarium samples were taken of all the species on the field plots in 1971. In addition, the species which were growing on the field plots outside the sample quadrats were listed during each study year.

The *Alchemilla* species group is taken as a whole: *Alchemilla vulgaris* coll. (in text and tables *A. vulgaris*). 69 *Alchemilla* sample plants were collected systematically from all the field plots at the beginning of July 1977 in order to identify the species composition. Sample plants were taken at 10 steps apart along lines 10 m apart.

Taraxacum (*Taraxacum officinale* Weber, s.lat.) *Hieracium* and *Pilosella* are not dealt with below the generic level.

In this study *Agrostis tenuis* Sibth. also refers to *A. gigantea* Roth and *Poa pratensis* L. to *P. angustifolia* L. Otherwise the species nomenclature is according to Hämet-Ahti et al. (1981) and Koponen et al. (1977).

312. Trees and shrubs

The above-ground wood biomass of the trees and shrubs on the field plots were estimated in 1979. The shrub biomass (50—200 cm) was obtained using the mean shrub method. 2 x 2 m quadrats were marked out systematically on all the 10 x 10 m subplots in each field plot.

The shrubs in the 2 x 2 m quadrats were then identified and all the separate shoots protruding from the ground counted and their length measured. The shoot of average length was then chosen from each species, the diameter at the base measured, the shoot cut off at the base, dried for 48 hrs at 105 °C and weighed. The dry-weights of the mean shrubs are converted into dry mass per unit area by multiplying them by the number of shoots. Herbarium samples of *Salix* species growing in the quadrats were taken for later identification. In addition, the percentage coverage of each species in the quadrats was estimated.

The biomass of the trees (> 200 cm) in each field plot was estimated by measuring the height, base diameter and breast height diameter (DBH) of all the trees in each of the above-mentioned 2 x 2 m quadrats, as well as the coverage of each tree species. In P65, however, all the trees both within and without the planted area were measured. In addition, the height and diameter at the base and half-height of the conifers less than 2 m tall were measured on the planted area.

Maps of the location and crown coverage of the different taxons of the trees and shrubs on all the field plots were also drawn on graph paper. Julin (1948) and Sjörs (1954) have used a similar method. Reasonable species indentification was used in identifying the *Salix* species. The identifying characteristics may vary. If more strict criteria had been used possibly more hybrids would have been identified.

The nomenclature is according to Hämet-Ahti et al. (1981).

313. Soil samples

Soil measurements were made in 1972 and 1976. Soil samples were taken from all field plots studied in June 1972 using the method developed by Anderson (1970) and Ahti Mäkinen (pers. comm.). Two samples (0.5 l) were taken of the soil down to a depth of 12 cm from all the succession sample quadrats examined in 1971. The thickness of the cultivated layer (mull layer) at all the sampling points was also measured. In addition, two 0.25 l samples were taken from the mineral soil below the cultivated layer (sub-soil) in each field plot. Each sample was treated separately. In 1976 new samples were taken (40 subsamples/ha) using a soil auger down to a depth of 12 cm. The subsamples were combined in each plot.

The soil samples were analysed by Viljavuuspalvelu Co. (a soil testing service). The following analyses were performed: soil type, organic matter content, acidity, exchangeable calcium and potassium and easily-soluble phosphorus. The results were expressed per unit volume of dry milled sample (mg/dm^3). The terminology used is in accordance with that of Kurki et al. (1965).

32. Estimation methods for vegetation biomass and production

321. Correction of field layer biomass

The mean biomass and frequency values, calculated directly from the results of the plant analyses (Appendix 1), were used in the classification method and the diversity method, and in the graphic presentation of the abundance distribution of the most dominant species (Appendix 2). The biomass values, corrected according to the temperature sum from the above-mentioned mean biomass values, were used in the calculation of the production of individual species, or of entire plant communities, and in the succession model. The biomass collected at different temperature sum values (p. 11) were corrected so as to correspond to 650 d.d. All the samples collected in 1977 were taken at the end of July when the temperature sum had reached 650 d.d.

The biomass values of individual plant species were corrected by drawing the bell-shaped growth curves of green biomass with respect to the temperature sum for the 20 most abundant species. This was done on the basis of the phenological samples collected in 1972 (see p. 11). If the point on the growth curve which corresponds to a temperature sum of 650 d.d. is denoted as 1.0, then a correction value, with which the mean biomass value for each species is to be corrected, is obtained for all the temperature sums. Correction is done with the assumption that the temperature is the most important factor affecting plant growth. The total biomass values for the whole community are obtained by adding the uncorrected biomass values of the rest of the species to the corrected ones.

322. Estimation of the above-ground net primary production

A number of methods based on harvesting have been developed for estimating the net primary production of grasslands. There are methods based on the standing crop (Golley 1960, Traczyk 1968, 1971, Gyllenberg 1969, Kosonen 1969, Törmälä 1982) and methods in which the sum of the green peak biomass values for each species are used as the estimate of primary production (Odum 1960, Golley 1965, Traczyk 1968, Mellinger & McNaughton 1975, Törmälä & Raatikainen 1976, Sims & Singh 1978). In addition, Wiegert & Evans (1964) have developed a method based on the decomposition of litter (Łomnicki et al. 1968, Wiegert & McGinnis 1975, Törmälä & Eloranta 1982).

All three methods were used in this study. In addition, four different modifications of the first method and two of the third method were used. Production estimates for species and plant community were obtained for 1972 and 1973 because in these years phenological samples were collected. It was also possible to obtain some estimates of the production in 1971. The maximum green biomass (MB, g/m^2) and the maximum total biomass (MTB, living and dead) were calculated for each field plot in 1972 and 1973 from the phenological samples. The green biomass (JB), and the total biomass (JTB, living and dead) at the end of July (temperature sum 650 d.d.) were calculated for 1971 and 1973 from the succession samples on the basis of the corrected biomass.

The sum of the green peak biomass values for each species (PB) was calculated by applying the method used by Traczyk et al. (1973). However, this could only be done for the results for 1973 since it was the only year when species sorting from succession samples and species phenology was monitored at the same season. The biomass values were corrected to correspond to the peak biomass values for each species because the species sorting was made only once during the growing season. It was possible to do the correction for the 20 most abundant species because phenological samples were collected for these species in 1973 in order to determine mean shoot weights (g/shoot) (p. 11). The correction has been done by assuming that the shoot densities are the same at harvest time and during the maximum biomass stage of the species. In addition, it was assumed that the sterile-fertile ratio remained the same during this period.

The peak biomass for a species (B_h) was obtained using the formula:

$$B_h = s_n \cdot b_s + f_n \cdot b_f$$

where s_n is the mean number of sterile shoots ($shoots/m^2$), b_s the mean maximum sterile shoot weight (g/shoot), f_n the mean number

of fertile shoots, and b_f the mean maximum fertile shoot weight. PB were obtained by summing 20 species peak biomass values (B_h) and other species uncorrected biomass values.

In order to use the Wiegert & Evans (1964) estimation method for net primary production (WE), based on the litter disappearance rate, it is necessary to know the mean amount of litter and the disappearance rate at different seasons. Wiegert & Evans (1964) have developed two methods for determining the disappearance rate, they are the paired plots and the litter bag methods. The former method was used to calculate the disappearance rates during the spring and early summer (25.5.—20.6.72) in 1972 and in winter 1972/73 (12.10.72—25.5.73). The disappearance rate during summer 1972 could not be calculated because the litter biomass started to increase after the beginning of July. The disappearance rate for the period 21.6.—11.10.72 was estimated as 10 mg/g/day. In addition to this, the production was calculated according to a value for the summer disappearance rate of 6 mg/g/day, presented by Törmälä & Raatikainen (1976).

In 1973 the amount of litter remained the same in the spring and already began to increase in early summer. The disappearance rate could be measured in only P65. This value was used to estimate the rates for the other field plots. The summer disappearance rates were estimated to be the same as in the previous year, i.e. 6 and 10 mg/g/day. As samples were not collected in spring 1974, the mean values for spring 1972 and 1973 were taken as the litter biomass for spring 1974. The annual above-ground net primary production is obtained by multiplying the mean disappearance rate by the mean litter biomass (Wiegert & Evans 1964). Biomass samples were collected on 11 occasions during the two-year period described above. In addition, the production for 1971 was calculated from only three samples. The production estimates for summer 1971 were calculated from the corrected (to 650 d.d.) biomass values. The litter disappearance rate was calculated for the periods 25.7.71—25.5.72 and 26.5.—24.7.72.

323. Herbivory estimation

The effect of herbivores on the vegetation has been examined by observing the field vole (*Microtus agrestis*) as an example. The effect of voles on the vegetation can be elucidated either by measuring or estimating the phytomass consumed by the voles, or by measuring the changes that occur in the vegetation with respect to the density of the vole population. Both methods have been used in this study, the first in 1972 and 1973, and the second throughout the duration of the experiment. Consumption during the summertime has been estimated with the help of consumption values presented in the relevant literature (Drożdż 1968, Hansson & Grodziński 1970, Babińska 1972).

According to Ryszkowski et al. (1973), the ratio between the damaged and consumed biomass by small rodents is 1.8, while according to Babińska-Werka (1979) it is even 17. Two alternative ratios were tested here - 1.8 and 10. The estimates of Chitty et al. (1968), that field voles destroy 15 g of living dry phytomass a day under winter conditions, were used for measuring consumption and damage during the winter. The vole densities for the summer period (V—X) are mean values from 5—6 live trappings, and for the winter period (XI—IV) the final live trapping in the autumn in each field plot (Hytönen 1975, Teivainen, pers. comm.). The effect of voles on the vegetation during the summer is depicted by the proportion of destroyed plant material out of the potential primary production on each field plot. These damage percentages are calculated on the basis of MB and WE (see p. 13) for the summer season and on the basis of the October standing crop biomass for the winter season.

Another method for studying the effect of voles on the vegetation is to follow changes occurring in the vegetation with respect to the vole density. This has been done both at the plant community level and at the species level, and at the food preference level of the field vole (Marttila 1974, Teivainen & Jukola-Sulonen 1983, see also Hansson 1971). The species growing on the fields have been divided into three preference classes on the basis of the relative feeding (in feeding experiments). The proportion of the plant species tested in feeding trial was at least 80—90 % in each field plot. The effect of voles on the vegetation has been studied by comparing the biomass values in other years with the biomass values in 1971 (= 100) (corrected biomass values). Fluctuation of the field vole popula-

tion was described by the total number of voles caught during each year in all the field plots (Hytönen 1975, Teivainen pers. comm.).

324. Biomass estimation of trees and shrubs

Several methods were used to estimate tree biomass. Firstly, the above-ground fresh wood biomass of deciduous species were obtained using the functions developed by Simola (1977). The calculations were made using both the DBH and height. Separate formulae were used for *Betula pendula, Alnus incana* and *Populus tremula* x *P. tremuloides* (Simola 1977). The function for Populus was adapted for use with *Salix* species. The dry-weights were obtained using the moisture percentages measured by Simola (1977). The fresh biomass of coniferous species were obtained using the functions of Kanninen et al. (1979) for *Pinus sylvestris* and *Picea abies*. The calculations were also done as a function of DBH and height. The dry-weights were obtained using the moisture percentages measured by Harstela & Tervo (1977).

The fresh biomass of the conifers less than 2 m tall on the planted area in P65 were estimated as follows: The volume of the stemwood was calculated using the taper curves of Lahtinen & Laasasenaho (1979). The volume values were converted into dry weights by the method presented by Hakkila et al. (1977). The dry-weights were calculated in a similar way as for the larger conifers. The dry-weight of the branches was estimated according to Hakkila (1971). The dry-weight of the other shrubs was obtained by the mean shrub method (p. 12). *Salix* species were treated as one group. The ratio values of the *Salix* species identified on each field plot are presented according to the collected samples.

33. Methods of vegetation analysis

331. Clustering and ordination methods

The clustering and ordination analyses were made using the biomass values (g/m^2) and frequency percentages of 121 species from 19 different-aged sample plots on four field plots. Clustering of the sample plots was made from five different variations of the agglomerative hierarchic clustering (polythethic, non-overlapping) methods (Pritchard & Anderson 1971): nearest neighbour; furthest neighbour; group average; centroid and minimum variance clustering. Alternative indices for the dissimilarities between the sample plots were used in the different methods (Pakarinen 1976, Teivainen et al. 1979). The success of clustering and the homogeneity of the groups are examined by means of similarity comparisons (Jalas 1962).

Four ordination methods were tested: correlation analysis, factor analysis, polar ordination, and reciprocal averaging (Gauch et al. 1977). Correlation analysis (CA) was carried out on species which occurred more than twice in the material. Only positive correlations greater than 0.5 ($p < 0.05$) were taken into account. The result are shown in a plexus diagramme.

The same factor loading solution as used by Pakarinen (1976, 1979) was employed in the factor analysis (FA) using the HYLPS library programme developed at the University of Helsinki. The correlation matrices are treated further and, after factorization and rotation, a varimax solution which contains the required number of factors obtained as the end result. Two, three, four, five and six factor solutions were tested in the plot analysis, and two, five and ten factor solutions in the species analysis. The aim was to obtain so many factors, that the inclusion of new factors would not increase the overall variance explained nor break up easily interpretable factors. All species were included in the analysis, but those species which occurred once or twice are omitted in the species analysis of the results.

Bray-Curtis (Bray & Curtis 1957) (PO, polar/Wisconsin) ordination was the third ordination method tested. In this method, the basis of the analysis is the dissimilarity indices of the sample plots. Two indices were tested in this study: the percentage dissimilarity and the euclidean distance (Gauch & Whittaker 1972). Polar ordination gives only the ordination of the sample plots with respect to two axes, but not the species ordination. The end points of the axes are selected subjectively on the basis of available study materials.

Reciprocal averaging (RA, correspondence analysis) is the most recent of the ordination

methods tested. Hill (1973) has developed a direct iteration algorithm for calculations. A Fortran program provided by Dr. H. G. Gauch, Jr. of Cornell University was used in this study. The output contains sample plot and species scores on three axes. Species and sample plot ordinations can be compared on the same scale. Sample plot analyses were made with both the biomass and frequency values using all the above-described methods, but in the case of the species analyses only with the biomass values.

The reciprocal averaging ordination of the sample plots were also tested on a more extensive material covering abandoned fields. In addition to the hay fields material studied here, it also comprised material collected from abandoned fields in southern and central Finland (data from Teivainen et al. 1979). The control material comprised data from 26 abandoned field plots of rather varying age in which water voles (*Arvicola terrestris*) had damaged tree seedlings planted on the field plots. The water vole habitats included a number of old fields, some of which had been ploughed before planting and others not. The control material and the reseach material comprised a total of 45 abandoned fields of various ages. The precise age of all the field plots in the control material was not known (Korhonen 1978), but they can be divided into two age classes: young fields less than eight years old and those equal to or greater than eight years. The analysis was carried out according to the frequency values.

The clustering and ordination analyses described above were carried out on a Burroughs 6700 Computer at the Computing Centre of Helsinki University using library programmes obtained by the Department of Botany (Library programmes from Pritchard & Anderson 1971, Gauch et al. 1977, cf. also Pakarinen 1976).

332. Diversity methods

The diversity of the plant community developing on the field plot has been estimated numerically using different diversity indices, and graphically using dominance-diversity curves (Whittaker 1972, Bazzaz 1975, Squiers & Wistendahl 1977). The diversity functions have been calculated separately for the field layer and for the whole plant community. The species diversity has been calculated for each sample plot as follows:

1. Total number of species of the sample (S).
2. Average number of species per unit area (ASR), Areal Species Richness, which is obtained as the mean sum number of species per square metre.
3. Shannon's (Shannon & Weaver 1949) diversity index

$$H' = - \sum_{i=1}^{s} p_i \ln p_i$$

where S is the number of species and p_i is the biomass of the i:th species divided by the total biomass.

4. Simpson's (1949) diversity index

$$D = 1 - \sum_{i=1}^{s} p_i^2$$

5. Pielou's (1966) diversity index

$$J' = H'/\ln S$$

6. Whittaker's (1972) diversity index

$$E_c = S/\ln (p_1/p_s)$$

where p_1 is the relative biomass of the most abundant species and p_s that of the least one.

7. Kempton and Taylor's (1976) diversity index

$$Q = S/2 \ln (R_2/R_1)$$

where R_1 and R_2 are the lower and upper quartiles of the species abundance distribution.

8. Lamont et al.'s (1977) diversity index

$$E_b = (S_{90\,\%-1} - S_{10\,\%+1})/(\ln p_{10\,\%+1} - \ln p_{90\,\%-1})$$

where the numerator is 80 % of the total number of the species in the sample and $p_{10\,\%+1}$ is the relative biomass for the (10 % + 1)th species and $p_{90\,\%-1}$ for the (90 %—1)the species from the species abundance distribution.

All the diversity variables were calculated from uncorrected biomass values, apart from Simpson's index which was also calculated according to the corrected biomass values (D_2). The results for the field layer have been calculated to an accuracy of 0.1 g/m^2 and the results for the whole plant community to an accuracy of 0.01 g/m^2.

The diversity values for the whole plant community have been calculated at the end of the study period from the combined materials for 1977 and 1979. The dependence of the different diversity indices on each other and on external factors has been studied using correlation analysis. The correlations were calculated between the diversity indices of the field layer and the number of samples, surface-area sampled, size of sample quadrat, temperature sum at sampling date, succession age and production (JB).

34. The succession model

The same basic principle as that used by Kauppi et al. (1978) was used in developing the succession model: The species can be divided into groups according to their successional stage at which each species was most abundant. The pioneer species give way to the second and third group of species, the second in turn to the third group etc., until the climax where the changes with respect to time are the least, is reached. The plant species were divided using the aforementioned classification methods into three groups according to the succession stage. The proportion of these three groups out of the total biomass on each plot was then calculated using the corrected biomass values.

The model developed here is a matrix model which has been calculated through the use of the least squares method. It is possible using this model to depict the area and rate of replacement between the species successional classes. Changes between the first and the third species group are permitted in the model. The succession models have been calculated from the different combined materials of the field plots. The model was developed on the VAX 11/780 computer of the Finnish Forest Research Institute.

4. RESULTS AND DISCUSSION

41. Soil

The soil in the field plots was fine sand till, and in some places rather fine sand. The subsoil in all the field plots was fine sand till.

The northern and central parts of P68 were the most fertile and had the thickest mull layer (Fig. 4). There were no such trends in P65. The distinctive feature on P65 was that the parts with the highest potassium level were the same as those with a thin layer of mull soil. In P58, the soil on the eastern side of the field plot had the highest nutrient level, while the soil in the parts with a thick mull layer were the most acidic. The greatest change in the results of analyses made four years later was in the level of potassium (Table 1). The level of potassium had increased by 19—112 %, depending on the field plot. The other changes were only small.

The soil in the field plots were clearly below the approvable fertility level of fields, judging by all the different criteria of fertility (Kurki 1972) (Table 1). However, when these values are compared to those for forest soil of the OMT and MT site types. pH and Ca were either the same order of magnitude or greater, K and P lower than the levels for the uppermost layer of forest soils (A_0) (Urvas & Erviö 1974). The values for K and P content of field plot soil were 21—70 % of those for forest soil (Table 1).

Table 1. Soil analyses of the cultivated layer and the sub-soil samples of the field plots in 1972 and 1976. The terminology is according to Kurki et al. (1965). Comparison values for cultivated layer of fields (Kurki 1972) and for A_0 -layer of OMT (MT) forest soils (Urvas & Erviö 1974) are from corresponding soil types. HtMr = fine sand till, KHt = fine sand, Mull = the thickness (cm) of the cultivated layer (mull layer), m = medium high, and rm = high organic matter content of mull layer, pH = acidity, Ca = exchangeable calcium, K = exchangeable potassium, P = easily-soluble phosphorus. The results are expressed (mean ± SE) mg/l of dry milled sample.

Taulukko 1. Neljän eri ikäisen peltolohkon maa-analyysi v. 1972 ja 1976. Terminologia on Kurki ym. (1965) mukainen. Vertailuarvot peltojen muokkauskerrokselle ja OMT (MT) -metsien A_0 -kerrokselle (Urvas & Erviö 1974) ovat vastaavilta maalajeilta. HtMr = hietamoreeni, KHt = karkea hieta, Multa = multakerroksen paksuus (cm), m = multainen, rm = runsasmultainen, pH = happamuus, Ca = vaihtuvan kalkin, K = vaihtuvan kaliumin ja P = helppoliukoisen fosforin määrät (keskiarvo ± SE) milligrammoina litrassa kuivaa jauhettua näytettä.

Field plot *Peltolohko*	Year *Vuosi*	Soil type *Maalaji*	Mull *Multa*	Org.matter *Multavuus*	pH	Ca	K	P
		Cultivated layer — *Muokkauskerros*						
P68	1972	HtMr (KHt)	19 ± 1	m (rm)	5.6 ± 0.1	907.0 ± 58.6	37.7 ± 3.4	9.4 ± 0.2
	1976	HtMr		m	5.6	1050.0	80.0	11.0
P65	1972	HtMr (KHt)	21 ± 2	m (rm)	5.6 ± 0.1	801.0 ± 37.6	45.0 ± 2.5	8.9 ± 0.3
	1976	HtMr		rm	5.5	750.0	70.0	9.8
P58	1972	KHt (HtMr)	27 ± 3	rm (m)	5.9 ± 0.1	1105.0 ± 98.2	41.4 ± 7.2	8.6 ± 0.8
	1976	HtMr		rm	5.6	900.0	75.0	6.6
P53	1972	HtMr (KHt)	20 ± 2	rm (m)	5.6 ± 0.1	990.0 ± 41.5	32.2 ± 6.7	8.9 ± 2.7
	1976	HtMr		m	5.6	875.0	38.0	6.6
		Sub-soil — *Pohjamaa*						
P68	1972	HtMr			6.0	150.0	26.2	3.6
P65	1972	HtMr			5.5	175.0	22.0	3.4
P58	1972	HtMr			5.9	300.0	44.0	2.4
P53	1972	HtMr			5.7	300.0	18.0	4.2
		Comparison values — *Vertailuarvot*						
Field — *Pelto*					5.8	1400.0	150.0	10.0
Forest — *Metsä*					4.7 (4.4)	913.0 (676.0)	117.0 (150.0)	14.0 (15.8)

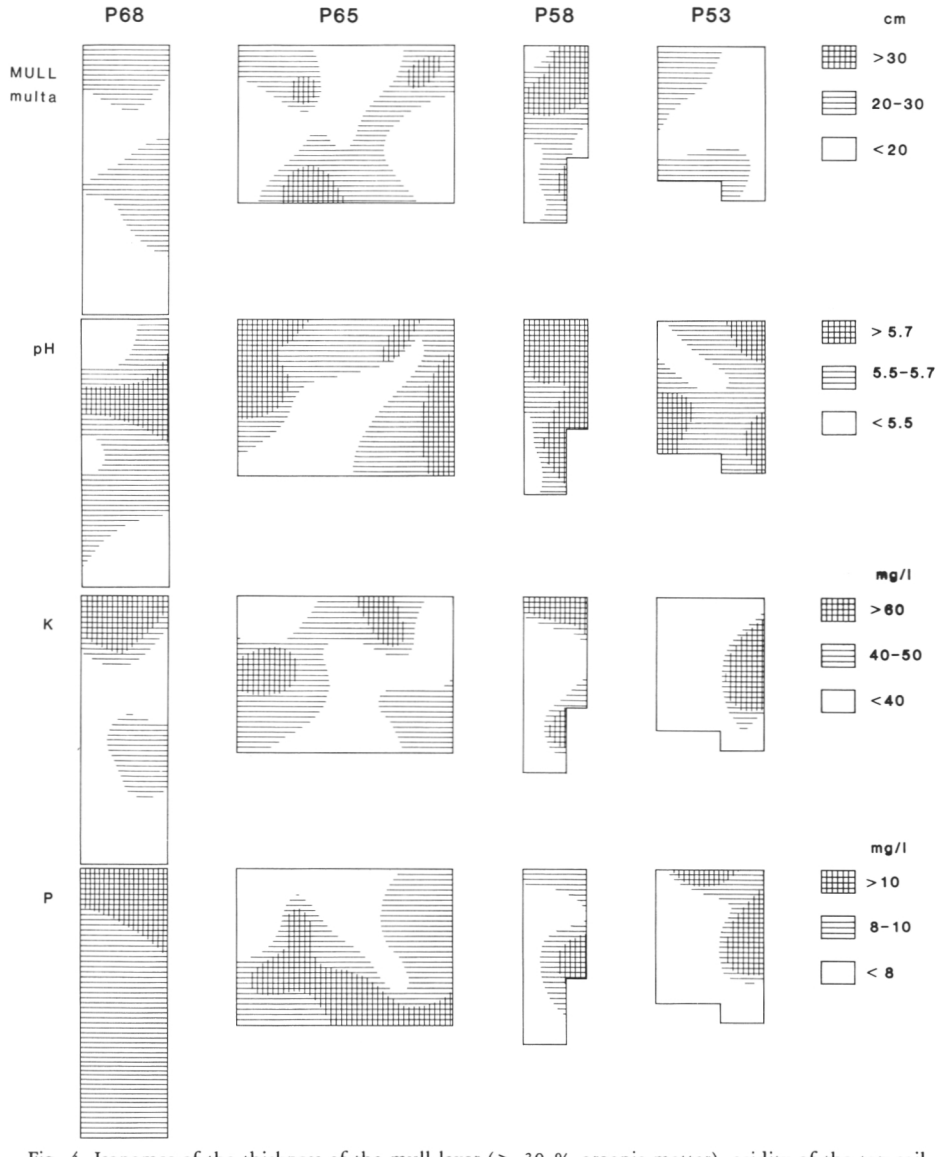


Fig. 4. Isonomes of the thickness of the mull layer (> 30 % organic matter), acidity of the top-soil (pH), exchangeable potassium (K) content and easily-soluble phosphorus (P) content mg/l of dry milled sample in the different field plots in 1972 (Table 1).

Kuva 4. Maa-analyysin pohjalta laaditut eri peltolohkojen isonomikartat multakerroksen paksuudesta (cm) (multa), pintamaan happamuudesta (pH), vaihtuvan kaliumin (K) ja helppoliukoisen fosforin (P) määristä milligrammoina litrassa kuivaa jauhettua näytettä v. 1972 (Taulukko 1).

42. Vegetation succession on the field plots

An overall picture of the vegetation succession occurring in the separate vegetation layers on each field plot is given in the following. The description of succession in the field and ground layers is based on the results of plant analyses made on four or five occasions during the course of the study, (Appendix 1, Table 3), and in the tree and shrub layers (Table 4) on studies done at the beginning and end of the study. In addition, the development of the ground, tree and shrub layers, as well as factors which may have had an effect on these layers, are also discussed in this section.

Table 2. The July green biomass (JB, dry weight g/m^2) on the sample plots (years from sowing). Biomass values are corrected (see text, p. 13) from the biomass values in Appendix 1 to a temperature sum of 650 for the 20 most abundant plant species. Uncorrected species are as in Appendix 1.

Taulukko 2. Heinäkuun vihreä biomassa (JB, kuivapaino g/m^2) eri ikäisillä näytealoilla (vuosia kylvöstä). 20 runsaimman lajin biomassat liitteestä 1 on korjattu (ks. s. 13) vastaamaan lämpösummaa 650 d.d. Muut lajit on otettu liitteestä 1 korjaamattomina.

Field plot — *Peltolohko*	P68					P65					P58				P53				
Sample plot — *Näyteala*	3	5	7	8	9	6	8	10	12	14	13	15	17	19	18	20	22	23	24
Study year — *Tutkimusvuosi*	1971	1973	1975	1976	1977	1971	1973	1975	1977	1979	1971	1973	1975	1977	1971	1973	1975	1976	1977
Ranunculus acris							0.5	1.0	0	0	10.8	7.3	23.0	9.2	21.3	15.7	43.6	28.8	11.6
Alchemilla vulgaris						2.2	4.3	+	11.4		235.4	173.7	244.0	276.8	67.7	77.4	31.6	139.6	83.4
Vicia cracca			13.9		2.1				1.7		3.6	16.1	10.4	0.2	48.3	25.2	27.4	23.6	12.7
Vicia sepium					0.1			1.0			0.2	0.7	9.6	5.3	0.1	5.6	15.1	3.9	7.8
Lathyrus pratensis												11.5	4.4	4.6	8.3	15.4	20.6	25.5	14.0
Epilobium angustifolium				31.5	13.9		9.0	13.3	20.0	9.3	10.0						4.0		
Hypericum maculatum	0.8	+	0.8	+	3.8	+	+	0.2	9.3	0.1	1.7	1.0	+	8.6	2.4	9.2	6.0	14.5	7.9
Rumex acetosella		0		3.2		5.6	0.2	0.7	0	0.1						0			0
Achillea ptarmica		0.3			3.1	3.0	2.8	9.5	2.5	6.4	0.5	3.0	+	1.4	14.1	8.4	9.2	10.0	6.8
Achillea millefolium	0.4	1.4	0.7	7.5	0.3	0.8	2.7	2.4	0.2	1.3	4.7	1.5	1.4	+	14.4	5.5	2.0	5.0	0.4
Cirsium helenioides					20.1											7.0	97.0	16.8	3.7
Leontodon autumnalis	0	0				32.5	8.0	6.8	+	0.6	3.3	0.1	0		0.7	+	0	0	+
Taraxacum officinale	6.2	4.5	19.0	14.4	24.2	26.5	78.2	81.5	42.5	60.2	58.9	28.6	32.3	13.7	35.1	52.9	61.1	74.1	38.6
Festuca rubra						1.3	0	3.5	0.3	0		3.3	1.5	1.2	9.1	7.7	14.8	32.2	14.4
Poa pratensis	+	2.3	14.3	4.0	19.2	6.7	5.7	9.6	19.7	15.3	17.1	14.5	32.9	22.9	47.8	30.9	39.4	40.7	33.1
Deschampsia cespitosa	0	+	35.0	1.0	13.9	0.5	3.6	21.7	6.2	3.7	2.6	29.0	3.5	0.5	70.0	52.0	39.2	70.0	30.4
Agrostis tenuis	48.8	61.1	81.0	144.7	115.7	200.3	257.2	173.2	149.6	152.6	189.5	86.7	81.5	38.2	77.4	70.5	45.0	70.0	33.9
Phleum pratense	738.5	345.6	163.6	156.6	153.2	335.8	123.8	81.4	50.3	17.7	166.6	90.3	47.1	27.1	17.1	16.2	30.7	88.4	33.5
Anthoxanthum odoratum						7.1	5.5	12.0	7.7	6.4	1.4	0.1	2.9	0.9	4.7	1.8	1.5	0.3	0.1
Elymus repens	117.5	136.3	318.8	276.0	109.0	99.7	92.5	68.0	19.2	18.3	64.5	44.6	51.0	16.9	31.3	20.5	41.2	77.3	45.0
Uncorrected species — *Korjaamattomat lajit*	10.6	4.3	4.5	23.7	33.3	14.0	4.8	16.9	25.0	9.2	1.2	19.7	25.6	10.6	13.8	27.4	17.4	17.4	23.1
Total — *Yhteensä*	922.8	555.8	651.6	662.6	511.9	736.0	598.8	502.7	365.6	301.2	772.0	531.7	571.1	438.1	483.6	449.3	546.8	738.1	400.4

Field Plot 68

When the study began, three years after the field had been sown, the vegetation was dominated by sown *Phleum pratense* (B 80 %). Of the two species sown, *Trifolium pratense* was gradually disappearing from P68 (B 1 %). After *Phleum*, the most abundant and commonest species were *Elymus repens* and *Agrostis tenuis* (Table 2, Appendix 2). Considerable changes took place in the vegetation during the six-year monitoring period, the most significant of which was the gradual decrease of *Phleum* (Fig. 5). The proportion of this species out of the total biomass decreased from 80 to 20 %. The other large change was the strong spread of *Elymus*. By the seventh succession year it comprised over 40 % of the total plant biomass. In later years, however, *Elymus* started to decrease. By the end of the study period, the dominant species grew in the field plot in almost equal amounts. *Phleum*, *Agrostis* and *Elymus* constituted over 80 % of the plant biomass throughout the study period. The percentage of herbs increased with time (2 to 20 %).

The hemicryptophyte group (the wintering buds at ground level) was the most abundant of the life form groups (Raunkiaer 1909, Ellenberg 1979) present. The proportion of this group had decreased from 90 to 60 % by the seventh succession year, while at the same time the proportion of geophytes (subsurface wintering buds) increased. In later years, however, the number of geophytes started to decrease and that of hemicryptophytes to increase. The number of therophytes (wintering as seeds) was quite low throughout the course of the experiment, as was the case with chamaephytes (buds above ground level).

At the onset of the study the ground vegetation was completely absent (Table 3). Even in later years it was very scant. The only moss species found were *Brachythecium albicans* (Hedw.) B.S.G. and *B. reflexum* (Starke) B.S.G.

The tree and shrub layers were not present at the onset of the study. In 1979 the most abundant and only species belonging to these layers was the shrub *Rubus idaeus* (Table 4). *Rubus* occured in low thickets, about 60 cm high, at a frequency of 44 % (Fig. 6). The species has spread onto the field plot from the uncultivated strips along the edges of the field plot. The directions of spreading of a number of thickets can be seen in Fig. 6. *Rubus idaeus*

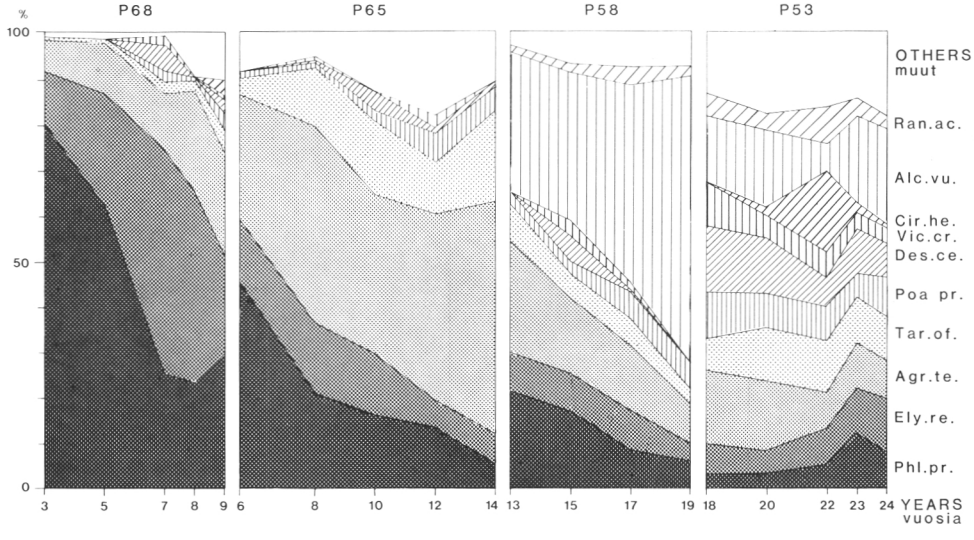


Fig. 5. Succession of the most abundant species in the field layer of the different field plots according to the corrected (650 d.d.) relative biomass values. Ran.ac. = *Ranunculus acris*, Alc.vu. = *Alchemilla vulgaris*, Cir.he. = *Cirsium helenioides*, Vic.cr. = *Vicia cracca*, Des.ce. = *Deschampsia cespitosa*, Poa pr. = *Poa pratensis*, Tar.of. = *Taraxacum officinale*, Agr.te. = *Agrostis tenuis*, Ely.re. = *Elymus repens*, Phl.pr. = *Phleum pratense*.

Kuva 5. Peltolohkojen kenttäkerroksen runsaimpien lajien sukkessio korjattujen (650 d.d.) suhteellisten biomassojen mukaan. Lajit, ks. engl. teksti.

Table 3. The species composition of the ground layer on the sample plots (years from sowing), the biomass values (B) (g/m^2) and the frequencies (F) (%).
Taulukko 3. Pohjakerroksen lajikoostumus, biomassat (B) (g/m^2) ja frekvenssit (F) (%) eri ikäisillä näytealoilla (vuosia kylvöstä).

Field plot — *Peltolohko*	P68										P65										P58								P53									
Sample plot — *Näyteala*	3		5		7		8		9		6		8		10		12		14		13		15		17		19		18		20		22		23		24	
Year — *Vuosi*	1971		1973		1975		1976		1977		1971		1973		1975		1977		1979		1971		1973		1975		1977		1971		1973		1975		1976		1977	
Method — *Metodi*	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F
Amblystegium serpens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.00	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.00	10	0.20	3	—	—
Amblystegium sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.00	3	—	—
Atrichum undulatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.00	4	—	—	—	—	—	—	—	—	—	—
Brachythecium albicans	—	—	—	—	0.12	10	—	—	—	—	1.11	10	3.32	12	0.63	6	0.00	3	—	—	0.52	10	—	—	0.02	20	—	—	0.68	20	1.46	20	3.84	20	0.52	6	—	—
B. curtum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.06	24	—	—	0.02	2	—	—	—	—	—	—	—	—	0.20	10	—	—	0.00	10	0.06	6	0.01	3
B. reflexum	—	—	—	—	—	—	—	—	0.01	4	—	—	—	—	—	—	—	—	0.17	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
B. salebrosum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.02	24	1.23	21	3.30	33	0.36	10	—	—	0.00	20	0.01	13	+	+	+	+	1.60	20	0.61	6	0.44	13
B. starkei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	0.20	10	—	—	—	—	—	—	—	—
Brachythecium sp.	—	—	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.00	4	—	—	—	—	—	—	—	—	0.01	3
Eurhynchium praelongum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.01	8	—	—	—	—	—	—	—	—	—	—
Plagiomnium ellipticum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	0.11	10	—	—	—	—	—	—	—	—	—	—	—	—	0.01	3
Pleurozium schreberi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	0.05	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhizomnium punctatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.00	10	—	—	—	—	—	—	—	—	—	—	—	—
Others — *Muut*	—	—	—	—	—	—	—	—	—	—	0.19	10	0.00	6	—	—	—	—	—	—	—	—	—	—	0.00	10	—	—	0.00	40	—	—	—	—	0.20	13	—	—
Total — *Yhteensä*	—	—	—	—	0.12	10	—	—	0.01	4	1.30	20	3.32	18	1.71	47	1.23	24	3.54	38	0.88	20	0.11	10	0.02	50	0.02	21	1.08	50	1.46	20	5.44	30	1.59	25	0.47	23

Table 4. The species composition of the tree and shrub layers in 1979, biomass value (B) (d.w. kg/ha), density (N) (stems/ha), frequency (F) (%), mean height (h) (m), mean diameter — butt (D_0) (cm) and breast height (DBH) (cm). See further explanation in text.

Taulukko 4. Puu- ja pensaskerrosten lajikoostumus 1979, biomassa (B) (kp. kg/ha), tiheys, (N) (runkoja/ha), frekvenssi (F) (%), keskipituus (h) (m), tyviläpimitta (D_0) (cm) ja rinnankorkeusläpimitta (DBH) (cm). Katso tarkempi selitys tekstistä.

Field plot — *Peltolohko*	P68					P65						P58						P53					
Sample plot — *Näyteala*	11					14						21						26					
Method — *Metodi*	B	N	F	h	D_0	B	N	F	h	D_0	DBH	B	N	F	h	D_0	DBH	B	N	F	h	D_0	DBH
Tree layer — Puukerros																							
Picea abies						46	76	30	2.2	4.1	2.1												
Pinus sylvestris						471	256	46	2.5	6.4	3.4												
Betula pendula						670	270	59	4.2	6.9	3.8												
Alnus incana												342	714	5	2.8	3.7	1.8						
Populus tremula						57	69	26	3.3	4.1	2.3												
Salix spp.						23[a]	14	7	3.5	7.8	2.7	165[b]	1309	10	2.5	2.9	1.0	592[c]	3438	28	2.5	1.3	1.0
Total — *Yhteensä*						1267	685	67				507	2023	14				592	3438	28			
Mean — *Keskimäärin*									3.1	5.9	2.9				2.7	3.3	1.4				2.5	1.3	1.0
Shrub layer — *Pensaskerros*																							
Picea abies						52	171	40	1.4	3.0								30	78	3	1.7	4.0	
Pinus sylvestris						54	149	41	1.6	3.9													
Juniperus communis																		8	78	3	1.2	3.0	
Betula pubescens																		31	313	3	1.4	1.4	
Alnus incana												11	119	5	2.0	1.3							
Rubus idaeus	195	40547	44	0.6	0.3	12	3607	13	0.5	0.3								10	1328	3	0.8	0.3	
Salix spp.						24[a]	249	4	1.6	1.3		321[b]	7190	19	1.2	1.0		415[c]	4453	25	1.5	1.0	
Total — *Yhteensä*	195	40547	44			142	4176	51				332	7309	24				494	6250	28			
Mean — *Keskimäärin*				0.6	0.3				1.3	2.1					1.6	1.2					1.3	1.9	
Trees and shrubs total																							
Kaikki yhteensä	195	40547	44			1409	4861	70				839	9332	29				1086	9688	34			

a *S. phylicifolia, S. caprea (1:1)*
b *S. phylicifolia, S. phylicifolia* × *myrsinifolia, S. myrsinifolia (1:2:1)*
c *S. phylicifolia, S. phylicifolia* × *myrsinifolia (1:2)*

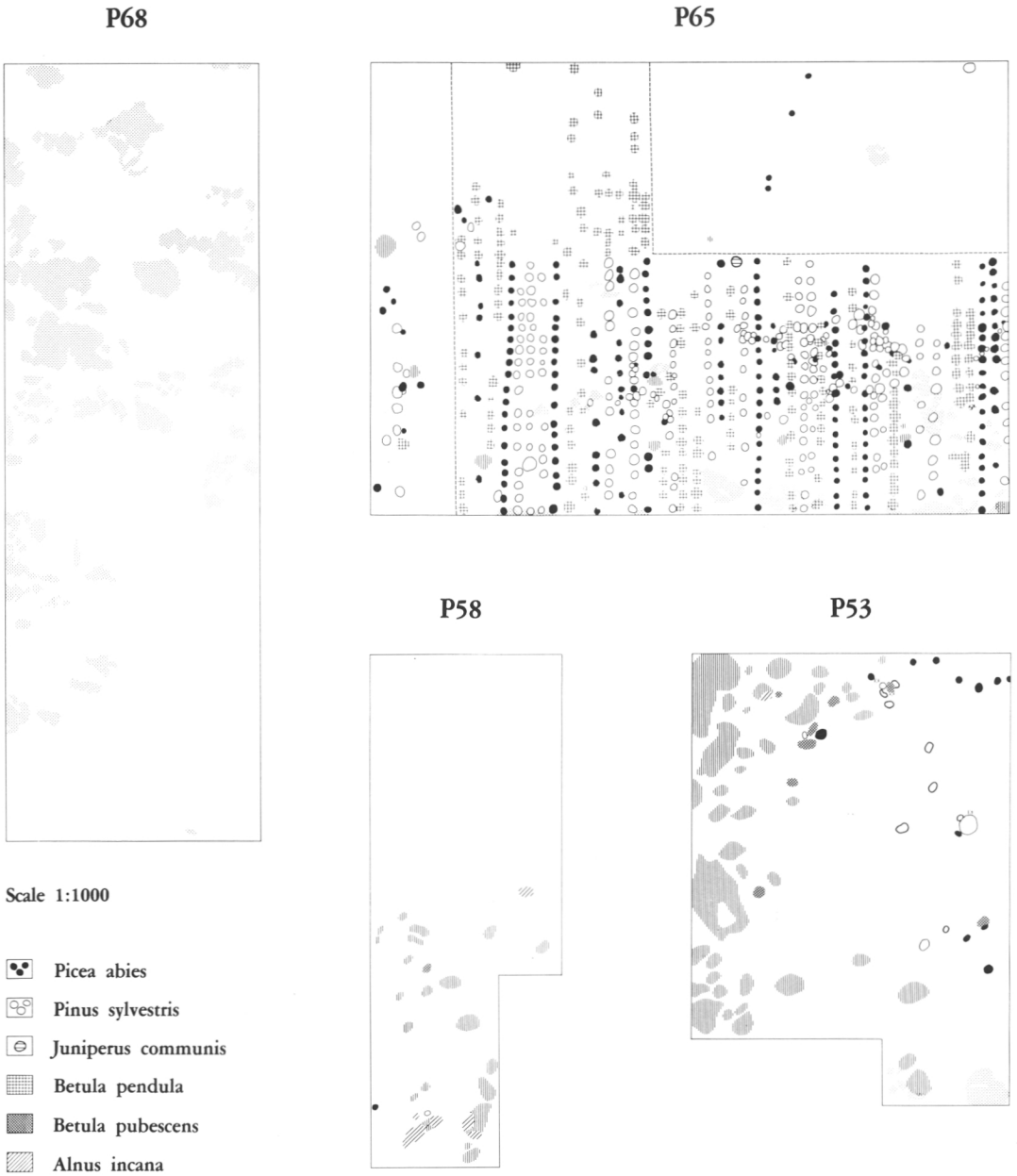


Fig. 6. Crown projections of the coverage of the trees and shrubs on the field plots, 1979. *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Populus tremula* x *P. tremuloides* seedlings were planted on P65 in 1972. The seedlings were planted two metres apart in alternate rows. Planting area is bordered with dashed line.

Kuva 6. Peltolohkojen puu- ja pensaslajiston peittävyyskartat latvusprojektiona v. 1979. Lohkolle 65 istutettiin v. 1972 Pinus sylvestris- Picea abies- Betula pendula- ja Populus tremula x P. tremuloides- taimia kahden metrin välein vuororiveihin katkoviivalla rajatulle alueelle.

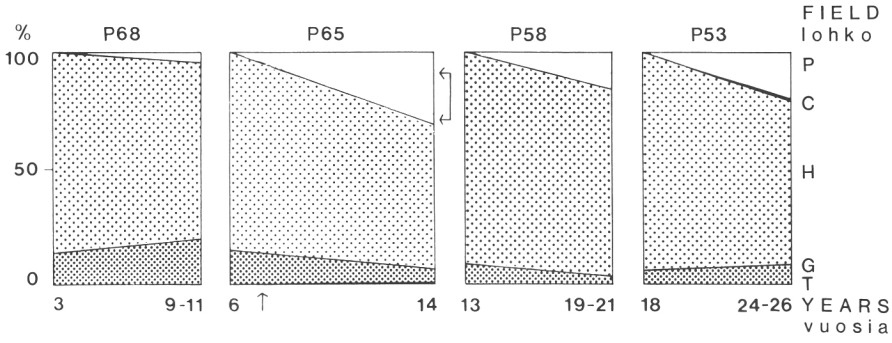


Fig. 7. The whole plant community of the four field plots divided into different life form groups (Raunkiaer 1909, Ellenberg 1979) as relative biomass, 1971 and 1977 — 1979. Planting year (1972) on P65 is marked with an arrow and the proportion of planted trees and shrubs in 1979 marked at the side of the P65 block. P = Phanerophytes, C = Chamaephytes, H = Hemicryptophytes, G = Geophytes, T = Therophytes.

Kuva 7. Neljän peltolohkon koko kasviyhteisö elomuotoluokittain (Raunkiaer 1909, Ellenberg 1979) vv. 1971 ja 1977—1979 suhteellisina osuuksina biomassasta. Puiden taimien istutusajankohta on merkitty lohkolle P65 nuolella ja istutettujen puiden ja pensaiden osuus v. 1979 lohkon P65 pylvään sivuun. P = Fanerofyytit, C = Kamefyytit, H = Hemikryptofyytit, G = Geofyytit, T = Terofyytit.

was the sixth most abundant species when compared to the results of the plant analyses made on the field layer in 1977. The proportion of shrubs out of the whole plant community grew from 0 to 4 % (Fig. 7). The remainder of the plant community consisted of the field layer.

Field Plot 65

The field layer was monitored five times at intervals of two years starting in 1971. The vegetation had been allowed to develop for six years before the study was started. Of the sown species, *Trifolium pratense* had disappeared almost completely, while *Phleum pratense* still represented half of the plant biomass (Table 2, Fig. 5 and Appendix 2). The other abundant species were *Agrostis tenuis* and *Elymus repens*. During the next eight years *Phleum pratense* gradually decreased, as did *Elymus repens*. On the other hand *Agrostis tenuis*, *Taraxacum officinale* and *Poa pratensis* increased. Between the succession age years 8—14, *Agrostis* was the dominant species on the field, constituting almost half of the plant biomass and occurring at a frequency of 100 % throughout the course of the study. The proportion of the grasses out of the total biomass decreased regularly along with the increase in herbs from 10 to 30 %.

Over 85 % of the field layer plant biomass consisted of hemicryptophytes throughout the course of the study. The proportion of such plants increased to some extent during the course of succession. The amount of geophytes was less than 14 %. The proportion of chamaephytes was less than 3 % and therophytes occurred only occasionally.

The ground layer remained very scattered throughout the course of the study (Table 3). Bryophytes occurred in less than half of the sample quadrats in each year. A total of seven species of bryophyte were found on this field, *Brachythecium albicans* being most abundant at the beginning of the study, but *B. salebrosum* (Web. & Mohr) B.S.G. at the end. *B. curtum*, (Lindb.) C. Jens., *B. reflexum* and *Pleurozium schreberi* (Brid.) Mitt. also occurred on the field plot at the end of the study.

The tree and shrub layers were absent at the beginning of the study. There were only a few seedlings, less than 50 cm tall, growing in the field plot. Eight years later there were 8 tree and shrub species (Table 4, Fig. 6), both planted and naturally regenerated. All species planted on the field in 1972 were still growing there 7 years later. Most of the introduced species had also regenerated on the field, both in the planted area and outside it. In addition to the planted *Betula pendula*, *Populus tremula* x *P. tremuloides*, *Pinus sylvestris* and *Picea abies*, the following species were also

present on the field plot: *Ribes nigrum* L., *Juniperus communis* L. and a few *Salix* spp. (*Salix caprea* L. and *S. phylicifolia* L. in the ratio 1:1). *Rubus idaeus* thickets mainly occurred along the edges of the field plot. The survival rate of the planted seedlings was 65 %. *Betula* and *Populus,* with a survival rate of 38 %, were damaged the most, *Pinus* (63 %) and *Picea* (90 %) the least. If the naturally regenerated seedlings on the planted area are taken into account, then *Pinus* decreased by 16 % and *Picea* increased by 4 %. Only a few *Populus* and *Betula* had regenerated naturally. The coverage of trees and shrubs was 18 % throughout the whole of the field plot, 13 % represented by planted seedlings and 5 % by naturally regenerated seedlings. Natural regeneration had been the most successful on the planted area, 76 % of the naturally regenerated seedlings being found in this area. Natural regeneration had been especially successful in the middle parts of the field plot. The soil in this area was drier than elsewhere in the field plot and the field vegetation lower.

The most abundant woody species was *Betula pendula*, then *Pinus sylvestris* and *Populus tremula* x *P. tremuloides*. The order based on stem number was *Betula*, *Pinus*, *Picea abies* and *Populus*. According to the biomass figures, *Pinus* and *Picea* were the most abundant shrub species, and according to stem number, *Rubus idaeus* and *Salix* spp.

In 1979 the trees and shrubs comprised 31 %, the field layer 68 % and the ground layer 1 % of the whole plant community (Fig. 7). Only 14 % of the trees and shrubs had regenerated naturally. The most abundant species in the whole plant community was *Agrostis tenuis*, followed by *Betula pendula*, *Pinus sylvestris* and *Taraxacum officinale*.

The effect of trees and shrubs on the succession of the field and ground layer was studied in 1979 by collecting samples from the planted area and from the treeless area of P65 (30 samples from each). The differences were tested using the Student's t-test (Table 5). The most abundant species on the treeless part of the field were *Agrostis tenuis*, *Taraxa-*

Table 5. Effect of the trees and shrubs on the field layer on P65 in 1979. The biomass values (B) d.w. g/m^2) and frequencies (F) (%) of the most abundant species in the field and ground layer on the treeless and planted area of the field plot. The statistical significance of the differences (*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ° = $p < 0.1$) with Student's t-test and the light indicator values of the species, 1 = shade plant, 9 = light plant, x = indifferent (Ellenberg 1979).

*Taulukko 5. Puiden ja pensaiden vaikutus kenttäkerrokseen P65:llä v. 1979, biomassa (B) (kp. g/m^2) ja frekvenssi (F) (%) kenttäkerroksen runsaimmilta lajeilta istutusalalta ja puuttomasta osasta lohkoa. Erojen tilastollinen merkitsevyys(*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ° = $p < 0.1$) Studentin t-testillä. Lajien valon osoitusarvot: 1 = varjokasvi, 9 = valokasvi, x = indifferentti (Ellenberg 1979).*

	Treeless area *Puuton alue*		Planted area *Istutettu alue*		t-test *t-testi* df = 58	Light indicator value *Valon osoitusarvo*
	B	F	B	F		
Field layer — *Kenttäkerros*						
Epilobium angustifolium	—	—	35.3	13	—	8
Achillea ptarmica	6.8	23	7.1	37	0.232	8
Cirsium arvense	5.1	3	—	—	—	8
Taraxacum officinale	37.3	53	34.9	57	0.186	7
Poa pratensis	22.5	70	8.0	73	1.684°	6
Deschampsia cespitosa	0.3	10	7.1	27	1.046	6
Agrostis tenuis	167.2	100	168.6	100	0.116	7
Phleum pratense	23.7	83	11.7	70	1.815°	7
Anthoxanthum odoratum	0.0	3	11.5	60	3.810***	X
Elymus repens	27.9	33	15.9	17	0.789	7
Others — *Muut*	6.8		11.1			
Field layer, total *Kenttäkerros, yhteensä*	297.6	100	311.2	100	0.385	
Ground layer, total *Pohjakerros, yhteensä*	0.7	17	6.4	57	1.621°	
Litter — *Karike*	604.2		497.3		2.478*	

cum officinale, *Elymus repens* and *Phleum pratense*, and on the planted area *Agrostis*, *Epilobium angustifolium* and *Taraxacum*. *Anthoxanthum odoratum* L. and *Epilobium* were more abundant on the planted area than on the treeless area. Similarly, there were more bryophytes on the planted area. *Phleum* and *Poa pratensis* were more abundant on the treeless area than on the planted area. The amount of litter was greater outside the planted area.

Trees and shrubs affect the amount of light reaching the field layer. Ellenberg (1979) has presented indicator values for the light of different species (Table 5). However, they do not provide an adequate explanation of the obtained results. *Anthoxanthum odratum* was more commonly found between the trees than on the treeless area, even though it is indifferent as regards light. The only factor which may have been affected by the tree cover was the biomass of bryophytes. The effect of trees and shrubs on the species composition of the plant community thus appears to be rather insignificant when the coverage is 18 %.

Field Plot 58

The field layer was monitored four times during the period 1971 to 1977. The vegetation on the field had developed for 13 years before the onset of the study. Of the sown species, *Trifolium pratense* had disappeared completely, while *Phleum pratense* accounted for 22 % of the field vegetation (Table 2, Fig. 5). *Alchemilla vulgaris* (31 %) and *Agrostis tenuis* (25 %) were present in greater numbers. The abundance of *Phleum* and *Agrostis* decreased to one fifth of the level in 1971 during the next six years. The abundance of *Alchemilla* increased so much during the same period that it comprised 63 % of the field layer by the end of the study.

According to the *Alchemilla* analyses conducted in 1977, almost 90 % of the *Alchemilla* include *A. acutiloba* Opiz and 7 % *A. subcrenata* Buser (Table 6).

When the proportion of grass species on the field plot decreased from 57 to 25 %, the proportion of herbs increased from 43 to 75 %. This took place almost exclusively as a result of the increase in *Alchemilla*.

No essential changes occurred in the distribution of life form groups during the course of the study. Hemicryptophytes accounted for over 90 % of the plant biomass throughout the study, and geophytes for less than 10 %. The importance of chamaephytes in the field layer remained very small, and that of the therophytes even smaller.

The ground layer on this field plot, as in the previously described field plots, was only poorly developed (Table 3). A total of seven bryophyte taxons were present on, at the most, half of the sample quadrats. *Brachythecium albicans, B. salebrosum* and *Plagiomnium ellipticum* (Brid.) T. Kop. were present on the field plot at the beginning of the study, but *Atrichum undulatum* (Hedw.) P. Beauv., *B. salebrosum*, *Brachythecium* sp. and *Eurhynchium praelongum* (Hedw.) B.S.G. by the end of the study.

The tree and shrub layers were missing from the field plot at the onset of the study. There were only a few 50 cm-high *Alnus incana* growing in the southern part of the field plot. Eight years later most of the field plot was still free of trees (Fig. 6). There were seven tree and shrub species growing in the lower part of P58 (Table 4). The most abundant species according to the biomass values was *Alnus incana*, and according to the stem number and coverage the *Salix* group. Two *Salix* species, *S. myrsinifolia* Salisb. and *S. phylicifolia*, as well as hybrids of these two species, were present on the field in the ratio 1:1:2. The most abundant taxon in the tree layer was *A. incana*, and in the shrub layer the *Salix* group. In addition, one *Pinus sylvestris*, one *Picea abies* and one *Betula pendula* were growing outside the sample quadrats. The coverage of woody plants was 5 %.

Table 6. Composition of *Alchemilla* species on the basis of the samples collected on 1.7.1977, the number (N) and frequency (F) (%) of *Alchemilla* samples. *Alchemilla* was not found on P68.

Taulukko 6. Alchemilla-pikkulajikoostumus 1.7.1977 kerättyjen satunnaisnäytteiden mukaan, näytteiden lukumäärä (N) ja frekvenssi (F) (%). Alchemilla ei esiintynyt P68:lla.

Field plot — *Peltolohko*	P65		P58		P53	
Sample plot — *Näyteala*	12		19		24	
Method — *Metodi*	N	F	N	F	N	F
Alchemilla acutiloba	—	—	24	89	6	19
A. monticola	16	23	—	—	7	22
A. subcrenata	3	4	2	7	5	16
Alchemilla sp.	—	—	1	4	1	3
Total — *Yhteensä*	19	27	27	100	19	60

The trees and shrubs formed 16 % of the plant biomass of the whole plant community when calculated on the basis of the combined 1977 and 1979 materials (Fig. 7). The field layer formed the other 84 %. The most abundant species in the plant community were *Alchemilla acutiloba*, *Agrostis tenuis* and *Alnus incana*

Field Plot 53

The field layer was monitored five times over the period 1971 to 1977. The vegetation had developed for 18 years before the onset of the study. Of the sown species, *Trifolium pratense* had disappeared completely and the proportion of *Phleum pratense* was only 3 %. The most abundant taxons on the field were *Agrostis tenuis*, *Deschampsia cespitosa* (L.) Beauv. and *Alchemilla vulgaris* (Table 2, Fig. 5, Appendix 2). Only rather slight changes took place in the species composition on the field plot during the following years. However, the same species were not dominant for any two years in succession. The following ten species formed a group of dominant species during the course of the study: *Alchemilla vulgaris*, *Agrostis tenuis*, *Taraxacum officinale*, *Deschampsia cespitosa*, *Elymus repens*, *Poa pratensis*, *Phleum pratense*, *Vicia cracca* L., *Cirsium helenioides* (L.) Hill. and *Festuca rubra*.

The vegetation on P53 varied in patches. In 1975 large clones of *Cirsium helenioides* occurred on two quadrats, with the result that it was the dominant species. Summer 1976 was poor. The temperature sum was low with the result that too large estimates of the biomass values, corrected according to the temperature sum, were obtained in comparison to the estimates for more normal years (Table 2). The dominant species in most of the years included *Alchemilla vulgaris*, *Agrostis tenuis* and *Taraxacum officinale* (Fig. 5). According to the *Alchemilla* analysis made in 1977, 37 % were *A. monticola,* 32 % *A. acutiloba* and 26 % *A. subcrenata* (Table 6). The percentage of grasses increased to some extent with time, from 47 to 53 %. The proportion of hemicryptophytes appeared to decrease as the proportion of geophytes and chamaephytes increased in 1976 and 1977.

The ground layer was heterogeneous throughout the course of the study (Table 3). A total of nine bryophyte taxons were found on, at the most, half of the sample quadrats. The most abundant bryophyte on the field plot at the beginning of the study was *Brachythecium albicans* and at the end of the study *B. salebrosum*. Other bryophytes found on the field plot were *B. curtum*, *B. starkei* (Brid.) B.S.G., *Brachythecium* sp. and *Plagiomnium ellipticum*.

There was no tree or shrub layer on the field at the onset of the study. Eight years later, there were nine species of trees and shrubs growing on the field (Table 4). The coniferous species were situated on the upper parts of the field on the northern side, and the deciduous species on the lower parts of the field on the southern side (Fig. 6). The *Salix* group was the most abundant taxon in both the tree and the shrub layers. There were *Salix* thickets on the lower part of the field, having spread from the edge of the adjacent forest. The *Salix* samples consisted of *S. phylicifolia* and *S. myrsinifolia* in the ratio 1:2. *Betula pubescens* Ehrh. and *Picea abies* were the most abundant of the other species. *Pinus sylvestris*, *Juniperus communis*, *Rubus idaeus*, *Alnus incana* and *Sorbus aucuparia* were also present on the field. The coverage of woody plants was 14 %.

Trees and shrubs comprised 23 % of the plant biomass of the whole plant community in P53 according to the combined materials for 1977 and 1979 (Fig. 7). The field layer accounted for the other 77 %. The percentage of the ground layer was only 0.1 %. The most abundant taxons in the whole plant community were the *Salix* and *Alchemilla* groups.

The field layer accounted for at least 70 % of the biomass of the plant communities in all the field plots throughout the course of the study. The hemicryptophytes comprised the major portion of the field layer. The proportion of geophytes and chamaephytes was small, apart from the youngest field. The most common and most abundant species were: *Phleum pratense*, *Agrostis tenuis*, *Elymus repens*, *Taraxacum officinale* and *Alchemilla vulgaris*. The most abundant species at the onset of the study were *Phleum* and *Elymus*, and at the end of the study *Alchemilla* and *Agrostis*.

The ground layer was poorly developed on all the fields. It did not comprise even 1 % of the plant biomass of the plant communities

on any of the field plots. The most abundant species was *Brachythecium albicans*, followed by *B. salebrosum*. A total of 13 taxons were present on the field plots. Some of the samples collected from certain areas were not identified (1.7 % of the biomass of bryophytes). The most abundant species, *B. albicans,* was more abundant on all the field plots during the initial and middle stages of the study, but was completely lacking by the end of the study. According to Koponen (1980), the species favours cultivated areas and thrives on dry grassy meadows, and does not belong to the original forest vegetation. All the other species which occurred on the field plots are, according to Koponen (1980), forest species growing in hygrophilous, partly mesophilous herbaceous forest stands. They were present on the youngest field plots towards the end of the study and occurred on the oldest field plots occasionally during the course of the study.

The coverage of the tree and shrub layers was not complete on any of the fields. Apart from the planted area, most of the woody plants were situated close to the edge of the adjoining forest. Natural reforestation proceeded rather slowly on the fields. It had not even started on the youngest (P68) in nine years. Reforestation had proceeded well on P65 even without any planting. Planting considerably accelerated reforestation. This took place even though only 65 % of the planted seedlings were still alive in 1979. The main reason for the high mortality rate appears to be the dense vole population which developed on the field plots (Teivainen, pers. comm.). When the seedlings were planted in spring 1972, the vole population on the fields reached a peak density of as high as 350 individuals/ha during the same summer (Koponen 1972, Hytönen 1975). A number of dead or damaged seedlings were observed the following summer. According to Teivainen, the most vole damage was done to *Populus*, followed by *Betula* and *Pinus*. *Picea* was damaged the least. Other reasons for the death of the seedlings can be put forward. According to Metsämuuronen et al. (1978), the field vegetation is a serious obstacle to tree seedlings planted on fields. The field vegetation competes for water and nutrients, and presses the seedlings down onto the ground during the winter following snowfall. Many insect and fungi which attack young trees at this stage can more easily attack seedlings which are weakened in this way (Juutinen et al. 1976, Löyttyniemi & Rousi 1979). There is no information available about the extent to which other damaging agents contributed to the seedling mortality in the studied fields.

The wood biomass in the oldest field plots was the greater, the older was the field plot. This applies to all the field plots when the planted trees in P65 are discounted. This was the case even though hay harvesting was stopped at the same time in 1968 in all the field plots. There appears to be differences in both the species involved and the rate of afforestation. *Salix* species and *Alnus incana* have spread vigorously by vegetative means using the underground network of roots developed prior to 1968, and thus reforestation has occurred at a faster rate than in the young field plots. For the same reason there were very little signs of the removal of thickets carried out in 1976 in the oldest field plots. According to the Field Reservation Act, shrub development has to be prevented and afforestation promoted in such abandoned fields. The *Salix* and *Alnus* thickets growing along the edges of P58 and P53 were removed in places. This only had a short term effect since new thickets had already developed from the stumps in the following year, in 1977.

One difference between the field plots was the abundance of *Pinus sylvestris* in P65. This occurred even without planting. *Salix caprea* was present in P65 but was completely absent from the others. *Alnus incana* was abundant in P58, but was almost completely lacking in the other field plots.

Natural afforestation of hay fields takes place at a slower rate than after open cultivation (Beckwith 1954). It was also slow on the fields studied. The coverage of trees and shrubs was only 14 % 26 years after grass had been sown and 12 years after the last mowing. Throughout most of the field plot areas studied here there was no tree cover at all.

Phleum pratense, which had been sown, and *Elymus repens* and *Agrostis tenuis*, which followed it in the succession, initially grew as a dense tall stand that effectively inhibited the initial development of the tree seedlings. Inhibition of seedling growth was so effective in P68 that only *Rubus idaeus* was found by the ninth year of succession. *Elymus repens*, which in the literature is frequently referred to as an allelopathic species (Quinn 1974, von

Schütt et al. 1975, Horsley 1977, Rice 1979), spread rapidly as *Phleum* gave way in P68 and, by the age of 7—8, it comprised almost half of the total plant biomass. The abundance and frequency of *Elymus* may alone account for the lack of trees and tree seedlings. In the upper part of the field where the abundance of *Elymus* was over 200 g/m^2, not even *Rubus* was able to grow (Appendix 2 and Fig. 6), even though it grew in the places where *Phleum* and *Agrostis* were at their most abundant.

Elymus repens was also abundant on the northern and southern areas of P65 where the mull layer was the thickest (Fig. 4. Appendix 2). Not one naturally-regenerated tree or shrub grew in 1979 in places where *Elymus* was growing at an abundance of at least 50 g/m^2 during the study (Appendix 2 and Fig. 6). The survival rate of planted seedlings on the planted area where *Elymus* was growing at an abundance of at least 50 g/m^2, was 41 %. The survival rate elsewhere in the planted areas was 70 %. Although there is much evidence to support the role of allelopathy in vegetation succession (Keever 1950, Klein & Miller 1980), it is not possible to conclude that *Elymus repens* definately prevents the growth and development of tree seedlings. Both phenomena may have some mutual explanation. The relationship between the presence of *Elymus* and reforestation was not as clear in the oldest field plots as on the young ones, even though in this case the main areas where natural regeneration occured were places where *Elymus* was not very abundant.

43. Classification and ordination of vegetation

431. Clustering

The material is divided on the basis of biomass and frequency into three clusters using five different clustering methods (p.15).

In this study, the minimum variance method was the best clustering method (Fig. 8) for both the biomass and the frequency values, and the furthest neighbour and group average methods were the second best. The nearest neighbour and the centroid methods were less suitable. The choice criteria were the same as those of Pakarinen (1976). When the minimum variance method is used with the biomass values, clusters of two, eight and nine plots are formed at the level of three clusters. The two youngest plots on P68 belong to the first cluster, the other plots on P68 and all the plots on P65 to the second cluster, and the plots on P58 and P53 to the third cluster. In the case of the frequency values, all the plots on P68 belong to the first cluster, and all the plots on P65 to the second cluster. Otherwise the clustering was the same as for the biomass values. The internal similarity of the sample plot clusters was used in the analysis of the results. The similarities were (B) 73 %, 31 % and 26 % and (F) 55 %, 51 % and 44 %. Westhoff & van der Maarel (1978) and Campbell (1978) have used a corresponding technique in the analysis of the classification levels of vegetation. The most homogeneous group was formed from the youngest plots and the most heterogeneous from the oldest ones. Dominance was emphasized when clustering was made on the biomass values. The frequency values depict the dispersal and the density of species and do not consider the abundance relationships between the different species to the same extent as the biomass values do. The succession changes were more quantitative than qualitative (Appendix 1), and thus analysis based on biomass values is more suited to this type of study. According to Jalas (1962) and Williams et al. (1973), the choice of data type (biomass versus frequency) is dependent on the heterogeneity of the material. The smaller the variation within the material, the greater is the need for quantitative information. Campbell (1978) and Dzwonko (1977b) propose that quantitative data should be used at the lower classification level and more qualitative data at the upper level.

The classification methods have originally been developed as a tool for numerical taxonomy (Sneath 1961, Sneath & Sokal 1973). The methods have since been applied in the classification of vegetation (Orlóci 1967). A great number of very diverse methods have been developed for this purpose (Orlóci 1975, Gauch 1982). Five clustering algorithms were used in this study. The furthest neighbour method and the minimum variance method are the most used and the most suitable (Pritchard & Anderson 1971, Pakarinen 1976, Dzwonko 1977a, Campbell 1978, Lausi &

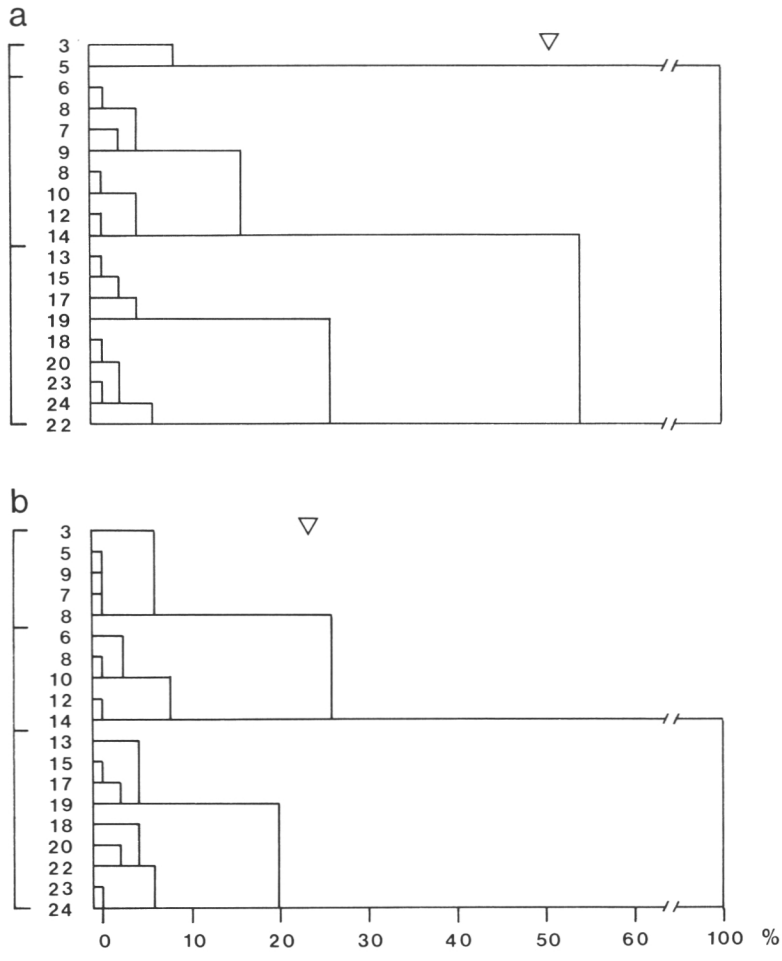


Fig. 8. Minimum variance clustering dendrogrammes for the sample plots calculated according to the biomass (a) and frequency (b) values. Clustering at the three group level on the basis of the relative dissimilarity (%) of the sample plots is marked with an arrow and depicted on the left. Sample plot symbols are succession age in years.

Kuva 8. Näytealojen luokitteludendrogrammit biomassojen (a) ja frekvenssien (b) mukaan minimivarianssiklusterimenetelmällä. Suhteellisen erilaisuuden (%) perusteella saatu ryhmittely kolmen ryhmän tasolla on merkitty nuolella sekä kuvattu vasemmalle. Näytealasymbolina on sukkessioikä vuosina.

Feoli 1979, Gauch 1980, Komarkova 1980, Gauch & Whittaker 1981). These methods gave the best results in this study, too.

Much development work has been done on these methods during the past few years and many new variations of clustering algorithms have been achieved (Jancey 1980, Gauch & Whittaker 1981, Gauch 1982, van der Maarel 1982). The present methods have simplified and speeded up the treatment and classification of vegetation materials owing to the fact that the role of the subjective element has been minimized.

432. Phytosociological classification

The minimum variance clustering method, based on the biomass data, was used for the phytosociological classification of the sample plots. The clusters, i.e. the meadow sub-associations, were named according to the most abundant and most frequent indicator species present on the plots belonging to each cluster. Each indicator species constituted at least 6 % of the total biomass on the sample plot and occurred at a frequency of at least 67 %. In addition, differential species were presented for each sub-association. Differential

species occurred almost solely in the association in question.

Agrostis tenuis, the species typical for all the sample plots, constituted at least 5 % of the total biomass on all the plots and occurred at a frequency of at least 67 %. The cluster of the two youngest plots on P68 was called a *Phleum pratense* meadow. *Phleum* constituted over 60 % of the biomass on these plots and occurred at a frequency of 100 %. The other common and abundant species were *Elymus repens* and *Agrostis tenuis*. The differential species of the sub-association were *Trifolium pratense* and *Lapsana communis*. The cluster comprising the other plots on P68 and all the plots on P65 was called an *Agrostis tenuis* meadow. *Agrostis* constituted at least 10 % of the biomass on the plots and occurred at a frequency of at least 67 %. The other common and abundant species were *Phleum pratense*, *Taraxacum officinale* and *Elymus repens*. The differential species of the sub-association were *Epilobium angustifolium* and *Rumex acetosella*. The cluster formed of the plots on the two oldest field plots (P58 and P53) was called an *Alchemilla* meadow because species of the *Alchemilla* group constituted at least 6 % of the biomass and occurred at a frequency of at least 77 %. The other common and abundant species were *Poa pratensis*, *Agrostis tenuis*, *Taraxacum officinale*, *Phleum pratense* and *Elymus repens*. The differential species of the sub-association were *Ranunculus acris*, *R. auricomus* and *Lathyrus pratensis*.

The difficulty in classifying grassland communities, i.e. plant communities consisting of herbs and grasses, is that their flora is extremely rich, ranging from the hygrophytes of the shore meadows to the xerophytes of dry meadows. Therefore a corresponding classification system has not been created for meadow vegetation in Finland like for forest and peatland sites. This was apparent already to the early classifiers of meadows in Finland (Norrlin 1870, Cajander 1907, Linkola 1916, 1921, Teräsvuori 1920, 1927a, b, c). Apart from the work of Teräsvuori, the earliest classifications were based on the moisture of the soil and only slight attention was paid to the floristic composition. Even later on, a more extensive classification of natural and seminatural grasslands has not been achieved, even though attempts have been made by Hansson & Myllymäki (1973) and Passarge (1976). Local meadow descriptions have been made, for instance, by Kalela (1939), Jalas (1946), Perttula (1950), Pudas (1961), Saarinen (1962), Kärkkäinen (1963), Jukola (1977), Hokkanen & Raatikainen (1977a), Hintsanen (1979) and Silfverberg (1980). The four last-mentioned references concern abandoned fields and the grouping presented in these studies corresponds to a great extent to the earlier classifications of natural and seminatural meadows. The difference is in the abundance of cultivated species and *Elymus repens* and *Epilobium angustifolium*.

The plant communities corresponding to the *Phleum pratense* meadows of this study are the young grass swards described by Paatela (1953), Jalas & Juusela (1959), Raatikainen & Raatikainen (1975), Silfverberg (1980) and Hokkanen & Raatikainen (1977a). Meadows corresponding to the *Agrostis tenuis* sub-association of this study have been described by Saarinen (1962), Larsson (1976) and Vepsä (1976). The *Anthoxanthum odoratum* type of Hokkanen & Raatikainen (1977a) also corresponds to these *Agrostis tenuis* meadows. The *Alchemilla* meadows of this study correspond to the *Alchemilla*-dominated plant communities of seminatural slope meadows in northern Savo described by Teräsvuori (1920) and the meadows described by Linkola & Tiirikka (1936), Saarinen (1962) and Hintsanen (1979). *Alchemilla* meadows of this study are also close to the *Deschampsia* and *Ranunculus* meadows described by Linkola (1916) and Teräsvuori (1920). Vepsä (1976), Hokkanen & Raatikainen (1977a) and Hintsanen (1979) have also described *Deschampsia* meadows although presumably growing on wetter sites than those of this study.

433. Polar ordination (PO)

Polar ordination was used to expose two major features of environmental variation according to the floristic similarities. In this method the end points of the axes are chosen from sample plots which differ as much as possible from each other. A number of alternatives were tested as the end points of the axes. On the basis of the available study materials the best ordination was obtained with the index of dissimilarity. Ordination based on biomass data was obtained (POB) using plots 3 and 24, 13 and 14 as the end

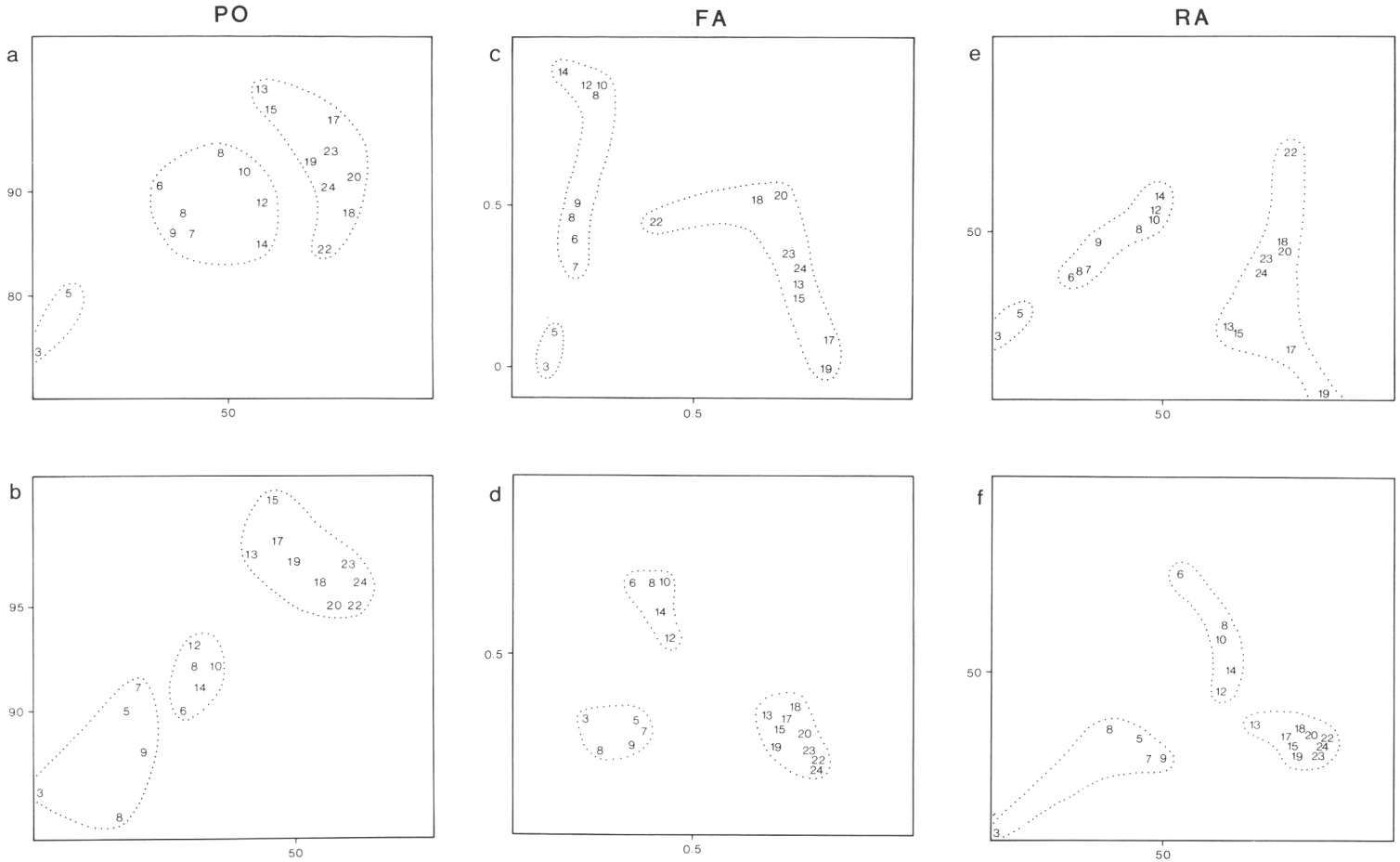


Fig. 9. Ordination of the sample plots with two axes of (a, b) polar ordination (PO), (c, d) factor analysis (FA) and (e, f) reciprocal averaging (RA), calculated using the biomass values (upper row) and the frequency values (lower row). Minimum variance clustering from Fig. 8 is depicted with dotted lines.

Kuva 9. Näytealojen ordinaatio kahden akselin suhteen (a, b) polaari ordinaation (PO), (c, d) faktorianalyysin (FA) ja (e, f) reciprocal averaging ordinaation (RA) avulla, biomassoista (ylärivi) ja frekvensseistä (alarivi) laskettuna. Kuviin on merkitty minimivarianssiryhmittely kuvasta 8 pisteviivalla.

points of the axes (Fig. 9a). The best result with the frequency values (POF) was obtained using plots 3 and 24, and 14 and 15 as the end points of the axes (Fig. 9b). The x axis of the ordination obtained according to both POB and POF could be interpreted as the time dimension. It arranged the field plots in the order of succession, but did not follow the order of succession age of the sample plots. The y axis also had features of the time dimension.

Sample plot ordination was tested using the index of similarity between the plots. Although the above-mentioned ordinations were the best, the distances between the sample plots did not correspond to those of the similarity indices.

434. Factor analysis (FA)

Factor analysis is an eigenvector method which can be used to summarize the vegetational variation by a required number of factors. A grouping of the sample plots can be attempted on the basis of the factor loading matrix (Q-analysis, cf. Wildi 1977, Kärenlampi 1972). The grouping is possible according to similar factor loadings while stressing, however, the maximum loadings. Three (frequency data, FAF) and five (biomass data, FAB) factor varimax solutions were chosen (Table 7). The five factor solution explains 95 % and the three factor solution 91 % of the total variance in the material. The first factor (F_1) in the five factor solution corresponds to elapsed time. F_2 is the inverse factor of the first one. F_3 mainly indicates the special features of P65, F_4 the special features of P53 and F_5 of P68. The three factor solution (FAF) gave essentially the same information as F_1, F_2 and F_3 in the five factor solution.

The sample plots formed six groups in the five factor solution (Table 7a). If three groups would be required, as suggested in the cluster analysis (Fig. 8), it would be difficult to

Table 7. The five factor (F) varimax solution of the sample plots on the basis of biomass values (a), the three factor solution on the basis of frequencies (b) and the corresponding groupings based on the maximum factor loadings (in boldface) and loadings over 0.3 (300). C = communality, S = variance explained (%). Minimum variance clustering (MVC) from Fig. 8 is depicted on the right.

Taulukko 7. Näytealojen viiden faktorin (F) varimax-ratkaisu biomassojen mukaan (a) ja kolmen faktorin ratkaisu frekvenssien mukaan (b) sekä maksimilatauksiin (paksut numerot) ja arvoja 0.3 (300) suurempiin latauksiin perustuva luokittelu. C = kommunaliteetti, S = selitysaste (%). Minimivarianssi klusteri (MVC) -ryhmittely kuvasta 8 on esitetty oikealla.

a

Field plot / *Pelto-lohko*	Sample plot / *Näyte-ala*	F 1	F 2	F 3	F 4	F 5	C	MVC
P68	3		**948**				956	
	5		**976**				985	
P65	6		**866**	386			971	
P68	9		**803**	469			978	
	8		**795**	422		341	965	
	7		**786**			478	948	
P65	8		433	**741**	426		960	
	10		387	**751**	466		967	
	12		311	**891**			970	
	14			**951**			975	
P53	22				**727**		658	
P53	18	**678**		381	465		873	
	20	**752**		438	359		928	
	23	**727**			603		964	
	24	**810**			383		958	
P58	13	**861**					971	
	15	**890**					980	
	17	**973**					974	
	19	**988**					980	
	S	31.9	27.9	21.1	10.3	3.4	94.5	

b

Field plot / *Pelto-lohko*	Sample plot / *Näyte-ala*	F 1	F 2	F 3	C	MVC
P68	3		**740**	353	721	
	7	387	**833**	326	950	
	5	367	**836**	341	951	
	9	358	**868**		959	
	8		**873**		897	
P65	12	465	585	**594**	911	
	14	438	496	**675**	894	
	6	359	456	**753**	904	
	8	410	416	**758**	915	
	10	436	432	**762**	957	
P58	13	**766**	419	352	887	
	19	**795**	396		862	
	15	**813**	398	320	921	
	17	**898**	327	337	906	
P53	18	**844**		385	905	
	20	**866**		301	922	
	22	**891**			917	
	23	**907**			963	
	24	**903**			926	
	S	41.5	29.2	20.2	90.9	

define the limits. The sample plots could be distinguished as three clear groups in the three factor solution (Table 7b).

The sample plot ordination was described with the first and third factors of the three factor (FAF and FAB) solution (Fig. 9 c, d). FAB ordination is more clearly related to the time dimension than FAF ordination. There were two clear contradictions in the FAB ordination and the similarities between sample plots: Plot 22 is too far away from other plots in P53 and the plots 13 and 24 were too near each other.

435. Reciprocal averaging (RA)

Reciprocal averaging provides three important environmental variations. The ordination is depicted by the first two axes. According to the biomass values (RAB), the first axis can be interpreted as a time dimension (Fig. 9 e). The second axis has features of the succession and it also expressed the difference between P58 and the other fields. The third axis contained features of the two previous axes, and its interpretation was difficult. The distance between plots corresponded to a large extent to the similarities between the sample plots.

The ordination according to the frequency values (RAF) is very different to that of RAB (Fig. 9 e, f). The first axis was also related to the succession (Fig. 9 f) dimension. The second axis expressed the special features of P65, although it also contained features of the succession. The sample plots were grouped in a different way than was obtained with RAB. The distance between the plots and the similarities have not been uniform in all respects. Plots 3 and 5 are too far away from each other.

436. Comparison of the methods

The comparison of different methods was made according to their ability to express succession. The methods used gave rather different results about ordination and grouping, although there were also common features.

The first axis is in all cases related to the succession dimension. Sample plots form a more or less clear bell-shaped curve with all three methods (Fig. 9). This means that the second axis expresses more than one dimension (Swan 1970, Noy-Meir & Austin 1970, Gauch et al. 1977). In this study the second axis contains features of succession but also other dimensions, which shall be analysed in Section 437. The succession order in each method is obtained by following the bell-shaped curve from left to right.

All the frequency based methods ordinate the field plots but not the sample plots according to their succession age. RAF gives the best indication of succession. FAB and RAB express P58 as the oldest field, otherwise the ordination of the field plots is like the succession age. The sample plot ordination on the succession is the most real in RA ordination.

All the above-mentioned methods resulted in groupings, partly even uniform ones, but it was hard to obtain grouping levels. Grouping is difficult on the basis of ordination methods because the distances between the sample plots at the two-dimensional level do not always correspond to the similarities. However, FA is not such a bad grouping method as would be deduced from the above. It gives the limited number of factors which could be included in the grouping. The classification obtained using the minimum variance clustering method (Fig. 8) was very close to the grouping of RAB (Fig. 9 e), the five factor solution of FAB and the three factor solution of FAF (Table 7 a, b, Appendix 1).

According to these results, PO was least suited to both the grouping and the ordination of the sample plots; the scores are scattered but they are situated in less of a bell-shaped pattern than with the other methods. There are some deficiencies of PO: the end points of the axes is selected before the analysis, as well as the algorithms to be used. A further drawback of PO is that it gives only two axes and it is not possible to use it for ordinating plant species.

FA produces as many factors as are required. As well as being an advantage, this is also a drawback of FA, because the researcher can thus affect the results. Another drawback is the linearity of the factors, the dimensions which they express not being linear in nature (Orlóci 1980).

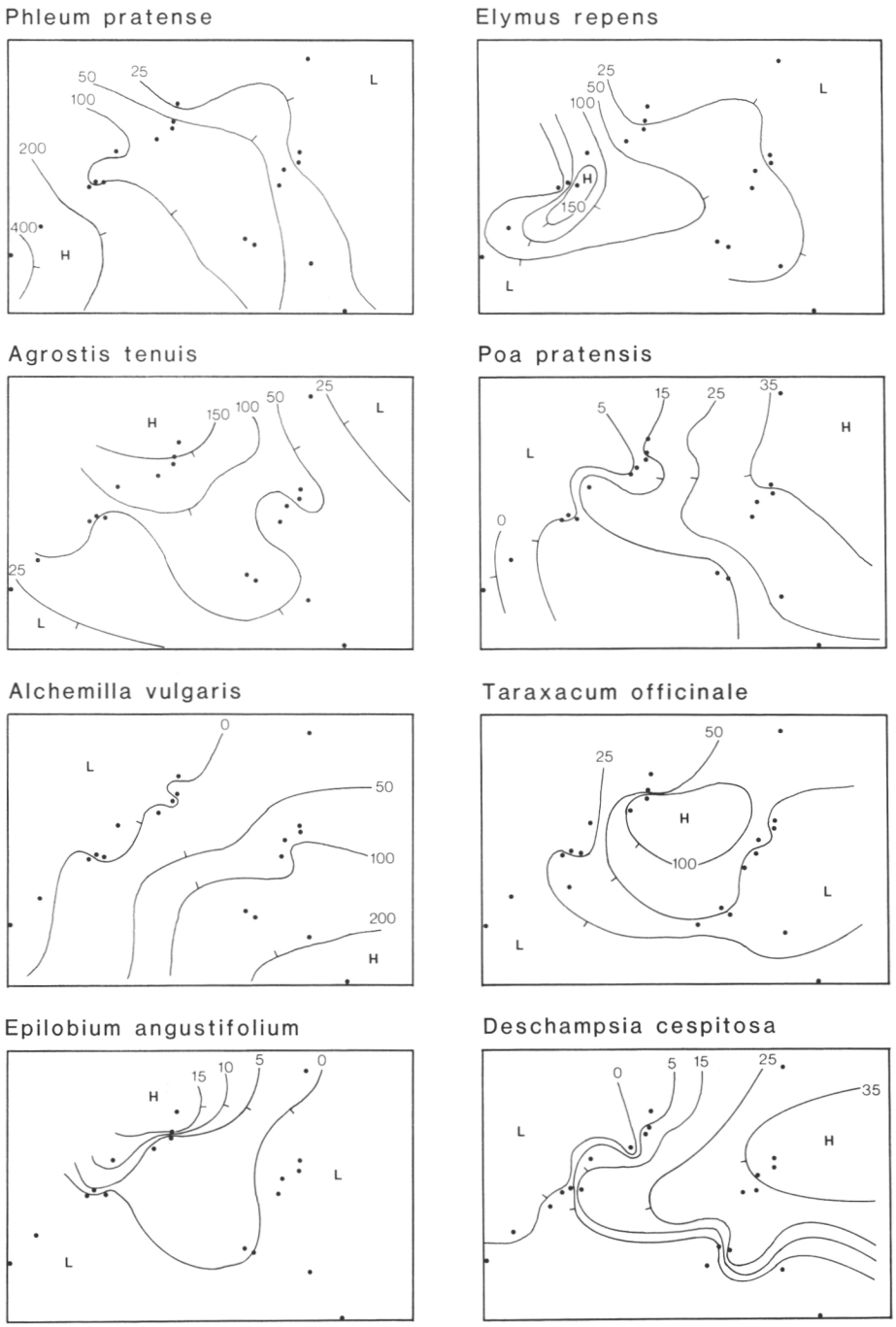


Fig. 10. Abundance distribution of some indicator species (g/m^2) on different sample plots in the RA ordination (See Fig. 9 e) by interpolating corrected biomass data. The high (H) and low (L) abundance patterns are marked on the ordination.

Kuva 10. Eräiden indikaattorilajien biomassajakautumat (g/m^2) näytealojen RA-ordinaatiossa (kuvasta 9 e) interpoloimalla korjatuista biomassoista. Ordinaatioon on merkitty lajien suurien (H) ja pienien (L) runsauksien alueet.

In comparison to the previous methods, RA has the advantage that the researcher cannot affect the results at any stage, and thus the ordination which is obtained is objective. In the programme used here, RA has at the most three axes. More are available, but they are difficult to interpret (Bouxin 1975). According to the results obtained here, RA appears to be a rather suitable method for the ordination of the sample plots in succession studies, and, on certain presumptions, for grouping. In fact, as Pakarinen (1976) suggests, a pure clustering method should be used for proper clustering and classification, as it will also provide the classification levels.

437. Ecological and phytosociological interpretation of ordination diagrammes

In order to make more precise analysis of the trends, the clusters obtained using RAB were depicted by interpolating the abundance of the different species from the measured biomass values (g/m^2) (Fig. 10). *Phleum pratense* had been sown on the field plots and thus was a species gradually declining with time, while the abundance of *Poa pratensis,* which is a species of mesophilic meadows, increased regularly. The succession proceeded vertically across the abundance curves of these species. The succession age, counted from the time of grass sowing, was thus depicted on both axes, although mainly on axis 1.

The succession age of a plant community is counted in succession studies from the last disturbance, which in the case of these field plots was the last time that they had been ploughed and sown. However, these field plots have also been disturbed to some extent more recently by mowing up until 1968. A second succession age can be counted from this period in time. According to this, these field plots were even-aged. No grass crop had been taken from P68, three from P65, eleven from P58 and sixteen from P53. Whether or not this is apparent in the vegetation of the field plots and, via this, in the ordination of the sample plots, is examined in the following.

Grass harvesting usually favours annual species and low rosette species, which remain relatively intact during mowing. All woody plants, high herbaceous plants and a number of tall non-tuft forming grasses, suffer from mowing (Paatela 1953, Tamm 1956, Raatikainen & Raatikainen 1975). The low rosette field plants included *Leontodon autumnalis* L., *Achillea millefolium* L., *Gnaphalium sylvaticum* L., *Rumex acetosella* L., *Campanula patula* L. and *Plantago major* L. The abundance curves of these species did not show any clear effects of the mowing in the RAB ordination (Fig. 10), but the effect was clear in the frequency curves of RAF ordination (Fig. 11). These species occurred in small amounts or not at all on P68. Large-sized herbs, which suffer from mowing at the best growing time, included *Vicia sepium* L., *Anthriscus sylvestris*, *Cirsium helenioides*, *Epilobium angustifolium*, *Filipendula ulmaria* and *Geranium sylvaticum*. Trees and shrubs, whose development is possible after yearly mowing has been discontinued, included *Pinus sylvestris*, *Picea abies*, *Betula pendula*, *Betula pubescens*, *Alnus incana*, *Juniperus communis* and several *Salix* species (Table 4). All of these species were either missing or were present in small numbers on all the field plots in the beginning of the study in 1971, but spread strongly during the course of the study. *Elymus repens*, which also suffers from mowing, had attained a very strong position before the age of ten years was reached on P68, which had not been mowed at all (Fig. 5). It accounted for 40 % of the biomass on this field plot, its abundance on the other plots not exceeding 12 % at any stage of succession. The time dimension of the second axis of the RAF ordination can thus be interpreted as representing succession following the termination of mowing.

In addition to the above time dimension, the second axis also contained a trend of another kind especially in RAB ordination. The occurrence of certain species was depicted in the RAB ordination in order to permit interpretation of this trend (Fig. 10). The abundance of *Agrostis tenuis* was concentrated on the upper side in the ordination. *Epilobium angustifolium* also formed similar curves (Fig. 10). *Agrostis* and *Epilobium* both favour acidic fresh soil (Ellenberg 1979). The results of the soil analyses supported this (Table 1). The amount of exchangeable calcium was smallest and the acidity highest in the soil on P65. Other species indicating acid

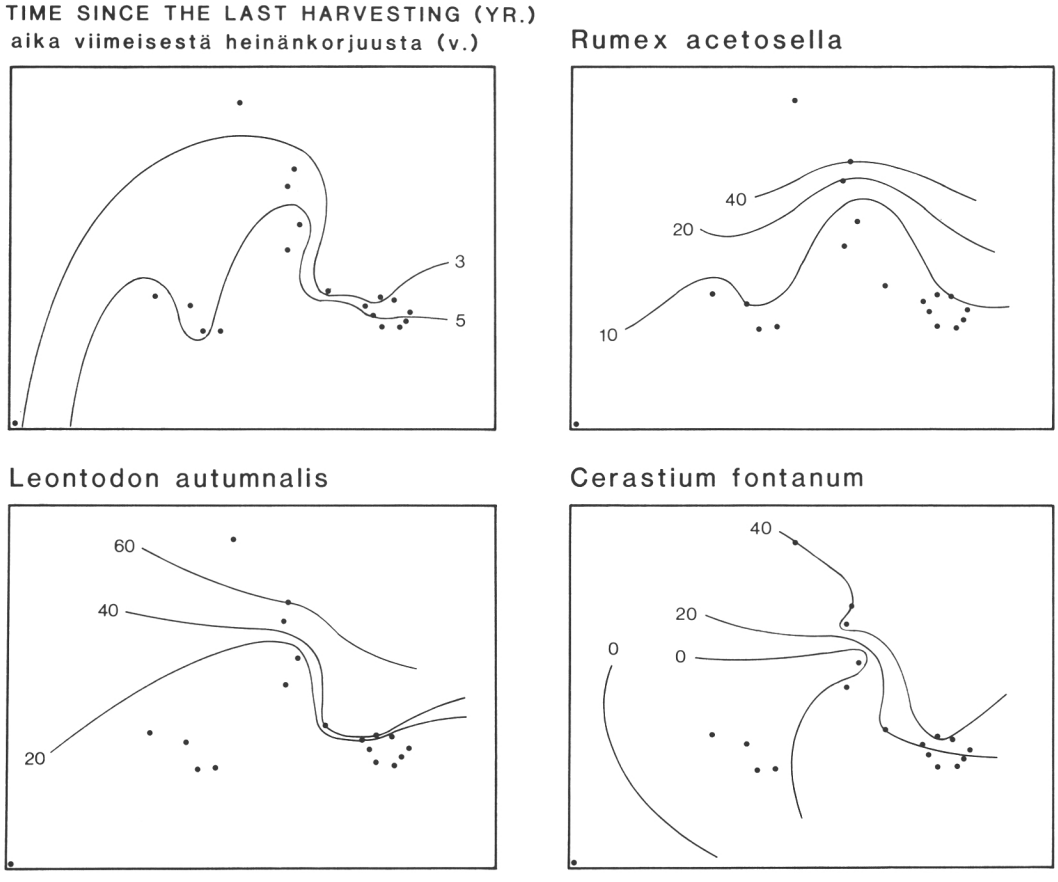


Fig. 11. Frequency distribution (%) of some species benefitting by harvesting and time since the last harvesting in the RA ordination of the sample plots (See Fig. 9 f).

Kuva 11. Eräiden heinänkorjuusta hyötyvien lajien frekvenssijakautumat (%) ja aika viimeisestä heinänkorjuusta näytealojen RA-ordinaatiossa (ks. kuva 9 f).

conditions which were concentrated in P65 are *Gnaphalium sylvaticum*, *Rumex acetosella*, *Stellaria graminea* L. and *Hieracium umbellatum* L. All these species are also to be found on fresh or dry sites. *Ranunculus auricomus* L., *Lathyrus pratensis* L., *Geranium sylvaticum* and *Alchemilla acutiloba* were at their most abundant on P58, which was placed at the other end of the studied dimension (Appendix 1). These species require a moist and less acid site (Jalas 1965, Ellenberg 1979). This dimension thus represented both the fertility and the moisture conditions at the same time. According to this gradient, P58 was the most fertile and moistest field plot, followed by P53 and P68. The driest and least fertile was P65.

The results of the gradient analysis indicated that the sample plots do not form a fully parallel succession series, since the development trend on each field was slightly different. Two of the youngest fields best fit together.

Inspite of the above-described small environmental differences, the field plots together represent a mesophilic succession series. The earlier described (p. 32) *Phleum*, *Agrostis* and *Alchemilla* sub-associations are according to Cajander's forest site type theory (1926) and, using the terminology of Jalas and Juusela (1959), a successional sub-associations of one and the same site type. P58 differ from the other field plots owing to the large dominance of *Alchemilla* species. If each

species of *Alchemilla* would have been included separately in the analysis, then the difference between P58 and the other fields would have been more pronounced since 90 % of the *Alchemilla* species which occurred on P58 were *A. acutiloba*. This species occurred in small numbers on P53 or was completely absent on the other fields (P68 and P65) (Table 6). Perhaps the possible analysis of the other apomictic group, *Taraxacum*, would have indicated the same difference between P58 and other field plots as *Alchemilla* did.

438. The study material as part of a more extensive material

The above conclusions have been drawn on the basis of relatively small material comprising 19 sample plots. The validity of these conclusions has been tested by analysing the material together with a more extensive abandoned field material using RAF (data from Teivainen et al. 1979). This control material consisted of 26 different-aged abandoned fields, part of which were originally hay fields and part fields cultivated in different ways (Korhonen 1978).

The ordination of the sample plots was depicted on the first and second axes (Fig. 12). The sample plot scores formed a curve passing from the bottom left up to the right. The hay field material was placed separately up on the right, and the control material down on the left. The youngest of the hay fields was placed on the right side of the ordination and the oldest up on the left. The control material could be divided into two age groups, fields more than eight years old and younger than eight years old (Fig. 12). The first axis in this combined material also appeared to represent succession. Succession proceeded gradually from the bottom on the right up to the left. According to the ordination, the control material consisted of fields of approximately the same age as those in the hay field material.

The relative frequencies of the species were used in interpreting the second axis (Fig 13). The occurrence of *Agrostis tenuis* was concentrated in the upper part of the ordination diagramme. The frequencies of *Phleum pratense* decreased on the old hay fields where it had been sown, but on the other fields it

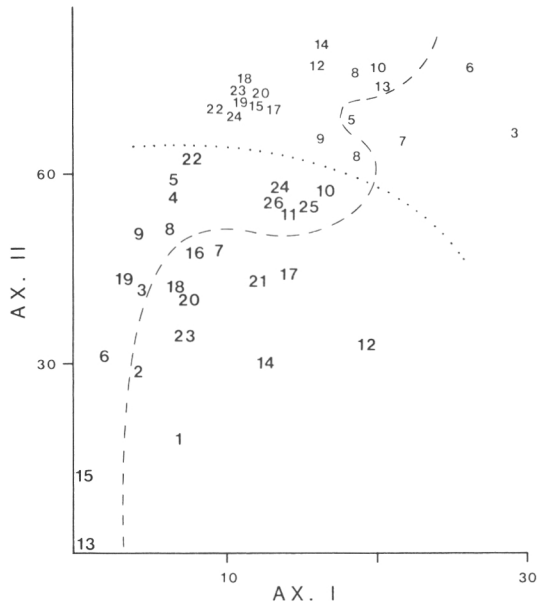


Fig. 12. The frequency based RA ordination with two axes for the research sample plots (small numbers) and the control fields (big numbers) (data from Teivainen et al. 1979). The numbers for the research field plots refer to the succession age of the plots, and for the control material to the sample plot number. The materials are separated by the dotted line. The plots younger than eight years are on the right of the dashed line.

Kuva 12. Heinäpeltoalojen (pienet numerot) ja kontrollipeltojen (isot numerot) (Teivaisen ym. 1979 aineisto) RA-frekvenssiordinaatio kahden akselin suhteen. Heinäpeltoaineiston numerot ovat alojen ikäsymboleita, kontrolliaineiston näytealanumeroita. Aineistot on erotettu pisteviivalla. Kahdeksaa vuotta nuoremmat alat ovat katkoviivan oikealla puolellla.

became more common as succession proceeded. *Alchemilla vulgaris* was concentrated on the upper and *Deschampsia cespitosa* on the lower side. *Elymus repens* was common on the hay fields of all ages, but in the control material it was concentrated in the fields which were younger than eight years. The frequencies of *Rumex acetosella* were concentrated in the upper part of the ordination, and that of *Filipendula ulmaria* in the bottom part. According to the ecological indicator values of the plant species (Ellenberg 1979), the second axis represents the moisture gradient. The most hygrophilic end represents the *Filipendula ulmaria* dominated, tall herb field (Teivainen et al. 1979), and the driest, mesophilic end the *Agrostis tenuis* dominated field (P65). It would appear to be possible to determine the succession age of an unknown

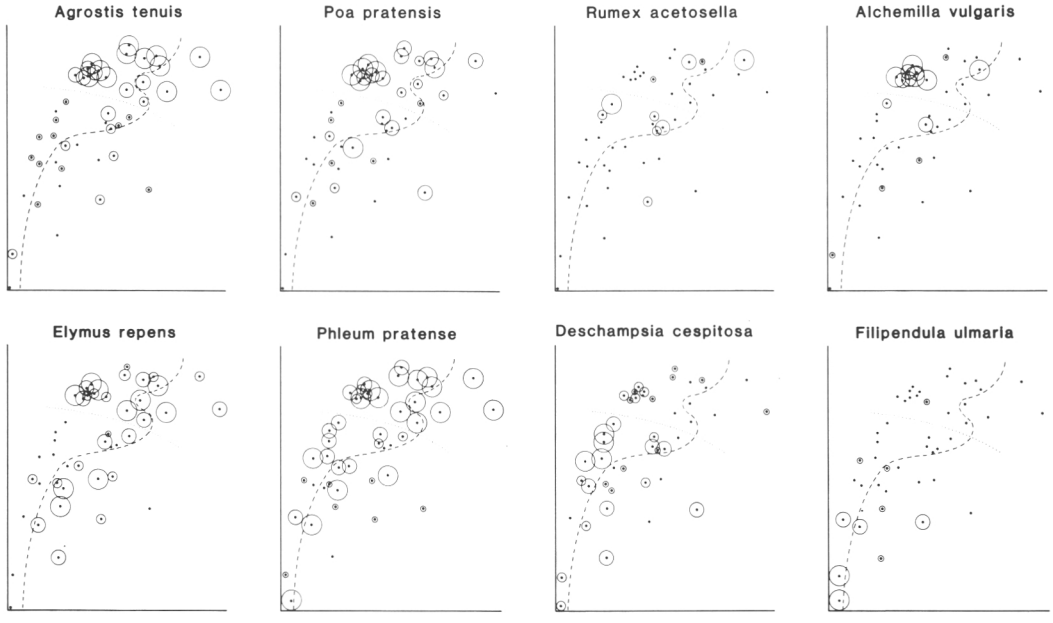


Fig. 13. The concentration of occurrence of some indicator species in the frequency based RA ordinations of the research and control sample plots. The circle size indicates frequency. See Fig. 12 for further explanations.
Kuva 13. Eräiden indikaattorilajien yleisyyden painopisteet heinäpelto- ja kontrollinäytealojen frekvenssipohjaisessa RA-ordinaatiossa. Ympyrän koko kuvaa frekvenssiä. Ks. kuva 12.

material using RA if the analysis includes a material representing a clear succession series. The ordination results obtained using the hay field material alone, also appear to be valid in the control material.

44. Grouping of the plant species

441. Correlation analysis (CA)

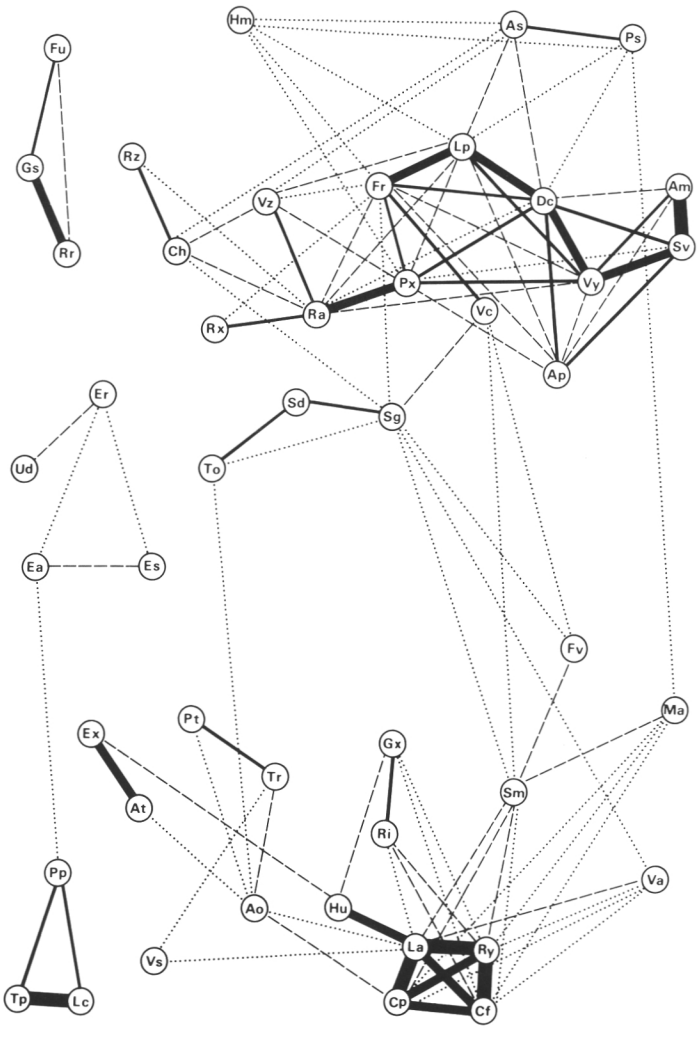
A plexus diagramme was drawn of all the positive correlations greater than 0.5 in the correlation matrix (according to the biomass values) (Fig. 14). Those species which occurred at the most on two plots were omitted from the material. The principle followed in drawing the figure was that highly positively correlated species were placed close to each other and were joined together by a thick line. Species which occurred at their most abundant at the same time on the same fields, form more or less tight groups.

Succession proceeds from the bottom part of the figure upwards. The method separates out the species on the different fields into their own loose clusters, and certain species groups and gradients can be found in the material. However, this method is not suitable for making a more detailed analysis of the trends because the figure on which the clustering is based is a monoplane and there is considerable leeway in the placing of the points representing the species.

442. Factor analysis (FA)

In addition to the sample plots, factor analysis can also be used for classifying plant species. Since it was found during the analysis of the sample plots that the succession changes become most clearly apparent when the biomass values are used, only the results calculated according to the biomass values are presented.

The two factor solution was used to depict the ordination of the species (Fig. 15a). This solution accounted for 28 % of the total variance among the variables. The proportion of the first factor was 15 % and of the second 13 %. The species which were concentrated in P68 are at the bottom on the left of Fig.



Am Achillea millefolium
Ap A. ptarmica
At Agrostis tenuis
Ao Anthoxanthum odoratum
As Anthriscus sylvestris
Cp Campanula patula
Cf Cerastium fontanum
Ch Cirsium helenioides
Dc Deschampsia cespitosa
Ea Equisetum arvense
Es E. sylvaticum
Er Elymus repens
Ex Epilobium angustifolium
Fr Festuca rubra
Fu Filipendula ulmaria
Fv Fragaria vesca
Gs Geranium sylvaticum
Gx Gnaphalium sylvaticum
Hu Hieracium sp.
Hm Hypericum maculatum
Lc Lapsana communis
Lp Lathyrus pratensis
La Leontodon autumnalis
Ma Myosotis arvensis
Pp Phleum pratense
Ps Pimpinella saxifraga
Px Poa pratensis
Pt P. trivialis
Ra Ranunculus acris
Rx R. auricomus
Rr R. repens
Ri Rubus idaeus
Rz Rumex acetosa
Ry R. acetosella
Sd Silene dioica
Sv S. vulgaris
Sg Stellaria graminea
Sm S. media
To Taraxacum officinale
Tp Trifolium pratense
Tr T. repens
Ud Urtica dioica
Va Veronica arvensis
Vc V. chamaedrys
Vs V. serpyllifolia
Vy Vicia cracca
Vz V. sepium

CORRELATIONS
korrelaatiot

0.500–0.599
0.600–0.699
0.700–0.799
0.800–0.899
0.900–0.999

Fig. 14. Plexus diagramme of the statistically significant ($p < 0.05$) interspecific correlations. The thickness of the line and distance between species are related to the magnitude of the correlations.

Kuva 14. Plexus-diagrammi lajien välisistä tilastollisesti merkitsevistä ($p < 0.05$) korrelaatioista. Viivan paksuus ja lajien välinen etäisyys ovat suhteessa korrelaation suuruuteen.

15a, those which were concentrated in P65 are in the upper central part of the figure, and the species from P53 are at the bottom on the right. *Phleum pratense* received the largest negative loadings for F_1, *Festuca rubra* the largest negative loadings for the second factor, and *Leontodon autumnalis*, *Rumex acetosella* and *Campanula patula* the largest positive ones. This factor corresponded partly to elapsed time but had also characters of fertility status. The latter species were found to be species which withstand mowing. The interpretation thus appears to be approximately the same as that for the sample plot material (p. 37). The species could be arranged in the order of succession according to these factors when the nonlinearity of the species in the ordination diagramme was taken into account. However, the problem was that a number of the abundant species were missing from this solution (e.g. *Agrostis tenuis, Alchemilla vulgaris*).

There were more species in the five factor solution, and even more in the ten factor solution. However, the drawback with these solutions was that factors which had been

relatively clear in the two factor solution were broken up into sub-factors when the five or ten factor solution was applied. The different fields, or even single sample plots, had their own factors.

The five factor solution accounted for 52 % and the ten factor solution for 79 % of the total variance among the species. The first factor of the two factor solution divided in the five factor solution into two parts: F_1 and F_5, and the second factor also into two parts: F_2 and F_3. A further factor was formed, F_4, which was difficult to interpret.

The classification of the plant species into ecological species groups was made using the five factor solution (Table 8). The species were arranged according to uniform factor loadings while stressing maximum loadings. Annual weeds and species sown on the fields belong to the first species group. These species were at their most abundant on the young plots. All the species in the second species group were geophytes and occurred at their most abundant on the youngest field between the ages of 5—9 years. Most of the species belonging to the third species group were low,

Table 8. A five factor varimax solution of species occurring on the sample plots on the basis of biomass values. (See further explanations in Table 7).
Taulukko 8. Näytealoilla esiintyneiden lajien viiden faktorin varimax-ratkaisu biomassojen mukaan (ks. tarkemmat selitykset taulukosta 7).

	Species — *Lajit*	Factors — *Faktorit* 1	2	3	4	5	C
1	*Lapsana communis*					**—933**	902
	Trifolium pratense					**—908**	850
	Phleum pratense	396				**—808**	857
2	*Equisetum arvense*	**408**					385
	Equisetum sylvaticum	395			**—424**		420
	Elymus repens	**378**					327
3	*Rubus idaeus*	363	**—640**				637
	Rumex acetosella		**—967**				952
	Cerastium fontanum		**—939**				908
	Leontodon autumnalis		**—916**				934
	Campanula patula		**—911**				854
	Stellaria media		**—704**				629
	Gnaphalium sylvaticum		**—599**				429
	Myosotis arvensis	—406	**—580**				552
4	*Anthoxanthum odoratum*		—472	**—527**			594
	Epilobium angustifolium	429		**—538**			623
	Agrostis tenuis	464		**—629**		365	769
	Fragaria vesca			**—771**			660
	Silene dioica	—387		**—685**			658
5	*Veronica serpyllifolia*		—373	—405	**469**	—359	719
	Taraxacum officinale	—375			**438**	302	522
	Alchemilla vulgaris			377	**377**		460
6	*Ranunculus auricomus*	**—513**			314		493
	Veronica officinalis	**—528**					338
	Stellaria graminea	**—639**	—333	—482			764
	Achillea ptarmica	**—619**		—374	—346		690
	Hypericum maculatum	**—453**			—345		368
	Anthriscus sylvestris	**—515**			—426		476
	Deschampsia cespitosa	**—671**			—394		683
	Vicia cracca	**—626**					600
	Veronica chamaedrys	**—719**					583
	Poa pratensis	**—725**				381	758
	Vicia sepium	**—748**					586
	Ranunculus acris	**—774**					735
	Lathyrus pratensis	**—851**					816
	Festuca rubra	**—922**					866
	Variance explained % Selitysaste %	14.2	11.8	9.2	7.8	8.6	51.6

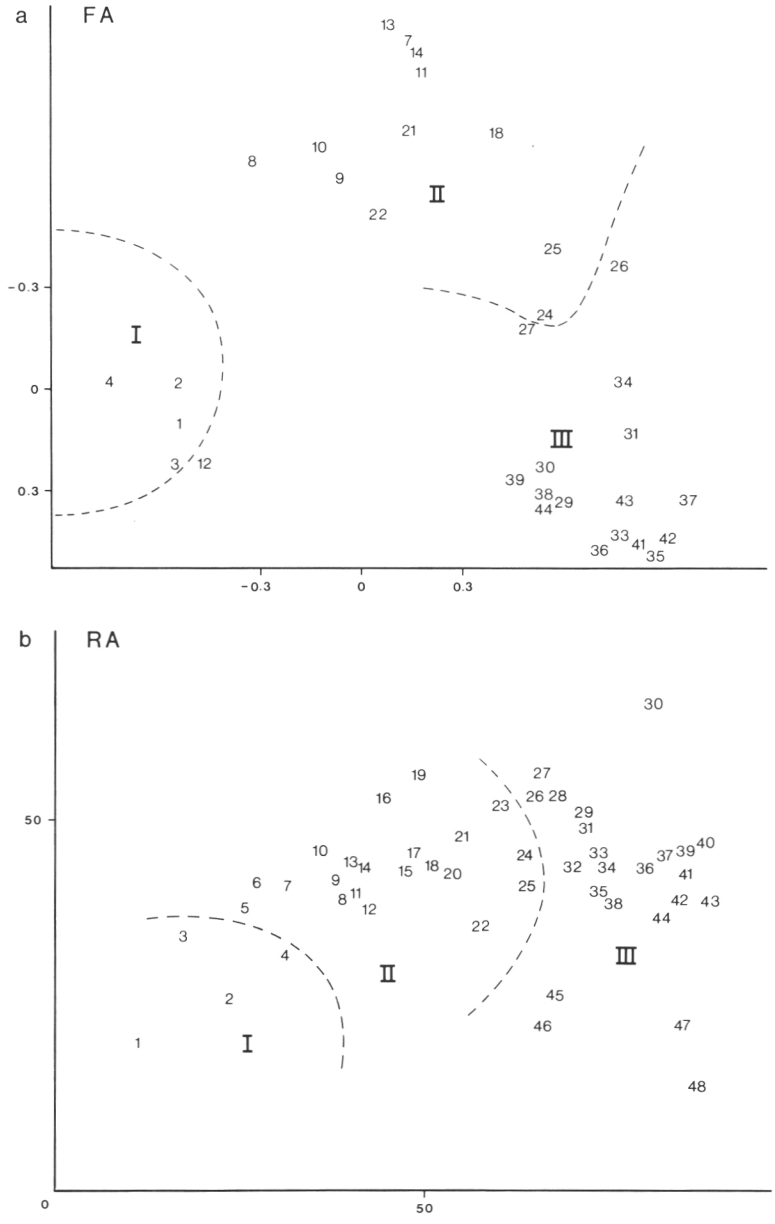


Fig. 15. Ordination of the species according to the biomass values as a two factor varimax solution of FA (a) and with respect to the two axes of RA (b). The species in succession classes I—III are separated by the broken line. I succession class (I sukkessioluokka): 1 = *Trifolium pratense*, 2 = *Lapsana communis*, 3 = *Equisetum arvense*, 4 = *Phleum pratense*, II succession class (II sukkessioluokka): 5 = *Urtica dioica*, 6 = *Equisetum sylvaticum*, 7 = *Rumex acetosella*, 8 = *Veronica serpyllifolia*, 9 = *Gnaphalium sylvaticum*, 10 = *Rubus idaeus*, 11 = *Cerastium fontanum*, 12 = *Elymus repens*, 13 = *Leontodon autumnalis*, 14 = *Campanula patula*, 15 = *Trifolium repens*, 16 = *Epilobium angustifolium*, 17 = *Poa trivialis*, 18 = *Stellaria media*, 19 = *Hieracium* sp., 20 = *Agrostis tenuis*, 21 = *Anthoxanthum odoratum*, 22 = *Cirsium arvense*, 23 = *Fragaria vesca*, 24 = *Taraxacum officinale*, 25 = *Myosotis arvensis*, III succession class (III sukkessioluokka): 26 = *Stellaria graminea*, 27 = *Silene dioica*, 28 = *Rumex acetosa*, 29 = *Anthriscus sylvestris*, 30 = *Cirsium helenioides*, 31 = *Achillea ptarmica*, 32 = *Achillea millefolium*, 33 = *Deschampsia cespitosa*, 34 = *Veronica chamaedrys*, 35 = *Poa pratensis*, 36 = *Vicia cracca*, 37 = *Festuca rubra*, 38 = *Hypericum maculatum*, 39 = *Silene vulgaris*, 40 = *Pimpinella saxifraga*, 41 = *Ranunculus acris*, 42 = *Lathyrus pratensis*, 43 = *Vicia sepium*, 44 = *Ranunculus auricomus*, 45 = *Ranunculus repens*, 46 = *Filipendula ulmaria*, 47 = *Alchemilla vulgaris*, 48 = *Geranium sylvaticum*. See text for further explanation.

Kuva 15. Lajien ordinaatio biomassojen mukaan kahden faktorin varimax-ratkaisuna (a) sekä RA:n kahden akselin suhteen (b). Sukkessioluokkien I—III lajit on erotettu katkoviivoin. Tarkemmat selitykset tekstissä. Lajit, ks. engl. teksti.

rosette hemicryptophytes. These occurred at their most abundant on P65 between the succession ages of 6—10 years. The species in the fourth species group were hemicryptophytes and occurred at their most abundant on P65 between the succession ages of 10—14 years. The fifth and sixth species groups consisted almost solely of hemicryptophytes: three grasses and a large group of herbs characteristic of old meadows.

443. Reciprocal averaging (RA)

It was possible using RA-analysis to arrange the species with respect to the same three axes as was the case with the sample plots. The species are presented with respect to the first two axes in Fig. 15 b. The species scores are ordinated nonlinearly, as was the case with the sample plots. The species for P68 are down on the left, for P65 in the upper centre, for P58 at the bottom on the right, and for P53 at the top on the right in the diagramme. The species ordination confirms the interpretation of the axes presented in connection with the ordination of the sample plots: the succession axis is nonlinear, time progresses from the bottom left up and down towards the right, and the moisture and nutrient status increases from the top left down to the right. The species can be put into a succession order, but clear classification is not possible using this method. Both the plots (Fig. 9 e) and the species (Fig. 15 b) have been ordered with the aid of RAB by taking into account arch distortion of the axes (Appendix 1).

444. Comparison of the methods

RA appeared to be the best of the ordination methods used here. It gave the position coordinates for all the desired species. It could be used to ordinate the species into the order of succession. It separated the species on P58 into their own group. However, it could not be used for classifying the species. RA stressed the importance of the first two and the clearest gradients and it was not possible to obtain more interpretable axes. When succession is to be elucidated from a more heterogeneous material than this, the other gradients may be more powerful than succession and thus succession could be remained completely unobserved.

The superiority of the methods used for the ordination of sample plots and species has been tested by, for instance, Austin (1977), Gauch et al. (1977) and del Moral (1980). All have come to the conclusion that RA is the most satisfactory method so far developed. Del Moral (1980) has used the degree of distortion and skewness of the ordination, the ability to separate stands, the efficiency of species ordination, ease of interpretation, objectivity and how the method recovers a classification of the same data as the evaluation criteria. Gauch et al. (1977) have reported that RA produces the most successful ordination when treating a heterogeneous material and long vegetation gradients. Hill & Gauch (1980) have observed that there are two problems associated with RA: (1) arch effect of the axis, (2) distances at the ends of the first axis are compressed relative to the middle. Both these drawbacks were evident in the RA ordination done in this study. The distortion of the second axis was clear in both the sample plot and the species ordinations (Figs. 9 e and 15 b). The compression of the first axis was most clearly apparent as a concentration of the older plots on the right side of the ordination. Hill & Gauch (1980) have corrected both these errors in a new RA programme which is called detrended correspondence analysis (Decorana).

FA gave the required number of factors and thus brought out the weaker trends. FA could be used to classify the plant species, although not the classification levels. Despite these advantages, there were found to be a number of drawbacks: values were not obtained for all the species, the factors were not necessarily the same in the species and plot analyses. In addition, the species group of P58 could not be included in the five factor FA solution, but only in the 10 factor solution. As the relationships between species change with time, linear correlation does not always give, according to Orlóci (1980), the correct picture of the relationships between species during the progression of succession. This is also the fact with factor analysis and with other methods used for classifying species. In the comparisons of ordination methods mentioned above, a method relatively closely related to FA, principal component analysis (PCA), has in most cases been used instead of FA. The FA used in this

study is based, however, on a product-moment correlation matrix, as opposed to the case for PCA, in which standardized similarities are used (Noy-Meir & Whittaker 1977). According to Pakarinen & Ruuhijärvi (1978), this method gives a considerably better result than PCA does. Pakarinen & Ruuhijärvi have come to the conclusion that FA is better than RA in depicting more than two gradients. They suggest that both methods are just as suitable for depicting two gradients.

445. Succession classes

The most significant trend in the material, according to both RA and FA, was time dimension. Both the axes of RA, as well as the factors of all the solutions of FA, were for the most part succession axes. Thus the species in the material could be divided into succession classes using these methods. The principle used here was that the succession order obtained from RA in Fig. 15 b was followed and the classification from FA was applied to it (Appendix 1). The species were divided into three classes The first group of FA-grouping (Table 8) rearranged to form the first succession class, the second, third, fourth and fifth group to form the second succession class and the sixth group to form the third succession class. As an exception, *Equisetum arvense* belonged to the first, *Ranunculus repens*, *Silene dioica* and *Alchemilla vulgaris* to the third succession class. The abundance of the species belonging to the first succession class decreased throughout the course of the study. The abundance of the species in the second class initially increased, but later on decreased with time. The abundance of the species in the third class was at its greatest on the oldest fields. Division of the sample plots by the clustering method into three groups agreed with the classification of the plant species obtained with FA and RA to the extent that the abundance of the species in the first succession class was concentrated in the *Phleum pratense* sub-association stage, the second succession class in the *Agrostis tenuis* stage and the third succession class in the *Alchemilla vulgaris* stage (Appendix 1).

Species of succession class I (pioneers) on hay fields are also, according to Raatikainen & Raatikainen (1975) and Paatela (1953), at their most abundant on very young fields. However, *Urtica dioica*, *Equisetum sylvaticum*, *Rumex acetosella*, *Cerastium fontanum*, *Elymus repens*, *Epilobium angustifolium*, *Stellaria media*, *Cirsium arvense* and *Myosotis arvensis*, which belong to the second class in this study, are also regarded as pioneers in the above-mentioned studies. The contradiction with these studies is due in the case of some of the species to pure chance (*Stellaria media*, *Myosotis arvensis* and *Cirsium arvense*) and also to the fact that grass harvesting ceased on the fields before the study was started (*Elymus repens*, *Equisetum sylvaticum* and *Epilobium angustifolium*). Thus the materials are not in this respect comparable. Similarly, mowing resulted in the fact that the species of the old fields in this study, *Stellaria graminea*, *Filipendula ulmaria*, *Anthriscus sylvestris*, *Achillea ptarmica*, *Ranunculus repens* and *Cirsium helenioides*, were not according to the previously-mentioned studies species which clearly increased in abundance as the grass leys aged. *Silene vulgaris* is known to be a common species on young areas influenced by human activities, but in this study it occurred on the oldest field and appeared to be even on the increase as time went by. According to Jalas (1965), the species may occur in Savo on just the same sort of grass meadows as were included in this study.

45. Succession models

An attempt was made to estimate the changes in the proportions of species successional classes over time using the succession model. This study is primarily concerned with the succession stage of so-called treeless open fields and the model is only valid for the field layer of the treeless stage (tree coverage < 18 %). Changes occur in the succession as the effect of the tree cover on the field increases, but this is not taken into account in this model.

The matrix model used here has been constructed using the method of least squares (Kauppi et al. 1978). The corrected relative biomass values (Table 2) of the species were used as the material in developing the model, and the species classification obtained using RA and FA (Table 8, Fig. 15 and Appendix 1).

Succession models were calculated separate-

ly for each field and also for different combinations of the fields (Table 9). The matrix model depicts how much and at what rate each species group occupies the area of the other groups.

The suitability of the models with the field plots can be examined visually in Fig. 16. The matrix models calculated from the different field plots and combinations for the field plots have been fitted to the material for each field plot. The fit of the model for each field plot calculated from its own material differed only very slightly from the measured values. The only exception to this was the oldest field plot, whose model could not be fitted to any material due to the fact that it gave meaningless values. This is due to the fact that the small changes which occurred in the species classes took place in an opposite direction to the situation on the other fields. The estimates given by the model for P58 differed the least from the measured values. If models 1, 2 and 3 are fitted to the materials for other fields, then the first model (i.e. for P68) best fits the material of all the fields. The model for P65 gives too large a value for the proportion of the second species group, and the model for P58 too small a value.

Of the models calculated from the combined materials for two, three or four field plots, the models of P68, P65 and P58, as well as from all the fields, best fitted all the materials. Some of the other models gave negative values, and some of them values which did not in other respects fit the material.

Overall, it can be said that almost all the models predicted extremely well the development of the pioneer species (class I) during the course of succession. On the other hand, the different models gave rather a deviating picture of the succession of the second and third species group. Rather few changes took place on P65 and P53 during the course of the study between species classes II and III. This is also apparent in the models calculated from the plots in question, in that the second species group is very slowly replaced by the third one. The displacement is faster if the model includes P68 or P58. In addition, there is a clear level difference between species classes II and III when the two youngest fields are compared to the two oldest ones. This is evident in almost all the models when they are fitted to other fields.

Table 9. The matrix models (1—13) constructed using the least square sums method for different field plots and combinations of the field plots in order to predict the replacement rate in three succession classes of species (I—III) (Fig. 16) over time on the basis of corrected relative biomass values. The matrices are read from the top of the columns. The residual square sums (RSS) for the models are given. See text for further explanations.

Taulukko 9. Matriisimalleja (1—13), jotka on laadittu pienimmän neliösumman menetelmällä eri peltolohkoille ja niiden yhdistelmille tarkoituksena ennustaa kolmen sukkessioluokan lajien korvautumisnopeus ajassa suhteellisten korjattujen biomassojen mukaan. Matriiseja luetaan sarakkeiden yläpäästä alkaen. Mallien jäännösneliösummat (RSS) annetaan. Katso tarkemmat selitykset tekstistä.

Model- *Malli*	Fields plot *Peltolohko*	Yearly rate of replacement between biomass proportions of succession classes *Sukkessioluokkien biomassaosuuksien väliset vuotuiset korvautumisnopeudet*				RSS
			I	II	III	
1	P68	I	0.811	0.000	0.000	
		II	0.201	0.943	0.000	
		III	—0.012	0.057	1.000	8.02
2	P65	I	0.765	0.000	0.000	
		II	0.197	0.990	0.000	
		III	0.038	0.010	1.000	5.18
3	P58	I	0.822	0.000	0.000	
		II	0.192	0.794	0.000	
		III	—0.014	0.206	1.000	3.15
4	P53	I	1.252	0.000	0.000	
		II	0.214	0.922	0.000	
		III	—0.466	0.978	1.000	4.26
5	P68 + 65	I	0.802	0.000	0.000	
		II	0.172	0.990	0.000	
		III	0.026	0.010	1.000	6.56
6	P68 + 58	I	0.822	0.000	0.000	
		II	0.302	0.796	0.000	
		III	—0.124	0.204	1.000	7.74
7	P68 + 53	I	0.812	0.000	0.000	
		II	0.176	0.974	0.000	
		III	0.012	0.026	1.000	7.80
8	P68 + 65 + 58	I	0.808	0.000	0.000	
		II	0.210	0.942	0.000	
		III	—0.018	0.058	1.000	11.56
9	P68 + 65 + 53	I	0.802	0.000	0.000	
		II	0.178	0.984	0.000	
		III	0.020	0.016	1.000	7.00
10	P68 + 65 + 58 + 53	I	0.808	0.000	0.000	
		II	0.200	0.952	0.000	
		III	—0.008	0.048	1.000	9.00
11	P65 + 58	I	0.842	0.000	0.000	
		II	0.408	0.848	0.000	
		III	—0.250	0.152	1.000	13.00
12	P65 + 53	I	0.780	0.000	0.000	
		II	0.228	0.974	0.000	
		III	—0.008	0.026	1.000	6.79
13	P58 + 53	I	0.874	0.000	0.000	
		II	—0.270	1.004	0.000	
		III	0.396	—0.004	1.000	6.29

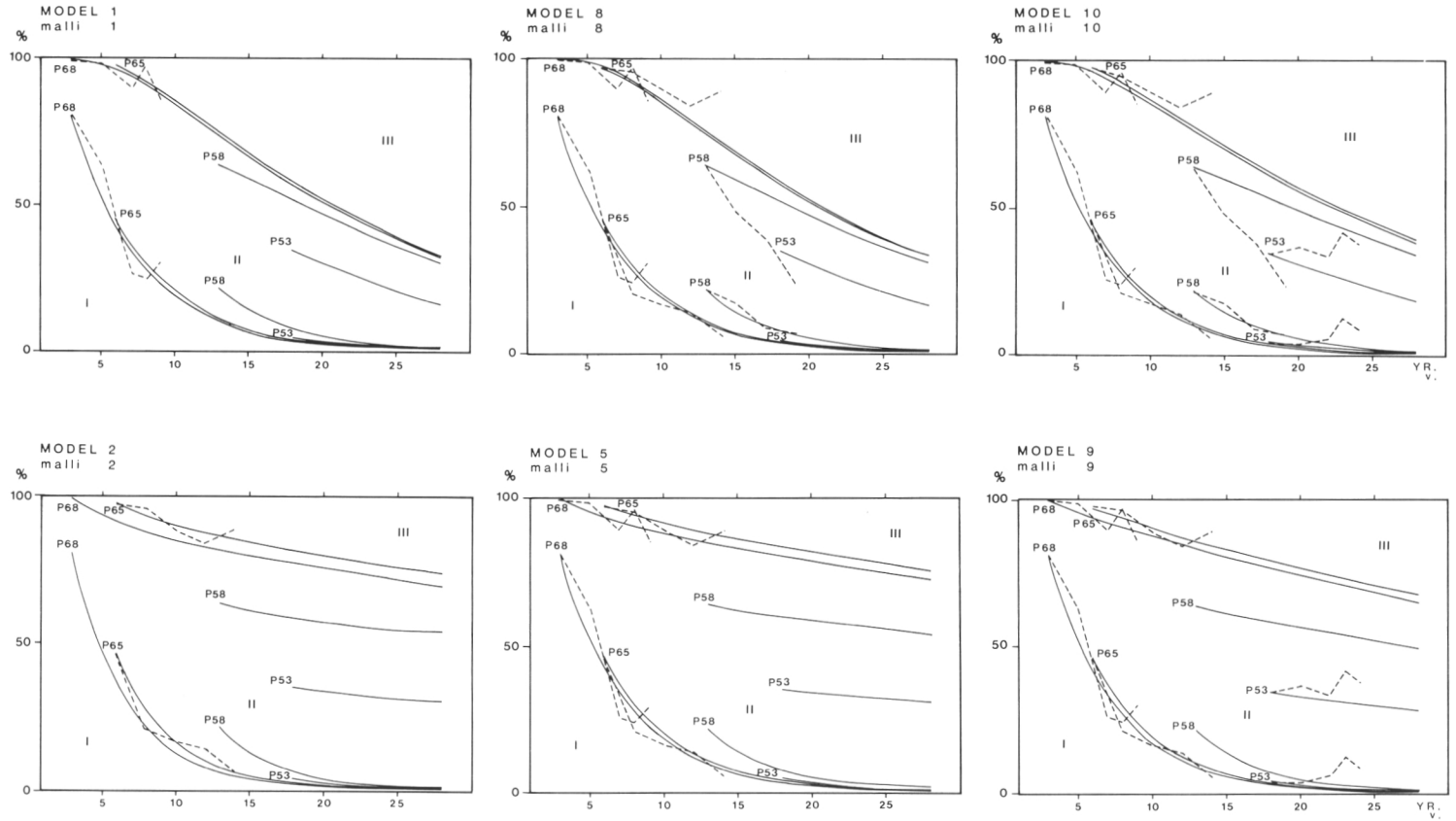


Fig. 16. Predictions (continuous lines) given by the matrix models 1, 2, 5, 8, 9 and 10 (Table 9) for the changes in the biomass proportions of succession classes I—III (y-axis) over time (x-axis) on all field plots. Each model is based on the measured biomass proportions (broken lines).

Kuva 16. Matriisimallien 1, 2, 5, 8, 9 ja 10 (taulukko 9) antamat ennusteet (yhtenäinen viiva) lajien I—III sukkessioluokkien osuuksien muutoksista (y-akseli) ajan kuluessa (x-akseli) kullekin lohkolle. Mallin pohjana oleva mitattu biomassa-aineisto on merkitty katkoviivoin.

The same feature also became apparent earlier in connection with the classification and clustering of the sample plots - the two oldest and the two youngest field plots formed groups which clearly differed from each other.

The basic question in modelling succession is whether succession is Markovian, i.e. whether information about the history of the vegetation cover, and for how far back, is essential in predicting the future vegetation on the area (Horn 1975b, van Hulst 1979a, b). It was possible in this study to predict what would happen for as many as 24 years ahead on the basis of a monitoring period lasting for nine years. It will be interesting to see whether the predictions given by these models come true in the succession taking place in the future on the fields.

Models resembling the matrix models used in this study have also been prepared by Anderson (1966), Stephens & Waggoner (1970), Horn (1975a), Redetzke & van Dyne (1976, 1979), Kauppi et al. (1978) and Enright & Ogden (1979). Succession models have also been drawn up by adapting the Lotka-Volterra equation for competition between species (Horn 1981, van Hulst 1979a, Lepš & Prach 1981). However, most of the models have been prepared from heterogeneous material and not from permanent plots as in this study.

46. Growth dynamics of the plant species

461. Abundance distribution

The classification of both the sample plots and the species was based on the extent to which species occur simultaneously on the same sample plots. How the abundance (biomass) of the species is distributed horizontally, what regularities are apparent, and how the aforementioned succession changes are apparent in the distribution is examined in the following. The abundance distribution was depicted using the isonomes of the seven most abundant species on all the fields at the start of the study (in 1971 and 1973) and at the end of the study (in 1977), on P65 also in 1979. The curves were obtained by interpolation from the green biomass dry-weight values for the sample quadrats (Appendix 1).

The abundance of the species was distributed rather irregularly on the field plots (Appendix 2). *Phleum pratense* had the smallest local variations on P68 at the start of the study, *Agrostis tenuis* on P65 at the end and *Alchemilla vulgaris* on P58 throughout the course of the study. Thus the distribution was the most regular when the species was dominant. The species were most irregularly distributed in the initial stages of their spreading and if the species has a strong tendency to form tussocks (*Deschampsia cespitosa*). The local variation in the soil was also apparent in the distribution of the abundance of the species. The quality of the soil in different parts of the fields in 1972 is presented in Fig. 4. Appendix 2 shows that *Elymus repens* was concentrated in the parts of P68, P65 and P58 where the mull layer was the thickest. *Phleum pratense* disappeared at the fastest rate on areas where the mull layer was thin. *Agrostis tenuis* spread the fastest on the parts of P65 where the potassium level was high and the pH low. *Alchemilla vulgaris* was concentrated in areas low in phosphorus and was completely absent from P68 which had a higher phosphorus level in all parts of the field plot.

The moisture conditions also had an effect on the distribution of the species on the field plots. Water from melting snow flowed down the slope on P58 in the spring and there were especially abundantly *Alchemilla* in these places. The species group disappeared from the central part of this plot in 1973, which was an area where the water flowing down the slope in the spring had collected (Appendix 2). *Alchemilla* obviously does not tolerate standing water. On the other hand, *Poa pratensis* and *Agrostis tenuis* rapidly colonised this area which had earlier been occupied by *Alchemilla*.

A large number of different factors e.g. exposition and gradient of the slope, shading by trees and shrubs in general have an effect on the distribution of the species. It was not possible to draw any definite conclusions as regards the role of these factors from the charts in Appendix 2. However, the clearest factor affecting the distribution of the species was time. The strongest changes occurred on the youngest field plots. Only slight changes were visible on the oldest field during the

course of the study. Conversion of an almost evenly-productive hay field into a meadow with considerable local species variation occurred during a succession period lasting for 20 years. The results are in agreement with the results for the succession of the species obtained earlier using mean values for the individual sample plots.

Three features of the method made it difficult to compare the results between different years. Firstly, the maps in Appendix 2 have been drawn on the basis of measured dry-weight values which have not been corrected using the temperature sum values. Secondly, the sample squares could not be set out at exactly the same points on the fields because a harvesting method was used. Thirdly, the number of sample quadrats in different years and on the different field plots varied (p. 11). Therefore the number of details in the figure of Appendix 2 is less in 1971 and 1973 than in 1977 and 1979, when the number of sample quadrats was greater.

462. Competition between the species

Competition between species is one of the most studied areas in the field of community ecology. Animal ecologists, in particular, have concentrated a considerable amount of research resources on the study of this subject and on the development of a general theory (Birch 1979, Simberloff 1982, Haila 1982).

The effects of plant species on each other have been studied in many different ways. Investigated indicators of competition are a reduction in the production, a decrease in the shoot weight, a decrease in the reproductive capacity or a reduction in the shoot density (Waring & Major 1964, Cook 1965, Erviö 1975, Pulli 1980a, c). Bornkamm (1961) has used the shoot weight as a measure of the effect of competition. The weight is the smaller, the stronger the competitor it is growing close to. Models for estimating the competitive capacity have been developed on the basis of the production and the shoot densities (Curtis & McIntosh 1950, de Wit 1960, Harper 1977, Snaydon 1979). However, all of the above-mentioned studies have been done under experimental conditions and most of them using crop plants. The study of competition under natural conditions is considerably more difficult.

In this study an attempt has been made to study competition power using correlation and regression analyses in individual sample quadrats (cf. Lefébvre & Simon 1979, Haggar 1979, Smith & Crespo 1979). The correlations between biomass and shoot weight, and between densities and shoot weight, have been calculated for the different species. Comparison has been done for each quadrat so that only those quadrats where both of the species have occurred at the same time are included in the study. The comparisons for each pair of variables were conducted separately for each field, the two youngest fields (P68 and P65) together and the two oldest (P58 and P53) together. The ratios between the biomass of the species were calculated separately for the period 1971—75 and for the period 1971—79. However, the ratios between the shoot weight and the biomass, and between the shoot weight and the densities, were only obtained for the material collected during 1971—1975 (Table 10) because the number of shoots had not been counted in the other years. The biomass and shoot weight values are corrected to correspond to a temperature sum of 650 d.d.

Correlation analysis was made on the following species: *Phleum pratense, Elymus repens, Agrostis tenuis, Taraxacum officinale, Poa pratensis, Deschampsia cespitosa, Alchemilla vulgaris*, *Ranunculus acris* L., *Festuca rubra* and *Vicia cracca* (Table 11). Regression analyses were also made on the relationship between *Phleum pratense* and *Agrostis tenuis* (Fig. 17).

There were no species pairs on the youngest fields which would have had only positive significant correlations. However, on the oldest fields there were such correlations between *Phleum pratense, Elymus repens, Agrostis tenuis, Taraxacum officinale* and *Alchemilla vulgaris,* and between *Poa pratensis, Deschampsia cespitosa* and *Festuca rubra.* The correlations between these two groups were negative or not significant. Neither *Vicia cracca* nor *Ranunculus acris* were significantly correlated with any species.

When interpreting the results it was presumed that two species are competing with each other if there is statistically significant negative correlation between the shoot weight of one of the species and the biomass or shoot

Table 10. The mean shoot weight (g/shoot) for each species and succession class according to the uncorrected (a) and corrected (b) biomass values. See further explanation in text.

Taulukko 10. Laji- ja sukkessioluokkakohtaiset keskimääräiset versokoot (g/verso) korjaamattomien (a) ja korjattujen (b) biomassojen mukaan. Katso tarkempi selitys tekstistä.

Field plot — *Peltolohko*		P68			P65			P58			P53		
Sample plot — *Näyteala*		3	5	7	6	8	10	13	15	17	18	20	22
Year — *Vuosi*		71	73	75	71	73	75	71	73	75	71	73	75
Temperature sum — *Lämpösumma*	a	432	567	462	347	411	462	404	667	462	529	765	462
	b	650	650	650	650	650	650	650	650	650	650	650	650
I succession class													
I *sukkessioluokka*	a	0.67	0.55	0.39	0.32	0.26	0.34	0.40	0.51	0.41	0.26	0.46	0.36
	b	1.11	0.68	0.56	0.79	0.52	0.48	0.79	0.51	0.58	0.32	0.42	0.52
Phleum pratense	a	0.69	0.55	0.39	0.32	0.26	0.34	0.40	0.51	0.41	0.25	0.46	0.36
	b	1,14	0.68	0.56	0.79	0.52	0.48	0.79	0.51	0.58	0.32	0.42	0.52
II succession class													
II *sukkessioluokka*	a	0.26	0.17	0.16	0.09	0.11	0.11	0.13	0.16	0.13	0.10	0.11	0.19
	b	0.56	0.23	0.28	0.24	0.19	0.15	0.24	0.15	0.18	0.12	0.11	0.23
Rumex acetosella	a	—	—	—	0.06	0.02	0.07	—	—	—	—	—	—
	b	—	—	—	0.11	0.04	0.10	—	—	—	—	—	—
Elymus repens	a	0.51	0.31	0.23	0.31	0.24	0.20	0.20	0.36	0.25	0.27	0.19	0.18
	b	1.26	0.45	0.46	1.04	0.61	0.40	0.50	0.36	0.50	0.45	0.18	0.37
Leontodon autumnalis	a	—	—	—	0.04	0.03	0.23	0.05	0.10	—	0.08	—	—
	b	—	—	—	0.22	0.09	0.57	0.16	0.10	—	0.14	—	—
Epilobium angustifolium	a	—	—	—	—	1.80	4.00	2.00	—	—	—	—	0.40
	b	—	—	—	—	9.00	13.30	10.00	—	—	—	—	2.00
Agrostis tenuis	a	0.12	0.09	0.06	0.05	0.05	0.06	0.07	0.10	0.07	0.06	0.07	0.06
	b	0.23	0.11	0.11	0.17	0.14	0.10	0.17	0.10	0.11	0.08	0.07	0.10
Anthoxanthum odoratum	a	—	—	—	0.05	0.04	0.04	0.06	0.03	0.05	0.05	0.03	0.04
	b	—	—	—	0.05	0.04	0.04	0.05	0.03	0.05	0.05	0.03	0.04
Taraxacum officinale	a	3.33	1.36	4.12	1.56	2.03	2.87	1.70	0.73	1.17	0.68	0.92	1.84
	b	3.10	1.13	3.17	1.20	1.56	2.20	1.31	0.73	0.90	0.57	1.15	1.42
III succession class													
III *sukkessioluokka*	a	0.04	0.06	0.19	0.10	0.10	0.12	0.53	0.32	0.40	0.16	0.25	0.24
	b	0.10	0.06	0.27	0.16	0.21	0.16	0.77	0.32	0.46	0.20	0.26	0.29
Cirsium helenioides	a	—	—	—	—	—	—	—	—	—	—	5.84	5.05
	b	—	—	—	—	—	—	—	—	—	—	7.00	5.11
Achillea ptarmica	a	—	0.20	—	0.15	0.16	0.11	0.10	0.18	—	0.17	0.21	0.13
	b	—	0.30	—	0.50	0.40	0.19	0.25	0.18	—	0.24	0.19	0.22
Achillea millefolium	a	0.10	0.60	0.20	0.08	0.11	0.24	0.16	0.13	0.10	0.11	0.09	0.08
	b	0.20	0.70	0.35	0.20	0.27	0.48	0.39	0.13	0.20	0.16	0.09	0.15
Deschampsia cespitosa	a	0.08	—	0.13	0.05	0.09	0.24	0.11	0.15	0.10	0.17	0.23	0.15
	b	0.17	—	0.21	0.13	0.18	0.40	0.22	0.15	0.17	0.24	0.21	0.25
Poa pratensis	a	—	0.04	0.24	0.07	0.05	0.08	0.07	0.06	0.07	0.06	0.07	0.06
	b	—	0.04	0.26	0.10	0.06	0.09	0.09	0.06	0.08	0.06	0.07	0.07
Vicia cracca	a	—	—	0.51	—	—	—	0.60	0.70	0.43	0.72	0.88	0.36
	b	—	—	0.73	—	—	—	1.20	0.70	0.61	0.89	0.93	0.51
Festuca rubra	a	—	—	—	0.06	0.04	0.03	—	0.04	0.04	0.03	0.06	0.04
	b	—	—	—	0.19	0.06	0.05	—	0.04	0.07	0.05	0.05	0.07
Hypericum maculatum	a	0.08	—	0.40	—	—	0.10	0.25	0.50	—	0.28	1.68	0.43
	b	0.20	—	0.80	—	—	0.20	0.85	0.50	—	0.40	1.53	0.86
Ranunculus acris	a	—	—	—	—	0.40	0.74	0.37	0.43	0.74	0.46	0.38	0.68
	b	—	—	—	—	0.50	1.00	0.47	0.43	0.82	0.46	0.42	0.75
Lathyrus pratensis	a	—	—	—	—	—	—	—	1.28	0.55	0.83	0.84	0.49
	b	—	—	—	—	—	—	—	1.28	1.10	1.04	0.77	0.98
Vicia sepium	a	—	—	—	—	—	0.23	—	0.23	0.39	0.10	0.52	0.38
	b	—	—	—	—	—	0.33	—	0.23	0.56	0.10	0.47	0.54
Alchemilla vulgaris	a	—	—	—	1.30	0.75	—	1.43	0.79	1.14	1.22	0.66	0.77
	b	—	—	—	2.20	1.08	—	2.05	0.79	1.42	1.35	0.91	0.96
All species — *Kaikki lajit*	a	0.53	0.30	0.19	0.14	0.12	0.13	0.24	0.26	0.25	0.14	0.18	0.23
	b	0.92	0.38	0.32	0.33	0.21	0.17	0.39	0.26	0.32	0.17	0.17	0.27

density of the other (Table 11). Such interspecific competition is also seen as negative correlation between the biomass values of the species. The species whose biomass or shoot density increases as the other species shoot weight decreases is the stronger competitor. This was the case with *Agrostis tenuis* with respect to *Phleum pratense* and *Elymus repens* on the youngest fields. There were no such relationships between species on the oldest fields. According to this result, *Agrostis* is occupying the space held by *Phleum* on the youngest fields. This can be seen in the quadrats such that where *Agrostis* was growing densely or abundantly, *Phleum* was only small-sized, but where *Phleum* was growing densely or abundantly, *Agrostis* was large-sized (Fig. 17 a, b). This situation results in the disappearance of *Phleum* over time (see also Appendix 2). The relationship between these species had changed to such an extent on the oldest fields that negative correlations were no longer found. The relationship between *Agrostis* and *Phleum* was analysed using the regression models (Fig. 17). The biomass of *Agrostis* explained 18 % and density 39 % of the variation in the shoot weight of *Phleum*. The biomass of *Phleum* explained 19 % of the variation in the shoot weight of *Agrostis*. The slopes of the regression lines, which have also been used as measures of the effect of competition (Wu & Jain 1979, Gulmon 1979), were statistically significant in the models presented in Figs. 17a, b, c, e, f and h. The relationship between *Agrostis* and *Elymus* is not as clear as that described above, but there was a state of competition between these two species on the youngest fields (Table 11).

Apart from *Elymus repens* and *Agrostis tenuis*, all the species had positive intraspecific correlation between the biomass and their own shoot weight. Correlations were smaller although still significant on the oldest fields (Figs. 17e and g). The intraspecific correlation between the density and the shoot weight was statistically significant only in the case of *Phleum pratense* and *Agrostis* on the youngest fields. The correlation for the former was positive and for the latter negative (Figs. 17f and h). There is evidence to show that intraspecific competition is strong in *Agrostis* on the youngest fields. This can be seen as a decrease in the shoot weight as the shoot density increases. In *Phleum* the trend is the opposite since the shoot weight increases as the shoot density increases. This is a rather surprising result. There is no intraspefic competition in *Phleum* on the youngest fields, although being sown it forms almost pure stands. It is generally accepted (Pulli 1980b) that intraspecific competition prevails in pure stands, and interspecific competition in mixed stands. There were no statistically significant correlations between the densities and the shoot weights on the oldest fields. Whether or not we can conclude from this that there was no intraspecific competition in these cases, is uncertain. It may be that it is not possible to determine whether there is any intraspecific competition in mixed stands consisting of so many different species using this method, or that the material was too small as regards certain species.

Phleum pratense was a species whose biomass was positively correlated with the shoot weight of *Elymus repens, Agrostis tenuis* and *Alchemilla vulgaris*. *Phleum* appears to prefer the rather fertile sites where the aforementioned species also grow large-sized.

If there is a negative correlation between the abundances of two species, the species either compete with each other and reduce each others abundances or else the species have different environmental requirements. The following species pairs were of this sort: *Phleum pratense* and *Taraxacum officinale*, *Elymus repens* and *Agrostis tenuis*, on the youngest fields, the species pair *Phleum* and *Elymus* on P68, and *Poa pratensis* and *Alchemilla vulgaris* and *Alchemilla* and *Festuca rubra* on the oldest fields.

Positive correlations between the abundances of the species means that these species grow abundantly on the same quadrats and are thus in association with each other. Such species do not have a reducing effect on each other's shoot weight, but are adapted to growing together. There were no such relationships on the youngest fields, but on the oldest fields *Phleum pratense* and *Elymus repens*, *Phleum* and *Alchemilla vulgaris* and *Phleum* and *Taraxacum officinale*, were associated with each other. One reason for this may be that such species live on different environmental resources, e.g. their root systems develop in different layers in the soil (Linkola & Tiirikka 1936, Berendse 1979).

The interspecific correlations change with time: negative correlations become positive.

Table 11. The statistically significant correlations (*** = p <0.001, ** = p <0.01, * = p <0.05) between biomass (B) (g/m^2, corrected to the 650 d.d. level) and shoot weight (W) (g/shoot), shoot density (D) (shoots/m^2) and shoot weight, weight and weight, biomass and biomass of the most abundant species *Phleum pratense, Elymus repens, Agrostis tenuis, Taraxacum officinale, Deschampsia cespitosa, Poa pratensis, Festuca rubra* and *Alchemilla vulgaris* (species variables 1 and 2), on P68 and on the combined two youngest (P68 + P65) and two oldest (P58 + P53) field plots.

*Taulukko 11. Runsaimpien lajien, Phleum pratense, Elymus repens, Agrostis tenuis, Taraxacum officinale, Deschampsia cespitosa, Poa pratensis, Festuca rubra ja Alchemilla vulgaris (lajimuuttujat 1 ja 2) biomassojen (B) (g/m^2, korjattuja biomassoja) ja versokokojen (W) (g/verso), versotiheyksien (D) (versoja/m^2) ja versokokojen, versokokojen ja versokokojen sekä biomassojen ja biomassojen väliset tilastollisesti merkitsevät korrelaatiot (*** = p <0.001, ** = p <0.01, * = p <0.05) lohkolla P68 sekä kahden nuorimman (P68 + P65) ja kahden vanhimman (P58 + P53) lohkon yhdistetyissä aineistoissa.*

Field plot *Peltolohko*	Variables — *Muuttujat* 1.—2.	1971—1975						1971—1979
		B_1—W_2	D_1—W_2	B_2—W_1	D_2—W_1	W_1-W_2	B_1—B_2	B_1—B_2
P68	*Phleum — Elymus*	.720***				.719***	—.520**	—.236***
P68 ja P65	*Phleum — Phleum*	.837***	.543***	.837***	.543***			
	Phleum — Elymus	.406***				.503***		
	Phleum — Agrostis	.453***		—.447***	—.573***	.577***	—.492***	—.304***
	Phleum — Taraxacum						—.306**	
	Elymus — Agrostis				—.443***	.487***	—.390***	—.297***
	Agrostis — Agrostis		—.396***		—.396***			
	Taraxacum — Taraxacum	.651***		.651***				
	Poa — Poa	.698***		.698***				
P58 ja P53	*Phleum — Phleum*	.714***		.714***				
	Phleum — Elymus			.312*		.489***		.287***
	Phleum — Agrostis	.576***	.493***			.612***		.216*
	Phleum — Taraxacum							.217*
	Phleum — Alchemilla	.425*				.444*	.368*	
	Elymus — Elymus	.526**		.526**				
	Elymus — Agrostis					.358*		
	Elymus — Taraxacum			.524***		.368*		
	Agrostis — Agrostis	.370*		.370*				
	Agrostis — Alchemilla					.410*		
	Taraxacum — Taraxacum	.410**		.410**				
	Taraxacum — Alchemilla			.426*				
	Deschampsia — Deschampsia	.656***		.656***				
	Poa — Poa	.444**		.444**				
	Poa — Alchemilla						—.307*	—.342***
	Poa — Festuca					.357*		
	Alchemilla — Alchemilla	.550***		.550***				
	Alchemilla — Festuca							—.273*

Changes take place e.g. between *Phleum pratense* and *Elymus repens*, and between *Phleum* and *Agrostis tenuis*.

The competition between seeded species and other species is very severe in young hay fields. This results in the seeded species decreasing. As time passes and the number of species increases, the relationships between the species become so complicated that it is not possible using the method applied here to obtain any statistically significant negative correlations which would be indicators of interspecific competition. According to the results, the competition situation changed, but whether or not competition decreases with time, as the correlations would suggest, is not certain. Competition may appear in such a way that it is not revealed in the correlations. In addition, interpretation of the results is difficult because *Taraxacum officinale*, *Poa pratensis*, *Agrostis tenuis* and *Alchemilla vulgaris* are not taxonomically uniform species.

A number of plant species have been found to effect others (Cable 1969, Sharitz & McCormick 1973) However, in most cases it has not been a question of real competition but of environmental factors eg. weather, predators and pathogens (Simberloff 1982). It is not certain whether it is a question of real competition in this study. According to Ellenberg (1979) and Jalas (1958), *Phleum pratense* and *Agrostis tenuis* grow on rather different sites. This may partly explain the decrease of *Phleum*. Competition, if it exists, does not however exclude *Phleum* because it is present for a long time on its optimum sites.

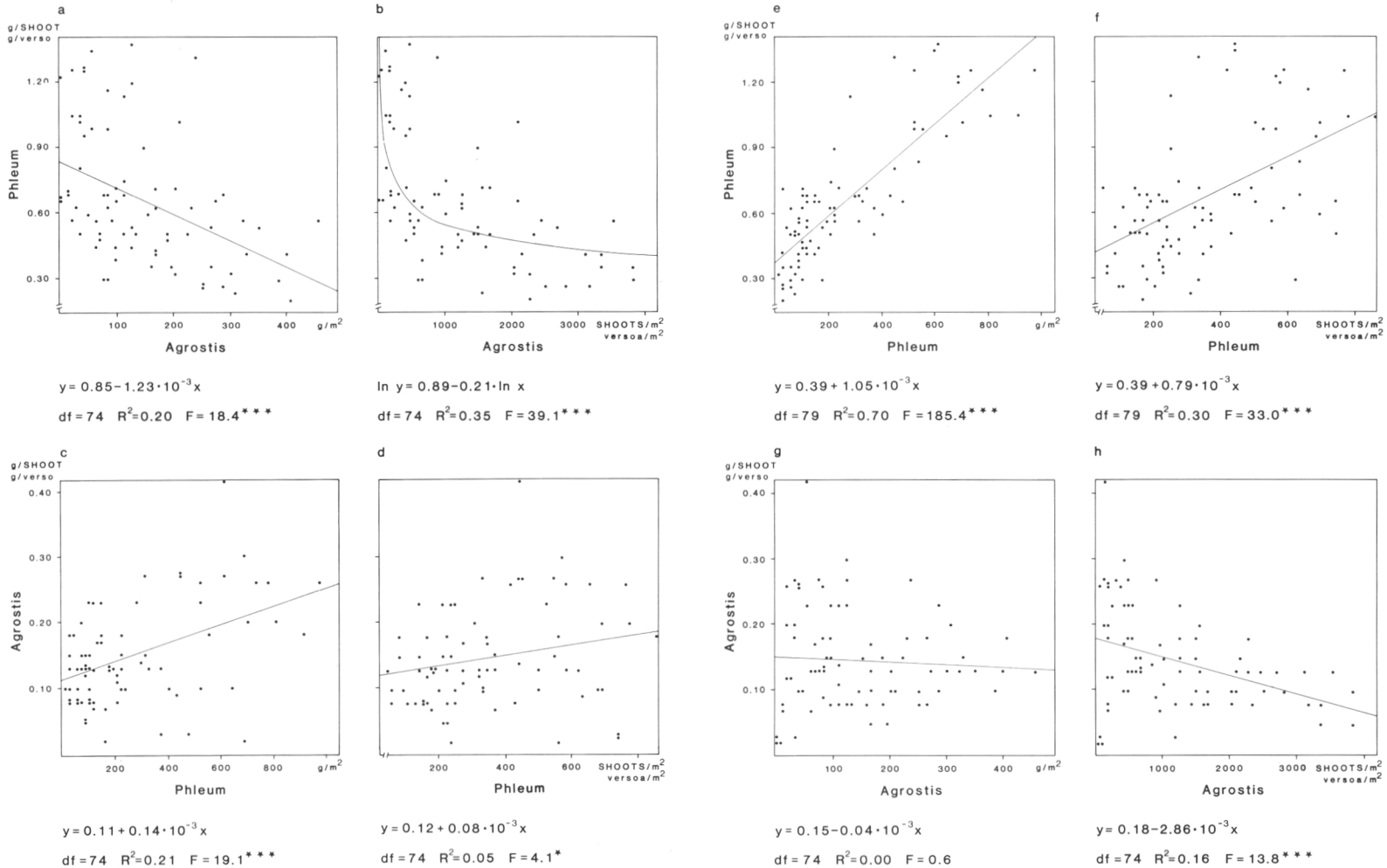


Fig. 17. Interspecific (a, b, c, d) and intraspecific (e, f, g, h) competition in *Phleum pratense* and *Agrostis tenuis* on the basis of the regressions between the biomass (g/m^2), shoot density ($shoots/m^2$) and shoot weight (g/shoot). Statistical significance ***: $p < 0.001$, *: $p < 0.05$.

*Kuva 17. Phleum pratensen ja Agrostis tenuiksen lajienvälinen (a, b, c, d) ja lajinsisäinen (e, f, g, h) kilpailu. Kuvat perustuvat biomassan (g/m^2), versotiheyden ($versoa/m^2$) ja versokoon (g/verso) välisiin regressioihin. Tilastollinen merkitsevyys ***: $p < 0.001$, *: $p < 0.05$.*

A large number of plant properties affect competitiveness, such as the way of reproduction and growth, shoot weight, site requirements, efficiency of the root system and degree of allelopathy. In other words the whole strategy with which species are adapted to their environment. MacArthur & Wilson (1967) have determined two, and Grime (1977, 1979) three ways in which plants react to their environment. The r-strategists of MacArthur & Wilson (1967) are species of disturbed, open or semi-open sites, are typically small-sized, have a rapid reproductive capacity and poor competitiveness (Pianka 1970, Southwood et al. 1974). These species expend a large portion of their energy in reproduction, and fast changes and instability are typical of the communities which they form. Species obeying the K strategy (MacArthur &Wilson 1967) are large-sized, show reproducers, long-lived and strong competitors. They expend more energy in survival. The communities which they form are long-lived, stable and shape the environment in which they live. However, many species do not fulfill all the requirements of either of the strategy types described here, but a gradual change in reproductive strategy is apparent. At one extreme are the annual species and at the other trees (r - K continuum). The material of this study does not fit especially well in this strategy division, although the species in the first and second succession classes have more of the properties of the r type, and those of the third class more of the K type strategy. The same can be said of the suitability of Grime's (1979) typing system. Neither have Newell & Tramer (1978) been able to obtain clear evidence of the validity of the r - K theory in the succession of an old field. Strategy typing appears to be relative. The type of each species can be defined with respect to other species. For example, *Elymus repens* is a K strategist in comparison to

Table 12. Application of the power law (Yoda et al. 1963) and the "ultimate thinning line" (White 1980) to the most abundant species and the whole field layer in 1971—1975, to the tree and shrub layers in 1979, and to the OMT spruce stands, re-calculated from Ilvessalo's (1920) data tables, w = mean plant weight (g/plant), d = mean plant density (plants/m^2), K = a constant, and R^2 % = coefficient of determination of the equation.

Taulukko 12. Potenssilain (Yoda ym. 1963) ja "äärimmäisen harvennusrajan" (White 1980) soveltaminen runsaimpiin lajeihin ja koko kenttäkerroksen v. 1971—1975, puu- ja pensaskerroksiin v. 1979 sekä OMT-kuusikoihin laskettuna Ilvessalon (1920) taulukoista. w = keskimääräinen versokoko (g/verso), d = keskimääräinen versotiheys (versoja/m^2), K = vakio ja R^2 % = yhtälön selitysaste.

	Equation — *Yhtälö*	R^2 %	Reference — *Lähde*
The power law *Potenssilaki*	$w = Kd^{-3/2}$		Yoda et al. 1963
The "ultimate thinning line" *"Äärimmäinen harvennusraja"*	$\lg w = 4.4 - 1.5 \lg d$	100	White 1980
Species — *Lajit*			
Phleum pratense	$\lg w = -0.86 + 0.28 \lg d$	61	
Elymus repens	$\lg w = -0.05 - 0.12 \lg d$	2	
Agrostis tenuis	$\lg w = -0.40 - 0.18 \lg d$	10	
Taraxacum officinale	$\lg w = 0.50 - 0.28 \lg d$	36	Own data
Poa pratensis	$\lg w = -0.75 - 0.16 \lg d$	11	*Oma aineisto*
Ranunculus acris	$\lg w = -0.17 - 0.06 \lg d$	9	
Alchemilla vulgaris	$\lg w = 0.23 - 0.08 \lg d$	17	
Field layer total *Kenttäkerros yhteensä*	$\lg w = 4.26 - 1.45 \lg d$	89	
Trees and shrubs total *Puut ja pensaat yhteensä*	$\lg w = 1.63 - 0.14 \lg d$	85	
OMT *Picea abies*	$\lg w = 3.50 - 1.90 \lg d$	99	Re-calculated from Ilvessalo's (1920) tables — *Laskettu Ilvessalon (1920) taulukoista*

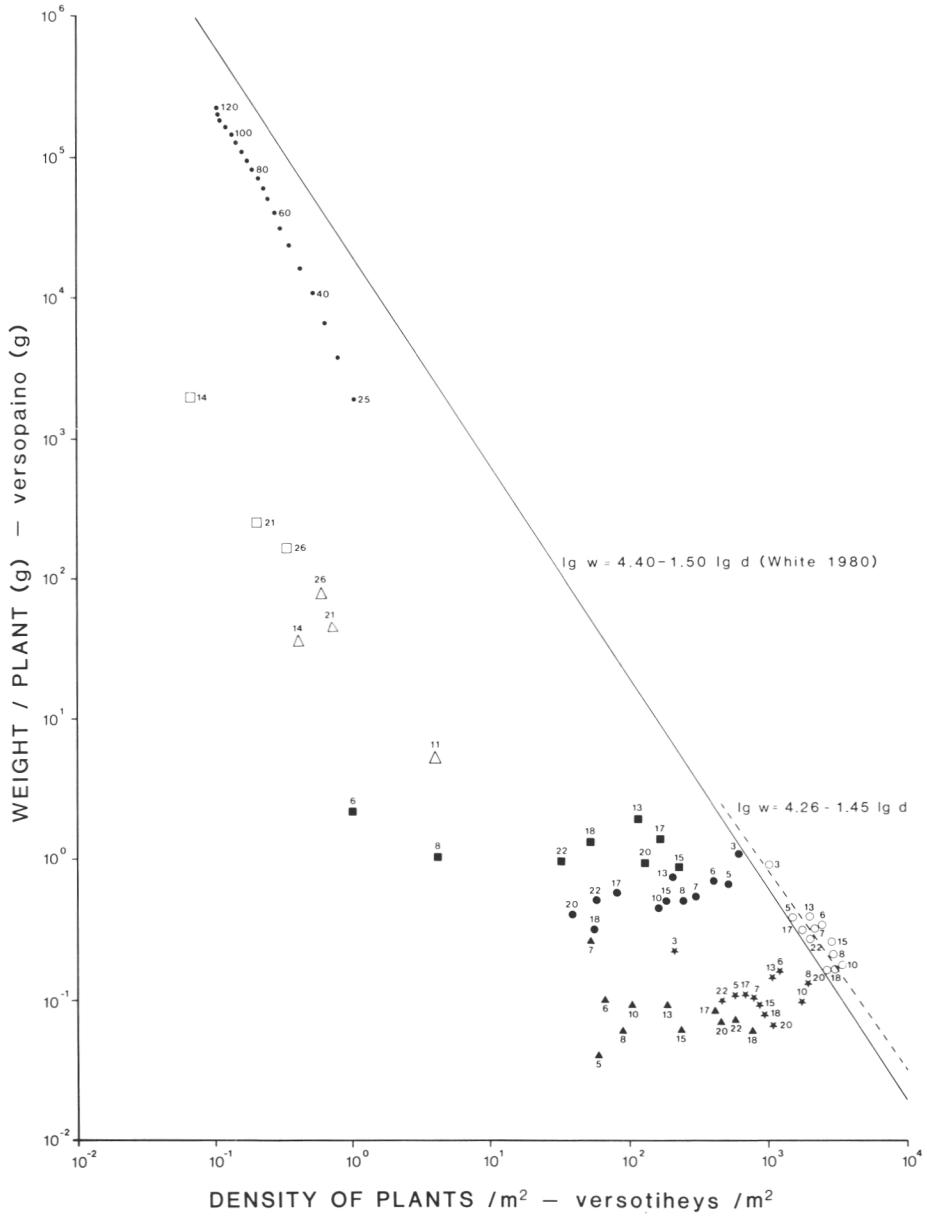


Fig. 18. The relationship between mean density (plants/m^2) and mean plant weight (g): in 1971—1975 for the whole field layer (○) and for some species in the field layer *Phleum prtense* (●). *Agrostis tenuis* (★), *Poa pratensis* (▲) and *Alchemilla vulgaris* (■) and in 1979 for the tree (□) and shrub (▵) layers separately and for the OMT spruce stands (•) (data from Ilvessalo 1920) compared with the "ultimate thinning line" (continuous line) as calculated from White (1980). Both axes are in lg scales. Equation for the whole material of the field layer (broken line) is given. Other equations are given in Table 12. The numbers denote the succession age of the plots.

Kuva 18. Keskitiheyden (yksilöitä/m^2) ja keskipainon (g/verso) välinen suhde vuosina 1971—1975 koko kenttäkerroksessa (○) ja kenttäkerroksen lajeilla Phleum pratense (●), Agrostis tenuis (★), Poa pratensis (▲) ja ALchemilla vulgaris (■) ja v. 1979 puu- (□) ja pensas- (▵) kerroksessa sekä Ilvessalon (1920) OMT-kuusikossa (•) verrattuna Whiten (1980) laskemaan "äärimmäisen harvennusrajan" yhtälön kuvaajaan (yhtenäinen viiva). Kummatkin akselit ovat logaritmissa. Kenttäkerroksen kokonaisaineiston yhtälön kuvaaja on merkitty katkoviivalla. Muut yhtälön ovat taulukossa 12. Symbolien numerot merkitsevät näytealan sukkessioikää.

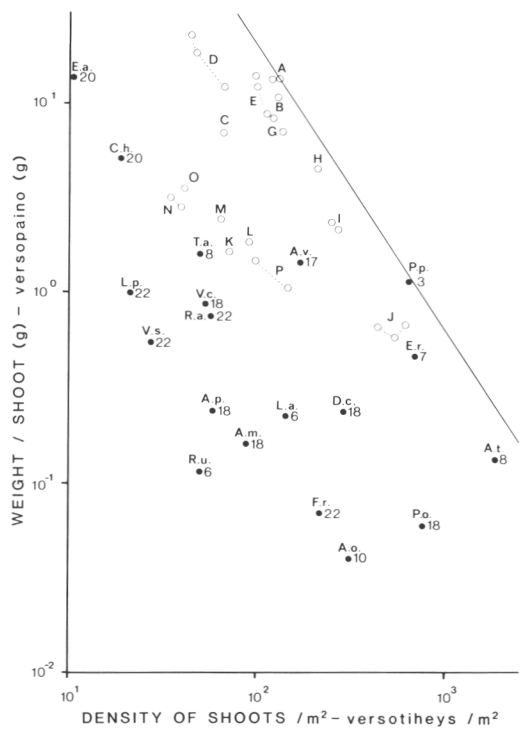
Lapsana communis, but an r strategist in comparison to *Festuca rubra.*

463. Weight-density ratios

The relationship between shoot density and shoot weight has interested population ecologists during the last few years. Most of the studies have been concerned with either monocultures of weed plants or forests comprising only one tree species (Yoda et al. 1963, White 1980). Perennial clones of herb plants have also been studied (White 1980, Hutchings 1979, Pulli 1980a and c, Prach 1982). Yoda et al. (1963) have developed the -3/2 power law or thinning rule between shoot weight and shoot density, which White (1980) considers to be one of the most general principles in plant population ecology. The law describes the ratio between the mean shoot weight and the mean shoot density in a plant population. The law appears over time as the mortality rate depending on density or as self-thinning.

$$w = Kd^{-3/2}$$

where w is the mean weight of the plant, d the density of the surviving plants, and K a constant which varies within certain limits depending on the species. Yoda et al. (1963) have originally developed the law for monocultures of weed species, but it has since proved to be true for many woody and herbaceous species in pure stands and in some mixed stands consisting of two species (White & Harper 1970, Gorham 1979, Hutchings 1979, White 1980, Hutchings & Budd 1981).



A.m. *Achillea millefolium*
A.o. *Anthoxanthum odoratum*
A.p. *Achillea ptarmica*
A.t. *Agrostis tenuis*
A.v. *Alchemilla vulgaris*
C.h. *Cirsium heleniotdes*
D.c. *Deschampsia cespitosa*
E.r. *Elymus repens*
E.a. *Epilobium angustifolium*
F.r. *Festuca rubra*
L.a. *Leontodon autumnalis*
L.p. *Lathyrus pratensis*
P.o. *Poa pratensis*
P.p. *Phleum pratense*
R.u. *Rumex acetosella*
T.a. *Taraxacum officinale*
V.c. *Vicia cracca*
V.s. *Vicia sepium*

Data re-calculated by Hutchings (1979) — *Hutchingsin (1979) eri lähteistä laskema aineisto:*

A *Phragmites communis*
B,C *Phragmites communis*
D *Typha angustifolia*
E *Solidago altissima*
F *Carex cordorrhiza*
G *Carex lacustris*
H, I *Carex rostrata*
J *Carex aguatilis*
K—O *Mercurialis perennis*
P *Glyceria maxima*

Fig. 19. Mean shoot weight and density ratios plotted on the lg scales for the most abundant species in the research material in (1971—1975) (●) and for some clonal perennial species re-calculated by Hutchings (1979) (○), in comparison to the "ultimate thinning line" (White 1980). The points for the species are those placed closest to the thinning line. The numbers denote the succession age of the plots.

Kuva 19. Keskimääräisen versokoon ja tiheyden suhteet lg skaaloissa runsaimmilla heinäpeltoaineiston lajeilla vuosina 1971—1975 (●) sekä eräillä Hutchingsin (1979) laskemilla lajeilla (○), verrattuina "äärimmäiseen harvennusrajaan" (White 1980). Lajien pisteet ovat lähimpänä harvennusrajaa sijainneita pisteitä ja numerot alojen ikäsymboleita.

The constant K varies in most cases between 3.5—4.3 when the density is one shoot/m^2. By defining the value of K as 4.4, Hutchings (1979) and White (1980) have achieved the so-called ultimate thinning line, which no population can exceed. As the shoot densities were only calculated in 1971, 1973 and 1975, only this part of the material can be examined with respect to the thinning rule. The shoot weight was calculated according to the corrected (temperature sum 650 d.d.) biomass values (Table 10). In addition, the trees and shrubs analysed in 1979 were included in the comparison (Table 4). The degree to which Finnish single-species tree stands follow the power law and self-thinning during the course of succession was calculated using the material of Ilvessalo (1920) for control purposes. The natural spruce stands growing on fresh, fertile sites (OMT) in Ilvessalo's material were used. The material consisted of growth and production tables which were used to calculate the ratios between stem weight and stem density for stands older than 25 years. The volume figures were converted into weight values using the measurements of Hakkila (1966, p. 58).

None of the species in the field layer follow the power law, nor the thinning line in their succession (Fig. 18, Table 12). In the first succession class, *Phleum pratense* is close to the thinning line during the first year of the study, but later on draws away more from it each year. *Agrostis tenuis*, in the second succession class, approaches the thinning line obliquely from above, but did not actually reach it on any of the plots. It is closest to the line on plots with a succession age of 8 and 10 years, and furthest from it at the succession age of 3 and 22 years. *Alchemilla vulgaris*, in the third succession class, is closest to the line on P58 and furthest from it on P65. *Poa pratensis*, also in the third succession class, approaches the line obliquely, but remains at quite a distance from the line on the oldest field. The points for the plots where the species were at their most abundant, were closest to the thinning line. All the species examined showed this feature (Fig. 19).

In the above, the populations of the species are examined separately. A different result is obtained if the plant community in the field layer is examined as a whole. The equation for the ratio between the mean shoot weight and mean shoot density in the combined material is almost the same as White's (1980) ultimate thinning line (Fig. 18). The cluster of points is situated right next to the thinning line. The points for the two youngest fields are placed along the thinning line, the older plots lower than the younger. The trend in the case of the older plots is not so clear, although a slight upward trend can be seen.

The points representing the tree and shrub layers are situated far from the thinning line, running from the bottom upwards almost in the order of succession. The advancing effect of the succession with planting is evident in the position of the points.

The mean stem weight in Ilvessalo's (1920) forest material is greater, and the density the smaller, the older is the forest stand. Stands comprising one tree species in Finland appear to obey the power law within certain limitations. The same result has been obtained by O'Neill & DeAngelis (1981) for the Leningrad district forests (data from Kazimirov & Morozova 1973). The slope of the regression calculated from the material of Ilvessalo (1920) is larger than that of the power law, and the constants smaller (Table 12). In other words, self-thinning, takes place at a lower level than the ultimate thinning line.

The power law and the thinning line do not only concern monocultures of single species, but also mixed stands of perennial harbaceous species as a whole. White & Harper (1970) and White (1980) have earlier presented results which confirm this. White (1980), citing unpublished results, has proposed that ratios in agreement with the power law are also valid in mixed stands of forest trees when all the species are taken into account collectively, but not in the case of the individual species. According to this study, this is also valid in mixed stands of herbaceous plants at the meadow stage. Although none of the individual species in the plant community obey the power law, the whole community appears to obey the thinning line. The death of the above-ground parts of perennial herbaceous species results in there being no such increase in mean size as supposed in the power law. At least in the initial stage of succession, the mean weight of individual plants decreases.

Hutchings (1979) has shown in his studies of perennial herbaceous species which form clones, that these species do not obey the -3/2 power law when growing naturally. Kays & Harper (1974) have shown that *Lolium peren-*

ne at least obeys the law under experimental conditions. According to Hutchings (1979), the ultimate thinning line acts as a line which not even perennial clone-forming herbaceous species exceed, although they approach it in their maturity stage (Fig. 19). The results of this study show that the individual perennial herbaceous plants, also in mixed stands, do not exceed the ultimate thinning line, but the power law proves to be true in the mixed stands at the plant community level. Hutchings (1979) states that the power law can be used when determining the optimum shoot density and biomass for each site. According to White (1980), this sort of weight—density study has not been conducted earlier in forestry. As far is known, such shoot weight—density studies have not been done in Finland either, although it might give an interesting new approach to the discussion on growth models and short-rotation cultivation methods.

47. Production dynamics

471. Primary production in 1971, 1972 and 1973

Methods based on the standing crop, on the sum of the maximum biomass of each species, and on the decomposition rate of the litter, were used to estimate the above-ground net primary production (p. 13). They provided an estimation of the amount of above-ground living plant biomass produced during one year, apart from the amount of energy consumed in the respiration of the plants and the energy utilised by the herbivores.

The method based on the standing crop is the simplest method for estimating production. Four different variations of this method were used: maximum living biomass (MB), maximum total biomass (living and dead) (MTB), the green biomass on July 25 (temperature sum 650 d.d.) (JB) and the total biomass (living and dead) on July 25 (JTB). MB and MTB were obtained during 1972 and 1973 using the phenological samples (Jukola 1977), JB and JTB in 1971 and 1973 (Table 2) using succession samples collected once during the summer.

Depending on the field plot, the method used and the year in question, the production according to the standing crop on the plots varied from 410.7 to 1 311.2 g/m^2 (Table 13). The largest yields were obtained on P68 (549.8—1 311.2 g/m^2), and the smallest using most methods on P53 (449.3—791.6 g/m^2). The production was largest in 1971 and 1972, and smallest using most methods in 1973. Of the methods, MB gave the smallest values for the two youngest fields, and JB for the two oldest fields. The largest values were obtained with the method which included the litter (JTB and MTB).

The sum of the peak biomass values for each species (PB) was calculated using the

Table 13. Estimates of the above-ground net primary production (d.w. g/m^2/yr) for 1971—1973 made on the basis of maximum green biomass (MB), the maximum total (living + dead) biomass (MTB), July (650 d.d.) biomass (JB) (from Table 2), the July total biomass (JTB) (from Table 2 and Appendix 1), sum of peak biomass values for species (PB) (from Table 13) and rate of litter decomposition (WE). See further explanation in text.

Taulukko 13. Maanpäällisen nettoprimaarituotoksen estimaatteja (kp. g/m^2) vuosille 1971—1973 maksimaalisen vihreän biomassan (MB), maksimaalisen kokonais- (elävä + kuollut) biomassan (MBT), heinäkuun (650 d.d.) biomassan (JB), heinäkuun kokonaisbiomassan (JTB) (taulukosta 2 ja liitteestä 1), lajien huippubiomassojen summan (PB) (taulukosta 13) ja karikkeen hajoamisnopeuden (WE) avulla. Katso tarkempi selitys tekstistä.

Field plot *Peltolohko*	P68			P65			P58			P53		
Sample plot *Näyteala*	3	4	5	6	7	8	13	14	15	18	19	20
Year — *Vuosi*	1971	1972	1973	1971	1972	1973	1971	1972	1973	1971	1972	1973
MB	—	733.0	549.8	—	410.7	419.3	—	647.7	568.6	—	450.6	509.7
MTB	—	1083.2	940.1	—	739.4	842.7	—	855.7	818.0	—	683.9	781.1
JB	922.8	—	555.8	736.0	—	598.8	772.0	—	531.7	483.6	—	449.3
JTB	1311.2	—	873.8	974.0	—	782.4	1054.5	—	755.9	791.6	—	722.8
PB	—	—	742.5	—	—	666.0	—	—	661.0	—	—	617.1
WE	1467.7	1163.0	956.1	995.0	994.2	862.5	1103.0	856.0	613.0	716.2	917.3	655.6

Table 14. The relative and absolute peak biomass values for each species (B_h, from equation p. 13) and sums of these for each field plot (PB) (d.w. g/m^2) in 1973. Uncorrected species biomass calculated from Appendix 1.

Taulukko 14. Runsaimpien lajien absoluuttiset ja suhteelliset huippubiomassa (B_h, kaavasta s. 13) sekä niiden summat lohkoittain (PB) (kp. g/m^2) v. 1973. Muiden lajien biomassat laskettu liitteestä 1.

Field plot — *Peltolohko*	P68		P65		P58		P53	
Sample plot — *Näyteala*	5		8		15		20	
	B_h	%	B_h	%	B_h	%	B_h	%
Phleum pratense	475.0	64.0	123.8	18.6	98.4	14.9	18.1	2.9
Rumex acetosella	0.0	0.0	0.1	0.0			0.0	0.0
Elymus repens	168.5	22.7	92.5	13.9	45.2	6.8	45.8	7.4
Leontodon autumnalis	0.0	0.0	9.8	1.5	0.1	0.0		
Epilobium angustifolium			9.0	1.4				
Agrostis tenuis	70.3	9.5	257.2	38.6	122.1	18.5	84.6	13.7
Anthoxanthum odoratum			9.9	1.5	0.1	0.0	3.2	0.5
Taraxacum officinale	12.4	1.7	130.9	19.7	51.1	7.7	88.8	14.4
Cirsium helenioides							7.0	1.1
Achillea ptarmica	0.2	0.0	2.8	0.4	4.4	0.7	21.6	3.5
Achillea millefolium	3.2	0.4	4.5	0.7	4.0	0.6	11.5	1.9
Deschampsia cespitosa			3.6	0.5	52.1	7.9	56.4	9.1
Poa pratensis	8.6	1.2	13.6	2.0	16.1	2.4	38.0	6.2
Vicia cracca					26.1	3.9	26.0	4.2
Festuca rubra			0.1	0.0	4.9	0.7	9.2	1.5
Hypericum maculatum					1.0	0.2	9.2	1.5
Ranunculus acris			1.4	0.2	8.7	1.3	19.7	3.2
Lathyrus pratensis					11.5	1.7	16.9	2.7
Vicia sepium					0.8	0.1	6.6	1.1
Alchemilla vulgaris			2.0	0.3	194.7	29.5	127.1	20.6
Uncorrected species								
Korjaamattomat lajit	4.3	0.6	4.8	0.7	19.7	3.0	27.4	4.4
Peak biomass (PB)								
Huippubiomassa	742.5	100.1	666.0	100.0	661.0	99.9	617.1	99.9

1973 succession samples (Table 13). The measured standing crops for each species were corrected so as to correspond to the peak biomass of each species (p. 13) (Traczyk et al. 1973). The above-ground net production was 617.1—742.5 g/m^2/yr, being greatest on P68 and smallest on P53. The pattern of species succession given by the peak biomass values corresponds well to the concept presented above.

The above-ground net primary production can be calculated with the aid of the decomposition rate of the litter by means of a method (WE) developed by Wiegert & Evans (1964) (p. 14). The highest mean annual litter decomposition rates, 2.2 mg/g occurred in 1972 on P58. The next fastest decompostion rates were found on P65 (2.1) and on P68 (1.9). The lowest decomposition rate occurred on P53 (1.8 mg/g). The largest mean amount of litter was found on P68 and the smallest on P58. The above-ground net primary production was 613.0—1 467.7 g/m^2/yr (Table 13). Production in the study period was greatest on P68 and smallest on P58 and P53. Apart from the oldest field, the largest values were obtained in 1971 and the smallest in 1973. Production on the oldest field was at its greatest in 1972 and at its lowest in 1973.

The estimates for the above-ground net primary production obtained using different methods varied considerably. Wiegert & McGinnis (1975), as well as researchers cited by Coupland (1979), have arrived at the same results. In this study, the smallest estimates were obtained with MB and the largest with WE and JTB. The estimates given by PB fell in between. The ratio between MB (or JB) and the other estimates of primary production was 1.4—1.7 on P68, 1.4—2.4 on P65, 1.1—1.5 on P58 and 1.2—1.8 on P53. When all the fields are included together, the ratio was 1.5 (WE/JB) in 1971, 1.8 (WE/MB) in 1972, and 1.5 (WE/MB) and 1.3 (PB/MB) in 1973. Wiegert & McGinnis (1975) have obtained ratio values of a very similar order of magnitude (1.6—2.5), depending on how favourable is the growing season. According to the results of the IBP studies (Coupland 1979), the ratio for grasslands is 0.72—3.78.

One surprising feature is that WE and JTB gave almost the same results in this study. There is highly significant correlation (0.989, $p < 0.001$) between the production estimates given by the parts of these two parameters which are comparable. This is an especially interesting result because JTB is the simplest and the cheapest of the harvesting methods used. The costs of the different methods follow the order: JTB < JB < MTB < MB < WE < PB. JTB presupposes that the samples are collected once during the summer, at the end of July when the temperature sum is ca. 650 d.d. (55 % of the total temperature sum). Species identification and separation of the living and dead parts of the plant samples is not needed in this connection since measurement of the total plant biomass is sufficient. The method has been used earlier in Finland by Kosonen (1969). The method has been criticized because the total plant biomass also includes the dead remains of the previous year's plant biomass (Törmälä & Raatikainen 1976). Observations suggest that it may include plant biomass from a number of years, depending on the decomposition rate of the litter, the plant species composition and the weather.

Too small estimates of production are obtained when the amount of plant biomass is measured only once during the summer (Odum 1960, Wiegert & McGinnis 1975, Coupland 1979), because the species do not reach their maximum biomass values at the same time. Only in large dominance stands does it approach the correct result (Odum 1960). PB is considered to be a rather good method for estimating the production, although it is the most expensive of the available methods. However, PB does not include the dead biomass preceeding species peak, and hence, according to Golley & Gentry (1966), it gives underestimates of the production. This also applies to the two youngest fields in this study if the estimates are compared to the result given by WE. The results given by PB and WE were also the same on the oldest fields. The peak biomass values of the individual species can be measured either directly from the results of species identification on sample plots (Odum 1960, Wiegert & Evans 1964, Golley & Gentry 1966, Törmälä & Raatikainen 1976) or indirectly on the basis of the soot densities and the mean individual growth, as has been done in this study (cf. Traczyk et al. 1973). The former method is the most expensive and time-consuming of these methods.

However, Odum (1960) and Wiegert & McGinnis (1975) have shown that the sum of the peak biomass values can give overestimates of the production if all the species present at low abundance values are summed together. Wiegert & McGinnis (1975) have also shown that the estimates obtained with this method contain errors if the vegetation is very heterogeneous. They have shown that the best and most accurate method for estimating the annual above-ground net production is to calculate the annual amount of litter and determine the litter decomposition rate (WE).

The main problem with WE is the determination of the decomposition rate of the litter at a time when new litter is continuously being formed (July, August and September). It has been found that the rate of litter decomposition slows down in July in comparison to that at the beginning of summer, but increases again in August when the species that reached their production peak in early summer start to wither. The same value was chosen for the summer decomposition rate on all the fields in summer 1972 and 1973 (10 mg/g/day). Törmälä & Raatikainen (1976) arrived at an estimate of 6 mg/g/day in summer 1973 at a site 100 km to the south of the study area. Their value was too small to apply in this study because, if a 6 mg/g/day value would have been used, production on the fields would have been smaller than the maximum standing crop (MB). 10 mg/g/day is not an exceptionally large figure for the decomposition rate (Rychnovská 1979, Törmälä & Eloranta 1982).

The proportion of the root system, i.e. the below-ground primary production, was not measured in this study. According to various studies, its amount usually varies considerably (Wiegert & Evans 1964, Traczyk 1968, Tokarwińska 1978, Coupland 1979, Pulli 1980 b). According to Törmälä & Raatikainen (1976), the ratio of the above-ground and below-ground primary production is 1.2.

If this ratio is applied to the results of this study, then a net primary production (using WE) of 1 124.8—2 690.8 g/m^2/yr is obtained, which corresponds to the value of 18 817—45 055 kJ/m^2/yr according to Lieth & Pflanz (1968). When estimating the efficiency of energy capture, the amount of

energy received by the vegetation under study should be used (Botkin & Malone 1968). The closest meteorological station where radiation measurements are made is, however, at Jyväskylä, which is 70 km to the south-west of the study area. The total amount of radiation during the growing season was 2.53×10^6 in 1971, 2.67×10^6 in 1972 and 2.58×10^6 kJ/m^2 in 1973. 45 % of the total radiative energy is in a form available for plants (Sims et al. 1978). According to the above, the ecological efficiency (%) of the vegetation was:

Field plot	Sample plot	Study year	EECT	EECG
P68	3	1971	1.7	4.0
	4	1972	1.3	3.0
	5	1973	1.1	2.5
P65	6	1971	1.2	2.7
	7	1972	1.1	2.5
	8	1973	1.0	2.3
P58	13	1971	1.3	3.0
	14	1972	1.0	2.2
	15	1973	0.7	1.6
P53	18	1971	0.9	1.9
	19	1972	1.0	2.3
	20	1973	0.8	1.8

where EECT is the efficiency of energy capture from growing season total energy and EECG from usable energy. However, these figures do not include the amount of energy used in respiration nor that used by consumers. According to Golley (1960, 1965), Ryszkowski (1975) and Detling (1979), from 12 to 73 % of the production may be consumed in respiration. The proportion used by consumers is presented in the following section (p. 65).

The ecological efficiency decreases rapidly during the first ten years after cultivation ceases and the decrease then starts to taper off. These estimates are based on the assumption that the root/shoot ratio remains constant over time. According to Mellinger & McNaughton (1975), this is not necessarily the case because as the field ages an ever increasing proportion of the biomass of the community builds up under ground. According to Hokkanen & Raatikainen (1977a), in the succession of hay fields the root/shoot ratio does not change to a significant extent over time.

Values for the ecological efficiency of abandoned fields equivalent to 0.51 % of the total radiation (Törmälä & Raatikainen 1976) and 1.16 % of the photosynthetically available radiation (Törmälä 1982) have been obtained in Finland. The reason for the disagreement with the results of this study lies in the methods used and in differences in site fertility, as well as in cultivation differences (hay field/open cultivation).

Pulli (1980a) has obtained efficiencies of 0.7—1.1 % (of the total radiation) for young hay fields in 1974 and 1975. The results have been obtained on fields fertilized with nitrogen, and the production has been calculated from the above-ground standing crop on July 7.—9. In addition, the growing season has been defined using a different method than that used in this study, i.e. cumulatively from frost to frost. On the basis of the above, it is possible to achieve efficiency values greater than 2 % at least on young hay fields under Finnish conditions. Values for the efficiency of energy capture of 0.1—5.1 % have been obtained on grasslands in different parts of the world (Golley 1960, 1965, 1968, Botkin & Malone 1968, Sims & Singh 1978, French 1979, Coupland 1979).

Estimates for the primary production of meadows vary considerably. Wiegert & Evans (1964), Kosonen (1969), Williamson (1976), Coupland (1979) and Teivainen & Jukola-Sulonen (1983) have obtained the largest estimates for the above-ground net primary production. Their estimates of 691—1 211 g/m^2/yr are of the same order of magnitude as the production on the young hay fields in this study. Gyllenberg (1969), Törmälä & Raatikainen (1976), Törmälä (1977, 1982) and Törmälä & Eloranta (1982) have obtained considerably smaller production estimates in Finland (371—415 g/m^2/yr), which are of the same order of magnitude as the maximum standing crops on P65 in 1972 and 1973. Traczyk (1968), Scott et al. (1979), Coupland (1979) and Dickinson & Polwart (1982) have obtained similar or even smaller production estimates (138—290 g/m^2/yr). The production estimates obtained in this study for the youngest fields correspond to the size of a good crop from cultivated hay fields in Finland (Pulli 1980a). The great differences between these estimates of the primary production are due to differences in the precipitation and evaporation conditions and in the amounts of solar radiation (Sims & Coupland 1979), as well as to differences in the moisture and nutrient status of the soil, to the intensity of human activities

(Steen 1980) and to differences in the methods used (Wiegert & McGinnis 1975).

The methodological weakness of this study is that MB, and also to a great extent WE, were based on a relatively low number of samples, even though the samples were collected repeatedly from around the same posts. However, as these results are to a sufficient extent in agreement with the larger material collected once during the growing season, they can be considered to be rather reliable, despite the fact that they had to be scrutinized at many stages during the calculation of WE.

472. Production during 1971—1979

In the previous section, large differences were found both in the living and the dead biomass values between different seasons and between different years. Regular changes in production with respect to time in 1971—1979 were also studied. Succession samples were collected once at slightly different times during the summer for a period of nine years. Samples were also taken from all the fields at the same time in 1975 (2.7.) and in 1977 (27.7.). The standing crops measured on the different fields at the beginning of July 1975 did not differ significantly from each other. The greatest production was on P68, and the smallest on P65 (Appendix 1). The standing crop at the end of July 1977 was significantly greater ($p < 0.05$) on P68 than on P65 and P53.

The living standing crop measured in different years has been corrected so as to correspond to the temperature sum (650 d.d.) at the time of harvesting in 1977 (JB) (Table 2). The dead plant biomass has not been corrected because, according to the above, the amount of litter is at its smallest in June — July. Neither have the shoot densities been corrected — they were assumed to have remained unchanged. The shoot densities were calculated for 1971, 1973 and 1975 (Jukola 1977), since it was possible to calculate the mean individual production for each species and each field in these years (Table 10). The living standing crop at the end of July 1977 was half that at the corresponding time in 1971. However, the-oldest field, where no great changes occurred throughout the course of the study, was an exception to this. The reduction in the production on the fields is clearly evident in Fig. 20. When the distribution charts for species abundance in Appendix 2 are compared with these yield charts, it is apparent that the abundance of *Phleum pratense* was concentrated in most cases in the parts of the fields where the production was high. No such connections were found between the total yield and the abundance distribution of the other species. The original almost evenly distributed production of the cultivated hay fields had changed to a very irregular distribution of production on all the fields.

The standing crop of dead plant biomass (litter) in June - July varied considerably on the different fields and in different years. It was greatest on P68 (350—1 030 g/m^2) almost every year during the course of the study, and was smallest on P65 (184—238 g/m^2) at the beginning of the study and on the older plots (247—387 g/m^2) at the end of the study. The amount of litter on all the fields was greater at the end of the study than at the beginning (1.3—2.7 times). This was not due to an increase in production along with succession - according to the above the production in fact decreased - but to the prevailing weather conditions. The summers at the onset of the study (1971—1974) were warmer than normal and the winters, in part, were mild and litter decomposition was thus approximately equivalent to the amount that was produced during the summer. Later on the summers were cool and wet, litter decomposition was much slower. The amount of litter thus increased from year to year. 1976 and 1977 were especially bad years. As well as being affected by the weather conditions, the rate of litter decomposition is also affected by the species composition (cf. Bleak 1970, Miroshnichenko et al. 1972). This was evident in the fact that the accumulation of litter was nowhere near as great on the oldest herb-dominated fields as on the youngest grass-dominated fields, even during bad years. According to Hokkanen & Raatikainen (1977a) and Törmälä & Eloranta (1982), the amount of litter increases as succession proceeds after cultivation has ceased both on old hay fields and after open cultivation.

It became apparent in connection with the estimation of the net primary production, that JTB, i.e. the total biomass by the end of July, gives a good estimate of the net primary

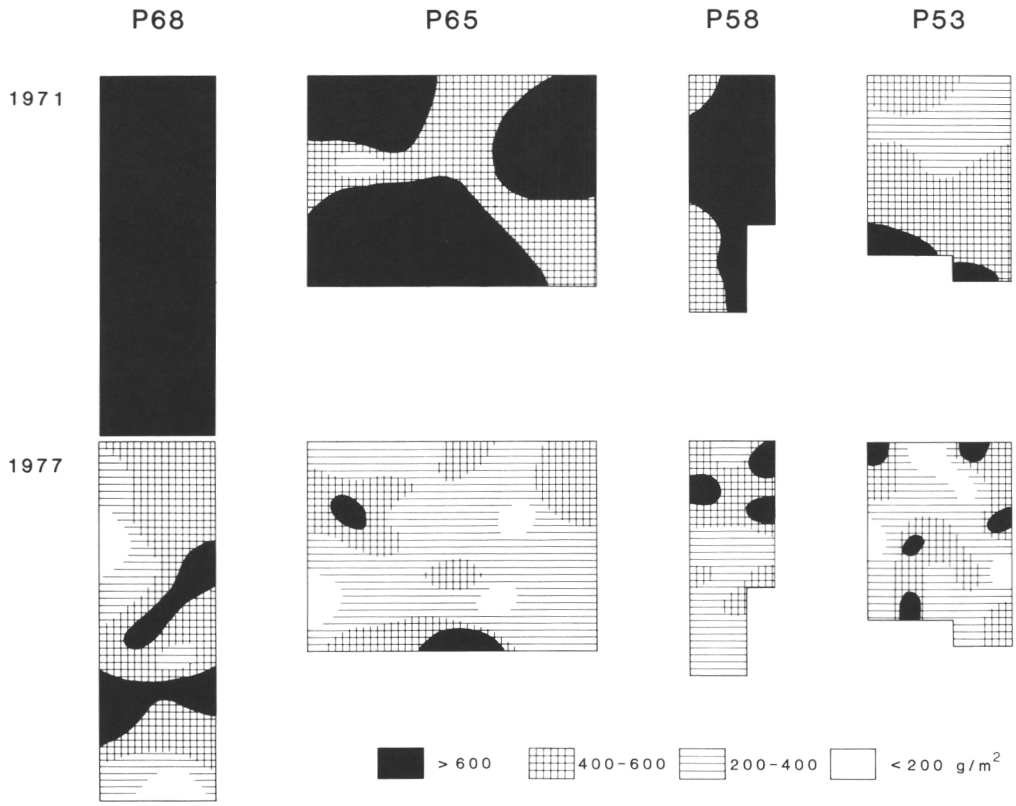


Fig. 20. Distribution pattern of the above-ground living biomass (g/m^2, JB, 650 d.d., Table 2) on the field plots on the basis of the isonomes for 1971 and 1977.

Kuva 20. Maanpäälisen elävän kasvimassan (g/m^2, JB, 650 d.d., Taulukko 2) jakaantuminen peltolohkoilla v. 1971 ja 1977 isonomikarttana.

production of the plant community during the period 1971—1973. However, owing to the heavy accumulation of litter in later years this does not apply to the youngest fields at least, where the accumulation was the greatest. JTB is thus an uncertain method for estimating primary production, as it depends on the weather conditions and the species composition.

The ratio between the shoot density and the production appeared to show a certain amount of regularity: a small shoot density was associated with a large production, and a large shoot density with a small production. This ratio and the regularity in the different vegetation layers and in different species is described in Section 465. The shoot density increased to a highly significant degree as the production decreased on the fields older than three years, but appears to decrease later on before the fields revert to forest land. This relationship between the shoot density and the production is also apparent in the mean changes of the shoot weight (g/shoot) (Table 10). Changes in the mean shoot weight appear to be reflected as changes in the production of the whole plant community.

The above-ground production of P68 was very high, over 900 g/m^2 at the age of three years, from where it decreased rapidly by the succession age of ten years to 500 g. A similar trend occurred on P65, where the decrease continued in almost a linear fashion upto the succession age of 14 years. The initial level on P58 was relatively higher than on the younger fields, but even so the production appeared to decrease on this field plot, too. The production on the oldest field remained at approximately the same level

from year to year. These observations concern the field and bottom layers. If the total production for the tree and shrub layers estimated on the basis of the analysis carried out in 1979 (Table 4) is included, then the situation does not change to any great extent. The production on the youngest field was still the greatest, and that on P65 the smallest, despite the fact that a few hundred seedlings of different tree species were planted on P65 (p. 9) in 1972. When the fact that the fields were treeless at the time that the study was started in 1971 is taken into account, it is apparent that the production of P65 decreased to almost one half in ten years. Production subsequently started to increase gradually along with reforestation, but did not reach the production level of the young hay field even at the succession age of 25 years (12 years after the last mowing).

The results presented in the literature about the relationship between succession and the production of abandoned fields vary considerably. Oosting (1942) states that the production increases as the age of the plant community which develops on the field increases. According to Odum (1960), Mellinger & McNaughton (1975) and Hokkanen & Raatikainen (1977a), however, the production decreases during the early stages of succession, and according to Wiegert & Evans (1964), the differences in production in different years are greater than the changes which occur along with succession. Such contradictory results may be due to differences in the initial stage of succession (hay/open cultivation) (cf. Hokkanen & Raatikainen 1977a), the treatments carried out on the field during cultivation and, possibly, to methodical differences. The geographical location and climatic factors may also have an effect on the succession of production.

The production and species composition of hay fields have been comprehensively studied on two occasions in Finland (Paatela 1953, Raatikainen & Raatikainen 1975). One of the factors which have been found to affect the production in these studies is the age of the ley (1—5 and over 5 years). The samples were collected, as was partly the case in this study, at the end of June and beginning of July. The results of this study correspond to those concerning the effect of the age of the ley on the production. The production obtained in earlier studies are considerably smaller than those of this study. The results of Raatikainen & Raatikainen (1975) compared here are mean values for Central Finland, and the production at the time when Paatela (1953) made his studies was generally much smaller than today (Raatikainen & Raatikainen 1975). In addition, the production of the ley decreased as the age of the ley increased at a faster rate than nowadays. According to Raatikainen & Raatikainen (1975), the largest production is obtained during the second year after seeding. The production remains rather large even after four years. In this study the production decreased rapidly on the fields at the age of three years, presumably because fertilization was discontinued already in 1968.

473. Herbivory

The most significant above-ground consumers on abandoned fields are herbivorous invertebrates. According to Hokkanen & Raatikainen (1977b), the most numerous of such invertebrates under Finnish conditions are cicadas (*Homoptera — Auchenorrhyncha*). The second important group are the small mammals, the most abundant of which in southern Finland are, according to Teivainen (1979), the field voles (*Microtus agrestis*). There are great local and seasonal variations in the abundance of these two groups (Andrzejewska & Wójcik 1971, Kalela 1962, Andrzejewska 1979a). Herbivorous invertebrates may consume, depending on the conditions, from 0.6 to 15.5 % of the annual net primary production (Gyllenberg 1969, Andrzejewska 1971, 1979b, Andrzejewska & Wójcik 1971, Breymeyer 1978, Törmälä 1982) or even as much as 20—30 % (Golley 1960, Odum et al. 1962, Breymeyer & van Dyne 1980). Herbivorous small mammals may correspondingly consume 0.5—12 % (Golley 1960, Grodziński et al. 1966, Myllymäki 1969, Gębczyńska 1970, Babińska 1972, Petrusewicz & Grodziński 1975, Ryszkowski 1982). Herbivores destroy living plant material in other ways than by merely consuming it, e.g. by shredding it and by building nests and corridors. The proportion of the energy consumed is only a very small part of the total amount of energy lost (Babińska—Werka 1979).

The effect of the dominant small mammal on the studied fields, i.e. the field vole (*Microtus agrestis*), on primary production and production of the individual plant species, is calculated in the following on the basis of the results obtained partly from the literature (p. 14). This example also acts as a demonstration of how results of this kind can be utilized in other branches of science if the research methods are compatible and the same sample plots used.

The proportion of energy consumed by the voles out of the primary production during the growing season corresponds to the values which have usually been obtained for the proportion of production consumed by the dominant consumer (0.2—2.9 %) (Table 15). Consumption when the vole density was at its peak is 0.8—2.9 % of production, but during declining years it is only 0.2—0.8 %. Relative consumption during the winter season is almost ten times that in summer. Depending on how the calculations are made, the total amount of plant biomass destroyed during the growing season in peak years is 1.6—5.3 % (smallest values A) or 8.3—23.6 % (largest values B), and in declining years 1.6—7.2 %. The damage percentages for the winter were so large on all the fields (36—85 %), that the vegetation would have been almost completely destroyed if the vole density had remained at the October level throughout the winter. This was not the case, however, as the vole population decreased dramatically with the onset of winter (Hytönen 1975). The damage percentages are so large that they should have some effect on the measured production. The damage should also be reflected as a decrease in the production during peak vole years, and especially as a reduction in the production after the peak year. At least part of the biomass lost during the growing season is replaced by new growth, but damage which occurs during the winter is concentrated on the buds of plants with the result that growth is slow during the following spring and the production may be poor throughout the following summer. This was apparently the case on the fields studied here. Growth in spring 1973 was slow even though the weather conditions did not differ from those during the previous spring. In addition, the winter 1972/1973 had been mild. The production throughout the growing season was clearly below that for the previous year. This was also evident in the values for the potential primary production (Table 15). The effect of the peak vole year on the production was also apparent in the yields at the end of July (corrected to a temperature sum of 650 d.d.) (Fig. 21). The production for 1971 is marked in the figure with the value 100 and the yields for different years are compared to this value. The effect of the vole peak on the production is strongly apparent in the year after the vole peak. The vegetation appears to have at least partly recovered during the time when the vole population was low.

The field vole forages selectively. Voles are very particular about which plant species and which parts of the plant they eat (Hansson 1971, Marttila 1974, Teivainen & Jukola-Sulonen 1983). The extent to which the effect of the voles is apparent in the production of the individual species and of species belonging to different preference classes is examined in the following. As has been done in the above, the comparisons are carried out on the production for 1971.

According to Teivainen & Jukola-Sulonen (1983), *Anthoxanthum odoratum*, *Leontodon autumnalis*, *Vicia sepium*, *Poa pratensis*, *Dactylis glomerata*, *Festuca rubra*, *Trifolium pratense*, *Taraxacum officinale*, *Phleum pratense* and *Capsella bursa-pastoris* belong to the first preference class, i.e. those species eaten the most (17—44 % of those offered). The combined biomass of these species decreases to almost one half from 1971 to 1973 in the material formed from combining all the fields (Fig. 21). The second preference class (eaten 6-16 % of those offered) includes *Deschampsia cespitosa*, *Trifolium repens*, *Vicia cracca*, *Agrostis tenuis*, *Sonchus arvensis*, *Viola arvensis*, *Myosotis arvensis*, *Equisetum arvense*, *Rumex acctosella* and *Elymus repens*. The biomass of these species also decreases from 1971 to 1973, but not to the same extent as for the species in the first preference class. The trend is also the same for the species in the third preference class (eaten 0—5 %). *Lapsana communis*, *Ranunculus repens*, *Alchemilla vulgaris*, *Lathyrus pratensis*, *Cirsium arvense*, *Rubus idaeus*, *Veronica chamaedrys*, *Epilobium angustifolium*, *Galeopsis bifida*, *Ranunculus acris*, *Poa trivialis* and *Hypericum maculatum* belong to this class.

A dense vole population has a strong effect both on the production in general and selectively on the production of the individual

Table 15. The amounts of plant biomass (d.w.g) consumed and destroyed by the field vole (*Microtus agrestis*) populations in the field plots according to different estimates in summer (A and B) and in winter (C) in 1972—1973, and the proportion of consumed and destroyed biomass out of the potential net primary production (I = MB, II = WE, see Table 14).

Taulukko 15. Peltolohkojen peltomyyrä (Microtus agrestis) -populaatioiden kuluttama ja tuhoama kasvimassa (kp. g) eri arvioiden mukaan kesäkaudelle (A ja B) sekä talvikaudelle (C) v. 1972—1973 ja kulutetun ja tuhotun biomassan osuus potentiaalisesta nettoprimaarituotoksesta (I = MB, II = WE, ks. taulukko 14).

Field plot — *Peltolohko*		P68			P65			P58			P53		
Year — *Vuosi*		1972		1973	1972		1973	1972		1973	1972		1973
Months — *Kuukaudet*		V—X	XI—IV	V—X	V—X	XI—IV	V—X	V—X	XI—IV	V—X	V—X	XI—IV	V—X
Voles/ha[1]		169	131	26	166	165	18	129	179	19	108	136	52
Myyriä/ha													
Individ.days		31 096	23 711	4 784	30 544	29 865	3 312	23 736	32 399	3 496	19 872	24 616	9 568
Yksilöpäiviä													
Consumption g/ind/day[2]		4.15	3.58	4.15	4.15	3.58	4.15	4.15	3.58	4.15	4.15	3.58	4.15
Kulutus g/yks/pv													
Destroyed kg/ha[3]	A	232		36	228		25	177		26	148		71
Tuhottu kg/ha	*B*	1291		199	1268		138	986		145	825		397
	C		356			448			486			369	
Consumption %	IA	1.7		0.4	2.9		0.3	1.5		0.3	1.8		0.8
Kulutus %	IB	1.5		0.4	2.4		0.3	1.3		0.3	1.6		0.7
	IC		16.1			20.3			16.5			8.7	
	IIA	1.1		0.2	1.3		0.2	1.1		0.2	0.9		0.6
	IIB	1.0		0.2	1.1		0.2	1.0		0.2	0.8		0.6
Destroyed %	IA	3.1		0.7	5.3		0.6	2.7		0.5	3.2		1.4
Tuhottu %	IB	15.0		3.5	23.6		3.2	13.2		2.5	15.5		7.2
	IC		67.2			85.2			68.9			36.5	
	IIA	2.0		0.4	2.5		0.3	2.0		0.4	1.6		1.1
	IIB	10.0		2.0	11.3		1.6	10.3		2.3	8.3		5.7

[1] Hytönen 1975, Teivainen (pers. comm.)
[2] Chitty et al. 1968, Drożdż 1968, Hansson & Grodziński 1970, Babińska 1972 (1 g = 16.75 kJ, Lieth & Pflanz 1968)
[3] Chitty et al. 1968, Ryszkowski et al. 1973, Babińska-Werka 1979

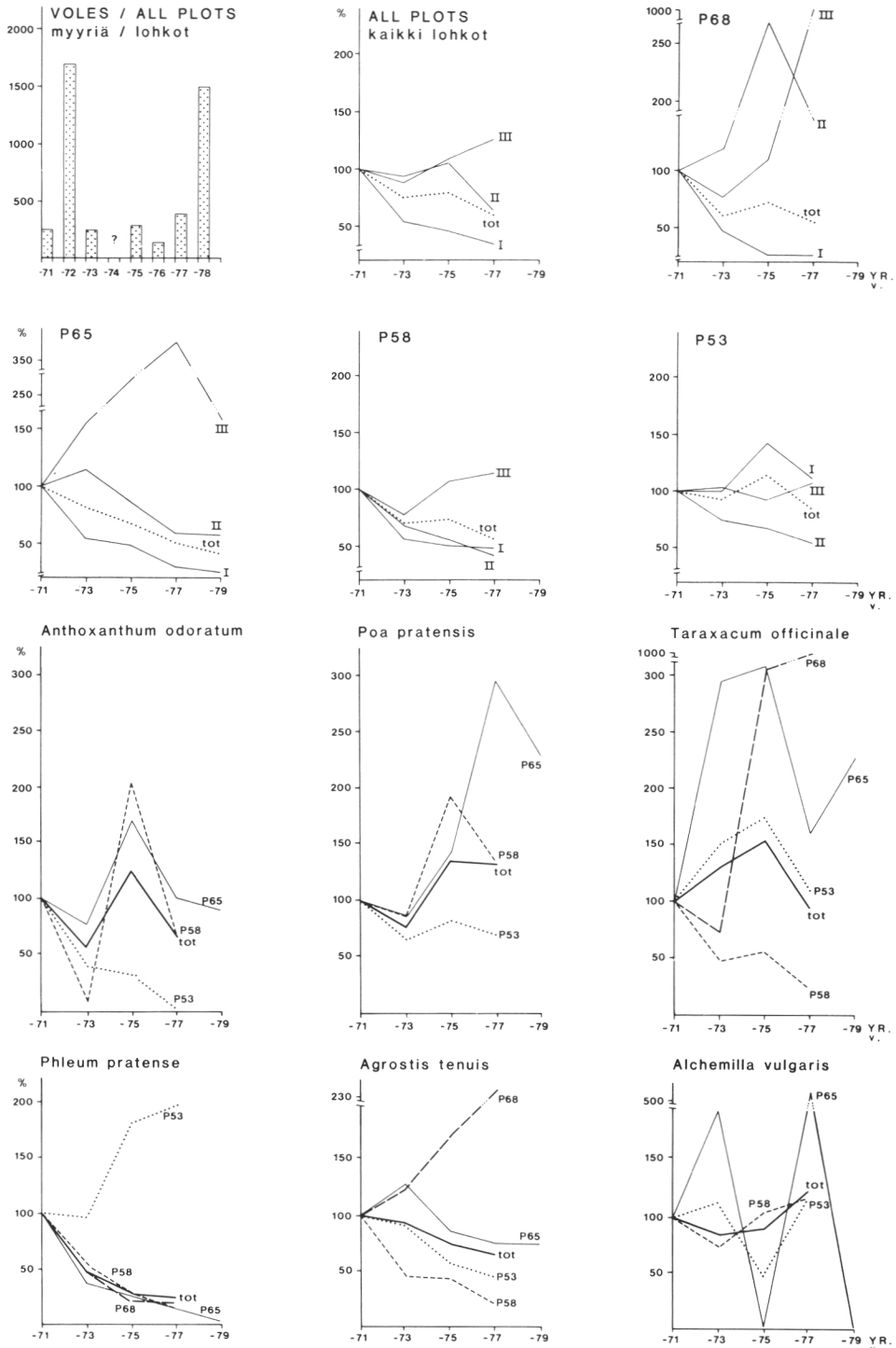


Fig. 21. The total numbers of different field vole (*Microtus agrestis*) individuals found on all field plots studied (1.71 ha) compared with the relative biomass values of three preference classes (I - III) for food plants and of particular species on each field plot and in the total (TOT) material of all field plots. Biomass in 1971 = 100 %. See text for further explanation.

Kuva 21. Peltolohkoilla (1.71 ha) tavattujen eri peltomyyräyksilöiden (Microtus agrestis) kokonaismäärän suhde kolmen ravintokasvipreferenssiluokan (I—III) sekä kunkin lohkon yksittäisten lajien suhteellisiin biomassa-arvoihin ja kaikkien peltolohkojen kokonaissadon (TOT) määrään. Vuoden 1971 sato = 100 %. Lisäselvityksiä on tekstissä.

species and hence on succession. By foraging selectively, the voles reduce permanently or only temporarily the production of their preferred species. The effect was permanent in the case of the seeded species, *Phleum pratense*. The effect was even more pronounced for *Leontodon autumnalis*, *Dactylis glomerata*, *Trifolium pratense* and *Capsella bursa-pastoris*. These species are favoured by the voles (preference class 1). They even occurred abundantly on some of the fields at the beginning of the study (*Leontodon*), but were completely absent by the end of the study (cf. however, p. 37). A dense vole population is even able to cause the removal from succession of certain species which are favoured. Crop plants and species which occur at the peripheral limits of their distribution, or are otherwise growing in biotopes which are unsuitable, are especially sensitive to the effect of voles.

The plant species favoured by voles also includes species whose production do not apparently decrease, or else decrease only very slightly, after a vole peak. Such species are *Vicia sepium* and *Taraxacum officinale*. In the case of *Vicia sepium*, the voles concentrated almost exclusively on the seeds, which is not fatal to the plant, because on old fields this species reproduces almost only by vegetative means. Voles feeding on this species thus did not result in a decrease in the production. *Taraxacum*, on the other hand, has a very strong reproductive capacity. A new plant can even develop from a small detached root segment. Thus this plant can withstand heavy grazing without it resulting in a decrease in the production. In spring 1972 when the vole peak was starting to develop, *Taraxacum* individuals which had been gnawed deep down into the ground were found on the fields. These survived, however, by means of buds formed on the roots.

The different preference classes contained species from all the different succession classes (Fig.15b). The major proportion of the combined biomass of the first preference class constituted *Phleum pratense* from the first succession class, *Taraxacum officinale* from the second succession class, and *Poa pratensis* from the third succession class. The most common species in the second preference class were *Agrostis tenuis* and *Elymus repens* from the second succession class, and *Alchemilla* and *Ranunculus acris* from the third succession class. Although species from the different succession classes were in all the preference classes, it does appear that there are certain connections between these classifications (Fig. 5). The production on the youngest sample plot mainly consisted (81 %) of species from the first preference class, while on the oldest plot all three preference clases were represented equally. The younger the hay field is, the greater the amount of food suitable for the field vole. This was also evident in the vole population density at the start of the study, which was at its greatest precisely on the youngest field plot (360 voles/ha). Cates & Orians (1975) have also found in their study on the palatability of plant species in different stages of succession using snails, that the species occurring in the early succession stages had the highest palatability indices. They state that species of early succession have not developed chemical and physical defence mechanisms, neither do they need to because they act in accordance with the r strategy (MacArthur & Wilson 1967). Species associated with later succession stages (K strategists) are the opposite in that their defence mechanisms are the stronger, the later the stage they belong to (trees). Oksanen (1980), in his studies on reindeer grazing areas in the fells of Fennoscandia, has found that the K strategists are concentrated in areas where the grazing pressure is low and the r strategists in areas subjected to a high grazing pressure.

The results in the literature are in general agreement about the effects of a dense vole population on the vegetation (Richter 1958, Tast & Kalela 1971, Batzli & Pitelka 1970, Kokeš 1976, Stenseth et al. 1977, Ryszkowski 1982). The effect of the vole density is evident, as in this study, both in the reduction in the production and the species composition, but also in changes in the relationships between the abundances of different species. Stenseth et al. (1977) have found that the field vole eats plant species in different ratios to that of the species which are available and so the peaks in the occurrence of this vole species have a considerable effect on the species composition of its habitats. According to Batzli & Pitelka (1970), there are two factors which have the greatest effect on the yield of grasslands: the amount of precipitation in early summer, and the vole density. They state that a dense vole

population has a strong effect on both the production and on the species composition. This was apparently the case in this study. This supports the theory of Fretwell (1977) about the effect of strong grazing in shaping natural plant communities Oksanen (1978, 1980) has also come to the same conclusion. However, the effect is not one-sided but, as found in this study, a complicated interrelationship exists between the vegetation and herbivores. For instance, Freeland (1974) and Haukioja (1980) have shown that the large variations in the abundance of herbivores can be explained using the dynamic changes which occur in the capacity of plants to protect themselves against herbivores.

48. Diversity

A total of 130 taxons were recorded on the fields in this study. There were 13 bryophytes, 104 field layer species, and 13 tree and shrub layer species. Diversity in its simplest meaning refers to the number of different species per unit surface area. Two different measures of the number of species were determined on the sample plots: the number of species in the sample (S), and the species richness (ASR), which is the mean sum number of different species occurring on an area of one square metre (Table 16).

In addition to the number of species, many indices have been developed for depicting the diversity of a vegetation, which is related to the stability of the community (p. 16). The abundance values for individual species or relative abundance values are also used in calculating these indices. Six indices have been used in this study. The most commonly used of these is Shannon's (Shannon & Weaver 1949) index, H'. Pielou (1966) has developed a modification, J', of Shannon's index, which gives similar but smaller values than Shannon's index. Simpson's (1949) index, D, gave similar results to the previous indices, lying between the values for Shannon's and Pielou's indices. Simpson's index values were also calculated for the field layer using corrected biomass values (D_2). This index differed from D_1 by + 0.038 . . . -0.059.

The next three indices differ considerably from the previous ones. A number of modifications have since been developed of Whittaker's (1972) index, E_c, so-called "log-cycle" by Whittaker and Niering (1975), Kempton and Taylor (1976) and Lamont et al. (1977). The two latter modifications were tested here.

In the above, the diversity of the sample plots was depicted using the number of species and a number of indices calculated in different ways. An attempt was made, using the diversity indices, to depict the nature of the relationships between the importance values of the species in the community. The distribution of the importance values between the species can also be depicted by means of the importance value curves (Whittaker 1972, Bazzaz 1975). Changes take place in the shape and slope of these so-called dominance-diversity curves as succession proceeds. These changes are reflected in the structural and functional changes which take place in the plant community. The dominance-diversity curve of a young hay field is almost geometrical on the log scale, but when the field reaches the age of 24 years the curve is logarithmical (Fig. 22).

The graphical and numerical depictors of diversity show that the concept of diversity is not unambiguous. The mathematical complexity of the indices means that they are difficult to interpret (Whittaker 1972). The relationship between the indices, and their relationship with different environmental factors, were studied by carrying out correlation analysis on the indices for the field layer (Table 17). Highly significant positive correlations were found between the indices ASR, H', J' and D, and between the indices S, E_c, E_b and Q. In addition, ASR was correlated with the indices S and E_c. These two groups of indices differ from each other and presumably measure very different features. The correlations between indices H', J' and D (dominance indices) were very high. The correlations between these three indices and ASR were somewhat smaller, although they were statistically significant. The other index group (equitability indices) consisted of the indices E_c, E_b and Q. Indices J' and D differed the most from indices E_b and Q.

The diversity increased along with the course of succession, irrespective of whether diversity refers to the number of species or the division of the biomass between the different species. Although the diversity increased in the field layer, the increase was

Table 16. Diversity analysis of the field layer in 1971—1979, and the whole plant community in 1971 and 1977—1979. S = number of species in sample, ASR = sum of species in one square metre, H' = Shannon's, J' = Pielou's, D_1 and D_2 = Simpson's, E_c = Whittaker's, Q = Kempton and Taylor's and E_b = Lamont et al.'s indices calculated from the uncorrected biomass, D_2 from the corrected biomass. (Equations on p. 16).

Taulukko 16. Diversiteettianalyysi kenttäkerroksesta v. 1971—1979 ja koko kasviyhteisöstä v. 1971 ja 1977—1979. S = otoslajiluku, ASR = neliömetrin summalajiluku, H' = Shannonin, J' = Pieloun, D_1 ja D_2 = Simpsonin, E_c = Whittakerin, Q = Kemptonin ja Taylorin sekä E_b = Lamontin ym. indeksit korjaamattomien biomassojen mukaan, D_2 korjatuista biomassoista (kaavat sivulla 16).

Field plot *Peltolohko*	P68					P65					P58				P53				
Sample plot *Näyteala*	3	5	7	8	9	6	8	10	12	14	13	15	17	19	18	20	22	23	24
Field layer — *Kenttäkerros*																			
S	24	12	15	16	20	32	31	36	27	29	31	24	28	25	26	30	32	33	39
ASR	11	8	11	16	17	18	17	19	20	17	20	15	20	21	22	24	25	29	29
H'	0.697	1.021	1.597	1.782	2.000	1.762	1.710	2.023	2.054	1.684	1.780	2.092	2.009	1.504	2.521	2.608	2.546	2.473	2.587
J'	0.219	0.411	0.590	0.643	0.668	0.508	0.498	0.569	0.623	0.500	0.518	0.658	0.603	0.467	0.774	0.767	0.735	0.707	0.740
D_1	0.303	0.533	0.731	0.779	0.809	0.731	0.761	0.804	0.787	0.668	0.781	0.822	0.769	0.583	0.901	0.899	0.890	0.883	0.901
D_2	0.341	0.541	0.681	0.720	0.809	0.696	0.732	0.808	0.790	0.632	0.787	0.822	0.775	0.583	0.912	0.919	0.917	0.905	0.901
E_c	2.858	1.514	2.034	2.381	2.727	4.443	4.469	5.024	3.693	3.005	4.185	3.217	3.696	3.154	4.055	4.446	4.653	4.793	5.798
Q	5.121	1.876	2.415	3.685	4.519	4.802	5.035	5.525	3.213	3.448	5.341	3.827	4.767	3.506	3.806	3.952	3.783	4.017	4.083
E_b	3.878	1.292	2.525	3.036	4.255	5.631	6.266	5.548	3.787	4.060	4.141	2.787	3.513	3.508	3.558	3.838	4.287	4.148	4.997
Whole community — *Koko yhteisö*																			
S	24				22	34				44	33			35	30				51
ASR	11				17	19				20	21			24	23				32
H'	0.697				2.075	1.798				2.291	1.794			1.896	2.541				2.790
J'	0.219				0.671	0.510				0.605	0.513			0.533	0.747				0.710
D_1	0.303				0.819	0.731				0.814	0.781			0.687	0.901				0.918
E_c	2.119				2.629	3.173				4.179	3.148			3.167	3.113				5.255
Q	3.047				4.892	4.298				5.624	2.743			4.995	3.126				4.653
E_b	2.542				4.858	3.807				4.863	3.055			3.737	3.890				4.839

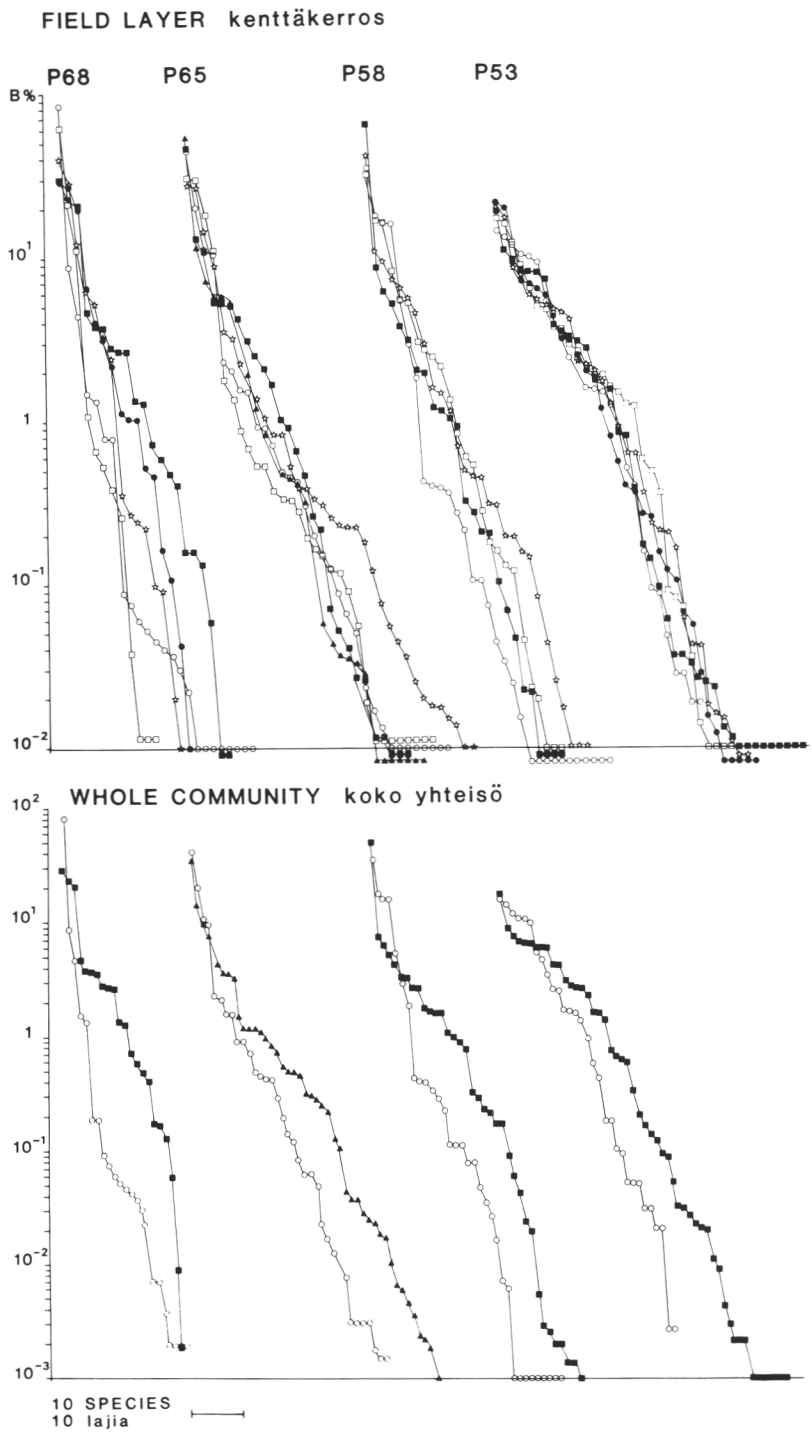


Fig. 22. Dominance-diversity curves for the field layer throughout the study period and for the whole community in 1971 and 1977—1979. The species have been arranged in order according to the relative abundances (B %) on the logarithmic scale. Symbols: ○ 1971, □ 1973, ☆ 1975, • 1976, ■ 1977, ▲ 1979.

Kuva 22. Dominanssi-diversiteetti-käyrät kenttäkerroksesta kaikkina tutkimusvuosina ja koko yhteisöstä v. 1971 ja 1977—1979. Lajit on järjestetty suhteellisten runsauksien (B %) mukaiseen järjestykseen logaritmiskaalassa. Selitykset: ○ 1971, □ 1973, ☆ 1975, • 1976, ■ 1977, ▲ 1979.

Table 17. Correlations between the diversity indices S, ASR, H', J', D_1, D_2, E_c, Q, E_b (Table 16) and the succession age in years (A_1), combined surface area of the sample quadrats (Sa), quadrat size (Qs), number of sample quadrats (Ns), time since mowing (A_2), the temperature sum at harvesting time (Ts) and the July biomass (JB) (Table 2). Statistically significant correlations are marked with an asterisk ($p < 0.05$).

Taulukko 17. Diversiteetti-indeksien S, ASR, H', J', D_1, D_2, E_c, Q ja E_b (taulukko 16) ja sukkessioiän vuosissa kylvöstä (A_1), näyteruutujen yhteispinta-alan (Sa), ruutukoon (Qs), otoskoon (Ns), ajan vuosissa niitosta (A_2), keruuajan lämpösumman (Ts) ja heinäkuun biomassan (JB) (taulukko 2) keskeiset korrelaatiot. Tilastollisesti merkitsevät korrelaatiot ($p < 0.05$) on merkitty tähdellä.

	S	ASR	H'	J'	D_1	D_2	E_c	Q	E_b
S	1.000								
ASR	0.763*	1.000							
H'	0.551*	0.833*	1.000						
J'	0.267	0.675*	0.948*	1.000					
D_1	0.428	0.692*	0.946*	0.943*	1.000				
D_2	0.472*	0.733*	0.964*	0.941*	0.987*	1.000			
E_c	0.980*	0.821*	0.669*	0.415	0.561*	0.597*	1.000		
Q	0.613*	0.253	0.078	—0.134	0.052	0.092	0.543*	1.000	
E_b	0.791*	0.454	0.286	0.055	0.269	0.264	0.775*	0.750*	1.000
A_1	0.557*	0.838*	0.785*	0.676*	0.613*	0.680*	0.637*	0.041	0.117
Sa	0.429	—0.138	—0.099	—0.277	—0.052	—0.071	0.384	0.358	0.555*
Qs	—0.021	—0.337	—0.143	—0.180	—0.096	—0.069	—0.031	0.213	—0.015
Ns	0.291	0.262	0.091	0.007	0.028	—0.000	0.261	—0.125	0.233
A_2	0.029	0.258	0.199	0.241	0.173	0.129	0.030	—0.317	—0.023
Ts	—0.017	0.073	0.171	0.193	0.064	0.083	—0.019	—0.375	—0.221
JB	—0.143	—0.277	—0.429	—0.444	—0.386	—0.380	—0.190	0.379	0.024

especially pronounced in the whole plant community. Diversity increased on all the fields up until the succession age of 24 years at least, rapidly during the first ten years but then more slowly. There was a negative correlation between dominance and diversity, as well as between production (JB) and diversity (H', J' and D). Mellinger & McNaughton (1975) have also arrived at the same result.

As was mentioned earlier, the different indices gave a differing result for diversity. Of the dominance indices, Simpson's (1949) index (D) emphasizes dominance the most. Only a few (1—3) abundant species affect the magnitude of the index, and it completely ignores species whose relative abundance is less than one (Fig. 22). Over half of the species present on all the plots were of this type.

Shannon's index can also be considered to be a dominance index, although not to the same extent as Simpson's index because it is affected by small abundance values even, and it emphasizes species which are moderately abundant. Shannon's index is the most commonly used diversity index. Considerable discussion has recently centred on the superiority of the different indices (Peet 1975, Routledge 1977, 1979, 1980, Alatalo & Alatalo 1977, Shaukat & Khan 1979, Alatalo 1981). Shannon's index has been the subject of much criticism. In this study, however, it proved to be, in addition to the ASR, the best indicator of changes taking place over time before the forest stage.

Pielou (1966) has developed a modification, J', of Shannon's index. The result is an index resembling H' and D, which has aspects of both indices. The correlations between these three indices were very high.

The species richness, ASR, increased almost linearily along with succession both in the field layer and in the whole plant community. However, there were a number of problems in calculating the species richness. The mean sum number of species counted on four 0.25 m^2 sample quadrats is not necessarily compatible with the mean sum number of species on sixteen 0.0625 m^2 quadrats. However, as no statistically significant correlation was found between the quadrat size and the species richness (Table 17), it was considered justified to count the species richness in this manner. The most effective measure of species richness is, in Peet's (1974) opinion, however, the number of species in sample (S) if all the sample plots have the same surface-area, the same quadrat size and the same number of samples. However, S provides only a small amount of information about the internal structure of the plant community. ASR, on

the other hand, gives information about both the species number and the structure of the community. This is the reason why ASR and H' are strongly inter-correlated. As S was calculated in this study from different number of samples and different-sized sample quadrats, it cannot be used as a measure of the species richness. However, ASR can only be used as a measure of species richness on a locally restricted area because the number of species per unit surface-area varies by area and by vegetation type. On the other hand, the diversity indices are intercomparable on much wider areas.

The two aspects which appear in the diversity concept, namely the species richness and the evenness of the abundance values, are inter-correlated and, according to Whittaker (1972), they cannot be measured separately. Instead, a number of indices which fulfill certain criteria should be used, these indices being such that they can be interpreted. The above-mentioned dominance indices depict the extent to which the abundance values are concentrated in the upper end of the dominance-diversity curves. Equitability indices depict the slope of the dominance-diversity curves in slightly different parts of the curves. E_c, namely the log-cycle index, is a measure of the slope of the curve throughout its length. It expresses the number of species per log-cycle of the abundance values. As the direction of the upper and lower ends of the curve differs from that in the central part of the curve, Kempton & Taylor (1976) and Lamont et al. (1977) have developed indices which measure only the slope of the central part of the curve. Kempton & Taylor (1976) have proposed that if 25 % of the species at the upper and lower end of the curve are omitted, then the slope (Q) which depicts the actual steepness of the curve would be obtained. Lamont et al. (1977, 1978) have shown that removal of 25 % of the species is absolutely too much and have developed an index which removes only 10 % from each end.

A number of drawbacks were found, however, in all these three indices in this study. The indices for the youngest stage of P68 have been calculated for the field layer and the whole plant community using the same material. As the bottom layer is missing, the only difference is in the calculation accuracy. The indices for the field layer were calculated to an accuracy of 0.1 g/m^2 and for the whole community to 0.01 g/m^2. This was almost the same as regards other materials collected in 1971. These equitability indices thus appear to be sensitive to differences arising from the accuracy of the calculations and the measurements. In addition, they are strongly correlated with the species number S, which was earlier found to be a poor depictor of diversity. It was also found that the equitability indices, apart from the E_b index, were poorly correlated with the succession age of the field layer although the dominance-diversity functions were clearly logarithmical. As the shape of the dominance-diversity curve does not change uniformly, the removal of the species from both ends of the curve results in the measurement of the slope at very haphazard points. This happened in the field layer of plot 68-3 when 25 % was removed from both ends of the curve. The result was a too large value for the index. In any case, it is quite inappropriate to remove as much as one half of all the species present, when calculating diversity indices to be used for describing the stability and diversity of the plant community. Removal of 50 %, at least, is too much. Both Q and E_b have given good results on areas with many species and were more highly correlated with succession than was the case in this study (Kempton & Taylor 1976, 1978, Lamont et al. 1977, Kempton & Wedderburn 1978).

Each of the above-described diversity indices has its own advantages and disadvantages. Each of them describe how the resources of the plant community are divided between the plant species in the community. These resources, which were divided into resource gradients in connection with the ordination analyses, limit, according to Whittaker (1972), the hypervolume of the plant community. Each of the species in the plant community occupies its own ecological niche in this space, which diversify with time. The proportion of the utilized resources can be interpreted as the productivity of the species. When the species are ranked according to their relative productivity, the dominance-diversity curve is obtained. According to the results of this study, the dominance-diversity curves illustrate what the diversity indices describe numerically. They show how the low diversity and the high dominance of a young hay field changes over

time into high diversity and low dominance, and how the distribution of limited resources between an increasing number of species makes the dominance-diversity curve change to a more logarithmical form. The dominance-diversity curve does not only show the distribution of resources within the community, but by comparing the curves of different plant communities it is also possible to find out the structural similarities between them. In other words, comparing the curves provides the same results as are obtained by ordination methods. For instance, the curves for the oldest stage of P65 are closer to those for the older stages of P68 than for the younger stages of P65. This is the same result as was obtained using some ordination methods (Fig. 9). The similarity between plant communities does not apper in the species composition only, but also in the structure.

In general, the diversity of an abandoned field increases along with succession up until the afforestation stage (Odum 1960, Margalef 1962, Bazzaz 1975, Mellinger & McNaughton 1975, Hokkanen & Raatikainen 1977a). Törmälä (1982) did not find any changes in diversity between the succession ages of 5—13 on the field covered in his study in Central Finland. He attributed this to the ecological heterogenity of the study area.

According to Odum (1969), however, the comparison of diversity studies is difficult because the indices used behave differently. In addition, the calculation methods and the materials differ from each other, which makes comparison difficult. Tramer (1975), Törmälä (1982) and Teivainen & Jukola-Sulonen (1983) have found that the time when the samples are collected has an effect on the indices.

Squiers & Wistendahl (1977) have studied the effect of the addition of species on diversity and the shape of the dominance-diversity curve. They found that the addition of species can cause a faster curving in the dominance-diversity function than takes place in nature. In other words, succession can be accelerated in a structural sense. The planting of tree seedlings has the same effect on the community diversity.

The development which takes place on abandoned hay fields during the first ten years depends on the state at the start of succession. If succession starts from bare soil, then diversity is initially very high. It decreases for a few years and then gradually starts to increase (Beckwith 1954, Tramer 1975, Squiers & Wistendahl 1977, Hokkanen & Raatikainen 1977a, Teivainen & Jukola-Sulonen 1983). In this study the diversity in the succession of hay fields is initially low owing to the strong dominance of the sown species, but then rapidly increases during the first ten years. Beckwith (1954), Nicholson & Monk (1974), Mellinger & McNaughton (1975) and Hokkanen & Raatikainen (1977a) have come to the same conclusion as regards the diversity of hay fields. According to this study, diversity appears to increase or to remain at a high level at least on the oldest fields throughout the course of the study. Whittaker (1972) and Bazzaz (1975) state that a plant community reaches its maximum diversity in the early forest stage. At this stage both shade and light-seeking species and many kinds of physiognomical groups are present in the same plant community.

In this study the oldest field appeared to have reached a fairly stable phase in the meadow stage. However, the woody plants have a competitive advantage which changes the situation. As they are the tallest species, they are able to capture a greater part of the resources in the niche hyperspace and completely change the conditions. This results in a new division of the whole niche hyperspace. Shading of the trees results in so large changes in the environmental conditions that the original species are forced out almost completely. Only on field layer species of the corresponding forest type — *Melampyrum sylvaticum* — occurred on the oldest field during the course of the study.

The results presented in the literature about the succession of diversity at the forest stage are rather variable. According to some studies, diversity always increases right upto the climax stage (Margalef 1962, Monk 1967) and according to others it decreases towards the climax following the peak in the early forest stage (Cajander 1926, Margalef 1969, Loucks 1970, Whittaker 1972, Malmer et al. 1978, Dyrenkov et al. 1981). They explain the decrease in diversity as a result of tree foliage closure in the forest. The strong dominance is caused by the superiority in competition of only a few climax tree species which suppress the species in the lower layers of vegetation that had earlier been dominant.

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SELOSTE

Kasvillisuuden sukkessio viljelemättä jätetyillä heinäpelloilla Keski-Suomessa kvantitatiivisin menetelmin tarkasteltuna

Johdanto ja tutkimuksen tarkoitus

Vuosisadan alkupuolella kaskiviljelyn loputtua ja Cajanderin (1909) kehitettyä metsätyyppioppinsa heräsi Suomessa kiinnostus erityisesti metsäkasvillisuuden sukkessiotutkimuksiin. Viime vuosina kiinnostus on herännyt uudelleen monestakin syystä: 1) 1960-luvun lopulta lähtien laajat peltoalueet jätettiin viljelemättä maatalouden ylituotannon hillitsemiseksi säädetyn pellonvarauslain 216/1969 seurauksena. 2) Metsänkäsittelyssä siirryttiin 1950-luvulta lähtien käyttämään avohakkuuta ja siihen liittyen metsänviljelyä. 3) Suomalaisten metsätyyppien käyttökelpoisuus käytännön työssä on joutunut uudelleenarvioinnin kohteeksi erityisesti siksi, että tyypittelyn perustana olevia kliimaksvaiheen metsiä on yhä vähemmän eikä eri tyyppeihin johtavia sukkessiovaiheita tunneta.

Vuonna 1969 voimaan tulleen pellonvarussopimuksen seurauksena oli enimmillään noin 240 000 ha peltoalueita jätetty viljelemättä. Vuoteen 1983 mennessä tuosta pinta-alasta oli otettu uudelleen viljelykseen noin 80 000 ha. Alle 100 000 ha oli edelleen sopimuksen piirissä ja 26 000 ha oli metsitetty. Viljelemättä jätettyjen peltojen saattaminen uudelleen tuottavaan tilaan metsittämällä kohtasi monia vaikeuksia: Peltojen maaperä todettiin sopimattomaksi metsäpuiden taimille. Lisäksi pintakasvillisuuden, myyrien, hyönteisten ja sienien aiheuttama haitta on vaikeuttanut peltojen metsittämistä. Sukkessiotutkimusohjelma, johon käsilläoleva tutkimus kuuluu, liittyy läheisesti tähän problematiikkaan ja on saanut alkunsa peltomyyrän elinympäristöselvityksenä, mutta on laajentunut myöhemmin metsänviljelyalojen ekosysteemien sukkessioanalyysiksi.

Tämä tutkimus on suoritettu Metsäntutkimuslaitoksen metsänsuojelun tutkimusosastossa vuosina 1971—1983. Vuonna 1971 aloitettiin osastossa fil.toht. Terttu Teivaisen johdolla tutkimusohjelma "Viljelemättä jätettyjen peltojen ja hakkuualojen kasvipeitteen muutokset ja niiden vaikutus myyräkantojen kvalitatiivisiin ja kvantitatiivisiin suhteisiin", jonka peltoja koskevaan osaan tämä heinäpeltojen sukkessiotutkimus kuuluu. Vuodesta 1979 tutkimus on kuulunut tekijän Suomen Akatemian rahoituksella tekemään tutkimushankkeeseen "Metsänviljelyalojen pintakasvillisuuden sukkessio ja sen merkitys taimien toimeentulolle ensimmäisinä viljelynjälkeisinä vuosina". Em. tutkimuksiin liittyen on julkaistu kasvillisuustutkimuksia vesimyyrän (*Arvicola terrestris*) tuhoaloista ja lyhytkiertoalojen sopivuudesta myyräbiotoopeiksi. Käsilläoleva tutkimus pellon kasvillisuuden sukkessiodynamiikasta on intensiivitutkimus, jolla on useita liittymäkohtia ja sovellutusmahdollisuuksia käytäntöön.

Tämän tutkimuksen tarkoituksena on:

1. Selvittää kasvillisuuden rakenteellisia ja toiminnallisia muutoksia neljällä eri-ikäisellä heinäpellolla yhdeksän vuoden aikana sekä suhteuttaa osa tuloksista laajempaan viljelemättä jätettyjen peltojen aineistoon.
2. Selvittää, muodostavatko pellot yhteneväisen sukkessiosarjan ja voidaanko tapahtuneiden muutosten avulla ennustaa tulevaa sukkessiosuuntaa.
3. Kokeilla sukkessiotutkimuksiin sovellettavia kasviekologian ja -sosiologian uusimpia menetelmiä.
4. Tehdä peltomyyrän (*Microtus agrestis*) elinympäristöstä ekologinen perusselvitys myöhempää myyrätuhoalojen luokittelua varten.

Tutkimusalue ja menetelmät

Tutkimusalue sijaitsee Suonenjoen kaupungin Jauhomäen kylän Heikkilän tilalla, 4 km Suonenjoen kaupungin keskustasta etelään Kuopio - Jyväskylä-maantien varressa. Tilan yhdeksän hehtaarin peltoala otettiin pellonvaraussopimuksen piiriin v. 1969. Tilalla oli kuitenkin jo aiemmin luovuttu osittain peltojen viljelystä niin, että tilan tässä tutkitut neljä peltolohkoa oli viimeisen kerran muokattu ja kylvetty heinälle (timotei ja apila) vuosina 1953, 1958, 1965 ja 1968. Peltolohkoilta oli korjattu heinää vuoteen 1968 saakka, mutta laitumina niitä ei oltu käytetty. Vuonna 1972 istutettiin osalle tutkimusalueesta männyn, kuusen, koivun ja hybridihaavan taimia 1300 kappaletta. Peltolohkojen tunnuksina käytetään em. viimeistä muokkausvuotta (P68, P65, P58 ja P53), mistä lasketaan pelloille kehittyvien kasviyhdyskuntien sukkessioikä näytteidenkeruuajankohtaan mennessä.

Tutkimuksen aloitusvuonna kasvillisuus oli saanut kehittyä peltolohkoilla 3, 6, 13 ja 18 vuotta. Kenttä- ja pohjakerroksen kasvillisuuden seurantaa suoritettiin 1—2 vuoden välein vuoteen 1979, jolloin saatiin sukkessiosarjat 3—24 vuotta vanhoilta näytealoilta. Kasvianalyysit tehtiin keskikesällä korjuumetodilla käyttäen lajierittelyä. Puu- ja pensaskerros analysoitiin vuonna 1979 käyttäen epäsuoraa biomassan arviointimenetelmää: pituuden ja läpimitan avulla laskettuja runko- ja tilavuusyhtälöitä. Tulokset on esitetty biomassoina (kuivapainoja g/m^2) ja esiintymisfrekvensseinä (%). Edellisten ns. sukkessionäytteiden lisäksi seurattiin kasvukaudenaikaisia lajistollisia ja kasviyhteisötason muutoksia ns. fenologianäytteiden avulla. Vuosina 1972—1973 kerättiin näytteitä 11 kertaa. Maa-analyysit tehtiin v. 1972 ja 1976.

Sukkessiotutkimuksissa aineistot kerätään siten, että niissä ilmenee aika enemmän tai vähemmän selvänä muutossuuntana. Tästä syystä näihin tutkimuksiin sovel-

tuvat erityisen hyvin uusimmat kasvillisuusaineistojen käsittelyyn kehitetyt monimuuttujamenetelmät, joiden avulla saadaan aineistosta esiin yksi tai useampia ympäristön muutossuuntia. Tässä tutkimuksessa on käytetty luokittelu- ja ordinaatiomenetelmiä. Luokittelumenetelmistä kokeiltiin eri klusterianalyysin muunnoksia, joilla voidaan aineisto jakaa kasvillisuudessa ilmenevien yhtäläisyyksien perusteella ryhmiin eri yhtäläisyyksien tasoilla. Ordinaatiomenetelmistä käytetään polaariordinaatiota, faktorianalyysiä ja reciprocal averaging -analyysiä. Ordinaatiomenetelmät määrittelevät joko näytealoille tai lajeille sijainnin muutossuuntien rajaamaan avaruuteen siten, että ekologisesti lähisukuiset alat tai lajit sijoittuvat lähekkäin.

Edelläkuvattujen kasvillisuusanalyysimenetelmien avulla on määritetty kasvillisuudessa ilmenevät muutossuunnat, yhtenä muutossuuntana aika viimeisestä muokkauksesta. Ajan suhteen on tutkittu tuotoksessa, lajikoostumuksessa ja monimuotoisuudessa (diversiteetti) tapahtuvia muutoksia, laadittu matriisimalli sukkessiomuutosten ennustamiseksi sekä analysoitu muutoksien syitä kuten lajien välistä kilpailua ja populaatioekologisia lainalaisuuksia sekä kasvissyöjien vaikutusta sukkessioon. Metsittymisen onnistumista, luontaista uudistumista ja istutuksen vaikutusta kasviyhteisöön on tutkittu.

Maaperä

Peltolohkojen maaperä oli kumpanakin tutkimusajankohtana selvästi alle tyydyttävän viljavuuden kaikilla viljavuuskriteereillä mitattuna. OMT- ja MT-metsämaihin verrattuna peltojen maaperän pH ja vaihtuva kalkki olivat samaa suuruusluokkaa tai selvästi korkeammat kuin metsän humuskerroksen (A_0). Peltomaan vaihtuvan kaliumin ja helppoliukoisen fosforin arvot olivat 21—70 % vastaavista metsämaa arvoista.

Kasvillisuuden sukkessio peltolohkoilla

Kenttäkerros muodosti kaikilla peltolohkoilla aluksi 100 % ja tutkimuksen lopussa vähintään 70 % kasviyhteisön biomassasta. Yleisimmät ja runsaimmat lajit olivat timotei (*Phleum pratense*), nurmirölli (*Agrostis tenuis*), juolavehnä (*Elymus repens*), voikukka (*Taraxacum officinale*) ja poimulehti (*Alchemilla vulgaris*). Tutkimuksen alussa runsaimmat olivat *Phleum* ja *Elymus*, mutta lopussa *Alchemilla* ja *Agrostis*.

Pohjakerros oli huonosti kehittynyt kaikilla lohkoilla. Millään lohkolla se ei muodostanut edes yhtä prosenttia kasviyhteisön kasvimassasta. Lohkojen runsain laji oli *Brachythecium albicans*, joka esiintyi runsaimpana kaikilla lohkoilla tutkimuksen alku- tai keskivaiheilla ja puuttui kokonaan tutkimuksen lopussa. Laji on kulttuurin suosija. Kaikki muut lohkoilta tavatut lajit ovat lehto- tai lehtomaisten metsien lajeja.

Puu- ja pensaskerros puuttui tutkimuksen alussa eikä ollut yhtenäinen millään lohkolla tutkimuksen lopullakaan v. 1979. Istutettuja lukuunottamatta suurin osa puuvartisista keskittyi lohkojen alaosiin, lähelle metsänreunaa. Metsittyminen eteni pelloilla varsin hitaasti. Nuorimmalla lohkolla metsittyminen ei päässyt vielä alkuun yhdeksässä vuodessa.

Lohkolla P65 pääsi metsittyminen ilman istutustakin hyvään vauhtiin. Istutetuista taimista oli elossa 7 v istutuksesta vain 65 %. Pääasiallinen kuolinsyy oli pelloilla esiintynyt tiheä myyräkanta. Istutetuista taimista oli v. 1979 elossa 38 % rauduksesta ja hybridihaavoista, 63 % männyistä ja 90 % kuusista. Puiden ja pensaiden peittävyys oli 18 %, istutettujen 13 % ja luontaisesti syntyneiden 5 %.

Vanhimmilla lohkoilla oli puubiomassan määrä tutkimuksen lopulla sitä suurempi mitä vanhempi lohko, mutta kuitenkin selvästi alle lohkon P65 määrän. Istutus on näin ollen jouduttanut metsittymistä suurista tuhoista huolimatta. Tosin istutetut lehtipuut ja osa männyistä olivat mutkarunkoisia ja huonokuntoisia.

Kasvillisuuden luokittelu ja ordinaatio

Aineisto on jaettu biomassojen ja frekvenssien pohjalta viidellä eri klusterimenetelmällä kolmeen ryhmään. Minimivarianssimenetelmä oli tämän tutkimuksen mukaan sekä biomassojen että frekvenssien mukaan paras klusterimenetelmä, seuraavina furthest neighbour ja group average menetelmät. Huonoimmat olivat nearest neighbour ja centroid menetelmät. Homogeenisimmat ryhmät syntyivät nuorimpien peltoalojen ryhmistä ja heterogeenisimmat vanhimpien alojen ryhmästä. Biomassojen mukaisessa ryhmittelyssä korostui dominanssi. Frekvenssit kuvaavat toisaalta hajallisuutta, toisaalta tiheyttä, eivätkä ota siinä määrin huomioon lajien runsaussuhteita kuin biomassat. Sukkessiomuutokset olivat enemmän kvantitatiivisia kuin kvalitatiivisia ja tällöin biomassapohjainen käsittely sopi paremmin tällaiseen tutkimukseen. Paras ordinaatiomenetelmä sekä alojen että lajien suhteen on reciprocal averaging menetelmä (RA), seuraavana faktorianalyysi (FA) ja huonoin polaari ordinaatio menetelmä (PO). Näytealat luokittuivat sukkession mukaan kolmeksi sukkessio-osakasvustoksi: 3—5 v. *Phleum pratense*-, 6—14 v. *Agrostis tenuis*- ja 15—24 v. *Alchemilla vulgaris*-, vaiheeksi. Sukkessioakselin lisäksi saatiin esiin kosteus- ja samalla ravinteisuusakseli. Akseleiden tulkinta oli sama myös kontrollina käytetyssä suuremmassa (26 peltoa) viljelemättä jätettyjen peltojen aineistossa.

Kasvilajien ryhmittely

Kasvilajit luokiteltiin FA:n ja RA:n avulla kolmeen sukkessioluokkaan: 3—5 v. mm.*Phleum pratense, Trifolium pratense, Lapsana communis*, 6—14 v. mm. *Elymus repens, Agrostis tenuis, Taraxacum officinale*, 15—24 v. mm. *Deschampsia cespitosa, Poa pratensis, Festuca rubra, Alchemilla vulgaris*.

Sukkessiomalli

Sukkessioluokkien suhteellisten biomassamuutoksien avulla on laadittu matriisimalli ennustamaan tapahtuvaa sukkessiota. Koko aineistosta saatu malli ei ennusta tapahtunutta sukkessiota kaikille peltolohkoille, mutta kunkin lohkon omasta aineistosta kehitetty malli kuvasi, vanhinta lohkoa lukuunottamatta, sukkession hyvin. Nuorimman lohkon malli laskettuna yhdeksän ensimmäisen sukkessiovuoden (muutokset nopeimpia) aineistosta

ennusti parhaiten kasvillisuuden sukkession 24 ikävuoteen saakka. Malleissa korostui samoin kuin ordinaatio- ja luokittelumenetelmilläkin kahden nuorimman ja vanhimman lohkon välinen ero.

Kasvilajien kasvun dynamiikka

Kasvilajien populaatioiden runsauden jakaantumista, paino-tiheyssuhteita, lisääntymisstrategioita sekä lajienvälistä ja lajien sisäistä kilpailua on kuvattu. Kilpailusuhde todettiin *Phleum pratensen* ja *Agrostis tenuiksen* välillä.

Lajien populaatiot eivät pelloilla sekakasvustoina toteuta Yodan ym. (1963) potenssilakia, mutta Whiten (1980) määrittämä äärimmäinen harvennusraja toimii rajana, jota ei ylitetä. Koko kasviyhteisössä sen sijaan Yodan -3/2 -potenssilaki toimii säädellen keskimääräisen tiheyden ja yksilöpainon suhdetta. Kontrolleina käytetyissä suomalaisissa yhden puulajin luonnontilaisissa metsissä (OMT) (Ilvessalo 1920) potenssilaki toteutuu.

Tuotoksen dynamiikka

Maanpäällisen nettoprimaarituotoksen arvioimiseen v. 1972 ja 1973 käytettiin hetken satoon, lajikohtaisten huippubiomassojen summaan ja karikkeen hajoamisnopeuteen perustuvia menetelmiä. Primaarituotos oli menetelmästä ja vuodesta riippuen 1.3.—1.8. -kertainen maksimibiomassaan verrattuna. Suurimmat arviot antoivat karikkeen hajoamisnopeuteen ja totaaliin heinäkuun (lämpösumma 650 d.d.) hetken satoon (elävä + kuollut) perustuvat menetelmät, jotka antoivat hyvin samansuuruiset tuotosarviot. Tuotos oli menetelmästä riippuen suurin nuorimmalla pellolla 549.8—1465.0 g/m^2 ja pienin vanhimmalla pellolla 450.6—917.3 g/m^2. Hyötysuhde oli 0.9—1.9 % kokonaissäteilyenergiasta. Mukaan ei laskettu hengityksen ja kuluttajien käyttämää energiaa, joten todellinen hyötysuhde oli tätä suurempi.

Vuosina 1971—1979 kerättyjen heinäkuun lopun hetken satojen mukaan kaikilla pelloilla sato kenttäkerroksessa pieneni, mutta puu- ja pensaskerros huomioon ottaen sato pieneni muilla paitsi vanhimmalla pellolla. Karikemäärä kasvoi kaikilla pelloilla sukkession mukana.

Kuluttajien vaikutusta tarkastellaan esimerkinluontoisesti peltomyyrällä. Peltomyyrä vaikuttaa tämän tutkimuksen mukaan voimakkaasti esiintymisensä huippuvuonna ja sen jälkeen suosimiensa ravintokasvien satoihin. Vaikutusta arvioitiin toisaalta myyrien kuluttaman energian mukaan käyttämällä kirjallisuudesta saatuja kulutusarvioita ja toisaalta mittaamalla peltomyyrän ravintokasvien satoja suhteessa myyräkantaan. Tulosten mukaan myyrät kuluttavat esiintymisensä huippuvuonna kesällä 1.5—3.1 % potentiaalisesta nettoprimaarituotosta ja talvella 9—20 %. Myyrät tuhoavat paljon suuremman määrän kuin kuluttavat, kesällä 2.7—23.6 % ja talvella lokakuun myyrätiheyden mukaan arvioituna 36.5—85.2 %. Näin suuria tuhoja ei kuitenkaan päässyt tapahtumaan, koska myyräkanta romahti ennen talvea. Myyrien vaikutus näkyi seuraavana kesänä myyrien suosimien ravintokasvien *Anthoxanthum odoratum, Leontodon autumnalis, Poa pratensis, Dactylis glomerata, Festuca rubra, Trifolium pratense, Phleum pratense* ja *Capsella bursa-pastoris* yhteissadon laskuna puoleen vuoden 1971 satoon verrattuna.

Diversiteetti

Diversiteettiä l. monimuotoisuutta on mitattu kahdeksan erilaisen indeksin avulla. Näistä kaksi on lajien lukumäärään perustuvia, otoslajiluku (S) ja neliömetrin alalla esiintyvien keskimääräinen summalajiluku (ASR) ja kuusi indeksiä, joissa on mukana lajiluvun lisäksi myös dominanssi, Shannon (H'), Pielou (J'), Simpson (D), Whittaker (E_c), Kempton (Q) ja Lamont (E_b). Kenttäkerroksen diversiteetti kohoaa sukkession myötä aluksi, mutta puu- ja pensaskerroksen kehittyessä kenttäkerroksen diversiteetti alkaa laskea. Koko kasviyhteisön diversiteetti kasvaa kaikilla indekseillä mitattuna. Tulosten mukaan indeksit mittaavat eri asioita. Indeksit voitiin jakaa kahteen ryhmään, toisaalta ASR, H', J' ja D sekä toisaalta S, E_c, Q ja E_b. Sukkessioiän kanssa korreloi parhaiten ASR ja H' sekä vähiten Q ja E_b. Tulosten mukaan näyttävät indeksit Q ja E_b sopivan huonosti tähän aineistoon.

Kasviyhteisöjen rakenteellisia muutoksia on kuvattu myös dominanssi-diversiteettikäyrien avulla. Ne havainnollistavat samaa asiaa kuin diversiteetti-indeksi, ts. resurssien jakoa lajien kesken. Niissä näkyi nuoren heinäpellon lähes geometristen käyrien muuttuminen vähitellen yhä logaritmisempaan suuntaan.

JUKOLA-SULONEN, E.-L. 1983. Vegetation succession of abandoned hay fields in Central Finland. A quantitative approach. Seloste: Kasvillisuuden sukkessio viljelemättä jätetyillä heinäpelloilla Keski-Suomessa kvantitatiivisin menetelmin tarkasteltuna. Commun. Inst. For. Fenn. 112: 1—85.

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Vegetation succession on 3 to 25-year-old abandoned hay fields in Central Finland was examined in this study. Both seasonal and annual changes in the vegetation at the species and community levels were followed using their biomass, shoot density and frequency values. Classification and various ordination methods indicated that there were three succession stages, successional subassociations: *Phleum pratense* L., *Agrostis tenuis* Sibth. and *Alchemilla vulgaris* coll. stages. Matrix models were constructed for estimating succession. Inter- and intraspecific competition and weight/density ratios were studied. While species dominance, production and ecological efficiency of the plant community decreased throughout the studied succession stages, their diversity and stability increased. These changes were continuous, greatest at the onset of field succession, but very slow on the older fields.

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Huomautuksia
Remarks

Appendix 1. Vegetation analysis of the abandoned hay fields. The order of sample plots and plant species is as in the reciprocal averaging ordination considering arch distortion of the axes (Figs. 9e and 15b). Classification of the sample plots is based on the minimum variance-clustering (Fig. 8) and of species (class I—III) is based closely on the factor analysis (Table 8). B = uncorrected (measured) biomass (g/m^2), F = frequency (%), field plot code = the last ploughing and seeding year, sample plot code = age in years since seeding, temperature sum = ($\Sigma > 5°C$/day) (d.d.) at harvesting, sub-associations = succesional sub-associations named by dominant species. See text for further explanations.

Liite 1. Viljelemättä jätettyjen heinäpeltojen kasvianalyysi. Näytealojen ja lajien järjestys on reciprocial averaging -ordination mukainen huomioonottaen akseleiden käyristyminen (kuvat 9e ja 15b). Näytealojen luokittelu perustuu minimivarianssiryhmittelyyn (kuva 8) ja lajien (luokka I—III) suurin piirtein viiden faktorin ratkaisuun (taulukko 8). B = korjaamaton (mitattu) biomassa (g/m^2), F = frekvenssi (%), peltolohkotunnus = viimeinen kyntö ja kylvövuosi, näytealatunnus = ikä vuosissa kylvöstä, lämpösumma ($\Sigma > 5°C$/päivä) (d.d.), osakasvusto = sukkessio-osakasvusto nimettynä dominantin lajin mukaan. Katso lisäselvitykset tekstistä.

Field plot - Peltolohko	P68		P68		P65		P68		P68		P68		P65		P65		P65		P53		P53		P53		P53		P53		P58		P58		P58		P58	
Sample plot - Näyteala	3		5		6		8		7		9		8		10		12		14		22		18		20		23		24		13		15		17		19	
Study year - Tutkimusvuosi	1971		1973		1971		1976		1975		1977		1973		1975		1977		1979		1975		1971		1973		1976		1977		1971		1973		1975		1977	
Temperature sum - Lämpösumma	432		567		347		390		462		651		411		462		651		860		462		529		765		390		651		404		667		462		651	
Method - Metodi	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F	B	F
Subassociation-Osakasvusto	Phleum pratense				Agrostis tenuis																Alchemilla vulgaris																
Class - Luokka																																						
I Trifolium pratense	7.1	70	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0.4	10	+	+	+	+	+	+	+	+	0.7	10	+	+		
I Lapsana communis	1.0	40	+	+	0	12	+	+	0	10	+	+	+	+	0	6	0.1	6	-	-	-	-	-	-	-	-	-	-	0	3	0	10	+	+	-	-	0	4
I Equisetum arvense	0.5	30	1.7	20	+	+	1.3	8	0.1	10	0.7	8	+	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
I Phleum pratense	443.1	100	276.5	100	134.3	100	78.3	92	114.5	100	153.2	92	61.9	100	57.0	100	50.3	91	17.7	77	21.5	80	13.7	80	17.8	100	44.2	69	33.5	45	83.3	100	90.3	100	33.0	100	27.1	67
II Urtica dioica	0.2	10	+	+	+	+	1.5	17	1.1	10	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	+
II Equisetum sylvaticum	1.0	30	2.6	40	-	-	9.1	50	1.0	40	14.5	33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	3	-	-	-	-	-	-	-	-
II Rumex acetosella	+	+	0	10	2.8	65	2.9	8	+	+	+	+	0.1	35	0.5	18	0	3	0.1	5	+	+	+	+	0	10	+	+	0	3	+	+	+	+	+	+	+	+
II Veronica serpyllifolia	0	10	+	+	0	41	+	+	+	+	+	+	+	+	0	6	+	+	0	2	-	-	-	-	-	-	-	-	0	20	+	+	-	-	-	-		
II Gnaphalium sylvaticum	0	10	+	+	0.2	12	+	+	+	+	+	+	+	+	0.1	6	0.2	6	+	+	+	+	+	+	+	+	0.1	3	+	+	-	-	-	-	-	-	-	-
II Rubus idaeus	0	10	+	+	1.4	12	+	+	+	+	0.9	4	0	6	+	+	1.0	6	0.1	3	+	+	+	+	0	10	+	+	+	+	0	10	+	+	+	+	+	+
II Cerastium fontanum	0.1	20	+	+	4.8	41	+	+	+	+	+	+	0.4	41	0.1	47	0.1	6	+	+	0.1	30	0.7	50	0.4	30	0.1	9	0	7	0	20	0	10	0.1	20	0	4
II Elymus repens	47.0	60	95.4	90	29.9	53	82.8	75	159.4	90	109.0	88	37.0	59	34.0	53	19.2	44	21.9	25	20.6	80	18.8	80	22.6	90	30.9	72	45.0	68	25.8	90	44.6	50	25.5	50	16.9	42
II Leontodon autumnalis	0	10	0	10	6.5	65	+	+	+	+	+	+	2.4	65	2.7	47	+	+	0.6	8	0	10	0.4	50	+	+	0	3	+	+	1.0	40	0.1	10	0	20	+	+
II Campanula patula	0.3	10	0	10	1.5	29	+	+	+	+	+	+	0.6	70	0.9	29	+	+	+	+	0.1	10	0.1	20	0.4	40	+	+	0.1	7	+	+	+	+	0	10	+	+
II Trifolium repens	0.2	10	+	+	+	+	+	+	+	+	+	+	0	6	1.0	12	+	+	+	+	-	-	-	-	-	-	-	-	-	-	0.2	20	+	+	0	10	+	+
II Epilobium angustifolium	+	+	+	+	+	+	6.3	8	+	+	13.9	8	1.8	6	4.0	6	20.0	9	17.6	7	0.8	10	+	+	+	+	+	+	+	+	2.0	10	+	+	+	+	+	+
II Poa trivialis	-	-	+	+	0.1	6	0.3	17	0.9	30	+	+	0.5	12	1.5	29	+	+	+	+	-	-	-	-	-	-	0.3	13	+	+	-	-	+	+	0.4	40	+	+
II Stellaria media	-	-	-	-	0	6	-	-	-	-	-	-	-	-	0	6	-	-	-	-	-	-	-	-	-	-	-	-	0	3	-	-	-	-	-	-	-	-
II Hieracium sp.	-	-	+	+	0.4	18	+	+	+	+	+	+	0.3	18	1.3	12	15.6	3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
II Agrostis tenuis	24.4	100	48.9	70	60.1	100	57.9	67	48.6	100	115.8	83	102.9	100	103.9	100	149.6	100	167.9	100	27.0	80	54.2	100	77.6	100	28.0	88	33.9	84	75.8	90	86.7	90	48.9	100	38.3	88
II Anthoxanthum odoratum	-	-	+	+	7.1	47	+	+	+	+	+	+	6.1	71	13.3	59	7.7	41	5.8	32	1.7	50	5.2	70	1.8	40	0.3	13	0.1	16	1.6	20	0.1	10	3.2	30	0.9	4
II Cirsium arvense	-	-	+	+	2.8	6	+	+	+	+	+	+	0.5	12	1.5	12	+	+	2.6	2	+	+	+	+	+	+	+	+	+	+	+	+	4.7	10	2.1	10	+	+
II Fragaria vesca	-	-	-	-	+	+	-	-	-	-	-	-	+	+	0.1	6	+	+	0	3	+	+	+	+	+	+	+	+	0	3	-	-	-	-	-	-	-	-
II Taraxacum officinale	8.0	50	4.9	50	34.4	94	18.7	25	24.7	70	24.2	29	101.6	100	106.0	94	42.5	65	36.1	55	79.5	90	42.1	100	42.3	100	96.4	94	38.6	77	76.6	100	28.6	100	42.0	100	13.7	63
II Myosotis arvensis	+	+	-	-	0	10	-	-	+	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	0	10	-	-	0	3	-	-	-	-	-	-	-	-
III Stellaria graminea	+	+	+	+	0	6	+	+	+	+	+	+	0	6	0.1	6	+	+	0.1	5	0.2	10	+	+	+	+	0	3	0.2	10	+	+	+	+	+	+	+	+
III Silene dioica	-	-	-	-	+	+	+	+	+	+	+	+	0.9	6	0.9	6	+	+	1.0	2	1.1	10	+	+	+	+	0.8	6	0.3	7	+	+	+	+	+	+	0	4
III Rumex acetosa	0	10	+	+	+	+	+	+	+	+	+	+	0	6	0.2	6	0.1	6	+	+	4.1	40	0.1	70	0.4	30	1.3	25	0.6	13	0	30	0	10	0.2	20	0.1	13
III Anthriscus sylvestris	+	+	+	+	+	+	0.1	8	1.4	10	7.0	13	1.3	6	0.2	6	0.8	3	0.2	5	8.1	40	+	+	12.9	20	2.8	19	3.4	10	+	+	+	+	+	+	0.1	4
III Cirsium helenioides	-	-	-	-	+	+	+	+	+	+	20.1	8	+	+	+	+	+	+	+	+	97.0	20	+	+	7.0	10	15.1	9	3.7	7	+	+	+	+	+	+	+	+
III Achillea ptarmica	+	+	0.2	10	0.9	18	+	+	+	+	3.1	8	1.1	18	5.7	41	2.5	32	7.0	30	5.5	50	9.9	30	9.3	50	4.0	38	6.8	39	0.2	10	3.0	10	+	+	1.4	13
III Achillea millefolium	0.2	10	1.1	20	0.3	18	3.0	17	0.4	30	0.3	8	1.1	24	1.2	29	0.2	3	1.4	10	1.0	70	10.1	100	6.0	100	2.0	59	0.4	36	1.9	60	1.5	40	0.7	30	+	+
III Deschampsia cespitosa	0	20	+	+	0.2	6	0.5	8	21.0	10	13.9	4	1.8	12	13.0	18	6.2	15	3.7	18	23.5	40	49.0	40	57.2	50	35.0	13	30.4	29	1.3	10	29.0	40	2.1	20	0.5	4
III Veronica chamaedrys	-	-	-	-	2.2	6	+	+	+	+	+	+	0.2	6	5.2	6	3.8	6	1.3	5	3.0	30	2.2	20	2.4	30	9.4	25	15.7	32	0.5	10	+	+	1.4	20	0.9	8
III Poa pratensis	+	+	2.3	60	4.7	71	3.2	25	12.9	40	19.2	46	4.6	59	8.6	71	19.7	74	15.3	72	35.5	100	43.0	100	30.9	100	32.6	100	33.1	97	13.7	100	14.5	80	29.6	80	22.9	83
III Vicia cracca	+	+	+	+	+	+	+	+	9.7	10	2.1	8	+	+	+	+	1.7	3	+	+	19.2	70	38.6	60	23.7	70	11.8	63	12.7	81	1.8	10	16.1	20	7.3	30	0.2	13
III Festuca rubra	-	-	+	+	0.5	12	+	+	+	+	+	+	0	12	2.1	18	0.3	9	0	2	8.9	20	6.4	70	9.3	70	16.1	63	13.4	45	+	+	3.3	20	0.9	30	1.2	8
III Hypericum maculatum	0.3	10	+	+	+	+	+	+	0.4	10	3.8	8	+	+	0.1	6	9.3	9	0.1	2	3.0	50	1.7	10	10.1	30	5.8	28	7.9	26	0.5	10	1.0	10	+	+	8.6	8
III Silene vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	6.2	10	2.8	10	+	+	1.6	7	-	-	-	-	-	-	-	-
III Pimpinella saxifraga	-	-	+	+	+	+	+	+	+	+	+	+	+	+	0.1	6	+	+	+	+	0.3	10	+	+	7.8	10	0.6	6	0.1	3	+	+	+	+	+	+	+	+
III Ranunculus acris	-	-	+	+	+	+	+	+	+	+	+	+	0.4	6	0.9	6	0	3	0	2	39.2	100	21.3	90	14.1	100	23.0	84	11.6	68	8.6	70	7.3	70	20.7	90	9.2	42
III Lathyrus pratensis	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	10.3	40	6.6	30	16.9	50	10.2	25	14.0	36	+	+	11.5	10	2.2	40	4.6	29
III Vicia sepium	+	+	+	+	+	+	+	+	+	+	0.1	4	+	+	0.7	6	+	+	+	+	10.6	60	0.1	20	6.2	30	1.9	16	7.8	32	0.1	10	0.7	10	6.7	30	5.3	17
III Ranunculus auricomus	-	-	-	-	+	+	-	-	-	-	-	-	0	6	0.1	6	+	+	+	+	1.0	30	0.1	10	0.2	40	1.3	28	0	3	0.4	30	0.9	30	0.9	20	0	13
III Ranunculus repens	-	-	+	+	0.6	24	0	8	+	+	+	+	0.1	12	0.3	18	0	6	0	7	+	+	+	+	0.1	20	0	3	+	+	0	10	+	+	1.4	20	0.3	8
III Filipendula ulmaria	-	-	+	+	+	+	11.4	8	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0.2	10	+	+	+	+	0.7	3	+	+	0.2	10	13.2	20	4.0	4
III Alchemilla vulgaris	-	-	+	+	1.3	6	+	+	+	+	+	+	3.0	6	+	+	11.4	12	+	+	25.3	90	60.9	100	85.2	80	97.7	84	83.4	77	164.8	100	173.7	90	195.2	100	276.8	92
III Geranium sylvaticum	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0.1	3	+	+	+	+	0.7	10	5.2	10	+	+
Others - Muut	0.2		0		0		0		0		10.2		0		3.3		3.3		3.9		0.4		3.8		0		0.5		0.4		0.1		13.2		0		5.1	
Total - Yhteensä	533.6		433.6		297.0		277.3		396.1		512.0		330.6		370.6		365.6		304.4		448.5		395.8		465.4		472.3		399.4		460.2		531.7		443.6		438.1	
Litter - Karike	388.4		318.0		238.0		752.5		349.1		1029.3		183.6		365.1		705.3		541.6		254.8		308.0		273.5		432.5		386.7		282.5		224.2		247.4		399.6	

Species found only on one or two sample plots. In parentheses: field code (field - age), biomass (g/m^2), frequence (%). Enintään kahdella alalla esiintyneet lajit, suluissa näytealatunnus (lohko - ikä), biomassa (g/m^2), frekvenssi (%): Equisetum pratense (68-3, 0, 10), Rubus arcticus (53-23, 0, 3), Potentilla erecta (53-24, 0.1, 3) (58-13, 0, 10), Epilobium montanum (53-24, 0, 3), Aegopodium podagraria (68-9, 0.9, 4), Viola canina (53-22, 0.1, 10) (53-23, 0.5, 3), Viola arvensis (65-8, 0, 6) (65-14, 0, 2), Capsella bursa-pastoris (58-13, 0, 10), Sagina procumbens (68-3, 0, 10) (58-13, 0, 10), Spergula arvensis (58-13, 0, 10), Rumex longifolius (68-3, 0, 10), Polygonum aviculare (58-13, 0.1, 10), Galium uliginosum (65-14, 0, 2), Galium verum (68-9, 6.8, 4), Galium album (65-14, 0.1, 2), Convolvulus arvensis (58-13, 0, 10), Veronica arvensis (65-6, 0, 6) (53-22, 0, 10), Veronica verna (65-6, 0, 6), Veronica officinalis (53-24, 0.2, 3), Melampyrum sylvaticum (53-22, 0.1, 10) (53-24, 0.1, 3), Plantago major (65-6, 0, 6), Galeopsis bifida (65-8, 0, 6) (65-12, 0, 3), Campanula glomerata (58-19, 5.1, 4), Solidago virgaurea (65-10, 3.3, 6), Erigeron acer (65-6, 0, 12) (65-12, 3.3, 3), Leucanthemum vulgare (53-23, 0, 3), Carduus crispus (65-14, 1.5, 5), Cirsium palustre (68-9, 2.5, 4) (53-18, 3.8, 10), Sonchus arvensis (68-3, 0.2, 10), Pilosella sp. (65-14, 2.3, 10) (53-24, 0, 3), Luzula multiflora (53-22, 0, 10), Festuca pratensis (58-15, 13.2, 10) (58-17, 0, 10), Poa nemoralis (53-22, 0.2, 10), Dactylis glomerata (65-6, 0, 6).

Species outside the sample quadrats, field code in parentheses (field - age). Näyteruutujen ulkopuolella esiintyneet lajit, suluissa näytealatunnus: Urtica urens (65-6,-8), Potentilla argentea (65-6,-8,-10), Potentilla norvegica (65-6, -8,-10),Geum rivale (65-8,-10,-12,-14, 58, 53), Trifolium hybridum (68-3,-5,-7), Arabis glabra (65-10), Dianthus deltoides (65-8,-10,-12), Rumex crispus (65-12, 53-22,-23,-24), Knautia arvensis (65, 58, 53), Prunella vulgaris (68, 65-6,-8,-10), Campanula rotundifolia (65, 58-13,-15,-17), Tanacetum vulgare (65, 53), Arctium tomentosum (58-13,-15), Centaurea jacea (65), Crepis paludosa (58-19), Gagea minima (58), Gymnadenia conopsea (53-20,-22,-23,-24), Alopecurus pratensis (65-6,-8,-10,-12).

P68 P65 P58 P53

1971 1973 1977 1971 1973 1977 1979 1971 1973 1977 1971 1973 1977

PHLEUM PRATENSE

ELYMUS REPENS

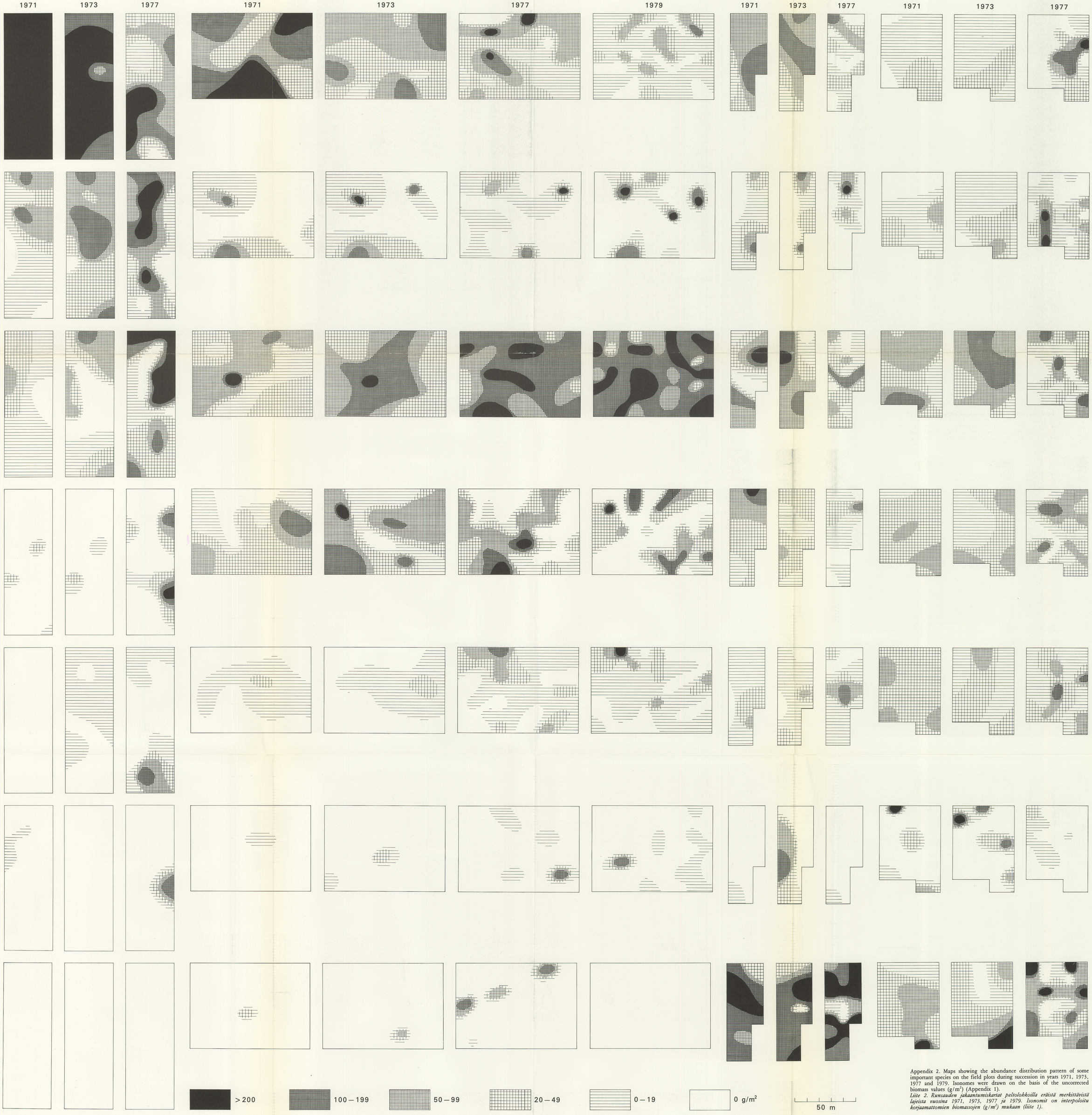
AGROSTIS TENUIS

TARAXACUM OFFICINALE

POA PRATENSIS

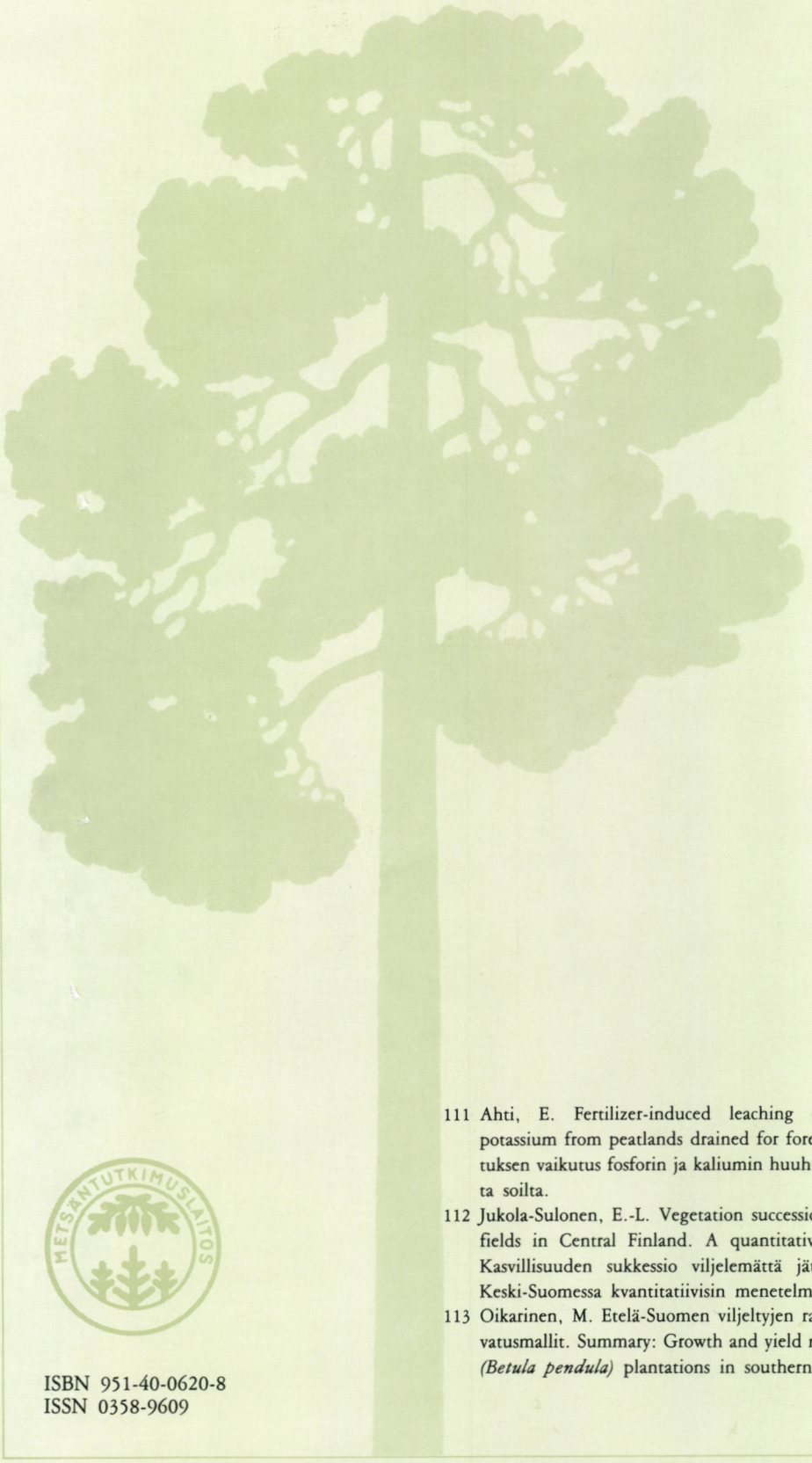
DESCHAMPSIA CESPITOSA

ALCHEMILLA VULGARIS



Appendix 2. Maps showing the abundance distribution pattern of some important species on the field plots during succession in years 1971, 1973, 1977 and 1979. Isonomes were drawn on the basis of the uncorrected biomass values (g/m^2) (Appendix 1).

Liite 2. Runsauden jakaantumiskartat peltolohkoilla eräistä merkittävistä lajeista vuosina 1971, 1973, 1977 ja 1979. Isonomit on interpoloitu korjaamattomien biomassojen (g/m^2) mukaan (liite 1).



111 Ahti, E. Fertilizer-induced leaching of phosphorus and potassium from peatlands drained for forestry. Seloste: Lannoituksen vaikutus fosforin ja kaliumin huuhtoutumiseen ojitetuilta soilta.

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