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Regulation of growth onset and cessation in Norway spruce, Scots pine and silver birch

Jouni Partanen

PUNKAHARJUN TUTKIMUSASEMA – PUNKAHARJU RESEARCH STATION

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ERRATA:

Article

I Page 813, left column, row 10:
The temperature *should be* fluctuating 20/10 °C *instead of* constant 10 °C *(cf. Table 1).*

III Page 5, row 28:
The formula (1)

should be $$\arcsin(\sqrt{p}) = m + T + S(T) + P + TP + \varepsilon$$

instead of $$\arcsin(\sqrt{p}) = m + S + T + ST + P + TP + \varepsilon$$

IV Page 495, left column, rows 13 – 17:
There *should read*
'In this study seedlings from the earlier sowings formed their terminal buds in the second growing season slightly earlier than the seedlings from the later sowings ($p < 0.001$). Also in the in the study by Koski and Sievänen (1985) ...' *instead of*
'In this study seedlings from the earlier sowings did not form their terminal buds in the second growing season earlier than the seedlings from the later sowings ($p > 0.1$). However, in the in the study by Koski and Sievänen (1985) ...' *(cf. page 493, right column, lines 1 - 6).*

V Page 147, left column, rows 27 – 28:
There *should read*
'… the cessation of height growth of silver birch seedlings occurred' *instead of*
'… the height growth of silver birch seedlings occurred'.

Regulation of growth onset and cessation in Norway spruce, Scots pine and silver birch

Kuusen, männyn ja rauduskoivun kasvun alkamisen sekä päättymisen säätyminen

Jouni Partanen

Academic dissertation

To be presented, with the permission of the Faculty of Forestry of the University of Joensuu, for public criticism in Auditorium C2 of the University, Yliopistokatu 2, Joensuu, on 21st June, 2004 at 12 o'clock noon.

Akateeminen väitöskirja

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Hakapaino Oy
Helsinki 2004

To my parents

Abstract

The photoperiodic and temperature factors affecting regulation of the annual growth rhythm of Norway spruce *(Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth) were studied by observing the onset and cessation of growth. The growth onset experiments were conducted by exposing rooted cuttings, seedlings and twigs of Norway spruce, from outdoors, to various controlled conditions of light and temperature. Timing of bud burst was observed visually. In the experiments relating to growth cessation, the seedlings were raised from seed periodically during the summer in a greenhouse. Light was natural and the photoperiod varied naturally. The temperature in the greenhouse fluctuated regularly and the accumulated daily temperature sum was approximately constant. Growth cessation was determined both by measuring the height of the seedlings and by observing timing of formation of the terminal bud. The effects of the first growing season on the annual rhythm of the seedlings in the second growing season were studied under the same greenhouse conditions as the first growing season.

The shortening photoperiod before winter solstice delayed bud burst, particularly in fluctuating temperature conditions. On the other hand, an increase in the accumulated sum of the daily light periods caused an earlier bud burst. Young spruces have a transitional time window during late autumn when ontogenetic development toward bud burst is possible, but between the turn of the year and the vernal equinox they seem to have a secondary rest. In old trees the bud burst was generally below 20% during autumn and winter. The bud burst percentages differed between plant materials of different age, which confirmed earlier results that showed the environmental response of bud burst in Norway spruce changes as trees get older.

In the first sowings, cessation of growth in experimental seedlings of all three species occurred earlier in the first growing season than it did in later sowings. However, they took longer and required a greater temperature sum than seedlings in the later sowings. These results suggest that the timing of growth cessation can be explained by the combined effects of night length and the stage of development the seedlings had reached, i.e. growth cessation is regulated both by photoperiod and accumulated temperature sum. By the second growing season, major timing differences in growth cessation between seedlings from different sowings had disappeared.

Seedlings raised from seeds originated in the north generally ceased growth earlier in the greenhouse than those from the south. In Scots pine, the photoperiod of the original site seemed to be the dominant factor in determining the environmental response of timing of growth cessation in the first growing season. In silver birch, the photoperiod and annual temperature sum of the original site had a smaller effect on the environmental response of timing of growth cessation than it did in Norway spruce.

Keywords: bud burst, cessation of height growth, phenology, *Picea abies* (L.) Karst., *Pinus sylvestris* L., *Betula pendula* Roth

Seloste

Kuusen, männyn ja rauduskoivun kasvun alkamisen sekä päättymisen säätyminen

Viileän ja lauhkean vyöhykkeen puiden on vuosittain kohdattava neljä eri vuodenaikaa erilaisine lämpö- ja valo-olosuhteineen, mikä edellyttää niiltä vuotuisen kehityksen sopeuttamista vuotuiseen lämpö- ja valo-olosuhteiden vaihteluun. Vuosirytmin säätely tapahtuu perinnöllisten tekijöiden ja ympäristötekijöiden yhteisvaikutuksesta. Vuosirytmiä säätelevistä ympäristötekijöistä tärkeimmät ovat lämpötila ja valo. Kasvun alkamisessa ilman lämpötilan merkitys on suurempi kuin valo-olosuhteiden. Kasvun päättyminen taas perustuu kriittisen yönpituuden antamaan signaaliin, joka käynnistää kasvun päättymiseen johtavan kehityksen. Toisaalta on osoitettu valo-olosuhteilla olevan merkitystä kasvun alkamisessa, ja kasvun päättymisen ajoittumista on kuvattu yönpituuden ja lämpösummakertymän yhteisvaikutuksena.

Tämän tutkimuksen tarkoituksena oli selvittää edelleen valo- ja lämpöolosuhteiden merkitystä sekä kasvun alkamisessa että kasvun päättymisessä. Kasvun alkamiseen liittyvät kokeet tehtiin siirtämällä kuusen juurrutettuja pistokkaita, siementaimia ja oksia ulkoa kontrolloituihin valo- ja lämpöolosuhteisiin, joissa silmujen puhkeamista havainnoitiin silmävaraisesti. Kasvun päättymiseen liittyvissä kokeissa männyn, kuusen ja koivun taimia kasvatettiin siemenistä kasvihuoneessa luonnonvalossa ja luonnollisesti vaihtelevassa valojaksossa. Lämpötila vaihteli kasvihuoneessa säännöllisesti, joten vuorokaudessa kertynyt lämpösumma oli suunnilleen vakio. Toistamalla kylvö kesän kuluessa viidesti kahden viikon välein luotiin erilaisia valojakson ja taimien kehitysvaiheen yhdistelmiä. Kasvun päättyminen määritettiin mittaamalla taimien pituutta ja havainnoimalla päätesilmun muodostumista samoissa kasvuolosuhteissa sekä ensimmäisenä että toisena kasvukautena.

Valo-olosuhteiden havaittiin osallistuvan puiden kasvun alkamiseen keväällä, mikä tasapainottaa ennustetun ilmaston lämpenemisen vaikutuksia. Valo-olosuhteet näet pysyvät tulevaisuudessakin käytännössä muuttumattomina vuodesta toiseen. Päivän lyhentäminen ennen talvipäivän seisausta viivästytti kuusen silmujen puhkeamista ennen kaikkea vaihtelevissa lämpöolosuhteissa. Toisaalta silmut puhkesivat sitä aikaisemmin, mitä enemmän päivittäisten valotuntien summaa kertyi. Nuorten (15-vuotiaiden) kuusten silmujen lepotila purkautui jo myöhään syksyllä. Vuodenvaihteesta kevätpäiväntasaukseen niiden lepovaihe syveni ja purkautui uudelleen huhti- – toukokuussa. Aikuisten (56-vuotiaiden) kuusten

silmuista sen sijaan puhkesi syksyn ja talven aikana yleensä alle 20%, ja silmujen lepotila purkautui vasta huhti- – toukokuussa. Silmunpuhkeamisprosenteissa havaittu ero eri ikäisten koemateriaalien välillä vahvisti aikaisempia tuloksia, joiden mukaan kuusella silmunpuhkeamisen riippuvuus ympäristötekijöistä muuttuu puiden ikääntyessä.

Männyn, kuusen ja rauduskoivun taimien kasvu päättyi ensimmäisenä kasvukautena aikaisemmin ensimmäisissä kylvöissä kuin viimeisissä. Ensimmäisten kylvöjen taimien kasvun päättyminen vaati kuitenkin kauemmin aikaa ja enemmän lämpösummaa kuin myöhempien kylvöjen taimien. Tämä viittaa siihen, että kasvun päättymisen ajoittumista voidaan selittää yönpituuden ja taimien saavuttaman kehitysvaiheen yhteisvaikutuksella. Toisena kasvukautena eri kylvöistä peräisin olevien taimien väliset erot kasvun päättymisen ajoittumisessa sen sijaan olivat suurimmaksi osaksi kadonneet. Taimien kehitysvaihe on kuitenkin huomioitava tuotettaessa taimia säädellyissä olosuhteissa taimitarhoilla metsänviljelyä varten.

Männyllä siemenen alkuperäpaikkakunnan valojakso näytti olevan vallitseva tekijä kasvun päättymisen ajoittumisen ympäristövasteelle ensimmäisenä kasvukautena. Koivulla siemenen alkuperäpaikkakunnan valojakson ja vuotuisen lämpösumman vaikutus kasvun päättymisen ajoittumisen ympäristövasteeseen ensimmäisenä kasvukautena oli pienempi kuin kuusella. Kaikkien kolmen puulajin pohjoisten alkuperien taimet päättivät yleensä kasvunsa kasvihuoneessa aikaisemmin kuin eteläisten alkuperien taimet, mikä on huomioitava siemenmateriaalin valinnassa. Mahdollisimman oikeaan osuneilla alkuperävalinnoilla voidaan parantaa metsänviljelyn onnistumista ja varmistaa viljelymetsien mahdollisimman hyvä menestyminen myös tulevaisuuden ilmasto-olosuhteissa.

Avainsanat: silmun puhkeaminen, pituuskasvun päättyminen, fenologia, kuusi, mänty, rauduskoivu

Preface

This study was financially supported by the Nordic Forest Research Cooperation Committee (SNS), the Academy of Finland, the Finnish Society of Forest Science, the Kemira Oyj Foundation, the Niemi Foundation, the Emil Aaltonen Foundation, the Finnish Cultural Foundation, the Foundation for Research of Natural Resources in Finland and the Ella and Georg Ehrnrooth Foundation. I thank the Head of the Punkaharju Research Station of the Finnish Forest Research institute, Dr. Juhani Häggman, for providing me excellent working facilities. I also thank for the facilities kindly provided by Ruotsinkylä Field Station and Joensuu Research Center of the Finnish Forest Research Institute, and by University of Joensuu, Faculty of Forestry.

I am most grateful to my supervisor Prof. Heikki Hänninen for his encouragement and guidance throughout this work. I also express my gratitude to Prof. Veikko Koski for inspiring me to start the study and to Dr. Risto Häkkinen for encouragement and fruitful discussions in the later phases of the work. Furthermore, I thank my other co-authors, Dr. Egbert Beuker, Dr. Ilkka Leinonen and Doc. Tapani Repo, for co-operation. The official reviewers of this thesis, Doc. Heikki Smolander and Prof. Marja-Liisa Sutinen, are greatly acknowledged for reading their constructive comments.

I want to thank the staff at Punkaharju Research Station for their friendship and assistance in the course of the work; especially Jouko Lehto, Pentti Manninen, Eija Matikainen, Esko Oksa, Markku Stenman and Tiina Tynkkynen for their technical assistance. I also want to thank for technical assistance the staff of the Ruotsinkylä Field Station, as well as Tapio Mäkelä from University of Joensuu, Faculty of Forestry. Furthermore, I thank Dr. Lisa Lena Opas-Hänninen for revising the language of papers II-V and thesis, Dr. Greg Watson for revising the language of paper I and Dr. Don Williams for revising the language of the thesis.

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Most of all, I thank my parents Kirsti and Unto Partanen for their support and patience during the past years.

Punkaharju 26th April 2004 Jouni Partanen

Contents

List of original articles

This thesis is based on the following publications, which are referred to in the text by the Roman numerals **I – IV**. Articles **I, II, IV** and **V** are reproduced with the publishers' permissions.

I Partanen, J., Koski, V. and Hänninen, H. 1998. Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (*Picea abies*). Tree Physiology 18: 811-816.

II Partanen, J., Leinonen, I. and Repo, T. 2001. Effect of accumulated duration of the light period on bud burst in Norway spruce (*Picea abies*) of varying ages. Silva Fennica 35: 111-117.

III Partanen, J., Hänninen, H. and Häkkinen, R. 2004. Bud burst in Norway spruce (*Picea abies*): Preliminary evidence for age-specific rest patterns. Submitted to Trees – structure and function.

IV Partanen, J. and Beuker, E. 1999. Effects of photoperiod and thermal time on the growth rhythm of *Pinus sylvestris* seedlings. Scandinavian Journal of Forest Research 14: 487-497.

V Partanen, J. 2004. Dependence of photoperiodic response of growth cessation on the stage of development in *Picea abies* and *Betula pendula* seedlings. Forest Ecology and Management 188: 137-148.

Partanen is the main author of articles **I – V**. The experiments in study **I** were planned by Prof. Koski and the experiment used in study **III** by Prof. Hänninen. In studies **II, IV** and **V**, Partanen participated in planning the experiment with the co-authors. In studies **I – V**, Partanen was responsible for analysing the results. Dr. Häkkinen performed the statistical analyses for study **III**.

1 Introduction

1.1 Basic concepts

Every year trees in boreal and temperate regions must withstand four seasons with different temperature and light conditions. Accordingly, their annual development becomes synchronised with the annual temperature and light cycle of the growing site (Weiser 1970, Sarvas 1972, 1974, Sakai and Larcher 1987). The annual cycle of trees describes the sequence of all developmental events, like bud burst and bud formation, that are repeated each year in basically the same way. Annual rhythm refers to the timing of the events in the annual cycle. Physiological changes in individual trees as a response to changing environment (= proximal reasons) are called acclimation. Changes in gene frequences in plant populations as a response to changing environment (= ultimate reasons) are called adaptation (Harper 1980, Hänninen 1986, 1990b). Accordingly, annual rhythm and its regulation at individual tree level is the outcome of acclimation, and the differences in annual rhythm and its regulation between tree species and seed origins result from adaptation.

In boreal and temperate regions, woody ecotypes and species are adapted to local seasonal photoperiod and temperature conditions (Sakai and Weiser 1973). Adaptation is two-part, capacity adaptation and survival adaptation (Levitt 1969, Heide 1985, Leinonen and Hänninen 2002). The predicted climate change may affect both the survival and capacity adaptation of trees. Capacity adaptation refers to the utilisation of growth site resources during the warm season. It may be inadequate if the onset of spring growth is delayed, or growth processes stop prematurely in autumn. In other words if the growth site resources are not fully utilised (Heide 1985). Survival adaptation refers to the tolerance or avoidance of unfavourable environmental conditions. It may be inadequate if growth onset is premature or growth cessation is delayed, and give rise to frequent frost damage (Heide 1985).

The regulation of annual rhythm denotes the interaction of genetic and environmental factors that determine the timing of events in the annual cycle. The internal factor that sets the limits of annual rhythm is the genotype. Because winter temperatures often fall below zero, only genotypes that manage to acquire adequate frost resistance before the onset of winter are able to survive. Favourable genetic factors affecting the annual rhythm of trees are exploited by forest breeding, and by using seeds and species from exotic origins for forest cultivation (Campbell 1974).

The major environmental factors affecting growth rhythm are temperature and light. These control the phenological behaviour of trees in boreal and temperate regions and finally determine their annual rhythm (Sakai and Weiser 1973). In addition, water and nutritional conditions are obvious controlling environmental factors (Kozlowski and Pallardy 1997). According to prevailing theories, processes relating to growth onset are regulated mainly by air temperature (e.g. Smith and Kefford 1964, Perry 1971, Fuchigami et al. 1982), whereas processes relating to growth cessation are regulated mainly by photoperiod (e.g. Wareing 1956, Vaartaja 1959). Environmental factors are exploited in nurseries where plants are produced in greenhouses for later forest cultivation (Grossnickle et al. 1991, Luoranen 2000).

1.2 Variation in temperature conditions

In Finland, as in boreal region generally, the effect of the year-to-year variations in temperature that ultimately determine the start and end of the growing season is considerable (e.g. Solantie 1987). The start of the thermal growing season, by definition, begins in spring when the mean daily temperature exceeds +5 °C and the sum of the daily mean temperatures of following five days is at least +20 °C. The thermal growing season ends in autumn when the mean daily temperature drops below +5 °C and remains under this level consecutively 5 to 10 days. According to local temperature observations for the years 1961 – 2000 in Punkaharju [61°48'N, 29°19'E] the start of the thermal growing season varied between day 106 (April 16 in 1990 and 1999) and 146 (May 26 in 1974). The end of the thermal growing season varied from day 254 (September 11 in 1973) to day 299 (October 25 in 2000) (Fig. 1A). The start of the thermal growing season varied by 40 days and the end by 45 days. At the start of the growing season the range of night length was 5 h 14 min, while at the end it was only 4 h 19 min. In other words, the range (in days) was bigger at the end than at the start of the growing season. However, the variation in the photoperiod was larger at the start of the growing season. The length of the thermal growing season in Punkaharju for years 1961 – 2000 varied from 125 days in 1972 to 190 days in 2000 (Fig. 1B).

Temperature conditions are changing as a result of climatic warming, but the photoperiod remains within its natural range. Consequently, the relationship between the temperature and light factors also changes. Since trees cannot move to avoid these new circumstances, they need to acclimate in order to survive. It has been predicted that the variation in temperature conditions between years will increase in the future and that the level of warming will be more pronounced in the north. It will also be greater during the winter than in summer (IPCC 1996). Consequently trees will need to acclimate to both the changing yearly temperature fluctuation and the changing temperature climate.

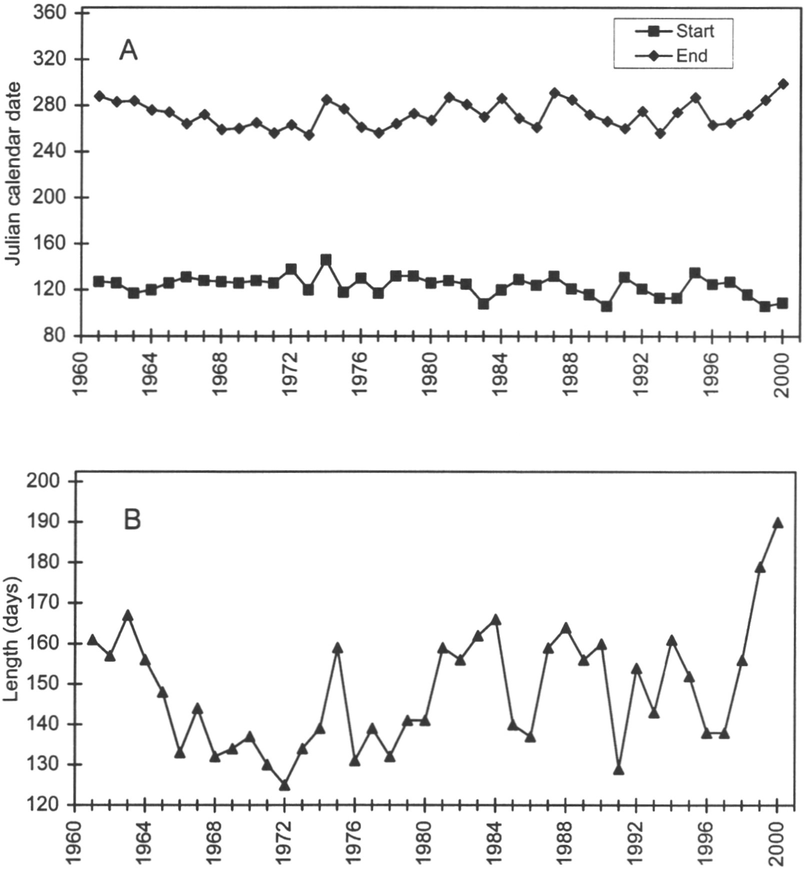

Figure 1. Start and end of the thermal growing season (A) and its length (B) in Punkaharju in years 1961 - 2000.

1.3 Factors affecting growth onset

There are several definitions of the concept of bud dormancy. In general, buds are considered to be dormant when there is no visible growth (e.g. Doorenbos 1953, Romberger 1963, p. 75). The vegetative buds of trees in boreal and temperate regions become dormant after growth cessation in autumn. Dormancy can be divided into a rest and a quiescent period. During the rest period physiological conditions in the bud itself are responsible for the arrest of growth. These buds have only a limited ability to develop ontogenetically towards bud burst, or none at all (Doorenbos 1953, Samish 1954). According to the prevailing theory, rest is completed as a result of exposure to low temperatures (–5 to +10 °C) for some weeks (Coville 1920, Smith and Kefford 1964, Perry 1971, Flint 1974, Sarvas 1974, Fuchigami et al. 1982, Cannell and Smith 1983). This exposure to low temperatures is called chilling.

Rest completion occurs as a result of physiological changes in the dormant bud that lead to a full internal ability to develop ontogenetically toward bud burst (Romberger 1963, Weiser 1970, Kobayashi and Fuchigami 1983, Hänninen 1990a). The rate of this ontogenetic development accelerates with rising temperature (Sarvas 1972, Landsberg 1977).

Period that follows rest completion is called quiescence (Hänninen 1990a, Kramer 1994, 1995, 1996). During this period, buds does not develop because of environmental factors unfavourable to growth such as low air temperature. Bud burst takes place as a result of exposure, for a prolonged period, to temperatures above a certain threshold, e.g. $T > +5$ °C (Smith and Kefford 1964, Perry 1971, Fuchigami et al. 1982, Cannell 1989, 1990).

During ontogenetic development toward bud burst, fluctuating day/night temperatures have been found to be more effective than constant temperature. It was shown by Campbell and Sugano (1975) and van den Driessche (1975), that a greater temperature sum accumulation was needed to bring about bud burst in one year old seedlings of *Pseudotsuga menziesii* (Mirb.) Franco when exposed to constant rather than fluctuating temperatures. It has been suggested that this efficiency of fluctuating temperature compared to constant temperature is related to the chilling requirement of the buds. Myking (1997) concluded that when the chilling requirement is fulfilled, there is no difference in timing of bud burst in *Betula pubescens* Ehrh. plants exposed to either constant or fluctuating temperature conditions.

Even though the role of photoperiod in growth onset is considered to be minor, the ability of ontogenetic development is not started solely by chilling. Long days are an absolute requirement for rest completion in Beech (*Fagus sylvatica* L.) and are needed to start bud development even in the case of fully chilled trees (Wareing 1953, Falusi and Calamassi 1990, Heide 1993). The onset of ontogenetic development in some other boreal tree species is also affected by increasing day length (Myking and Heide 1995, Olsen et al. 1997). In addition, long days can compensate for a lack of chilling during the rest break (e.g. Jensen and Gatherum 1965, Nienstaedt 1966, 1967, Hoffman and Lyr 1967, Worrall and Mergen

1967). According to a hypothesis put forward by Häkkinen et al. (1998), Häkkinen (1999), Linkosalo (2000a,b) and Linkosalo et al. (2000) adult silver birch and some other boreal trees require a special clue, in addition to the chilling requirement, for rest completion. It may come from light climate (e.g. critical night length, solar irradiance, light spectrum, shortening night), but also some other environmental factor, or interaction of several factors, may be involved.

1.4 Factors affecting growth cessation

In most tree species, in boreal and temperate regions, height growth cessation is a prerequisite for frost hardening. Consequently the timing of growth cessation is closely connected to frost resistance during early autumn (Weiser 1970, Sakai and Weiser 1973). The trees have phytochrome pigments that, in addition to night length, sense the red/far red ratio of light and initiate growth cessation in autumn (Junttila 1980, Junttila and Kaurin 1990). The photoperiod acts as an environmental signal for growth to cease and this prompts the start of the hardening process before the temperature drops. According to the photoperiod theory, a critical night length causes height growth cessation (Wareing 1950a,b, Vaartaja 1954, 1957, 1959; Dormling et al. 1968, Heide 1974, Ekberg et al. 1979, Junttila and Kaurin 1985). Tree species form latitudinal photoperiodic ecotypes that have become adapted to the prevailing photoperiod. In these the critical night length varies with the latitude of the tree's origins (Vaartaja 1951, 1954, 1957, 1959). However, successful geographic transfers have confirmed that tree species are quite well capable of adjusting their annual rhythm to new growing conditions (Beuker 1996).

In addition to temperature (Heide 1974), other environmental factors like soil moisture and water stress (Li et al. 2002), air humidity (Håbjørg 1972) and mineral nutrition (Landis et al. 1999) all have a modifying influence on the photoperiodic reactions that affect growth cessation. Moreover, variation in the timing of growth cessation has been explained by the joint effect of photoperiod and temperature sum accumulation (Koski and Selkäinaho 1982, Koski and Sievänen 1985). The combination of prevailing night length and accumulated temperature sum, at the time tree growth ceases, has been presented using fitted straight lines. These are called growth cessation lines in the present study (Fig.2).

According to earlier studies, at the start of the growing season the development of plants is mainly regulated by temperature (Hari 1968, 1972, Sarvas 1972). Consequently, the accumulated temperature sum is an estimate of the stage of development at any fixed time and has been used as a measure of this (Hari 1972, Sarvas 1972). Later during the growing season the role of the photoperiod becomes more important (Fuchigami et al. 1982).

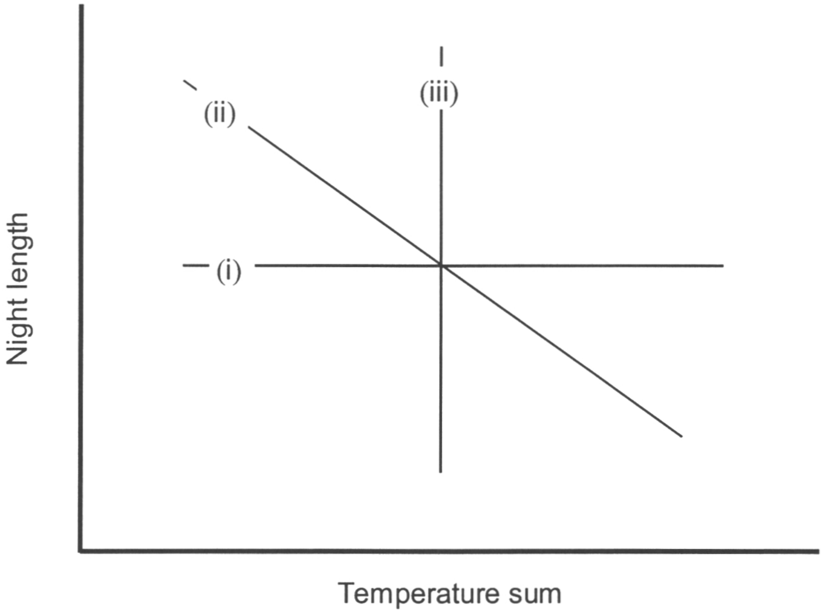

Figure 2. Theoretical growth cessation lines, i.e. combinations of prevailing night length and accumulated temperature sum, at the time of growth cessation of trees. (i) Prediction of the classical photoperiodic theory. Attainment of the genotype-specific critical night length triggers growth cessation regardless of the accumulated temperature sum (assuming, however, that the temperature sum is sufficient). (ii) Prediction of the joint factor theory of Koski and Selkäinaho (1982) and Koski and Sievänen (1985). The critical night length decreases with increasing temperature sum. (iii) Prediction of the temperature sum theory. Attainment of the genotype-specific temperature sum triggers growth cessation regardless of the prevailing night length. In (ii) and (iii), temperature sum is taken as an indicator of the stage of development of the trees. Cases (i) and (ii) consider free growth, whereas case (iii) considers predetermined growth. (Modified from Koski and Selkäinaho 1982, and Koski and Sievänen 1985).

1.5 Aims

The purpose of this study was to examine the photoperiodic and temperature factors affecting the regulation of the annual rhythm of Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth) by observing phenological events at certain points during growth onset and cessation in conditions of regulated light and temperature.

The specific aims were:

1) to test the effects of constant and fluctuating day/night temperatures in various combinations with natural, decreasing, constant and increasing photoperiods on the timing of bud burst in rooted cuttings of Norway spruce (**I**);
2) to test the effect of various light conditions and age of the trees in fluctuating day/night temperature on the timing of bud burst in seedlings and rooted cuttings of Norway spruce (**II**);
3) to test the effect of chilling, photoperiod and age of the trees on rest completion and timing of bud burst in Norway spruce (**III**);
4) to test the effects of night length and stage of development estimated with temperature sum accumulation, on the timing of height growth cessation and bud formation during the first and second growing seasons in seedlings of Scots pine from regions with different latitudes and altitudes (**IV**) and in seedlings of Norway spruce and silver birch from regions with different latitudes (**V**);
5) to test the effect of photoperiod and temperature sum of the original growing site on the environmental response of the timing of growth cessation in seedlings of Scots pine from regions with different latitudes and altitudes (**IV**) and in seedlings of Norway spruce and silver birch from regions with different latitudes (**V**).

2 Materials and methods

2.1 Plant materials

In the experiments relating to the timing of bud burst, rooted cuttings (**I** and **II**), seedlings (**II**) and twigs (**III**) of Norway spruce were used (Table 1). The rooted cuttings were from approximate latitudes of 60°N (**I**), 65°N (**I**) and 61°N (**II**), and the seedlings (**II**) and the twigs (**III**) were from latitude 62°N. In the experiments relating to the timing of growth cessation, seedlings of Scots pine (**IV**), Norway spruce (**V**) and silver birch (**V**) were used. Seedlings were raised with repeated sowings in the greenhouse. The origin of the seedlings of Scots pine varied approximately between 60°N and 70°N (**IV**), and the origin of the seedlings of Norway spruce and silver birch varied between 60°N and 67°N (**V**).

Table 1. Plant material and experiments used in the studies relating to growth onset (**I** – **III**) and cessation (**IV**, **V**).

Tree species	Plant material	Study
Norway spruce	10-year-old cuttings	I
Norway spruce	One-year-old seedlings (sown in June) One-year-old seedlings (sown in April) Two-year-old seedlings 14-year-old cuttings 18-year-old cuttings	II
Norway spruce	Twigs from 15-year-old trees Twigs from 56-year-old trees	III
Scots pine	First- and second-year seedlings	IV
Norway spruce	First- and second-year seedlings	V
Silver birch	First- and second-year seedlings	V

2.2 Experiments

The experiments relating to the timing of bud burst were conducted in Punkaharju Research Station [61°48'N, 29°19'E] (**I** and **III**), in Ruotsinkylä Field Station [60°21'N, 24°56'E] (**I**) of the Finnish Forest Research Institute and in the University of Joensuu [62°36'N, 29°43'E] (**II**). The experiments relating to the timing of growth cessation were conducted in Punkaharju Research Station (**IV** and **V**) and in Ruotsinkylä Field Station (**IV**).

Table 2. Photoperiod and temperature conditions used in the studies relating to growth onset (**I** – **III**) and cessation (**IV**, **V**).

Photoperiod	Temp.	Study
Natural with natural light (from 6 h 10 min)	10/10	I
Natural with natural light (from 6 h 10 min)	15/5	
Constant 6 h in natural light	10/10	
Shortening 10 min day^{-1} (from 12 h)	10/10	
Shortening 10 min day^{-1} (from 12 h)	20/10	
Lengthening 10 min day^{-1} (from 6 h)	10/10	
Lengthening 10 min day^{-1} (from 6 h)	15/5	
Lengthening 10 min day^{-1} (from 8 h 40 min)	20/10	
Constant 6 h	20/10	II
Lengthening 6 min 40 s day^{-1} (from 6 h)	20/10	
Shortening 6 min 40 s day^{-1} (from 6 h)	20/10	
Constant 5 h	20	III
Constant 10 h	20	
Constant 15 h	20	
Constant 20 h	20	
Natural with natural light	20/10	IV
Natural with natural light	20/10	V

In study **I** the rooted cuttings of Norway spruce were transferred in November and in December from outdoors to various photoperiod and temperature regimes in the greenhouse (Table 2). In study **II** seedlings of Norway spruce were transferred, on December 19, to three growth chambers where they were subjected to shortened, lengthened and constant photoperiods and fluctuating temperature conditions. In study **III** the twigs of Norway spruce were transferred from outdoors to constant photoperiods and constant temperature between September 14 and May 10 at intervals of one to three weeks.

In studies **IV** and **V** the seedlings were raised in greenhouses where natural light penetrating the glass provided the only illumination (Table 2). Sowing was repeated five times from late May and early June to late July. The daily temperature sum accumulation (+5 °C threshold) in the greenhouses was almost constant. Consequently the temperature sum accumulation and the age of the seedlings in these experiments were linearly confounded. At the end of October the seedlings were moved outdoors where they were exposed to natural snow coverage for the winter. The seedlings were moved back into the greenhouse the following May. The effects of the first growing season on the annual rhythm of the seedlings in the second growing season was studied under the same conditions as in the first growing season.

2.3 Measurements

The bud burst of the rooted cuttings, seedlings and twigs was observed at an interval varying between two and four days (**I, II, III**). The total height of the seedlings was measured once a week until their height, including the terminal bud, remained unchanged for at least three weeks. The seedlings were checked for terminal bud formation at the same time as the height measurements were made (**IV, V**).

2.4 Statistical analyses

In study **I** the number of days to bud burst was defined as the number of days from the start to the date by which 50% of the observed buds had burst. In study **II**, in addition to the number of days, the number of light hours and the temperature sum (+5 °C threshold) required for a 50% burst of observed buds (pooled data) were calculated for each treatment and for each material group. The bud burst percentage was calculated from the number of burst and observed buds (**III**).

The cessation of height growth for an individual seedling was defined as the moment by which 95% of height growth had been achieved. For individual origins and sowing dates it was taken as the average (of 95% height growth) of all the seedlings (**IV**, **V**). Timing of the formation of the terminal buds was defined as the moment by which 50% of the seedlings had set buds. In the first growing season, for each individual origin and sowing date, the night length prevailing at the time of growth cessation was plotted against the temperature sum accumulated until growth ceased (**IV**, **V**). The line on the plots of the observed data will be referred to the fitted growth cessation line (Fig. 2). Because the relationship between accumulated temperature sum and night length at the time of growth cessation is symmetric, it cannot be analysed in terms of dependent and independent variables. Therefore, growth cessation lines for individual origins were fitted using the maximum likelihood estimation method presented by Lappi and Sievänen (1993).

The differences in the number of days to bud burst between the treatments and between the two transfers were tested using analysis of variance and Tukey's multiple test procedure (**I**). The bud burst percentages of the twigs were analysed with ANOVA models (**III**). The differences in timing of growth cessation were tested separately in the first and second growing seasons using analysis of variance (**IV**, **V**). The effect of the photoperiod and temperature sum of the original growing site of the origin on the environmental response of the timing of growth cessation was examined by comparing the properties of the fitted growth cessation lines (Fig. 2) of the different origins using linear regression analysis (**IV**, **V**).

3 Results

3.1 Growth onset

3.1.1 Effects of photoperiod and accumulated light periods

In study **I** shortening the photoperiod delayed bud burst in Norway spruce cuttings especially at a day/night temperature of +20/10 °C, but also at constant temperature of +10 °C. When the photoperiod was lengthened and the day/night temperature was held constant at +10 °C, bud burst was accelerated compared with a natural photoperiod and constant temperature of +10 °C (**I**).

In study **II**, unlike study **I**, shortening the photoperiod seemed to promote bud burst compared with other photoperiod treatments. The probable reason for this was that the longer photoperiod, and thus higher number of accumulated daily light hours, at the start of the shorter photoperiod treatment reduced the temperature requirement of bud burst in all the samples of Norway spruce used. The promoting effect was clearest in the oldest material (18-year-old cuttings) (**II**).

3.1.2 Effects of temperature

Fluctuating day/night temperature conditions accelerated bud burst in Norway spruce cuttings compared with constant temperature conditions both in lengthening photoperiod and in natural photoperiod in natural light (**I**). In all temperature and photoperiod combinations, the cuttings in the second transfer, which had been exposed for a longer time to natural chilling and freezing temperatures, generally required fewer days to bud burst than the cuttings in the first transfer (**I**).

3.1.3 Age-specific patterns

In 18-year old cuttings bud burst was earliest in the treatment with a shortening (starting from 16 h) photoperiod and latest in the constant 6 h photoperiod (**II**). With 14-year-old cuttings and two-year-old seedlings, bud burst took place earliest in the shortening photoperiod, but there was no difference in timing of bud burst between the treatments with lengthening (starting from 6 h) and constant photoperiod (**II**). With one-year-old seedlings (sown in April and in July) bud burst was earliest in the shortening photoperiod and latest in the lengthening photoperiod (**II**).

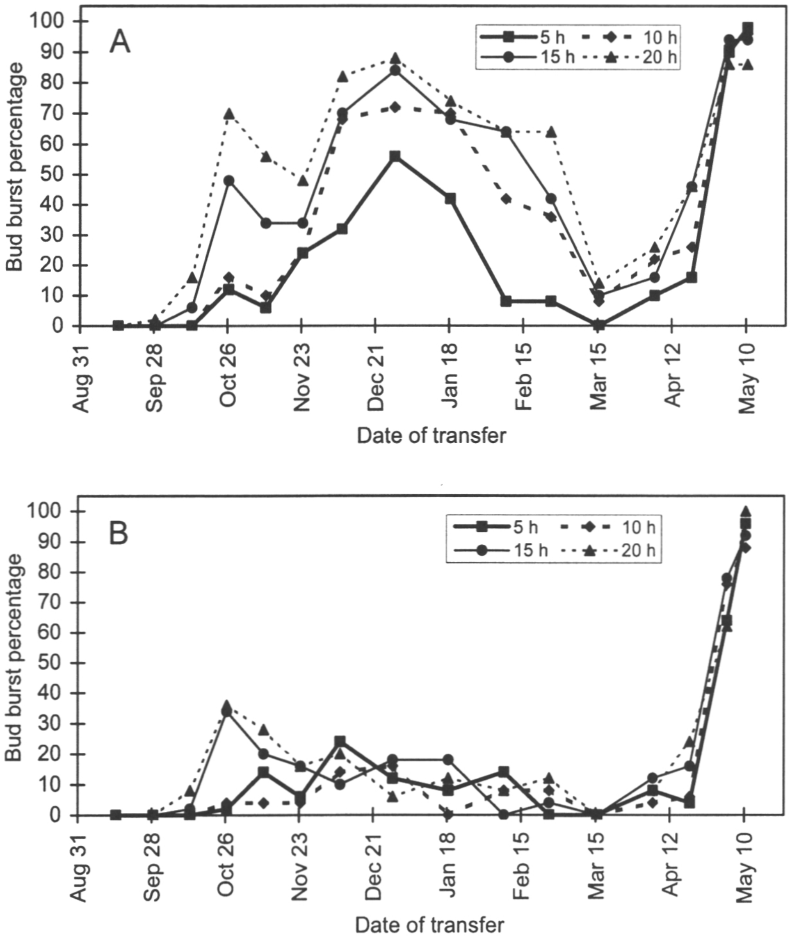

Figure 3. Bud burst percentage of (A) twigs of 15-year old ('young trees') and (B) twigs of 56-year old ('old trees') Norway spruce after transfer from natural conditions to forcing conditions (air temperature +20 °C, four different photoperiods) (III).

The bud burst percentage of the twigs of young (15-year-old) trees generally increased in all photoperiods until the end of the year. After that it decreased until the vernal equinox (March 20) (**III**), increasing again towards spring (Fig. 3A). In twigs of the old (56-year-old) trees the transient rest completion was much weaker as the bud burst percentages generally remained under 20% during autumn and winter (Fig. 3B) (**III**). During the time of vernal equinox no buds burst during any photoperiod. After that the bud burst percentage increased basically as it did in the young trees. The sine-curve-type secondary rest pattern was not as clear as in the twigs from the young trees (Fig. 3). Although the bud burst percentage of the twigs from young trees was generally higher with longer photoperiod, no evidence for a definite long photoperiod requirement for rest completion was observed (**III**).

3.2 Growth cessation

3.2.1 Effects of night length and stage of development

In the first growing season, there was neither a critical night length nor temperature sum (growth cessation lines (i) and (iii) in Fig. 2, respectively), which coincided with growth cessation in Scots pine (**IV**), Norway spruce (**V**) or silver birch (**V**) seedlings from different sowing dates. For growth to cease in seedlings from the first sowings a greater temperature sum and shorter night length was required than for seedlings from later sowings. These results (Fig. 4) support the prediction of the joint factor theory (declining growth cessation line (ii) in Fig. 2). Moreover, there was variation in the timing of growth cessation in Scots pine seedlings between experimental sites and years (**IV**).

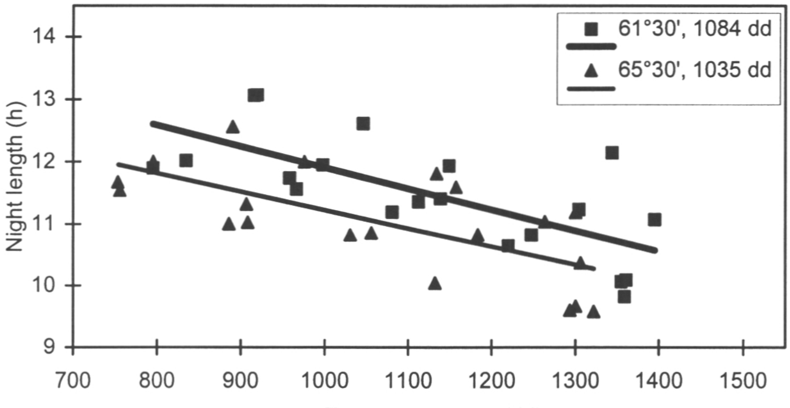

Figure 4. Average timing of growth cessation of two origins of Scots pine after the first growing season in terms of temperature sum and night length in two experimental sites and years. The temperature sum of the original growing sites of these origins is nearly similar, but the corresponding photoperiod is clearly different (IV).

For height growth to cease in the second growing season, Scots pine seedlings from the last two sowings needed a 400 dd higher temperature sum average than the seedlings from first two sowings. Furthermore, for terminal bud formation a slightly larger temperature sum was needed in seedlings from later sowings than in those from the first sowings (**IV**). While terminal bud formation in Scots pine was affected by sowing time, whether it was the first growing season or not, this was not the case in Norway spruce and silver birch seedlings. In the second growing season sowing time did not affect the timing of terminal bud formation and its effect on height growth cessation was minimal (**V**).

3.2.2 Differences among seed origins

Scots pine seedlings grown from seed from the most northern origins stopped growing before all the others. Those from the most southern origins were the last to stop growing (**IV**). Compared to the average annual temperature sum, the photoperiod, or latitude of the origin seemed to be the dominant factor in determining the level of the growth cessation line. Seedlings from seeds originating at sites with almost the same temperature sums, but different photoperiods, stopped growing at different times. (Fig. 4). However, those from seeds originating at sites with almost the same photoperiod, stopped growing almost at the same time, despite having different temperature sums. In the multiple regression model, latitude (photoperiod) of the origin was a significant predictor for the level parameter of the fitted growth cessation line for the origin, whereas temperature sum was not (**IV**).

Norway spruce and silver birch seedlings from seeds of northern origin generally ceased their growth earlier, i.e. with shorter night length and smaller temperature sum, than those from southern origins (**V**). Correspondingly, the average final height of the seedlings from northern origins was smaller than the average final height of the seedlings from southern origins. The difference in the timing of growth cessation between seedlings of northern and southern origins was smaller in silver birch than in the case of Norway spruce (**V**).

3.2.3 Differences among tree species

The fitted growth cessation lines for Norway spruce origins were more gently sloping than the corresponding lines for silver birch origins (**V**). In other words, the change in stage of development (estimated using either constant temperature sum accumulation or the age of seedlings) changed the critical night length of growth cessation less with Norway spruce than with silver birch. The fitted growth cessation lines of Scots pine origins were not as steep as those for silver birch origins, but they were steeper than those for Norway spruce (**IV**, **V**).

Because latitude (photoperiod) and average annual temperature sum of the original growing site in Norway spruce and in silver birch were strongly correlated, either one could be used to predict variations in the properties of the fitted growth cessation lines of origins (**V**). The linear regressions of the predicted night lengths of the fitted growth cessation lines at fixed temperature sums, using latitude (photoperiod) or average annual temperature sum as a predictor, were not as significant for silver birch as for Norway spruce. For Norway spruce, the slopes of the fitted growth cessation lines were dependent on the latitude (photoperiod) and the annual temperature sum of the original growing site, whereas in the case of silver birch the slopes of the fitted growth cessation lines were not dependent on either of them (**V**). In other words, the effect of photoperiod and annual temperature sum of the growing site of the origin on the environmental response of the timing of growth cessation was much weaker in silver birch than in Norway spruce.

4 Discussion

4.1 Growth onset

4.1.1 The role of photoperiod and temperature

Temperature has a far more important role in the onset of growth than photoperiod. It has been generally held that the timing of the onset of growth is regulated by temperature alone (Smith and Kefford 1964, Perry 1971, Fuchigami et al. 1982). This study has detected that the photoperiod also affects ontogenetic development. Shortening the photoperiod before the winter solstice (December 21) delayed bud burst in Norway spruce cuttings especially under fluctuating temperature conditions (**I**). It is possible, that in the case of climatic warming, this phenomenon may prevent the premature onset of growth during early winter.

According to earlier studies, short photoperiods do not prevent or delay growth onset when the chilling requirement has been fulfilled (Nienstaedt 1967, Worrall and Mergen 1967). In these studies, constant short photoperiods were used. However, a constant photoperiod does not simulate the photoperiod prevailing under natural conditions. Consequently, the lack of a photoperiodic effect in these earlier studies may be related to the use of a constant photoperiod.

A combination of fluctuating day/night temperature and continuously lengthening photoperiod was the most effective condition for promoting bud burst (**I**). Campbell and Sugano (1975) and van den Driessche (1975) found that fluctuating temperatures were more effective in promoting ontogenetic development in one-year-old seedlings of *Pseudotsuga menziesii* than a constant temperature. The fluctuating day/night temperature treatment included more chilling hours than the constant temperature treatment (**I**). This may partly explain the effectiveness of the fluctuating temperature in promoting bud burst and also suggests that the plant material may not have been fully chilled. Consequently, the difference in days to bud burst between cuttings in the first and second transfers was probably partly due to the differences in exposure to natural chilling and freezing temperatures, before the exposure to forcing conditions began (**I**).

The effect of direction of change in the photoperiod on the timing of bud burst in Norway spruce was further tested in uniform fluctuating temperature conditions (**II**). Bud burst was more dependent on the accumulated duration of the light period than on the direction of a change in the photoperiod. This partially contradicts the findings (**I**) considering that bud burst in Norway spruce was delayed several weeks by shortening photoperiod treatments. However, when the photoperiod was changed abruptly from 6 h to 16 h, the seedlings and cuttings in the shortening photoperiod treatment might have received a signal that the photoperiod was lengthening (**II**). Thus, the result does not preclude the possibility that the direction of a change in the photoperiod affects the response of bud development to forcing temperatures.

One possible reason for the observed differences in timing of bud burst between long and short day conditions (**II**) could be the consequent reduction in photosynthesis and increase in respiration under short day conditions resulting in low carbohydrate levels (Ögren 1997, Ögren et al. 1997). Another explanation for the observed differences could be the warming effect of absorbed radiation energy (Repo et al. 1991). Naturally the warming effect would be greater in plants subjected to a long photoperiod. The above factors alone do not satisfactorily explain the observed differences in bud burst time between long and short day conditions (**II**).

4.1.2 Age-specific reactions to environmental factors

In young trees the rest break was two-pronged. The bud burst percentage of twigs from 15-year-old trees, depending on the length of the photoperiod, increased (the rest was completed) up to the end of the year, but decreased toward March (**III**). The bud burst percentage in old trees generally remained under 20% in all photoperiods, and in the March 15 transfer, before the vernal equinox (March 20), there were no burst buds in any photoperiod. It would seem that mature trees, especially young ones, have a secondary rest culminating about the time of the vernal equinox. After that the bud burst percentages of both young and old trees increased rapidly toward early May.

In addition to chilling, another clue (Häkkinen et al. 1998, Häkkinen 1999, Linkosalo 2000a,b and Linkosalo et al. 2000) seems to be needed to satisfy the requirements for rest completion in silver birch and some other adult boreal trees. It would also seem evident that photoperiod alone does not comprise this additional clue needed for rest completion (**III**). After rest completion in May the decreased red/far-red ratio had no effect on the timing of bud burst of two-year-old seedlings of Norway spruce (Häkkinen et al. 2001). Moreover, as a rule even the two longest (15 h and 20 h) photoperiods did not cause the majority of buds to burst on twigs from either 15-year-old or 56-year-old trees until late spring (**III**). However, if the additional clue is mediated by substances originating in the roots, then its manifestation would be impossible (**III**) after the twigs were detached from the trees. Thus, these results do not conclusively invalidate the hypothesis that a long photoperiod is an absolute requirement for rest completion.

There was a clear difference in the bud burst percentages between the old and young twigs (**III**). Moreover, 18-year-old cuttings required a longer time for bud burst than 14-year-old ones and seedlings (**II**). Earlier Ununger et al. (1988) observed in rooted cuttings of Norway spruce, that the older plant material required a longer time for bud burst than the younger material. All these results suggest that changes takes place in the environmental responses of bud burst in Norway spruce as the trees age.

4.2 Growth cessation

4.2.1 The role of night length and stage of development

Growth of seedlings of all three species, in the first growing season, did not stop as a result of the constant night length or the same temperature sum accumulation (**IV, V**). For the growth cessation of seedlings from the first sowings, shorter night length and greater temperature sum was required than for seedlings from later sowings. Because the daily temperature sum accumulation in all the experiments was kept constant, it is likely that the seedlings from different sowing dates were in different stages of development at any given calendar date (night lengths) before height growth ceased. Consequently the results suggest that the variation in the timing of growth cessation in seedlings of all three species, in the first growing season, can be explained by both night length and stage of development. The stage of development being estimated using either constant temperature sum accumulation (or the age of the seedlings). The time of growth cessation also varied with experimental site and from year to year (**IV**). This suggests that other environmental factors such as nutrition and solar irradiance have an effect on the timing of growth cessation.

In the second growing season, Scots pine seedlings from later sowings required a greater temperature sum and a longer time for terminal buds to form and especially for height growth to stop than those from earlier sowings (**IV**). Because of predetermined growth, the sowing date should not have affected the phenology of Scots pine during the second rowing season. Possible reason for the longer time required for the height growth cessation in the later sowings compared to earlier ones, was that the elongation of the bud was partly included to the height measurement. A study by Koski and Sievänen (1985) demonstrated that the formation of terminal buds exhibited a similar after-effect, whereas the cessation of height growth showed an opposite after-effect. The sowing date did not affect the timing of terminal bud formation either in Norway spruce or silver birch in the second growing season because of free growth. It, however, had a slight effect on the timing of height growth cessation (**V**). Koski and Sievänen (1985), found no after effects on height growth in the second growing season in Norway spruce or silver birch. The time interval, in their study, between earliest and latest sowings was five months (March to July), whereas in this work (**IV** and **V**) it was only two months (June and July). Moreover, especially the last sowing in late July is quite late, and accordingly the seedlings were very small after the first growing season. These differences may partially explain the differences between Koski and Sievänen's (1985) findings and those presented here.

Short day treatment has been used in nurseries for many years to stop height growth and start the cold hardening of conifer seedlings (e.g. Heide 1974, Rosvall-Åhnebrink 1982, Colombo et al. 1982, Bigras and D'aoust 1992). For seedlings from northern origins the night length required for cessation of height growth and formation of the terminal bud is shorter than for the southern ones (Vaartaja 1951, 1957, Dormling 1973). Because Scots pine and especially Norway spruce seedlings are sensitive to an increase in night length and (**IV**, **V**), it is possible to stop the growth and hasten the development of dormancy by lengthening the night artificially (e.g. Rosvall-Åhnebrink 1977, 1980, 1982, 1990, Dormling and Lundkvist 1983). Growth in height of silver birch seedlings can be stopped when about two-thirds of the average temperature sum of the original growing site has been accumulated (Koski and Sievänen 1985, Luoranen 2000). In central Finland, an eight hour short day treatment, started earliest in July and lasting two to three weeks, stops height growth in silver birch (Luoranen and Rikala 1997, Luoranen 2000). In Study **V**, despite in the two latest sowings the required temperature sum had not been accumulated, a night length over 11 h seemed to be the factor that forced the silver birch seedlings to stop growing.

4.2.2 Differences among seed origins and tree species

Seedlings of Scots pine (**IV**), Norway spruce (**V**) and silver birch (**V**) from northern origins generally ceased their growth earlier, i.e. with a shorter night length, than seedlings from southern origins. Consequently, the final average height of the seedlings from northern origins remained smaller. The presence of latitudinally oriented photoperiodic ecotypes has earlier been demonstrated in several northern tree species (Pauley and Perry 1954, Vaartaja 1954, 1959, Dormling et al. 1968, Håbjörg 1972).

Photoperiod (latitude) of the original growing site of the tree seemed to be the dominant factor for determining the environmental response of the timing of growth cessation of the Scots pine seedlings in the first growing season (**IV**). Moreover, the role of the photoperiod seemed to become more important especially when moving northwards from latitude 65°N.

This is logical, because changes in length of the photoperiod (night length) occur more rapidly, and winter comes earlier, in the north than in the south. The results are in accordance with the earlier studies indicating a latitudinal cline for growth cessation in Scots pine origins (Wareing 1950a,b, Langlet 1959).

Dormling (1979) found that when Norway spruce from southern origins are moved northwards, their growth will cease later than trees of the autochthonous population. This is not only due to a previous longer critical night length, but also to their ability to register the twilight more effectively. According to Skre (1991) different birch origins might also respond to night length, solar irradiance and temperature in different ways when exposed to new growing conditions. However, in the case of silver birch origins the genetic variation in the environmental response of growth cessation among them seems to be weaker than in the case of Norway spruce.

5 Conclusions

The delaying effect of the shortening photoperiod on bud burst of Norway spruce cuttings, as well as the dependence of bud burst in seedlings and cuttings of this species on the accumulated sum of the daily light periods, go against prevailing theory that the timing of growth onset is regulated solely by air temperature. Because light conditions remain approximately the same from year to year, their contribution to the onset of growth stabilizes the ecological effects of predicted climate change (and warming) on bud development in temperate and boreal tree species.

Adult trees seem to have a secondary rest period that culminates at about the time of vernal equinox. In young trees this phenomenon is more obvious than in old trees. Consequently, adult trees generally attain a potential for ontogenetic development much later (late spring) than seedlings do (late autumn). However, young trees in particular appear to have a transitional time window during late autumn when ontogenetic development is possible. Long photoperiods generally enhanced rest break of twigs from young trees. However, no evidence for an absolute requirement for a long photoperiod for rest completion was found. Further studies are needed to clarify the role of the possible secondary rest in the onset of bud ontogenesis.

The photoperiodic regulation of height growth cessation of Scots pine, Norway spruce and silver birch seedlings in the sowing year is dependent on the stage of seedling development estimated using constant temperature sum accumulation (or the age of the seedlings). As a result it is necessary to take the stage of development of seedlings into account when they are produced in nurseries for forest cultivation under regulated growing conditions.

There are considerable latitudinal differences in the timing of growth cessation among Scots pine, Norway spruce and silver birch origins. Seedlings from seed of northern origin generally stop growing earlier (with a shorter night length) than those of southern origin. This fact must be taken into account in the selection of seed for forest cultivation. It is essential that seed from compatible origins be selected if we are to ensure the successful forest cultivation and future survival of the boreal population.

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Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (*Picea abies*)

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Summary We examined the effects of several photoperiod and temperature regimes imposed during the winter–spring period on the timing of bud burst in rooted cuttings of Norway spruce (*Picea abies* (L.) Karst.) grown in a greenhouse in Finland. The treatments were initiated in November and December after the cuttings had been exposed to natural chilling and freezing events. Irrespective of the treatments applied, time to bud burst decreased with increased duration of previous exposure to natural chilling and freezing events. Fluctuating day/night temperatures and continuous lengthening of the photoperiod hastened bud burst. Shortening the photoperiod delayed bud burst, suggesting that little or no ontogenetic development toward bud burst takes place during mild periods before the winter solstice. In the case of climatic warming, this phenomenon may prevent the premature onset of growth that has been predicted by computer simulations with models that only consider temperature regulation of bud burst.

Keywords: climate change, phenology, premature onset of growth.

Introduction

Synchronization of annual development with the annual temperature cycle of the growth site is essential for the survival of trees in cool and temperate regions (Weiser 1970, Sarvas 1972, 1974, Sakai and Larcher 1987). Early onset and late cessation of growth give rise to frequent frost damage, whereas late onset and early cessation result in loss of growth resources at the site (Heide 1985).

After growth cessation in autumn, the vegetative buds of trees are in a state of rest; i.e., they have limited or no growth competence and are unable to undergo ontogenetic development toward bud burst (Doorenbos 1953, Samish 1954, Hänninen 1990*a*). Rest break refers to changes in the dormant bud that lead to full growth competence (Romberger 1963, Weiser 1970, Kobayashi and Fuchigami 1983, Hänninen 1990*a*). Buds with full growth competence are able to undergo a sequence of morphological changes that culminate in bud burst (Romberger 1963, Sarvas 1972, 1974).

It is generally accepted that rest break occurs when buds are exposed to low temperatures (−5 to +10 °C) for several weeks (Coville 1920, Smith and Kefford 1964, Perry 1971, Flint 1974, Fuchigami et al. 1982, Cannell and Smith 1983). When the chilling requirement of the buds is fulfilled, they achieve full growth competence (Hänninen 1995). Several studies on peach have shown that a fluctuating day/night temperature is more effective than a constant temperature in bringing about rest break (Erez et al. 1979, Couvillon and Erez 1985, Erez and Couvillon 1987), implying that several biochemical reactions with different temperature optima are involved in bringing about rest break.

The rate of ontogenetic development depends on the growth competence of the bud (Hänninen 1990*a*, 1995) and increases with increasing temperature (Landsberg 1977). Bud burst occurs when buds are exposed for a prolonged period to temperatures above a certain threshold (Smith and Kefford 1964, Perry 1971, Fuchigami et al. 1982, Cannell 1989, 1990). Fluctuating day/night temperatures have also been found to be more effective than constant temperatures during ontogenetic development. Campbell and Sugano (1975) and van den Driessche (1975) found that a greater accumulation of thermal time was required for bud burst in one-year-old seedlings of *Pseudotsuga menziesii* (Mirb.) Franco when exposed to constant rather than fluctuating temperatures. However, Myking (1997) recently found that there is no difference in time to bud burst between constant and fluctuating temperatures in fully chilled *Betula pubescens* J.F. Ehrh. plants, indicating that the efficacy of fluctuating temperatures in enhancing bud burst is related to the chilling requirement of the buds.

A short photoperiod is a key factor in inducing bud dormancy in most tree species from cool and temperate regions (Wareing 1956), whereas photoperiod usually plays a subordinate role during dormancy release (Hänninen 1990*a*). However, long days have been shown to compensate partially for a lack of chilling during rest break in *Pinus sylvestris* L. (Jensen and Gatherum 1965, Hoffman and Lyr 1967), *Picea abies* (L.) Karst. (Nienstaedt 1967, Worrall and Mergen 1967), and several other tree species (Nienstaedt 1966, Farmer 1968, Hinesley 1982, Garber 1983). Heide (1993*a*, 1993*b*) found that long photoperiods reduced the thermal time required for bud burst in six northern deciduous tree species and that this effect was especially pronounced in beech (*Fagus sylvatica* L.). In *Betula pendula* Roth and *Betula pubescens*, long photoperiods significantly reduced the thermal time required for bud burst after short chilling periods (44 and 74 days, respectively), but had no effect when the chilling requirement was fully met after 105 chilling days (Myking and Heide 1995).

The aim of the present study was to test the effects of constant and fluctuating day/night temperatures in various combinations with natural, decreasing, constant and increasing photoperiods on the timing of bud burst in rooted cuttings of *Picea abies* that had previously been exposed to natural chilling and freezing events.

Material and methods

Material

Norway spruce cuttings were obtained from eight to ten clones of each of three origins: Suomussalmi (64°51′ N, 29°35′ E; 240 m asl); Tuusula (60°21′ N, 24°59′ E; 60 m asl); and Tammisaari (60°02′ N, 23°03′ E; 35 m asl). Clonal material was used to eliminate genetic differences among treatments and to permit study of plants that have passed the juvenile seedling stage. In 1985, the cuttings were rooted from six-year-old ortets growing at Paimio, Preitilä (60°27′ N, 22°45′ E), raised in a greenhouse for the first two growing seasons and subsequently moved outdoors.

Experiments

The experiments were carried out at the Ruotsinkylä Field Station (60°21′ N, 24°56′ E) and the Punkaharju Research Station (61°48′ N, 29°19′ E) of the Finnish Forest Research Institute during the winter of 1993–1994 and at the Ruotsinkylä Field Station during the winter of 1994–1995. The experimental material was transferred to a greenhouse from outdoors on two dates. After transfer, the cuttings were allowed to thaw in the natural photoperiod at 5 °C in Punkaharju and at 5–15 °C in Ruotsinkylä for one week before being exposed to the various combinations of temperature and photoperiod treatments. The temperature treatments were: constant day/night temperature of 10 °C; fluctuating day/night temperature of 15/5 °C; and fluctuating day/night temperature of 20/10 °C. The photoperiod treatments were: natural photoperiod with natural light, starting from 6 h 10 min at the time of transfer; constant 6-h photoperiod in natural light; shortening photoperiod at the rate of 10 min day^{-1}, starting from a 12-h photoperiod at the time of transfer; and lengthening photoperiod at the rate of 10 min day^{-1}, starting from a 6-h photoperiod at the time of transfer (8 h 40 min at the time of transfer for the 1994–95 experiment at Ruotsinkylä). In each treatment, each clone was represented by one cutting.

During the winter of 1993–1994, the experiments in Ruotsinkylä and Punkaharju were started on December 7 (Transfer 1) and December 20 (Transfer 2). During the winter of 1994–1995, the experiments were started on November 2 (Transfer 1) and December 2 (Transfer 2) in Ruotsinkylä. In 1993–1994, the mean temperature for all treatments was 10 °C. In 1994–1995, the mean temperature for all treatments was 15 °C (Figure 1). Temperature data from the greenhouse compartments were recorded hourly.

Shade curtains and artificial light were used to provide the different photoperiods (Figure 2). Daylength was extended with Philips (The Netherlands) SON-T (high pressure sodium) Agro lamps at Ruotsinkylä, and with cool white fluorescent tubes at Punkaharju. The photoperiods at the beginning of the second transfer were different from those at the beginning of the first transfer, because the same greenhouse compartments were used for cuttings from both transfers.

Observations and calculations

The developmental stage of ten uppermost buds of the cuttings, including the terminal bud, was checked twice each week. A bud was considered to have burst if new needles were visible. The mean number of days to bud burst (DBB) was calculated for each treatment as the number of days from the start of the treatment to the date when 50% of the observed buds had burst. The data were subjected to analysis of variance and Tukey's test for multiple comparisons. Because of large variations among clones and the limited number of clones per treatment, there were few statistically significant differences.

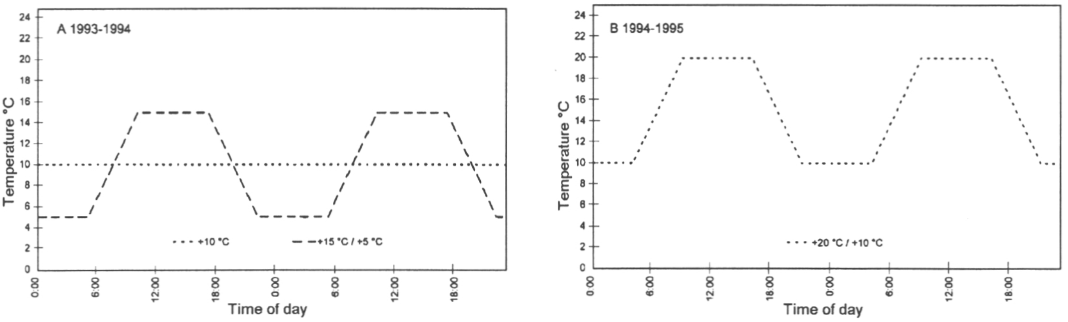

Figure 1. Day/night temperature treatments (A) in the winter/spring of 1993–1994, when the mean temperature was 10 °C, and (B) in the winter of 1994–1995, when the mean temperature was 15 °C.

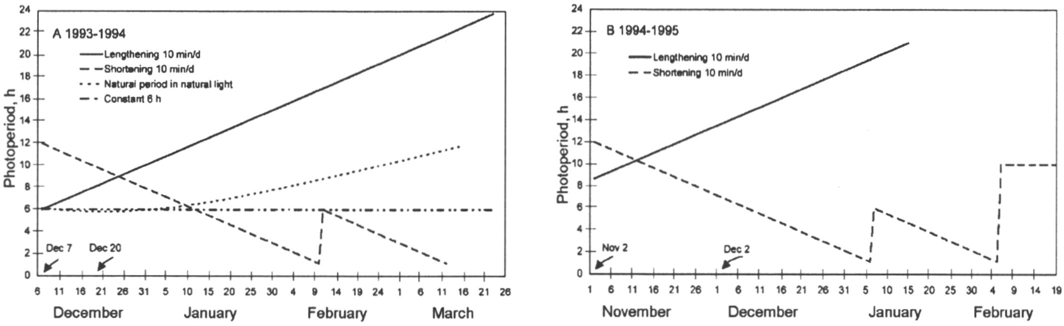

Figure 2. Photoperiod treatments (A) in the winter/spring of 1993–1994 at Ruotsinkylä and Punkaharju, and (B) in 1994–1995 at Ruotsinkylä. Arrows indicate starting dates of treatments. As indicated, the declining photoperiod treatment in the winter of 1994–1995 in Ruotsinkylä was continued as a 10-h constant photoperiod treatment.

Results

Effects of photoperiod

In 1994–1995, at a day/night temperature of 20/10 °C, shortening the photoperiod (see Figure 2B) delayed bud burst (Table 1). In the first transfer (November 2), half of the buds did not burst until 5 months had elapsed and the photoperiod had been changed to a 10-h constant photoperiod (Figure 2B). In the second transfer (December 2), half of the buds burst in 90 days. When the photoperiod was lengthened and the day/night temperature held constant at 10 °C, the DBB was 55 and 38 for cuttings in the the first and second transfers, respectively. In 1993–1994, shortening an initial 12-h photoperiod by 10 min per day generally delayed bud burst by more than 10 days compared with lengthening an initial 6-h photoperiod by 10 min per day (Figure 2A, Table 1). Most of the buds burst after the sudden lengthening of the photoperiod from 1 to 6 h on February 10 (Figure 2A).

In the northern origin (Suomussalmi) in 1993–1994, lengthening the photoperiod by 10 min a day at a 10 °C constant temperature hastened bud burst by an average of 13 (from 94 to 81) and 9 (from 80 to 71) days for cuttings in the first (December 7) and second (December 20) transfers, respectively, compared with DBB in the natural photoperiod (Table 2). In the southern origin (Tuusula), lengthening the photoperiod by 10 min a day at a 10 °C constant temperature hastened bud burst in cuttings in the first transfer (December 7) by an average of 16 days (from 94 to 78) and in the second transfer (December 20) by an average of 7 days (from 78 to 71) compared with cuttings in the natural photoperiod (Table 2).

Effects of temperature

A fluctuating day/night temperature accelerated bud burst by 10 days or more when the photoperiod was lengthened by 10 min per day from 6 h (Table 3). The effect was consistent over origins, temperature regimes and test sites. A fluctuating day/night temperature also promoted bud burst in the natural photoperiod in natural light (Table 3). In Ruotsinkylä in 1993–1994, fluctuating day/night temperatures caused buds to burst 28 days earlier in cuttings in the first transfer and 14 days earlier in cuttings in the second transfer compared with constant temperature conditions. This occurred in both the Suomussalmi and Tuusula origins. When the two transfers were combined, Tukey's test for multiple comparisons ($P < 0.05$) revealed a significant difference between fluctuating and constant temperatures during natural photoperiod in cuttings from the Suomussalmi origin.

Table 1. Effects of shortening and lengthening the photoperiod at constant and fluctuating day/night temperatures on mean days to bud burst (DBB). Temperature and photoperiod treatments are detailed in Figures 1 and 2.

Photoperiod	Day/night temperature (°C)	Origin	DBB in transfer 1 (Nov. 2)	Buds in transfer 1 (*n*)	DBB in transfer 2 (Dec. 2)	Buds in transfer 2 (*n*)
Ruotsinkylä 1994–1995						
Shortening from 12 h	20/10	Tammisaari	173	90	90	80
Lengthening from 8 h 40 min	20/10	Tammisaari	55	90	38	79
Ruotsinkylä 1993–1994						
Shortening from 12 h	10/10	Suomussalmi	90	99	84	90
		Tuusula	83	97	84	70
Lengthening from 6 h	10/10	Suomussalmi	79	97	70	90
		Tuusula	73	100	80	70

Table 2. Effect of lengthening the photoperiod at a constant day/night temperature of 10 °C on mean days to bud burst (DBB) at two test sites. Temperature and photoperiod treatments are detailed in Figures 1 and 2.

Photoperiod	Temperature (°C)	Origin	DBB in transfer 1 (Dec. 7)	Buds in transfer 1 (*n*)	DBB in transfer 2 (Dec. 20)	Buds in transfer 2 (*n*)
Ruotsinkylä 1993–1994						
Lengthening from 6 h	10/10	Suomussalmi	79	97	70	20
		Tuusula	73	100	80	50
Natural	10/10	Suomussalmi	97	100	77	20
		Tuusula	97	95	84	50
Punkaharju 1993–1994						
Lengthening from 6 h	10/10	Suomussalmi	83	81	72	27
		Tuusula	83	78	62	20
Natural	10/10	Suomussalmi	90	87	83	25
		Tuusula	90	72	72	20

Effects of prolonged exposure to natural chilling and freezing events

The cuttings in the second transfer, which had experienced more prolonged exposure to natural chilling and freezing events than cuttings in the first transfer, generally flushed earlier than cuttings in the first transfer. The only exception was in Ruotsinkylä in 1993–1994 where cuttings from the Tuusula origin in the second transfer (December 20) flushed on almost the same date as cuttings in the first transfer (December 7) (Tables 1, 2 and 3). When data for both transfers were combined and subjected to analysis of variance, a significant difference ($P < 0.05$) between the two transfers was detected in 1993–1994 at both test sites, except in Ruotsinkylä for the Tuusula origin.

Discussion

Shortening the photoperiod before the winter solstice (December 21) prevented ontogenetic development toward bud burst. If verified for other species, this is an important finding because it has been assumed that the timing of growth onset is regulated solely by air temperature (Smith and Kefford 1964, Perry 1971, Fuchigami et al. 1982).

According to several studies, short photoperiods do not prevent or delay growth onset in fully chilled trees (Nienstaedt 1967, Worrall and Mergen 1967, Hänninen 1990*a*); however, in all of these studies, constant short photoperiods were used. Based on our findings, we conclude that the lack of a photoperiodic effect on rest break in these earlier studies is related to the use of a constant photoperiod, which does not simulate the photoperiod under natural conditions.

It has been predicted that climate warming may cause premature growth onset during mild spells in winter and heavy damage during subsequent periods of frost in areas with a continental climate (Hänninen 1991). The computer model (Sarvas 1972, 1974, Hänninen 1990*b*) used to deduce this premature growth-induced frost damage hypothesis is based on the assumption that air temperature regulates the onset of

Table 3. Effects of constant and fluctuating day/night temperatures in a natural and a lengthening photoperiod on mean days to bud burst (DBB) at two test sites. Temperature and photoperiod treatments are detailed in Figures 1 and 2.

Day/night temperature (°C)	Photoperiod	Origin	DBB transfer 1 (Dec. 7)	Buds in transfer 1 (*n*)	DBB in transfer 2 (Dec. 20)	Buds in transfer 2 (*n*)
Ruotsinkylä 1993–1994						
10/10	Lengthening from 6 h	Suomussalmi	79	97	70	60
		Tuusula	73	100	80	60
15/5	Lengthening from 6 h	Suomussalmi	65	100	60	60
		Tuusula	69	100	66	60
Punkaharju 1993–1994						
10/10	Lengthening from 6 h	Suomussalmi	83	91	65	17
		Tuusula	83	96	58	10
15/5	Lengthening from 6 h	Suomussalmi	62	90	55	18
		Tuusula	69	97	55	10
Ruotsinkylä 1993–1994						
10/10	Natural	Suomussalmi	97	100	77	20
		Tuusula	97	95	87	60
15/5	Natural	Suomussalmi	69	100	63	20
		Tuusula	69	98	73	60

growth and that some ontogenetic development occurs before the winter solstice. However, our finding that bud burst was delayed when the natural photoperiod was shortened indicates that the predicted premature growth onset of trees may not occur under natural conditions. Similarly, Hänninen et al. (1993) and Hänninen (1995) found that the onset of growth of Scots pine saplings growing in open-top chambers under elevated temperature conditions took place about 70 days later than predicted by the computer model (Sarvas 1972, 1974, Hänninen 1990*b*, 1991).

A fluctuating day/night temperature enhanced the rate of bud burst more than a constant temperature, even though the mean temperature was the same in the two treatments. Among the treatments tested, a combination of fluctuating day/night temperature and continuously lengthening photoperiod promoted bud burst the most. Similar effects of fluctuating day/night temperatures versus constant temperatures have been observed on rest break in peach (Erez et al. 1979, Couvillon and Erez 1985, Erez and Couvillon 1987). A fluctuating temperature was also more effective than a constant temperature in enhancing ontogenetic development in one-year-old seedlings of *Pseudotsuga menziesii* (Campbell and Sugano 1975, van den Driessche 1975). However, Myking (1997) found no difference in time to bud burst between constant and fluctuating temperatures in fully chilled *Betula pubescens* plants. In our study, the fluctuating day/night temperature treatment provided more chilling hours to the cuttings than the constant temperature treatment, which may partly explain the effectiveness of the fluctuating temperatures in promoting bud burst.

For clones of all origins, bud burst generally occurred earlier in cuttings in the second transfer than in the first transfer, indicating that physiological changes occurred between the transfers. Presumably, these changes were associated with rest break because ontogenetic development requires higher temperatures than occurred during the period between Transfers 1 and 2. The cuttings in the second transfer were previously exposed to lower temperatures and shorter photoperiods before beings subjected to the treatments than the cuttings in the first transfer. Differences in exposure to natural photoperiod changes and natural chilling and freezing events probably account for the difference in days to bud burst between cuttings in the the first and second transfers.

Cuttings of northern origins generally flush earlier than those of southern origin (Kriebel and Wang 1962, Worral and Mergen 1967, Beuker 1994, Myking and Heide 1995). In the present study, the difference between the northern (Suomussalmi) and southern (Tuusula) origins was less than under natural conditions. This may be partly because of the small number of clones tested.

Rinne et al. (1997) found that a few hours' exposure to near-lethal freezing temperatures causes rest break in *Betula*. However, according to the prevailing theory, rest break involves a series of enzymatic reactions with temperature optima above 0 °C. Thus, neither our results nor those of Rinne et al. (1997) support the prevailing theory on the environmental regulation of rest break and subsequent growth onset. Further studies are needed to assess the ecological effects of predicted climate change on bud development of temperate and boreal tree species.

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II

Effect of Accumulated Duration of the Light Period on Bud Burst in Norway Spruce (*Picea abies*) of Varying Ages

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Partanen, J., Leinonen, I. & Repo, T. 2001. Effect of accumulated duration of the light period on bud burst in Norway spruce (*Picea abies*) of varying ages. Silva Fennica 35(1): 111–117.

One-year-old seedlings (two sowing times), two-year-old seedlings and 14- and 18-year-old cuttings of Norway spruce (*Picea abies* (L.) Karst.) were exposed to shortening photoperiod (initially 16 h), lengthening photoperiod (initially 6 h) and constant short photoperiod (6 h) treatments with uniform temperature conditions in growth chambers. The timing of bud burst was examined. In all plants, shortening photoperiod treatment seemed to promote bud burst compared with other treatments. This effect was clearest in the oldest material. The results suggest that, in addition to temperature sum, the accumulated duration of the light period may promote bud burst of Norway spruce.

Keywords growth initiation, phenology, photoperiod, Norway spruce

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1 Introduction

Light conditions control various events in the annual cycle of development of several tree species. Light is the primary source of energy for them and their morphogenic development is strongly affected by light conditions. The effects of photoperiod on growth cessation and dormancy have been observed for example by Wareing (1950a, 1950b), Vaartaja (1959), Heide (1974) and Ekberg et al. (1979). In this kind of response, the role of photoperiod is to act as an environmental signal which ensures the initiation of the hardening processes already before the occurrence of low autumn temperatures.

In dormancy release and growth initiation the role of temperature is more important than the role of light conditions. However, photoperiod may have effects similar to those of low temperatures for rest break. Long days compensate partially for a lack of chilling during rest break in *Pinus sylvestris* L. (Jensen and Gatherum 1965, Hoffman and Lyr 1967), *Picea abies* (L.) Karst. (Nienstaedt 1967, Worrall and Mergen 1967) and several other tree species (Nienstaedt 1966, Farmer 1968, Campbell and Sugano 1975, Hinesley 1982, Garber 1983). Some results indicate that there is a critical photoperiod for bud burst in beech (*Fagus sylvatica* L.) seedlings, even when they are fully chilled (Heide 1993a). In these cases, the photoperiodic signal may reduce the effect of temperature variation and stabilise the timing of bud burst in spring (Heide 1993a, 1993b). In addition, the results obtained by Häkkinen et al. (1998) suggest that mechanisms based on both light and temperature conditions control bud development in *Betula pendula* Roth.

It has recently been suggested that growth initiation in Norway spruce is affected by the direction of a change in the photoperiod, not its length per se (Partanen et al. 1998). In the event of climatic warming, this mechanism would be ecologically significant in autumn before winter solstice (December 21). It would prevent the ontogenetic development of buds and thus premature bud burst would be avoided. The delaying effect of shortening photoperiod on bud burst detected by Partanen et al. (1998) was especially pronounced in fluctuating temperature conditions.

The aim of this study was to test the effect of different light conditions on the timing of bud burst in Norway spruce. The effect of direction of change in the photoperiod (shortening, lengthening and constant photoperiod) was tested in uniform fluctuating temperature conditions. In light treatments, the duration of the light period, and consequently the accumulation of light hours, was different. The possible effects of the maturation of trees on the photoperiodic responses were also examined.

2 Materials and Methods

2.1 Plant Materials

The material consisted of seedlings and cuttings of Norway spruce of varying ages, forming five treatment groups. The youngest group consisted of one-year-old Norway spruce seedlings. The seeds produced at seed orchard number 111 in Kangasniemi (61°56´N, 26°41´E; 100 m a.s.l.) were sown on June 12, 1997 into PS-608 paper pots containing commercial fertilized peat (Vapo peat for forest trees) in the nursery at the Suonenjoki Research Station of the Finnish Forest Research Institute (62°40´N, 27°00´E; 130 m a.s.l.). The seedlings were grown in a plastic greenhouse and fertilized twice with 10 g/m^2 of the commercial fertilizer Kekkilä Superex-9 (N 19%, P 5%, K 20% and micronutrients).

The second youngest group also consisted of one-year-old Norway spruce seedlings. The seeds produced at seed orchard number 111 in Kangasniemi (61°56´N, 26°41´E; 100 m a.s.l.) were sown on April 28, 1997 into PS-508 paper pots containing commercial fertilized peat (Vapo peat for forest trees) in the nursery at Suonenjoki Research Station. The seedlings were grown in a plastic greenhouse with a shading net (30% shade). The seedlings were fertilized four times with 10 g/m^2 of the commercial fertilizer Kekkilä Superex-9 (N 19%, P 5%, K 20% and micronutrients), and once with 10 g/m^2 of Kekkilä Superex-5 (N 11%, P 4%, K 25% and micronutrients).

The third group consisted of two-year-old Norway spruce seedlings. The seeds produced at seed orchard number 111 in Kangasniemi (61°56´N, 26°41´E; 100 m a.s.l.) were sown on June 10, 1996 into PS-608 paper pots containing commercial fertilized peat (Vapo peat for forest trees) in the nursery at Suonenjoki Research Station. The seedlings were grown in a plastic greenhouse until October. During the second growing season the seedlings were grown outdoors on a rack 15 cm above the ground. Between the middle of June and the beginning of August a shading net was used (30% shade). During the first growing season, the seedlings were fertilized twice with 10 g/m^2 of the commercial fertilizer Kekkilä Superex-9 (N 19%, P 5%, K 20% and micronutrients). During the second growing season, the seedlings were fertilized six times with 15 g/m^2 of the commercial fertilizer Kekkilä Superex-9, and once with 10 g/m^2 of Kekkilä Superex-5 (N 11%, P 4%, K 25% and micronutrients).

The fourth group consisted of Norway spruce cuttings cut from the hedged motherplant V4208 in Haapastensyrjä Tree Breeding Centre. This plant was selected in 1990 from seedlings in early test number 1130/2. The seeds were sown in 1984 and the seedlings were planted in 1986 in Haapastensyrjä Tree Breeding Centre of the Foundation for Forest Tree Breeding (60°37´N, 24°27´E; 120 m a.s.l.). The seeds originated from plus clone E137 in Kalvola (61°05´N, 24°00´E; 120 m a.s.l.), which was pollinated by the trees from clone experiment number 125 in Haapastensyrjä (60°37´N, 24°26´E; 110 m a.s.l.). The cuttings were taken in autumn 1994. They were rooted in spring 1995 and grown in plastic trays of 45 cells filled with fertilized peat. The size of each cell was 5.0 cm × 5.4 cm × 10 cm (depth).

The fifth group consisted of Norway spruce cuttings from the hedged motherplant V3702 in Haapastensyrjä Tree Breeding Centre. This plant was selected in 1982. The seeds were sown in 1980 in Haapastensyrjä Tree Breeding Centre. The seeds originated from plus stand number 44 in Miehikkälä (60°47´N, 27°30´E; 60 m a.s.l.). The cuttings were taken in autumn 1994 and rooted in spring 1995. They were grown in plastic trays of 45 cells filled with fertilized peat. The size of each cell was 5.0 cm × 5.4 cm × 10 cm (depth).

2.2 Chilling Conditions

The seedlings were moved from the nursery at Suonenjoki Research Station to the Botanical Gardens of the University of Joensuu (62°36´N, 29°43´E; 81 m a.s.l.) on September 18, 1997. The cuttings were moved from Haapastensyrjä Tree Breeding Centre to the Botanical Gardens on October 14, 1997. After moving, the seedlings and cuttings were transplanted into plastic pots of 450 cm^3 volume containing commercial fertilized peat (Vapo B2, 1.2 kg m^{-3}: N 10%, P 8%, K 16%). After transplanting, the seedlings and cuttings were moved outdoors and exposed to natural chilling and freezing temperatures until December 5, 1997. On this date the material was presumed to be fully chilled (Worrall and Mergen 1967, Sarvas 1974, Hänninen 1990). The pots were isolated from each other with sand. The air temperature from the chilling conditions outdoors was monitored by a thermograph. The maximum and minimum air temperatures were 13 °C and –23 °C respectively. The seedlings and cuttings were moved indoors for two weeks into the growth room of the University of Joensuu (temperature 3 °C, relative humidity 90%, daylength 6 h, photon flux density approximately 100 µmol m^{-2} s^{-1}).

2.3 Forcing Conditions

The experimental material was moved and distributed evenly between the three growth chambers (Conviron PGW 36) of the University of Joensuu on December 19, 1997. In each of the three light treatments, 20 seedlings from each of the first three groups and five cuttings from each of the two other groups were used as experimental material. The treatments were: 1) shortening photoperiod (starting from a 16 h photoperiod, changing 6 min 40 s day^{-1}); 2) lengthening photoperiod (starting from a 6 h photoperiod, changing 6 min 40 s day^{-1}); and 3) constant 6 h photoperiod. At the beginning of treatment 1, the lights were switched on at 4 a.m. and off at 8 p.m. In treatment 3 and at the beginning of treatment 2, the lights were switched on at 9 a.m. and off at 3 p.m. Fluorescent (type F96T12/CW/VHO) and tungsten incandescent lamps (Sylvania 100W/227V) were used to give a photon flux density of approximately 200 µmol m^{-2} s^{-1}.

The accumulated duration of the light period was clearly different in the different light treatments. The number of accumulated light hours was greater in the shortening photoperiod treatment than in the lengthening photoperiod and much greater than in the constant 6 h photoperiod treatment. At the beginning of the experiment, the shortening photoperiod treatment presented long day conditions, whereas the lengthening and the constant photoperiod treatments presented short day conditions. With the shortening and lengthening photoperiod treatments the effect of direction of change in the photoperiod could also be tested.

In order to achieve the same temperature sum accumulation in all light treatments, the temperature conditions were identical in all treatments. During the whole experiment, the temperature was maintained at 20 °C between 8 a.m. and 4 p.m. and at 10 °C between 8 p.m. and 4 a.m. During the intervening times the temperature was changed steadily 2.5 °C per hour. The temperature data were recorded hourly. The water vapour pressure deficit was maintained at a maximum of 0.5 kPa during daytime and at 0.25 kPa during the night.

2.4 Observations and Calculations

The developmental stage of the terminal bud of one- and two-year-old seedlings and the terminal buds of the four uppermost twigs and the main shoot of the cuttings were checked at an interval of two days. Thus, the number of observed buds in each group in each treatment was 20 in the case of seedlings and 25 in the case of cuttings. A bud was considered to have burst if new needles were visible.

The temperature sum accumulation required for the bursting of the observed buds was calculated as the mean daily temperature sum (5 °C threshold) in degree days (d.d.) for each treatment and for each group. The number of days, the temperature sum and the number of light hours required for the bursting of 50% of the observed buds (pooled data) were calculated for each treatment and for each material group.

3 Results

In all plants, shortening photoperiod treatment seemed to promote bud burst compared with other treatments (Table 1). Furthermore, the higher number of accumulated duration of light period in the shortening photoperiod treatment seemed to reduce the temperature sum requirement of bud burst (Fig. 1). This phenomenon was clearest in the oldest material.

Table 1. Mean number of days required for 50% bud burst in Norway spruce seedlings and cuttings of varying ages in different light treatments.

Photoperiod in light treatment	One-year-old seedlings (June)	One-year-old seedlings (April)	Two-year-old seedlings	14-year-old cuttings	18-year-old cuttings
Shortening	19	21	21	21	27
Lengthening	25	25	24	25	33
Constant 6 h	21	23	24	25	35

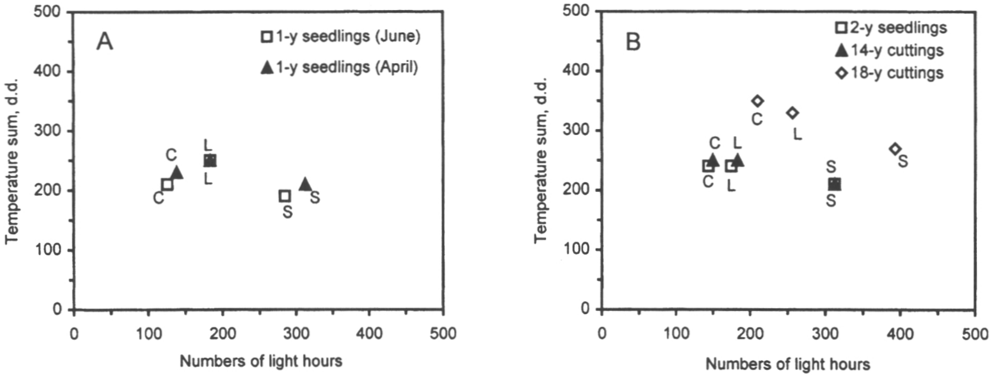

Fig. 1. Temperature sums and numbers of light hours required for 50% bud burst in one-year-old seedlings (A) and two-year-old seedlings and cuttings (B) in constant (= C), lengthening (= L) and shortening (= S) photoperiod. For one-year-old seedlings, the sowing time of the seeds is presented in parentheses.

Compared with other treatments, the shortening photoperiod treatment seemed to promote bud burst in all plant materials, but with respect to the other light treatments there were differences in timing of bud burst between the plant materials (Table 1). In 18-year-old cuttings bud burst was earliest in the treatment with a shortening photoperiod and latest in the constant 6 h photoperiod. With 14-year-old cuttings and two-year-old seedlings bud burst occurred first in the shortening photoperiod. In these material groups, however, there was no difference in timing of bud burst between the treatments with lengthening and constant photoperiod. With one-year-old seedlings (two sowing times) bud burst occurred first in the shortening photoperiod and last in the lengthening photoperiod.

4 Discussion

In this study, growth initiation in Norway spruce seemed to be more dependent on the accumulated duration of the light period than on the direction of a change in the photoperiod. Thus, the results are controversial to the results where bud burst in Norway spruce cuttings was delayed several weeks in shortening photoperiod treatments (Partanen et al. 1998). However, because the photoperiod had to be changed abruptly from 6 h (in controlled chilling conditions) to 16 h (in forcing conditions), the seedlings and cuttings in the shortening photoperiod treatment might have received a signal to the effect that the photoperiod is lengthening. Therefore, the results of this study do not exclude the possibility that the direction of a change in the photoperiod determines the response of bud development to forcing temperatures.

In the present study, bud burst of the four youngest material groups took place in the constant short photoperiod only two to four days later than in the long (= shortening) photoperiod (Table 1). This is in accordance with the results obtained with adult Scots pine trees (Hänninen 1995). In a study carried out by Leinonen et al. (1997) in elevated temperature conditions in midwinter, however, growth onset occurred approximately at the same time in a natural short photoperiod and in an artificially lengthened 17 h photoperiod. In the study by Leinonen et al. (1997) the initial growth rate of new shoots and the rate of dehardening of needles from the previous year were higher under the lengthened than the natural photoperiod. The difference was proposed to be due to the amount of total absorbed radiation, not to the photoperiodic effect itself.

The effect of the accumulated duration of the light period on photosynthetic production might explain the observed differences in timing of bud burst between long and short day conditions, assuming that the development and development rate of the bud is dependent on the carbohydrate level. The reduced photosynthetic production and the increased respiratory loss of carbohydrates in short day conditions lead to the low levels of carbohydrates (Ögren 1997, Ögren et al. 1997). In a study carried out with white spruce (*Picea glauca* (Moench) Voss) bareroot seedlings the delayed bud burst detected in fall-lifted seedlings stored at –2 °C could be related to low carbohydrate levels (Jiang et al. 1994) and/or slow photosynthetic recovery (Jiang et al. 1995). The reason for low levels of carbohydrates in fall-lifted seedlings compared with those lifted in spring could be respiration during cold storage (Cannell et al. 1990, Ögren et al. 1997). In a another study carried out with bareroot white spruce seedlings (Wang and Zwiazek 1999) the seedlings with higher carbohydrate levels produced more roots but the carbohydrate levels did not significantly affect the timing of bud burst following planting. In our study carried out with ball seedlings, however, the accumulated carbohydrates were more likely to be used for shoot growth and bud burst than for root growth.

The warming effect of the absorbed radiation energy might also be an explanation for the observed differences in the timing of bud burst between long and short day conditions (Repo et al. 1991). The possible warming effect of the absorbed radiation energy is stronger in treatments with long photoperiod than in treatments with short photoperiod. As a result, the actual temperature sum, based on the bud temperature, may be higher in long day conditions than in short day conditions during the same time period. In natural conditions during a sunny day, the temperature in the buds of Norway spruce graft may rise up to 7.5 °C above that of the air (Pukacki 1980). In the present study, a relatively low light level (approximately 200 μmol m^{-2} s^{-1}) was used in order to minimise the effects of light other than the photoperiodic signal effect. It has, however, been found earlier that light levels even below 140 μmol m^{-2} s^{-1} increase the bud temperature of Scots pine by about 2 °C compared to the surrounding air temperature (Repo et al. 1991).

The warming effect of the illumination on bud burst was possibly the largest in 18-year-old cuttings, because in this material group the differences in timing of bud burst between light treatments were the clearest. We estimated the presumed warming effect of the illumination on bud burst by using the differences in temperature sums and numbers of light hours and by supposing the physiological response of the bud to the temperature to be linear. According to our estimation the bud temperature of the 18-year-old cuttings in the shortening photoperiod should have been 10.5 °C higher during the light period than during the dark period in order to explain the results solely by the warming effect of illumination. According to the previous data, however, the bud temperature would have been elevated by 4 °C only at light level of 200 μmol m^{-2} s^{-1}. Thus, it seems that the warming effect of the absorbed radiation energy did not alone explain the observed differences in timing of bud burst between long and short day conditions.

In this study, the 18-year-old cuttings required a longer time for bud burst than the other groups (Table 1, Fig. 1). This refers to change in environmental responses of bud burst as trees get older and is in accordance with the results obtained in Norway spruce by Ununger et al. (1988). In the present study the differences in origin of the cuttings might also affect the timing of bud burst, in addition to age.

The results obtained from this study suggest that, in addition to temperature sum, the accumulated duration of the light period may promote bud burst of Norway spruce. This means that beside temperature, light conditions might also have an effect on bud burst in Norway spruce. The experiment used in this study could not, however, prove this effect unambiguously. Further studies concerning the accumulated duration of the light period and absorbed radiation energy are needed to explain the actual role of light conditions in the timing of bud burst.

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III

Bud burst in Norway spruce (*Picea abies*): Preliminary evidence for age-specific rest patterns

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Abstract

This study examines the effect of chilling and photoperiod on rest completion and bud burst in Norway spruce (*Picea abies* [L.] Karst.) using twigs from both 15-year-old (later 'young trees') and 56-year-old (later 'old trees') trees. The material was transferred between September and May from outdoors to experimental forcing conditions with four different photoperiods. The bud burst percentage of the twigs from young trees generally increased in all photoperiods until the end of the year. After that it decreased until vernal equinox (March 20) and then increased steeply towards spring. This new observation of transient rest completion during autumn suggests that young trees have (i) a transient time window during late autumn when ontogenetic development is possible and (ii) a secondary rest culminating approximately at the time of vernal equinox. In twigs from old trees the transient rest completion was much weaker as the bud burst percentages generally remained under 20 during autumn and winter. At vernal equinox there were no burst buds in twigs from the old trees in any photoperiod and after that the bud burst percentage increased basically in the same manner as in the young trees. The bud burst percentage of the twigs from young trees was generally higher the longer the photoperiod was. However, no evidence for absolute long photoperiod requirement of rest completion was observed.

Keywords: chilling, growth initiation, phenology, photoperiod, secondary rest

1. Introduction

The timing of vegetative bud burst of trees is determined by environmental factors. This response to environmental factors is under strong genetic control (e.g. Langlet 1960, Ekberg et al. 1991). Air temperature is a major environmental factor that regulates timing of bud burst. After growth cessation in autumn the vegetative buds of trees are in a state of rest, and they have no or limited ability to undergo ontogenetic development toward bud burst (Doorenbos 1953, Samish 1954). Rest break refers to the invisible physiological changes in dormant buds that lead to achievement of full growth competence, i.e. to the internal ability to develop ontogenetically toward bud burst (Romberger 1963, Weiser 1970, Kobayashi and Fuchigami 1983, Hänninen 1990). Rest is completed as a result of prolonged exposure to low chilling temperatures (e.g. –5 to +10 °C) (*chilling requirement of rest completion*, Coville 1920, Smith and Kefford 1964, Perry 1971, Flint 1974, Fuchigami et al. 1982, Cannell and Smith 1983). Bud burst takes place as a result of prolonged exposure to temperatures above a certain threshold, e.g. $T > +5$ °C (*thermal time requirement of bud burst*, Smith and Kefford 1964, Perry 1971, Fuchigami et al. 1982, Cannell 1989, 1990).

Compared to air temperature, photoperiod has been considered to have a minor effect during rest break. In experimental conditions, however, it has been observed that with several tree species long photoperiods compensate partially for the lack of chilling. This has been the case, for example, in *Picea abies* (L.) Karst. (Nienstaedt 1967, Worrall and Mergen 1967) and *Pinus sylvestris* L. (Jensen and Gatherum 1965, Hoffman and Lyr 1967). This compensation is manifested in the reduction of the thermal time requirement in partially chilled trees, but not in fully chilled ones (Myking and Heide 1995).

Beech (*Fagus sylvatica* L.), however, possesses an absolute long day requirement for rest completion, i.e. long days are required to start bud development also in the case of fully chilled trees (Wareing 1953, Falusi and Calamassi 1990, Heide 1993a). Furthermore, in some cases with other tree species it is not clear whether or not the reduction of thermal time requirement observed in long days is related to compensation of lack of chilling (Campbell and Sugano 1975, Heide 1993b). During the past few years, two different types of studies have suggested that photoperiod may have a greater influence on the timing of bud burst than merely compensating for the lack of chilling.

First, experimental studies with Norway spruce (*Picea abies*) have suggested that both direction of change of photoperiod (Partanen et al. 1998) and accumulated duration of light period (Partanen et al. 2001) affect the timing of bud burst. Second, analysis of phenological records gathered with adult individuals of several boreal tree species growing in natural conditions has suggested that rest completion takes place during mid- or late winter, i.e. considerably after the time when the chilling requirement is usually met. This was noted for Norway spruce by Hannerz (1999), who analysed bud burst of 17 spruce clones for up to seven years in field trials in Sweden. His study was carried out with rooted cuttings of chronologically old clones which were expected to correspond ecophysiologically to mature trees. A similar finding has been obtained in several recent studies where long-term historic phenological records of several boreal tree species have been analysed. This finding has led to the hypothesis that, in addition to meeting the chilling requirement, an additional clue, possibly from the light climate, is required for rest completion (Häkkinen et al. 1998, Häkkinen 1999, Linkosalo 2000a,b, Linkosalo et al. 2000). This suggestion was further supported by the unpublished findings of our small-scale experiment with twigs of four origins of approximately 70-year-old Norway spruce: despite several weeks of chilling in natural conditions, the bud burst percentage in forcing conditions was maximally 20 in twigs detached and transferred to forcing conditions during the autumn before the end of the year.

The aim of this study was to test experimentally the effect of chilling and photoperiod on rest completion and bud burst of Norway spruce (*Picea abies*). Moreover, the effect of ageing of the tree was examined using twigs from both 15-year-old (later 'young trees') and 56-year-old (later 'old trees') trees and by comparing the results with those of earlier experiments carried out with seedlings.

2. Materials and methods

2.1. Plant materials

The young trees were regenerated naturally at the Punkaharju experimental area of the Finnish Forest Research Institute (61°49'N, 29°19'E, 80 m asl) on an *Oxalis Myrtillus* type (OMT) site (Cajander 1949). The old trees originated from the seedlings produced from local seeds from the Savonlinna region at the nursery of the Punkaharju experimental area of the Finnish Forest Research Institute (61°48'N, 29°19'E, 80 m asl) in 1936 using standard nursery practices. The seedlings were four years old when they were planted out in the Punkaharju experimental area (61°48'N, 29°19'E, 90 m asl) in spring 1940 on an *Oxalis Myrtillus* type (OMT) site (Cajander 1949).

2.2. Experiment

The experiment was carried out at the Punkaharju Research Station. The twigs from both young (= 15-year-old) and old (= 56-year-old) trees were transferred in 16 batches from outdoors to forcing conditions (see below) using an interval of one to three weeks. The first samples of twigs were moved to forcing conditions on September 14, 1992 and the last samples on May 10, 1993. The air temperature was monitored in 1992 by a thermograph (model 'Fuess') and in 1993 recorded with a 'Squirrel' digital temperature logger. The winter 1992 – 93 was exceptionally mild, i.e. the daily mean temperatures dropped below –15 °C only occasionally and daily mean temperatures between –10 and –15 °C were also quite rare (Fig. 1). The experimental twigs (length about 40 cm) of both young and old trees were detached from the uppermost third of the tree crown. The average height of the young trees was approximately 3 m and the average height of the old trees approximately 25 m. After detaching, the ends of the twigs were placed into water. The twigs were kept in darkness at +10 °C for one day and their ends were placed in water before being exposed to various photoperiod treatments. The air temperature was monitored by a thermograph (model 'Fuess').

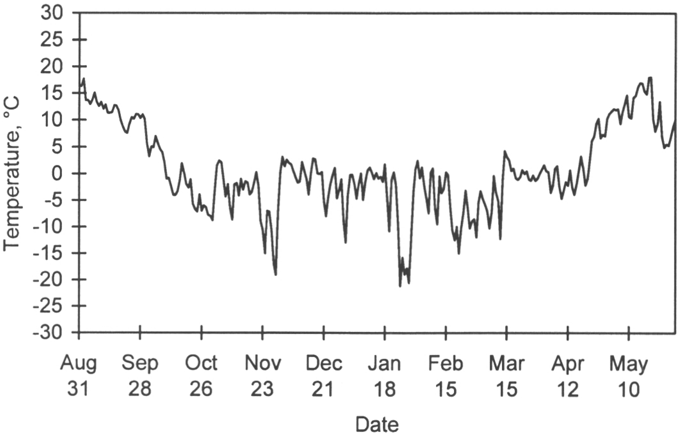


Figure 1. Average daily air temperature at Punkaharju Research Station during the experiment in 1992 – 1993.

In forcing conditions, in order to guarantee the water supply of the twigs, their ends were cut once a week and the water of the buckets was changed every other week. Constant 5-, 10-, 15- and 20-hour photoperiods were provided by using fluorescent tubes (type Sylvania F58W/154 – ST

Daylight). The air temperature was a constant +20 °C. In order to keep the temperature constant during warm periods in September and May, artificial cooling was used in the two longest (15 h and 20 h) photoperiods, where the warming effect of the fluorescent tubes was highest. The temperature was monitored by thermographs (model 'Fuess').

At each of 16 transfers, ten twigs from young trees and ten twigs from old trees were taken for each of the four experimental photoperiods. Due to practical restrictions, the following sampling procedure was applied. For *young trees*, at each transfer the 40 experimental twigs were obtained from ten experimental trees, i.e. four twigs were taken from each tree, one to each of four photoperiods. A new sub-population of ten experimental trees was used for each transfer, i.e. a total of 160 trees (16 transfers times 10 trees per transfer) were used in the experiment. In the case of *old trees*, the procedure was otherwise the same, but the same sub-population of ten trees was used in every other transfer, i.e. a total of twenty trees were used in the experiment.

The bud burst was observed visually three times a week at intervals of two or three days until either bud burst had taken place or the observed buds were visibly dead. The terminal bud of the main shoot of the twig and the terminal buds of the four uppermost collateral twigs were observed. A bud was considered to have burst if new needles were visible. The bud burst percentage was calculated as the proportion of the burst buds to the five observed buds of the twig.

2.3. Statistical methods

The effects of transfer time and photoperiod treatments on the bud burst percentages were analysed with the following statistical models and methods. The bud burst percentages of the twigs from the young trees were analysed with the ANOVA model

$$(1) \qquad \arcsin(\sqrt{p}) = m + S + T + S(T) + P + TP + \varepsilon$$

and the percentages of the twigs from the old trees with the ANOVA model

$$(2) \qquad \arcsin(\sqrt{p}) = m + S + T + ST + P + TP + \varepsilon\,.$$

In the above models

p = bud burst proportion,

T = factor of transfer time treatments (fixed),

P = factor of photoperiod treatments (fixed), and

S = factor of individual trees from which twigs were taken (random).

The inverse sine transformation was applied because some bud burst proportions equalled zero or one. The equality of effects of photoperiod treatments in each transfer were analysed with simple contrast F-tests (Model 1). The paired comparisons of equality of the transfer effects were analysed with Tukey's multiple test procedure (Model 2). The confidence limits of bud burst percentages of the twigs from young trees were calculated with the procedure for binomial proportions (Zar 1974).

3. Results

3.1. Twigs of young trees

The main effects of transfer time ($P < 0.001$) and photoperiod ($P < 0.001$) treatments on the bud burst percentage, as well as their interaction ($P < 0.001$), were highly significant. In spite of the interaction, the pattern of the effects was evident. The sine-curve-like effect of the transfer time on the bud burst percentage was explicit and similar in all treatments (Figs 2 and 3). The bud burst percentage increased, i.e. the rest was broken, from the September transfers until the end of the year from 0% to 56 – 88%, depending on the photoperiod. From the turn of the year until the transfer on March 15, the bud burst percentages decreased to 0 – 14% depending on the photoperiod. After this secondary rest development the bud burst percentage started to increase steeply, and exceeded 85% in all four photoperiods in the last two transfers of May 3 and May 10. The 95% confidence limits of the bud burst percentages confirmed the sine-curve-pattern, because in any photoperiod the confidence limits of low and high percentages did not overlap each other (Fig. 3).

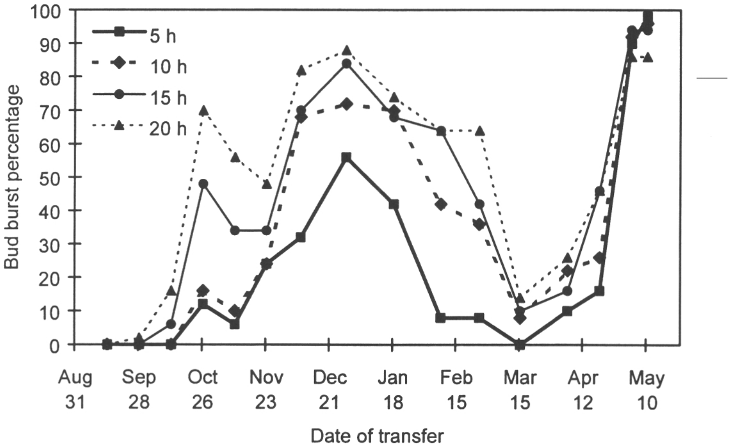


Figure 2. Bud burst percentage of twigs of 15-year old Norway spruce ('young trees') after transfer from natural conditions to forcing conditions (air temperature +20 °C, four different photoperiods).

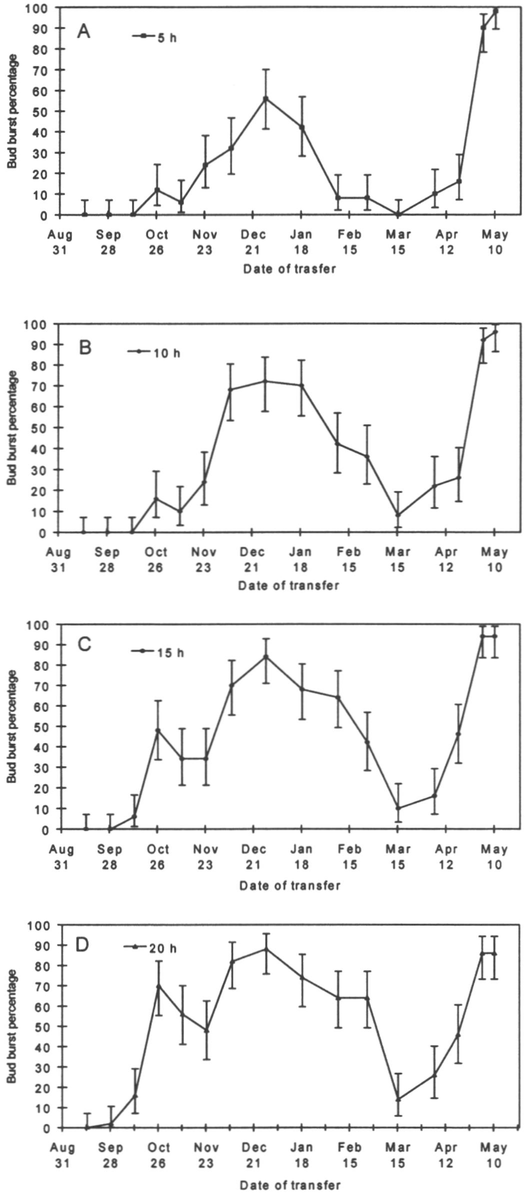


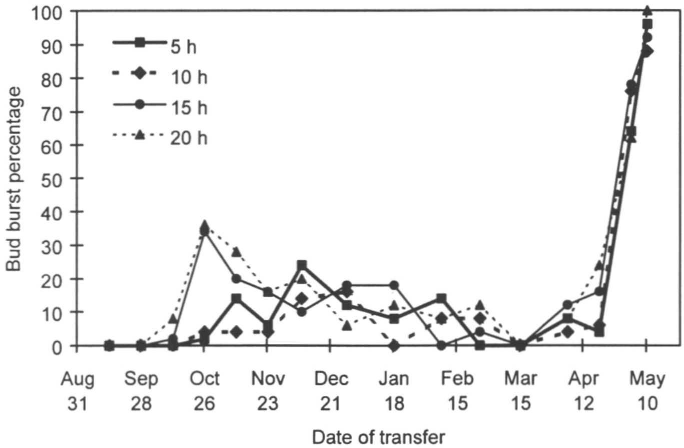
Figure 3. As Fig. 2, but with the 95% confidence limits of the bud burst percentages indicated for each of the four photoperiod treatments (A – D).

The pattern of the effect of photoperiod treatments on the bud burst percentage was also consistent in all transfers: the longer the photoperiod the higher the bud burst percentage was (Fig. 2). The differences between the photoperiod treatments were greatest, and also statistically highly significant, in the eight transfers from October 26 to February 25 ($P < 0.001$ in all transfers, except $P = 0.026$ in the November 23 transfer and $P = 0.003$ in the January 18 transfer). The photoperiod had no significant effect on the bud burst percentages close to zero (September 14, September 28, October 12, March 15 and April 5 transfers) or close to hundred (May 3 and May 10 transfers).

3.2. Twigs of old trees

The effect of the transfer time was highly significant ($P < 0.001$). However, unlike in the case of the twigs of the young trees, the interaction of the transfer time and photoperiod was not significant ($P = 0.284$). In addition, the effect of photoperiod treatments on the bud burst percentages was not significant ($P = 0.126$) when the exceptional October 26 transfer was excluded. Thus, the bud burst percentage of the twigs from the old trees depended significantly only on the transfer time.

Figure 4. Bud burst percentage of twigs of 56-year old Norway spruce ('old trees') after transfer from natural conditions to forcing conditions (air temperature +20 °C, four different photoperiods).



As in the twigs of the young trees, the effect of transfer time on old trees had a sine-curve-type rest pattern, but the pattern was much weaker (Figs 2 and 4). The bud burst percentage occasionally increased to above 20 up to the end of the year, and then decreased again to zero in the March 15 transfer (Fig. 4). After this, as in the case of twigs of young trees, the bud burst percentage increased steeply. The secondary rest pattern, although weak, was statistically significant since the zero bud burst percentages (September 14, September 28 and March 15 transfers) all differed from the percentages in the transfers of October 26, November 9 and December 8 ($P = 0.001$, 0.016 and 0.009, respectively). In addition, the effects of last two transfers (May 3 and May 10 transfers), in which the bud burst percentages were 62 – 100%, differed from all others ($P < 0.001$).

4. Discussion

4.1. Methodological considerations

All the classes of hormonal growth regulators (e.g. auxins, gibberellins, abscisic acid and cytokinins), except ethylene, apparently move long distances in plants. For example, Doumas et al. (1986) have detected in Douglas fir that cytokinins are carried from roots in xylem sap and accumulate in vegetative shoots before and during bud burst. Control of bud rest, however, seems to be very complex and involves the interactive effect of several growth hormones and other compounds. Moreover, the physiological significance of long-distance transport is not clear, because hormonal growth regulators can be synthesized in all the organs of plants (Kozlowski and Pallardy 1997).

In order to study experimentally the effect of chilling and photoperiod on bud burst in adult trees, twigs had to be used in the experiment because it is not possible to transfer whole trees to the forcing conditions. Using twigs, however, implied that the connection from the roots to the twigs was broken. In other words, the possible growth regulators which are transported from the roots to the twigs and which control the release of bud rest were not available. Should the breaking of the root – shoot connection have affected the results, then it should have been visible as the prevention of any photoperiodic effect caused by the experimental long photoperiod of 20 h (and possibly also 15 h) or as the prevention of any transfer time effect in forcing conditions. On the contrary, it is hard to find any mechanism that would explain how the breaking could have artificially caused the clear sine-curve-like effect with twigs of young trees (Figs 2 and 3) and the less clear effect with the twigs from old trees (Fig. 4).

Despite all the precautions taken in sampling and forcing the experimental twigs (see Material and Methods), it is possible that the methodology applied disturbed the water economy of the twigs, as they were transferred from outdoors to forcing conditions. The winter 1992 – 1993 in Punkaharju was, however, milder than on average. The average daily temperature was over

–15 °C except on November 29 and between January 25 and January 29, and it was slightly under –20 °C only on January 25 and January 29 (Fig. 1). Furthermore, every month there were a few days during which the average daily temperature was over 0 °C. There was a period of slightly colder weather in late February and early March, but even then the average daily temperature was under –10 °C only during a few days (Fig. 1). Thus, with respect to the temperature conditions, the twigs were not exceptionally stressed during the winter. In addition, the buds of the twigs from the old trees were alive in forcing conditions generally over one month, and those of the twigs from the young trees over one and a half months (data not shown). In the samples where it occurred, bud burst took place generally well before the remaining unburst buds in the sample started to die. Thus, even if these buds had not died, it is unlikely that they would have burst. Therefore, the death of these buds obviously had no significant effect on the bud burst percentages. Furthermore, the bud burst percentages (Figs 2 and 4) did not correlate with the air temperature at the time of sampling. Thus in conclusion, it is improbable that the clear sine-curve-like effect with the twigs of young trees (Figs 2 and 3) and the less clear effect with the twigs from old trees (Fig. 4) were artificially caused by problems in the water economy of the twigs.

4.2. Comparison with earlier studies

Earlier studies concerning the effect of chilling and photoperiod on rest break and bud burst in Norway spruce have been carried out using young seedlings (e.g. Nienstaedt 1967, Hänninen and Pelkonen 1988a,b, 1989, Hänninen 1990). In these studies rest break was caused by chilling, rest completion took place during autumn, and no secondary rest was found. When combined with these earlier results our findings suggest that as trees get older the environmental regulation of rest completion and bud burst changes. Earlier Ununger et al. (1988) and Partanen et al. (2001) have observed with seedlings and rooted cuttings of Norway spruce that the older plant materials required a longer time for bud burst than the younger materials.

In the present study, the buds of the twigs from old Norway spruce started to burst actively in spring only after vernal equinox. These results are in accordance with the results of Hannerz (1999), who tested different simulation models of bud burst with chronologically old rooted cuttings of Norway spruce growing in field trials in Sweden. In his study, models assuming that rest completion takes place on a fixed date during spring were more accurate than models where rest completion was modelled to depend on the accumulation of chilling. Similar findings have been obtained in several recent studies where long-term historic phenological records of adult trees of several boreal tree species have been analysed (Häkkinen et al. 1998, Häkkinen 1999, Linkosalo 2000a,b, Linkosalo et al. 2000). Thus, both the results of the present and the earlier studies suggest that rest completion takes place during mid- or late winter, i.e. considerably after the time when the chilling requirement is usually met.

The transient rest completion observed during late autumn with young trees (Figs 2 and 3) is also in agreement with the results of Häkkinen et al. (1998), Hannerz (1999), Häkkinen (1999), Linkosalo (2000a,b) and Linkosalo et al. (2000). Suppose that a similar transient rest completion occurred in some of the tree populations in the phenological records examined in these studies; in that case, the transient rest completion did not manifest itself in the phenological records, since the thermal time accumulation is minimal in natural conditions during the transient rest completion. Thus, the trees passed through a time window when they would have been able to undergo ontogenetic development, but due to the lack of high temperatures they entered the secondary rest without any substantial ontogenetic development. Ontogenetic development started only during spring, when the trees completed rest for the second time. Thus, models taking this time instant as a starting point for accumulating thermal time were more accurate in their predictions of timing of bud burst than models assuming earlier rest completion as a result of meeting the chilling requirement (Häkkinen et al. 1998, Hannerz 1999, Häkkinen 1999, Linkosalo 2000a,b, Linkosalo et al. 2000).

According to the hypothesis put forward by Häkkinen et al. (1998), Häkkinen (1999), Linkosalo (2000a,b) and Linkosalo et al. (2000), rest completion requires, in addition to meeting the chilling requirement, an additional clue. It may come from light climate (e.g. critical night length, light intensity, light spectrum, shortening night), but it can also be some other environmental factor, or interaction of several factors. In the present study, the experimental long photoperiods did not generally cause bud burst of the twigs during the early part of the year (Figs 2, 3 and 4). Accordingly, it seems evident that photoperiod alone at least does not comprise the additional clue required for rest completion. However, if the additional clue is mediated by substances originating from the roots, then its manifestation was prevented in the present study by detaching the twigs from the trees before the twigs were exposed to the experimental long photoperiods. Thus, our results do not provide conclusive falsification of the hypothesis of an absolute long photoperiod requirement of rest completion.

In this study, the bud burst percentages of the twigs from young (= 15-year-old) trees were generally higher in the long photoperiods (20 h and 15 h) than in the short (5 h and 10 h) photoperiods. This is in accordance with earlier studies. Worrall and Mergen (1967), using rooted Norway spruce cuttings, and Nienstaedt (1967), using Norway spruce seedlings, have detected that long photoperiod promotes bud burst by compensating partially for lack of chilling and that short photoperiods do not prevent bud burst of fully chilled trees. In a study by Partanen et al. (2001) the accumulated duration of the light period seemed to promote bud burst of Norway spruce rooted cuttings and seedlings, which is in accordance with the results obtained using twigs from young trees in the present study. However, in our study an age-specific pattern also in photoperiodic response was detected; the photoperiod did not affect the bud burst percentage of old trees.

4.3. Concluding remarks

Four conclusions arise from our study. First, our results show that as trees get older the environmental regulation of rest completion and bud burst changes. This conclusion is in agreement with several earlier studies. Second, our results suggest that rest completion in adult Norway spruces growing in natural stands does not take place until late winter. This suggestion is in agreement with a new developing theory recently discussed in the field. Third, our results suggest that young Norway spruces have a transient rest completion during late autumn and a secondary rest culminating approximately at the time of vernal equinox. This finding is completely new and as such the most important one in the present study. Due to the limited data and potential problems involved in the experimental method applied, however, this conclusion is only preliminary at this stage. Finally, no evidence for an absolute long photoperiod requirement of rest completion was observed.

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IV

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Effects of Photoperiod and Thermal Time on the Growth Rhythm of *Pinus sylvestris* Seedlings

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The effects of photoperiod and thermal time and their interaction on the timing of growth cessation were examined in seedlings of Scots pine (*Pinus sylvestris* L.) in greenhouses with 20°C day and 10°C night temperatures combined with the natural development of the photoperiod. Sowing was repeated five times during both 1995 and 1996 using origins from different altitudes and latitudes (> 60°N) in Sweden and Finland. In this way, gradients in temperature sums at a nearly constant photoperiod and different photoperiods at constant temperature sums were obtained. After the first growing season the timing of growth cessation of seedlings from different origins was flexible, i.e. it was determined by the specific combinations of accumulated temperature sum and night length illustrated by fitted straight lines. The photoperiod at the site of origin was a dominant factor in determining the timing of growth cessation in origins from northern latitudes. Because of predetermined growth, the sowing date did not affect the phenology during the second growing season. *Key words: climatic adaptation, growth cessation, phenology, photoperiod, Scots pine, temperature.*

INTRODUCTION

In cool and temperate regions the timing of growth cessation is an essential aspect of climatic adaptation of trees. Because winter temperatures often fall far below 0°C, only genotypes that manage to acquire adequate frost resistance before the onset of winter are able to survive. The phenological behaviour of trees indicates that they are able to respond to seasonal changes in environmental factors controlling growth processes. Photoperiod and temperature are the main environmental factors controlling phenological behaviour of trees in cool and temperate regions.

To project the timing of growth cessation of forest trees, at least three timing models have been presented. The first model is based on regulation through temperature sum accumulation (Sarvas 1972) and can be traced back to Réaumur (1735) and Linsser (1867). The second model is based on signals received from the critical photoperiod (night length) (e.g. Wareing 1950*a*,*b*, Vaartaja 1959, Heide 1974, Ekberg et al. 1979, Junttila & Kaurin 1985). This photoperiodic optimum shows a clinal variation with latitude. In a third model the timing of growth cessation is regulated jointly by temperature sum accumulation and photoperiod (Koski & Selkäinaho 1982, Koski & Sievänen 1985, Paus et al. 1986). Fuchigami et al. (1982) suggested a similar model with an increasing photoperiodic impact as the growing season progresses.

The existence of clines in photoperiodic response in Scots pine (*Pinus sylvestris* L.) has been revealed in several studies (Langlet 1959, Persson & Beuker 1997). Others, such as Vaartaja (1954), Wassink & Wiersma (1955) and Oleksyn et al. (1992), divide Scots pine into different ecotypes. Oleksyn et al. (1992) found that under different photoperiod conditions, i.e. those of 50° and 60°N, and similar temperature conditions, northern (> 55°N) and central (54–48°N) populations of Scots pine clearly behave differently. No single mechanism of height growth cessation could explain the response of all 24 European populations of 1-yr-old seedlings of Scots pine used in the study by Oleksyn et al. (1992). Even within an individual population a mechanism based solely on photoperiod could not explain their growth cessation. Northern populations responded to a combination of increasing night length and accumulated temperature sum according to a model by Koski & Sievänen (1985). Central and southern populations did not respond to increased night length. The study by Oleksyn et al. (1992) thus confirmed earlier studies claiming that timing of growth cessation is regulated by both genotypic and environmental (photoperiodic) control.

To distinguish between effects of temperature and photoperiod and their interactions on the growth and yield of Scots pine provenances, Persson & Beuker

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(1997) carried out studies where both the sites and the provenances were distributed over large altitudinal and latitudinal ranges. When the temperature sum did not change, effects of latitudinal transfer were not detected. This suggests that latitudinal transfers without changes in temperature sum do not affect the performance of the populations.

Successful geographic transfers of trees have shown that many species are capable of adjusting their annual rhythm (Beuker 1996). The combined regulation of growth cessation by temperature and photoperiod has been studied extensively (e.g. Doorenbos 1953, Samish 1954, Wareing 1956, 1969, Nitsch 1957*a*,*b*, Vaartaja 1959, Romberger 1963, Vegis 1964, Perry 1971, Kramer 1995). However, the regulation system of growth cessation has still not been fully revealed. A better knowledge of this regulation system may be crucially important to the existence of northern forests, especially as it has been predicted that winters will become essentially milder in the near future as a result of the greenhouse effect (e.g. Michell & Zeng 1990).

The results of the previous studies led to the hypothesis that the responses of trees to temperature and photoperiod have separate genetic controls. The combination of these two factors needed for the occurrence of a specific action during the annual cycle depends on the environment to which the tree is adapted.

The aims of the present study were: (1) to test the hypothesis that the responses of Scots pine seedlings to temperature and photoperiod in growth cessation have separate genetic controls and (2) to test the effect of the photoperiodic conditions on the annual rhythm of the first and second growing seasons when different sowing dates are used.

MATERIALS AND METHODS

Experiments

The experimental material comprised 10 Scots pine (*Pinus sylvestris* L.) origins from regions with different light and temperature conditions, of which three were from Finland and seven from Sweden (Table 1). By using origins from different altitudes and latitudes gradients in temperature sums with nearly constant photoperiod and different photoperiods at constant temperature sum were obtained.

A set of treatments repeated at certain time intervals in a consistent temperature regime combined with the natural development of the photoperiod provides a functional tool for testing the flexibility of growth cessation by observing the reactions of genetically similar material to various combinations of temperature sum accumulations and photoperiodic changes.

The experiments were conducted in greenhouses at the Punkaharju Research Station (61°48′N, 29°19′E) and the Ruotsinkylä Field Station (60°21′N, 24°56′E) of the Finnish Forest Research Institute during 1995, 1996 and 1997. The temperature in the greenhouses varied between 20°C (16 h during the day) and 10°C (8 h during the night). From June until the end of August during warm and sunny periods with warm nights, however, the temperature was up to 7°C higher, because no artificial cooling was available. Temperature data were recorded hourly. The accumulated temperature sum until time of growth cessation was calculated as the daily mean effective temperature sum (5°C threshold) in degree days (dd). For the first growing season, the accumulated temperature sums were calculated from the date of sowing. The total accumulated temperature sum in the greenhouse calculated from the first sowing was 1890 dd in Punkaharju in 1995 and 1822 dd in 1996. In Ruotsinkylä the corresponding figures were 1880 dd and 1810 dd.

Natural light penetrating the glass provided the only illumination. The night length for the date of growth cessation was given by the time interval between sunset and sunrise. The night length of Jyväskylä (62°13′N, 25°44′E) was used for Punkaharju and the night length of Helsinki (60°10′N, 24°57′E)

Table 1. *Average temperature sums of the growing season in the regions of origin of the Scots pine used in the study*

Origin number	Country	Latitude (°N)	Altitude (m)	Temperature sum (>5°C, dd)
1	Sweden	62°30′	300	785
2	Sweden	63°00′	300	936
3	Sweden	62°30′	400	875
4	Sweden	61°30′	200	1084
5	Sweden	61°00′	500	871
6	Sweden	62°30′	300	965
7	Sweden	65°30′	0–100	1035
8	Finland	60°02′	30	1330
9	Finland	62°49′	180	1057
10	Finland	69°16′	250	607

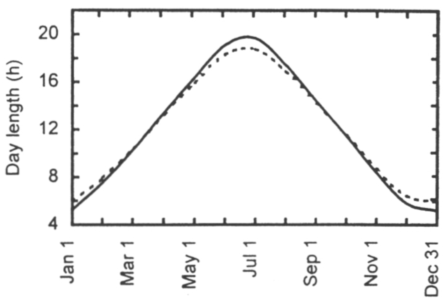

Fig. 1. Annual fluctuation in photoperiod at the latitudes of Jyväskylä (—; 62°13′N, 25°44′E) and Helsinki (----; 60°10′N, 24°57′E).

was used for Ruotsinkylä (Fig. 1). Both were as determined by the University of Helsinki (Anon. 1994, 1995).

The seedlings were raised in plastic trays of 45 cells filled with fertilized peat; no extra fertilization was carried out. The size of the cell was 5.0 × 5.4 × 10 cm (depth). Seeds from each origin were sown into 20 cells. Because the conditions in the greenhouse were assumed to be homogeneous, seeds of two successive sowing dates from each origin were sown into one tray. The peat substrate was watered manually. Sowing was repeated five times during both 1995 and 1996 (Table 2). The intention was to grow 20 seedlings per origin, 10 of which were chosen for the experiments. However, because of the low germinative capacity of some origins this did not always succeed.

In October, 2 weeks before the seedlings were moved outside (1 week in Ruotsinkylä in 1995), the temperature in the greenhouses was decreased to 5°C in order to attain winter-hardiness. The seedlings were removed from the greenhouse in 1995 on 30 October and in 1996 on 28 October. The seedlings overwintered under natural snow coverage. A protective net was used against voles. A survival inventory was made in spring, before the second growing season. The effects of the first growing season on the growth rhythm of the seedlings during the second growing season were studied by experiments under the same greenhouse conditions as in the first growing season. In 1996 the seedlings were transferred into the greenhouse on 21 May and in 1997 on 20 May.

Measurements and calculations

The total height of 10 seedlings in each batch was measured once a week until the height of the seedlings including the height of the terminal bud remained unchanged for at least 3 weeks. The height measurements were started 4 weeks after sowing. The timing of formation of the terminal bud was observed once a week at the same time as the height measurements were made. The terminal bud was considered to be developed when it was clearly visible.

The development of secondary needles during the spring of the second growing season was observed three times a week. The secondary needles were considered to be developed when the greenish tops had become visible. In addition, during the second growing season the total height of the seedlings and the formation of the terminal buds were determined once a week.

Growth cessation was defined as the instant at which 95% of the height growth of the seedlings had been achieved. The formation of terminal buds during the first and second growing seasons was defined as the instant when 50% of the plants had set buds. Development of the secondary needles during the second growing season was defined as the instant when 50% of the plants had formed secondary needles.

The data were subjected to analysis of variance (GLM). The effects of experimental year, location of the experimental site and their interaction after the first growing season were tested by using the following variables: average date, average temperature sum

Table 2. *Night lengths at the sowing dates*

		Sowing number				
Site	Year	1	2	3	4	5
Punkaharju	1995	June 1/4.90[a]	June 15/4.22	June 29/4.25	July 13/4.97	July 27/6.12
	1996	May 30/4.98	June 13/4.25	June 27/4.22	July 11/4.88	July 25/6.00
Ruotsinkylä	1995	June 1/5.68	June 15/5.13	June 29/5.15	July 13/5.73	July 27/6.70
	1996	May 30/5.75	June 13/5.15	June 27/5.13	July 11/5.67	July 25/6.60

[a] Sowing date/night length.

and average night length at the time of growth cessation. For the data of the first growing season accumulated temperature sum was used as the variable in analysing the differences between sowing dates with regard to timing of terminal bud formation and timing of growth cessation. The variance between the sowing dates in timing of formation of secondary needles, terminal bud formation and growth cessation during the second growing season was also analysed by using accumulated temperature sum as the variable.

For individual origin and sowing date, the means of the accumulated temperature sum at the time of growth cessation and of the corresponding night length were plotted for each experimental year and site. The relationship between these factors was estimated by breaking the natural correlation between them, using the method presented by Lappi & Sievänen (1993). According to them, the relationship between night length and accumulated temperature sum at the time of growth cessation is symmetrical and thus cannot be analysed in terms of dependent and independent variables. The problem lies in the special case of estimating the functional linear relationship: as the values of both of these variables fall only on a predetermined curve, the random errors of these values are functionally related. The maximum likelihood estimates for the basic model are derived from this functional relationship of the random errors. By using this method, the growth cessation lines were fitted separately for each of the 10 origins.

In order to test the differences in timing of growth cessation between the individual origins, the differences in the parameters of the fitted growth cessation lines of origins with similar photoperiod or temperature sum were tested using the natural logarithm of the likelihood function (Lappi & Sievänen 1993). The test equation was:

$$\chi^2 = n(L - L_1 - L_n) \qquad (1)$$

where $n =$ number of tested origins and $L =$ likelihood for all the tested origins. Three degrees of freedom, i.e. the number of tested parameters, were used in this test.

The intercept parameters (for night lengths) of the fitted growth cessation lines were calculated at the instant when the accumulated temperature sum was 1100 dd. This temperature sum was selected because it was approximately the mid-value of the accumulated temperature sum at the time of growth cessation for the whole experimental material. In order to obtain information about the significance of the predictor, i.e. how much of the variation can be explained by photoperiod and temperature sum separately and together, the intercept parameters were subjected to simple and multiple linear regression analysis. The dependent variables used in these analyses were latitude and temperature sum for the sites of the origins.

RESULTS

The timing of growth cessation in the first year was flexible with respect to photoperiod and thermal time, i.e. there was neither a fixed photoperiod nor a certain temperature sum which coincided with growth cessation (Tables 3 and 4). The variation among experimental sites and year at each entry was conspicuous (Table 5). The growth of the first-year seedlings did not cease at the same time in Punkaharju as in Ruotsinkylä. In the first-year seedlings the average growth period over sowing times was also different in 1995 to that in 1996. Both the average night length and the average accumulated temperature sum at time of growth cessation were different in these two years.

In the first growing season seedlings from the first sowings required a greater temperature sum for growth cessation and for formation of terminal buds than seedlings from the later sowings (Table 4, Fig. 6). Analysis of variance also showed significant differences between sowing dates ($p < 0.001$).

The difference in timing of growth cessation between the most northern and the most southern origin was clear. The seedlings of the most northern origin (10) ceased to grow first and the seedlings from the most southern origin (8) last (Fig. 2). The parameters of the fitted growth cessation lines of these origins differed significantly ($p < 0.001$) from each other.

Origins 1, 3, 6 and 9 have the same photoperiod. However, the temperature sums of their sites are clearly different, ranging from 785 to 1057 dd. In spite of this difference, the average timing of growth cessation for all these origins was almost the same (Fig. 3). The parameters of the fitted growth cessation lines of these origins did not differ from each other ($p > 0.1$).

Origins 2, 4, 5 and 7 have nearly similar temperature sums at their sites of origin. However, the photoperiods of these origins are clearly different, ranging from 61°00′N to 65°30′N. In spite of small differences in photoperiod and temperature sums, the

Table 3. *Average number of days from sowing to growth cessation and terminal bud formation in first growing season*

			Origin number									
Sowing number	Year	Site	1	2	3	4	5	6	7	8	9	10
			Days to growth cessation									
1	1995	Punkaharju	95	100	99	94	93	100	92	95	93	88
		Ruotsinkylä	88	95	96	95	97	96	91	98	93	87
	1996	Punkaharju	103	101	97	98	101	95	93	104	94	103
		Ruotsinkylä	98	98	103	108	111	106	100	111	102	100
2	1995	Punkaharju	91	97	94	95	88	95	94	90	82	75
		Ruotsinkylä	83	84	84	88	86	83	81	96	84	81
	1996	Punkaharju	91	91	92	92	86	94	94	97	88	94
		Ruotsinkylä	92	95	91	105	98	98	91	102	95	86
3	1995	Punkaharju	81	78	82	82	83	80	77	87	83	65
		Ruotsinkylä	71	78	75	80	78	77	76	86	79	70
	1996	Punkaharju	85	88	89	84	84	86	86	86	81	82
		Ruotsinkylä	87	86	86	89	96	89	88	92	85	88
4	1995	Punkaharju	71	70	73	74	73	69	64	74	73	56
		Ruotsinkylä	71	69	74	73	72	69	68	78	71	59
	1996	Punkaharju	84	80	69	71	69	73	66	75	71	73
		Ruotsinkylä	80	85	77	83	85	87	76	88	79	74
5	1995	Punkaharju	58	62	60	59	61	62	56	62	62	58
		Ruotsinkylä	61	64	70	72	68	68	57	69	63	36
	1996	Punkaharju	62	64	62	62	62	61	67	65	59	61
		Ruotsinkylä	72	74	73	74	70	67	62	77	74	64
			Days to bud formation									
1	1995	Punkaharju	93	96	96	95	97	95	87	101	99	82
		Ruotsinkylä	91	91	94	95	96	93	88	101	95	88
	1996	Punkaharju	104	105	100	105	110	100	94	119	100	89
		Ruotsinkylä	96	97	94	107	103	101	94	115	96	87
2	1995	Punkaharju	88	94	91	97	89	89	91	103	89	80
		Ruotsinkylä	88	86	85	91	87	85	81	97	87	85
	1996	Punkaharju	97	95	96	105	94	94	87	108	96	86
		Ruotsinkylä	92	98	98	106	98	98	82	109	96	81
3	1995	Punkaharju	84	83	82	88	87	84	77	91	84	73
		Ruotsinkylä	73	77	77	82	80	79	81	91	84	83
	1996	Punkaharju	97	96	96	99	98	98	96	109	94	88
		Ruotsinkylä	90	87	88	97	91	88	87	103	89	84
4	1995	Punkaharju	82	82	81	87	77	80	75		78	
		Ruotsinkylä	76	77	76	77	79	74	81	85	76	
	1996	Punkaharju	97	95		91		90	93			
		Ruotsinkylä		89	86	92	97	92			84	
5	1995	Punkaharju										
		Ruotsinkylä			87	86	86	83		85	86	
	1996	Punkaharju										
		Ruotsinkylä		88								

growth of origins 2, 4 and 5 all ceased at about the same time and clearly later than the growth of origin 7 (Fig. 4). The parameters of the fitted growth cessation lines of these origins differed significantly ($p < 0.01$) from each other, owing to origin 7.

The linear regression between the latitude of the site of the origins and the intercept parameters that determine the level of the fitted growth cessation lines when the accumulated temperature sum is 1100 dd was significant ($p < 0.001$). The latitude of the site of the origins accounted for 89.6% of the variability (Fig. 5A). The regression between the temperature sum of the site of the origins and the intercept parameters of the growth cessation lines was significant ($p < 0.05$). The temperature sum of the site of the origins accounted for only 54.0% of the variability (Fig. 5B). With the multiple regression model latitude was a significant predictor ($p < 0.001$) for the level of the fitted growth cessation line, whereas temperature sum was not a significant predictor ($p > 0.1$).

Some seedlings originating from the fourth and especially the fifth sowing had not formed all terminal buds by the time they were moved out after the first growing season (Table 3). After winter 1995–1996 in Ruotsinkylä, the average survival of the seedlings from the fourth sowing was 17% and from the fifth sowing only 10%. This was caused by

Table 4. *Average temperature sums and night lengths at the time of growth cessation in the first growing season*

			Origin number									
Sowing number	Year	Site	1	2	3	4	5	6	7	8	9	10
			Accumulated temperature sum									
1	1995	Punkaharju	1363	1427	1420	1359	1339	1431	1322	1375	1340	1270
		Ruotsinkylä	1264	1358	1374	1361	1377	1374	1300	1392	1334	1250
	1996	Punkaharju	1411	1395	1339	1355	1383	1314	1294	1425	1302	1379
		Ruotsinkylä	1282	1291	1348	1395	1433	1373	1306	1437	1335	1296
2	1995	Punkaharju	1258	1326	1298	1304	1227	1306	1300	1250	1140	1053
		Ruotsinkylä	1154	1168	1168	1220	1200	1161	1132	1317	1171	1126
	1996	Punkaharju	1243	1235	1247	1248	1177	1267	1263	1306	1207	1239
		Ruotsinkylä	1198	1233	1181	1344	1266	1260	1183	1312	1227	1128
3	1995	Punkaharju	1101	1067	1115	1112	1123	1085	1056	1165	1126	898
		Ruotsinkylä	967	1058	1021	1081	1068	1054	1030	1150	1071	963
	1996	Punkaharju	1149	1182	1197	1138	1144	1160	1157	1166	1108	1091
		Ruotsinkylä	1140	1115	1113	1149	1222	1143	1134	1185	1110	1140
4	1995	Punkaharju	961	957	981	998	988	939	886	995	987	778
		Ruotsinkylä	942	916	975	958	953	912	907	1013	938	798
	1996	Punkaharju	1102	1060	942	966	936	986	908	1010	967	981
		Ruotsinkylä	1056	1073	983	1046	1076	1093	976	1107	1011	953
5	1995	Punkaharju	783	818	799	795	817	826	756	823	819	775
		Ruotsinkylä	795	833	897	916	870	875	754	880	811	493
	1996	Punkaharju	838	856	838	835	837	819	890	870	807	808
		Ruotsinkylä	957	928	917	920	881	854	795	955	926	814
			Night length									
1	1995	Punkaharju	9.9	10.4	10.3	9.8	9.7	10.4	9.6	9.9	9.7	9.2
		Ruotsinkylä	9.4	10.1	10.2	10.1	10.2	10.2	9.7	10.3	9.9	9.3
	1996	Punkaharju	10.6	10.4	9.9	10.1	10.3	9.8	9.6	10.7	9.7	10.5
		Ruotsinkylä	10.2	10.2	10.7	11.1	11.4	10.9	10.4	11.4	10.6	10.3
2	1995	Punkaharju	10.8	10.8	11.2	11.2	10.6	11.3	11.2	10.8	9.9	9.3
		Ruotsinkylä	10.2	10.9	10.3	10.6	10.5	10.2	10.0	11.4	10.3	10.0
	1996	Punkaharju	10.8	11.3	10.8	10.8	10.2	11.0	11.0	11.4	10.5	11.1
		Ruotsinkylä	10.9	10.4	10.8	12.1	11.5	11.4	10.8	11.9	11.2	10.4
3	1995	Punkaharju	11.3	11.5	11.4	11.4	11.5	11.1	10.9	11.8	11.5	9.7
		Ruotsinkylä	10.4	11.7	10.7	11.2	11.1	11.0	10.8	11.7	11.1	10.4
	1996	Punkaharju	11.5	11.6	12.0	11.4	11.5	11.6	11.6	11.7	11.1	11.3
		Ruotsinkylä	11.7	11.6	11.6	11.9	12.6	11.9	11.8	12.2	11.6	11.9
4	1995	Punkaharju	11.6	12.8	11.8	12.0	11.9	11.4	11.0	11.9	11.9	10.1
		Ruotsinkylä	11.6	12.4	11.9	11.7	11.7	11.4	11.3	12.2	11.6	10.5
	1996	Punkaharju	12.8	11.8	11.3	11.6	11.3	11.8	11.0	12.0	11.6	11.7
		Ruotsinkylä	12.4	12.0	12.1	12.6	12.9	13.0	12.0	13.1	12.3	11.8
5	1995	Punkaharju	11.8	12.0	11.9	11.9	12.1	12.2	11.5	12.2	12.1	11.7
		Ruotsinkylä	12.0	12.9	12.9	13.1	12.7	12.7	11.7	12.7	12.2	9.8
	1996	Punkaharju	12.0	12.2	12.1	12.0	12.0	11.9	12.6	12.4	11.8	11.9
		Ruotsinkylä	12.9	13.1	13.0	13.1	12.7	12.5	12.0	13.4	13.1	12.2

Table 5. *Analysis of variance of timing of growth cessation after the first growing season*

Source of variation	df	SS	*F*-Ratio	$p>F$
Date of growth cessation				
Experimental year	1	16 598.49	114.31	0.0001
Experimental site	1	2 430.36	16.74	0.0001
Interaction year × site	1	5 340.47	36.78	0.0001
Temperature sum at the time of growth cessation				
Experimental year	1	897 286.23	20.86	0.0001
Experimental site	1	271.78	0.01	0.9366
Interaction year × site	1	157 810.67	3.67	0.0556
Night length at the time of growth cessation				
Experimental year	1	129.25	100.18	0.0001
Experimental site	1	34.90	27.11	0.0001
Interaction year × site	1	40.97	31.76	0.0001

df: degrees of freedom; SS: sum of squares.

dieback and canker fungus of pines [*Ascocalyx abietina* (Lagerb.)]. The other cases showed that even the latest sowing date at the end of July generally gave the seedlings sufficient time for winter hardening. In winter 1995–1996 in Punkaharju voles destroyed 20% and in 1996–1997 in Ruotsinkylä 62% of the material despite a protective net.

There seemed to be no major differences between the seedlings from different sowing dates in the formation of secondary needles in the second year (Fig. 6). Analysis of variance, however, showed significant differences ($p < 0.001$) in formation of secondary needles between different sowing dates.

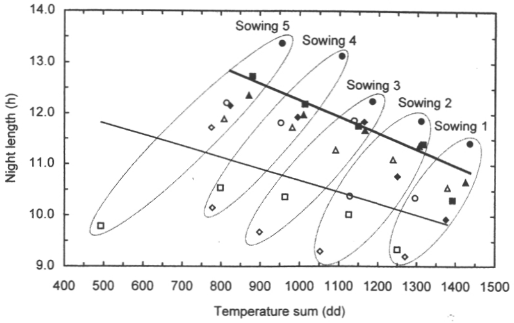

Fig. 2. Average timing of growth cessation after the first growing season in terms of temperature sum and night length in Punkaharju in 1995 (◆) and 1996 (▲), and in Ruotsinkylä in 1995 (■) and 1996 (●) for origins 8 (▬ 60°02′N, 1330 dd) and 10 (—; 69°16′N, 607 dd). Origin 8 is indicated with closed symbols and origin 10 with open symbols. Actual numbers are presented in Table 4.

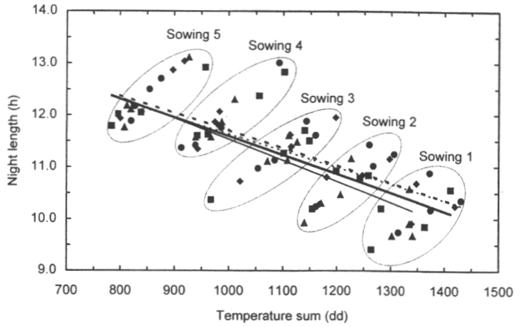

Fig. 3. Average timing of growth cessation after the first growing season in terms of temperature sum in two experimental sites and years for origins 1 (■ — 62°30′N, 785 dd), 9 (▲ —; 62°49′N, 1057 dd), 3 (◆ ---; 62°30′N, 875 dd) and 6 (●---; 62°30′N, 965 dd). Actual numbers are presented in Table 4.

The timing of the terminal buds in the second growing season occurred slightly earlier in seedlings from the first sowing dates than in seedlings from the later sowing dates (Fig. 6). Analysis of variance also showed significant differences between sowing dates ($p < 0.001$). The termination of shoot elongation took place clearly later in the later sowings than in the first sowings. The last two sowings needed a temperature sum average of 400 dd more than the first two sowings (Fig. 6). Analysis of variance showed significant differences ($p < 0.001$) in termination of shoot elongation between different sowing dates. The correlation between bud set and cessation of shoot growth in the second growing season was not statistically significant ($p > 0.1$), with a correlation coefficient of 0.011.

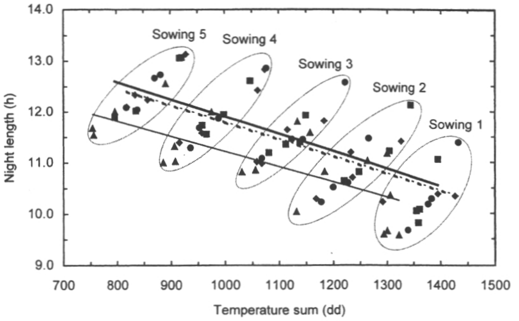

Fig. 4. Average timing of growth cessation after the first growing season in terms of temperature sum in two experimental sites and years for origins 4 (■ — 61°30′N, 1084 dd), 7 (▲ —; 65°30′N, 1035 dd), 2 (◆ ---; 63°00′N, 936 dd) and 5 (● ---; 61°00′N, 871 dd). Actual numbers are presented in Table 4.

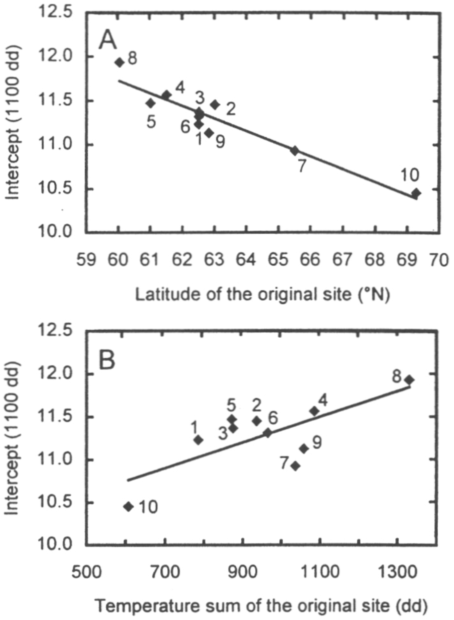

Fig. 5. Linear regression between (A) the latitude and (B) the temperature sum of the original sites of the origins and the intercept parameters of the fitted growth cessation lines at the instant when the accumulated temperature sum is 1100 dd. r^2, the coefficient of determination, is 0.896 in (A) and 0.540 in (B).

DISCUSSION

In this study a relationship between temperature sum and night length at the time of growth cessation of 1-yr Scots pine seedlings was consistently observed. This further confirms the flexibility of the growth cessation. The main reason for the differences in timing of growth cessation between experimental sites was presumably the difference in photoperiod between the sites. The experimental conditions between the two years were also dissimilar. In particular, temperature conditions differed. Hot summer seasons caused a rise in temperature sum accumulation in greenhouses, because no artificial cooling was available. In 1995 the average accumulated temperature sum in the greenhouse calculated from the first sowing was in Punkaharju 68 dd and in Ruotsinkylä 70 dd greater than in 1996. The inconsistency of thermal time versus photoperiod combinations from year to year and from one test site to another reveals that some other environmental factors must also be involved. As the deviations seem to be rather random, a minor heterogeneity in growing medium and water supply might be a source of error.

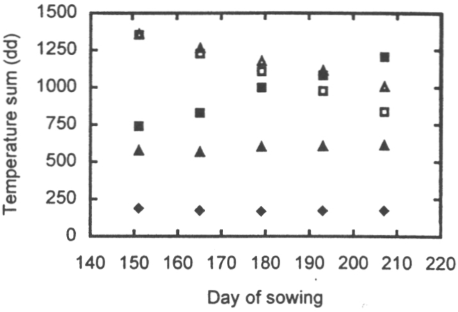

Fig. 6. Effect of sowing date on termination of shoot elongation (■), terminal bud formation (▲) and secondary needle formation in the second growing season (◆). Closed symbols indicate termination of shoot elongation and terminal bud formation during the second growing season and open symbols during the first growing season.

The photoperiod of the original site seems to be the dominant factor for determining the timing of growth cessation of the Scots pine seedlings. This confirms earlier studies indicating a latitudinal cline for growth cessation (e.g. Wareing 1950*a*, 1950*b*, Langlet 1959). In the present study the origins with almost the same photoperiod had almost the same timing of growth cessation despite different temperature sums (Fig. 3). The origins with almost the same temperature sums but different photoperiods had different timings of growth cessation (Fig. 4). In the multiple regression model photoperiod was a significant predictor ($p < 0.001$) for the level of the fitted growth cessation line, whereas temperature sum was not a significant predictor ($p > 0.1$).

The earlier growth cessation of the seedlings from origin 7 indicates that photoperiod seems to be particularly important north of latitude 65°N. In other words, the change in the photoperiodic conditions seems not to be linear when moving northwards. This non-linearity is logical because the changes in length of the photoperiod occur more rapidly further northwards. However, in this study there were only two sites of origin that were north of latitude 65°N. Further experimental studies are needed to improve our knowledge of the joint effects of temperature sum and photoperiod, especially studies using origins from more northern latitudes (> 65°N).

In the present study even the latest sowing date (27 July) generally gave the seedlings sufficient time for winter hardening. The only exceptions were the seedlings from the fourth and fifth sowings in Ruotsinkylä after winter 1995–1996. Owing to dieback and canker fungus of pines [*A. abietina* (Lagerb.)], the average survival of the seedlings from the fourth sowing was 17% and from the fifth sowing only 10%. The latest sowing date that Koski & Sievänen (1985) used in their experiments in Punkaharju was almost the same (29 July) and this date also seemed to give Scots pine seedlings sufficient time to prepare for winter hardening.

In both the present study and the study by Koski & Sievänen (1985) the start of the growth defined by bud burst or formation of the secondary needles after overwintering took place independently of the sowing date. In this study seedlings from the earlier sowings did not form their terminal buds in the second growing season earlier than the seedlings from the later sowings ($p > 0.1$) (Fig. 6). However, in the study by Koski & Sievänen (1985) the seedlings from the later sowing dates required twice the temperature sum accumulation for bud formation in the second growing season, compared with those sowed before the summer solstice. The seedlings from earlier sowings required a longer time and a larger temperature sum for the termination of shoot elongation than those from later sowings. Thus, observations by Koski & Sievänen (1985) indicated that the sowing time has an effect on both the duration of height growth and the formation of the terminal bud. In contrast to Koski & Sievänen (1985), the present results showed that the major differences in the timing of bud set seem to have disappeared after the first winter and the sowing time seems to have a converse effect on growth cessation. After the first growing season the height growth of Scots pine is predetermined. This means that differences in growth cessation and formation of the terminal buds in the second growing season reflect differences in the number of unit primordia which were formed during the bud formation at the end of the first growing season. This suggests that the explanation for the contradiction between the studies of Koski & Sievänen (1985) and the present study lies in differences in growth conditions during the first growing season.

An improved knowledge of the regulation system of growth cessation can be applied to the production of reforestation material. In order to be able to grow more than one crop per season, modern commercial nurseries use manipulated environments when raising seedlings for reforestation (Ryyppö 1998). In Swedish nurseries, long-night treatments of Scots pine are made at sowing dates earlier than August (Rosvall-Åhnebrink 1990). The seedlings need to cease their growth and become dormant in time before winter, both in the nursery and, later, in the forest. The results of this study confirm earlier studies that seedlings do not suffer from manipulated nursery environments after being transferred to the forest sites.

In order to anticipate the projected climate warming it has been suggested that more southern provenances from warmer regions should be used for the reforestation of boreal forests. As a result of the dominant effect of the photoperiod of the origin on growth cessation, as shown in this and earlier studies, trees will grow too far into the autumn, hardening will be delayed and thus they will be more liable to frost injury. Furthermore, Eiche's results (Eiche 1966) show that a transfer northwards will decrease survival and reduce the volume per hectare. In addition, because the projected increasing risk for spring frost damage as a result of climate warming seems to be less drastic than projected in the earliest models (Cannell & Smith 1986, Hänninen 1991, 1996, Beuker 1996), there seems, at least for the moment, little reason to recommend the use of more southern provenances in reforestation of Scots pine in Finland. Instead, southward transfers of the northern origins have been proven to increase survival and wood production, although they produce less wood than local southern origins (Beuker 1994).

In conclusion, the results of the present study demonstrate that the Scots pine seedlings carry genetic information that governs the regulation system of growth cessation and that the responses to temperature and photoperiod have separate genetic controls. Therefore, seedlings from different origins and sowing dates are able to cease their growth before winter with different combinations of accumulated temperature sum and night length. The photoperiod of the original site seems to be the dominant factor for determining the timing of growth cessation of the Scots pine seedlings. Because of predetermined growth, the sowing date does not affect the phenology during the second growing season.

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Dependence of photoperiodic response of growth cessation on the stage of development in *Picea abies* and *Betula pendula* seedlings

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Abstract

Dependence of photoperiodic response of growth cessation on the stage of development was examined in seedlings of Norway spruce (*Picea abies* (L.) Karst.) and silver birch (*Betula pendula* Roth) in greenhouses with 20 °C day and 10 °C night temperatures. Different combinations of photoperiod and stage of development were created by repeating sowing five times with 2 week intervals during the summer. During the experiment light conditions were natural but the daily temperature sum accumulation was regulated to be constant. Eight origins of spruce and seven origins of birch from different latitudes (60–67°N) in Finland were used. In the first growing season both Norway spruce and silver birch seedlings from the first sowings required a longer time for growth cessation than seedlings from the later sowings. However, because the seedlings from the first sowings ceased their growth on an earlier calendar date, the night length at the time of growth cessation was shorter for the seedlings from the first sowings. The results suggest that the variation in the timing of growth cessation of Norway spruce and silver birch seedlings during the first growing season was explained jointly by night length and stage of development. Seedlings from northern origins stopped their growth with shorter night length than those from southern origins. The effects of latitude and average temperature sum of the original growing site on the critical night length of growth cessation in the first growing season were stronger in Norway spruce than in silver birch. In the second growing season the sowing time did not affect the timing of the formation of the terminal buds, but slightly affected the timing of height growth cessation of Norway spruce and silver birch seedlings.

Keywords: Climatic adaptation; Growth cessation; Norway spruce; Photoperiod; Silver birch; Stage of development

1. Introduction

The growth rhythm of woody plants in cool and temperate regions is controlled by both internal and environmental factors. Genotype is the internal factor that sets the limits, whereas environmental factors determine the actual growth rhythm. The major environmental factors affecting growth rhythm are photoperiod and temperature. In cool and temperate regions, woody ecotypes and species are adapted to the local seasonal photoperiod and temperature conditions (Sakai and Weiser, 1973).

According to prevailing theory critical night length causes growth cessation and acts as an environmental signal which ensures the beginning of the hardening processes already before the temperatures drop (e.g. Wareing, 1950a,b; Vaartaja, 1954, 1957, 1959; Dormling et al., 1968; Heide, 1974; Ekberg et al., 1979; Junttila and Kaurin, 1985). The critical night

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length shows clinal variation with latitude, i.e. the northern geographical origins react to shorter critical night lengths compared to the southern ones. Accordingly, tree species which have wide range form photoperiodic ecotypes. These ecotypes are adapted to the local combination of photoperiod and temperature. Vaartaja (1954, 1959) has demonstrated the presence of latitudinally and altitudinally oriented photoperiodic and temperature ecotypes in 31 species of forest trees.

Environmental factors such as temperature, water stress and mineral nutrition have a modifying influence on photoperiodic reactions affecting growth cessation (e.g. Heide, 1974). In addition, the timing of growth cessation has been explained with a joint effect of temperature sum accumulation and photoperiod (Koski and Selkäinaho, 1982; Koski, 1985; Koski and Sievänen, 1985; Paus et al., 1986; Partanen and Beuker, 1999). This kind of regulation system would provide more flexibility in the timing of growth cessation compared to a regulation based only on one factor. In particular, a response only to the night length signal would mean that the growth cessation would take place at a fixed calendar date from year to year. This is, however, contrary to experience.

Physiological processes of plants can be described quantitatively on the basis of the concepts of rate of biological maturation and physiological stage of development (Hari, 1968, 1972). It may be assumed that the stage of development of seedlings is determined by several environmental factors, such as night length, light intensity, temperature and nutrition. In the beginning of the growing season, the rate of development is regulated mostly by temperature, and accordingly the accumulated temperature sum estimates the stage of development at a certain moment. Later during the growing season, the role of photoperiod becomes more important (e.g. Fuchigami et al., 1982). Koski and Selkäinaho (1982) presented a simple experimental technique where different combinations of photoperiod and stage of development of the seedlings are created by repeating sowing in natural light conditions in two different temperature conditions where the daily temperature sum accumulations are kept approximately constant. By using this kind of experimental technique, the effects of night length and stage of seedling development on the timing of growth cessation can be tested.

The first aim of the present study was to examine the effect of night length and stage of development on the timing of height growth cessation in seedlings of Norway spruce (*Picea abies* (L.) Karst.) and silver birch (*Betula pendula* Roth) in the first growing season. Further, the effect of the sowing date on the timing of bud formation and height growth cessation during the second growing season were tested. The second aim of the study was to examine the genetic variation among origins in the environmental response of growth cessation in the first growing season.

2. Materials and methods

The experimental material was obtained from eight Norway spruce and seven silver birch origins. These origins were from regions with different light and temperature regimes in Finland (Table 1). The seedlings were raised and observed in greenhouses at the Punkaharju Research Station (61°48′N, 29°19′E) of the Finnish Forest Research Institute during 1997 and 1998 in natural light. The temperature in the greenhouses was kept at a constant 20 °C between 7 a.m. and 5 p.m. and at 10 °C between 7 p.m. and 5 a.m. During the intervening times the temperature was changed steadily at a rate of 5 °C per hour. From June until the end of August during warm and sunny periods with warm nights, however, the temperatures in the greenhouses were up to 7 °C higher, because no artificial cooling was available.

The seedlings were raised in plastic trays of 45 cells (190 cm^3) filled with commercial fertilized peat (Vapo peat for forest trees; N 9.7%, P 7.5%, K 14.4% and micronutrients) as described in Partanen and Beuker (1999). Sowing was repeated five times during 1997 (Table 2). The aim was to grow 20 seedlings per origin, 10 of which were chosen for the experiments. However, because of the low germination capacity of northern origins this was not always successful.

In October, 2 weeks before the seedlings were moved outside, the temperature in the greenhouse was lowered to a constant 5 °C in order to attain winter hardiness. The seedlings were removed from the greenhouse in 1997 on 30 October. All the Norway spruce seedlings and the shorter silver birch seedlings overwintered wholly under natural snow coverage,

Table 1
Geographical information and average annual temperature sums for the original growing sites of the origins of Norway spruce and silver birch used in the study

Origin	Latitude (°N)	Longitude (°E)	Altitude (m)	Temperature sum (>5 °C, dd)
Norway spruce				
Tammisaari	60°02′	23°03′	35	1334
Tuusula	60°21′	24°59′	60	1321
Punkaharju	61°34′	29°13′	105	1226
Vilppula	62°04′	24°29′	105	1172
Laihia	62°52′	22°02′	35	1144
Lieksa	63°04′	30°17′	170	1046
Pihtipudas	63°17′	25°27′	165	1050
Rovaniemi municipality	66°21′	26°41′	295	873
Silver birch				
Karjalohja	60°14′	23°43′	50	1322
Taipalsaari	61°16′	27°54′	80	1288
Joutsa	61°40′	26°15′	110	1220
Punkaharju	61°49′	29°18′	92	1235
Ruovesi	62°03′	24°15′	100	1179
Oravainen	63°17′	22°20′	10	1132
Rovaniemi municipality	66°52′	24°55′	140	836

whereas the longer silver birch seedlings were covered with snow only partially.

The effects of the first growing season on the growth cessation of the overwintered seedlings in the second growing season were studied by experiments under the same greenhouse conditions as in the first growing season. In 1998 the seedlings were transferred into the greenhouse on 18 May. After transfer the silver birch seedlings were transplanted into plastic pots of volume 450 cm^3 containing fertilized peat (Vapo peat for forest trees; N 9.7%, P 7.5%, K 14.4% and micronutrients).

In the first and second growing seasons, the total height of 10 seedlings in each batch was measured and the timing of the development of the terminal bud was observed as described in Partanen and Beuker (1999). The temperature data was recorded hourly. Because the daily temperature conditions were kept approximately constant, the temperature sum accumulations (5 °C threshold) calculated from different sowing dates were almost linear. Accordingly, the temperature sum accumulation and the age of the seedlings were linearly confounded in this experiment. The night length for the date of growth cessation was given by the time interval between sunset and sunrise. In the calculations, the night length of Jyväskylä (62°13′N, 25°44′E) as determined by the University of Helsinki (Anon., 1996, 1997) was used.

Table 2
Night lengths on the sowing dates

Sowing	Date	Night length (h)
1	29 May	5.08
2	12 June	4.28
3	26 June	4.18
4	10 July	4.82
5	24 July	5.88

For an individual seedling, growth cessation was defined as the instant at which 95% of the height growth had been achieved, and for individual origins and sowing dates as the average over the seedlings. The formation of the terminal buds was observed from individual seedlings. For individual origins and sowing dates it was defined as the average over the seedlings, i.e. as the time when 50% of the seedlings had set buds. The effect of the sowing date on (1) temperature sum and (2) night length required for the average terminal bud formation and height growth cessation over all origins was tested separately in both growing seasons using analysis of variance.

In the first growing season, for each individual origin and sowing date, the night length prevailing at the time of growth cessation was plotted against the temperature sum accumulated until growth cessation. The lines that were fitted into these plotted observations, are called growth cessation lines. The relationship between accumulated temperature sum and night length at the time of growth cessation is symmetric and thus cannot be analysed in terms of dependent and independent variables. Therefore, the growth cessation lines were fitted using the maximum likelihood estimation presented by Lappi and Sievänen (1993). This was carried out separately for each of the eight Norway spruce and seven silver birch origins.

The genetic variation in the environmental response of growth cessation among origins was examined by comparing the properties of the fitted growth cessation lines of the different origins. The variation of the predicted night lengths between the different origins at fixed temperature sums and the variation in the slopes of the fitted growth cessation lines were analysed separately for Norway spruce and silver birch using linear regression analysis. The predictors in the regression analyses were latitude and average annual temperature sum of the original growing sites of the origins. The correlations between the latitude and average annual temperature sum of the original growing sites of the origins were also determined. For Norway spruce, the separate regression analyses were done at fixed temperature sums of 700, 800 and 900 dd, respectively. For silver birch, the analyses were done at fixed temperature sums of 900, 950 and 1000 dd, respectively. The fixed temperature sums were chosen to cover approximately the whole range of the growth cessation times for the experimental material.

Table 3
Average number of days from sowing to growth cessation and terminal bud formation of Norway spruce seedlings in the first growing season

Origin	Sowing				
	1	2	3	4	5
Days to growth cessation					
Tammisaari	86	75	66	53	41
Tuusula	81	79	64	51	38
Punkaharju	78	69	56	51	38
Vilppula	75	62	54	48	35
Laihia	71	63	55	47	34
Lieksa	69	59	54	46	33
Pihtipudas	73	64	60	45	35
Rovaniemi municipality	60	45	56	36	35
Days to bud formation					
Tammisaari	91	77	71	58	45
Tuusula	84	77	69	59	46
Punkaharju	82	72	55	57	45
Vilppula	79	63	55	53	40
Laihia	76	67	54	50	39
Lieksa	72	61	51	47	34
Pihtipudas	70	64	55	50	42
Rovaniemi municipality	59	55	43	39	36

3. Results

The length of the growing period of both Norway spruce and silver birch seedlings was dependent on the sowing time. Seedlings from the first sowings had a longer growing period (Tables 3 and 4), and thus also a greater temperature sum, at growth cessation than seedlings from the later sowings. However, because the seedlings from the first sowings stopped their growth on an earlier calendar date, the night length at the time of growth cessation was shorter for the seedlings from the first sowings than for those from the later sowings (Figs. 1 and 2). The average final height of both Norway spruce and silver birch seedlings was also dependent on the sowing time decreasing from the first to the last sowing (Fig. 3). Before the height growth ceased, the seedlings from different sowing

Table 4
Average number of days from sowing to growth cessation and terminal bud formation of silver birch seedlings in the first growing season

Origin	Sowing				
	1	2	3	4	5
Days to growth cessation					
Karjalohja	75	69	63	72	61
Taipalsaari	78	70	67	67	55
Joutsa	73	65	64	70	55
Punkaharju	76	68	60	67	58
Ruovesi	79	67	67	73	61
Oravainen	78	70	68	72	57
Rovaniemi municipality	67	65	59	61	47
Days to bud formation					
Karjalohja	84	79	64	74	64
Taipalsaari	81	73	62	68	77
Joutsa	79	72	63	71	64
Ruovesi	85	74	64	64	65
Punkaharju	83	71	60	82	73
Oravainen	78	71	62	71	73
Rovaniemi municipality	74	66	57	57	68

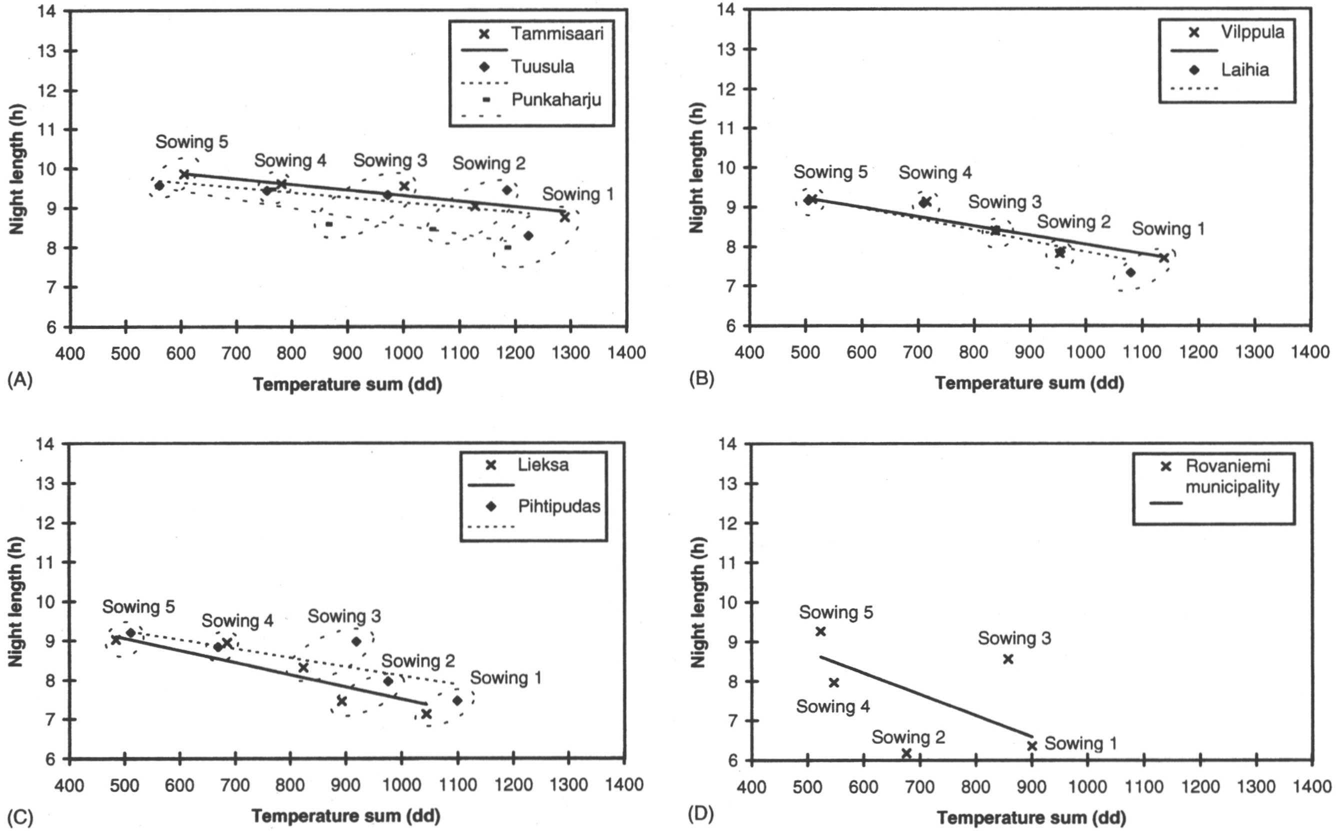

Fig. 1. Dependence of average timing of growth cessation on temperature sum and night length for different origins of Norway spruce seedlings in the first growing season.

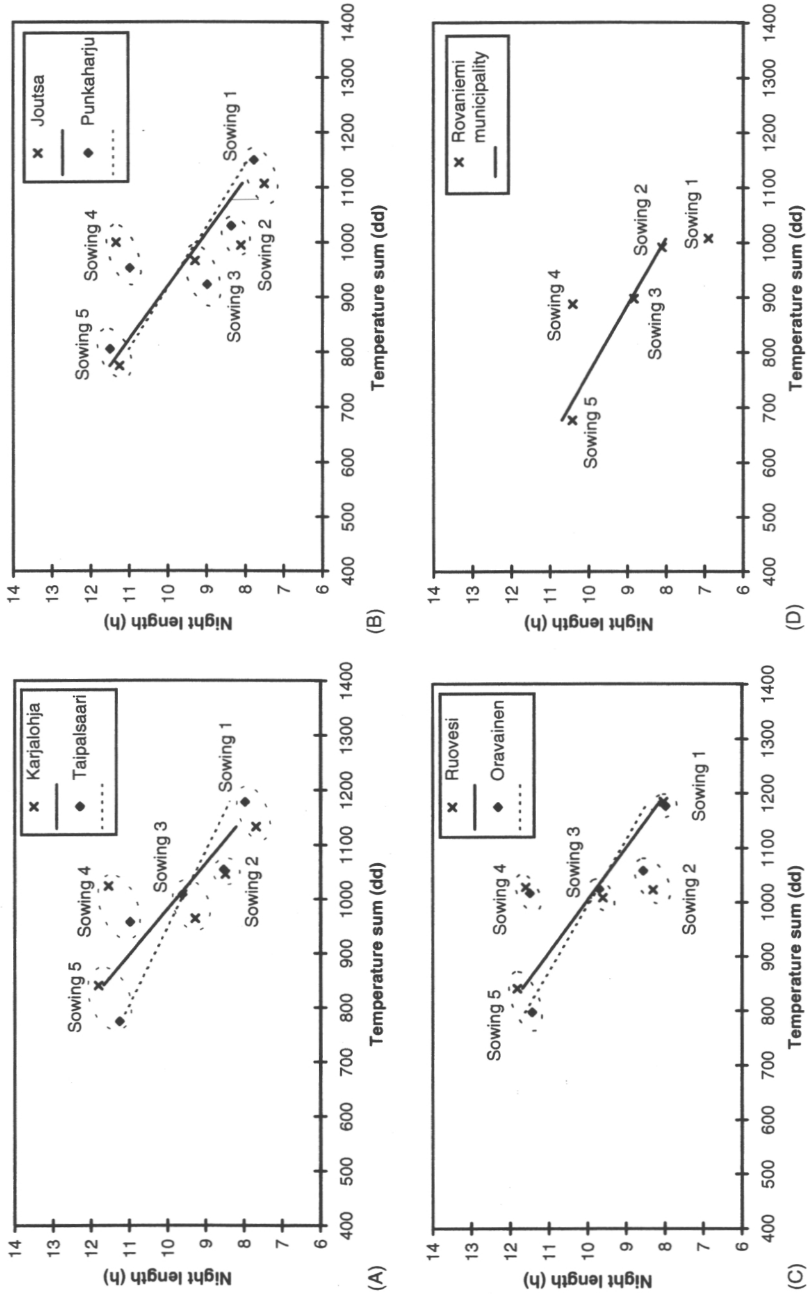

Fig. 2. As Fig. 1, but for silver birch seedlings.

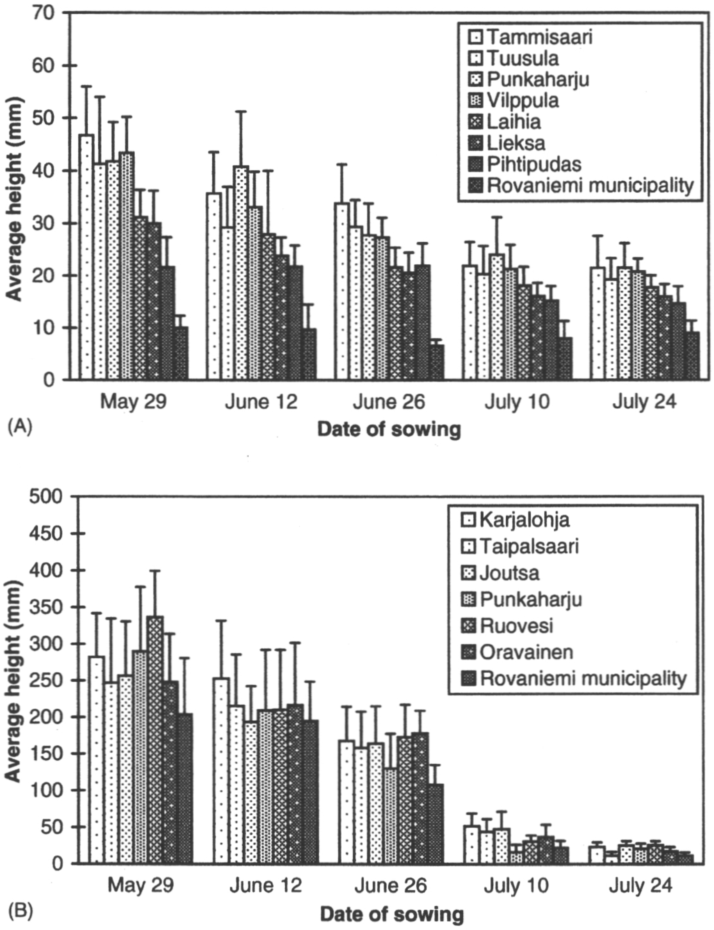

Fig. 3. Average final heights (±standard error) of the seedlings of Norway spruce (A) and silver birch (B) from different sowing dates and origins in the first growing season.

dates were at different developmental stages estimated with the temperature sum accumulation or, equivalently, with the age of the seedlings. Thus, the seedlings at earlier stages of development required a longer critical night length signal for height growth cessation.

There was latitudinal variation between southern and northern Norway spruce and silver birch origins both in the timing of height growth cessation and in the final height of the seedlings. Seedlings from northern origins generally stopped their growth earlier, i.e. with shorter critical night length than seedlings from southern origins (Tables 3 and 4). Correspondingly, the average final height of the seedlings from northern origins was smaller than the average final height of the seedlings from southern origins (Fig. 3).

In the first growing season the growth of the Norway spruce seedlings from different origins ceased with a temperature sum accumulation between 480 and 1300 dd and night length between 6 and 10 h (Fig. 3). The growth of the silver birch seedlings, however, ceased with a temperature sum accumulation between 670 and 1200 dd and night length between 7 and 12 h (Fig. 4). Consequently, the fitted growth cessation lines for Norway spruce origins were more gently sloping than the corresponding lines for silver birch origins (Figs. 3 and 4). In other words, the change in stage of

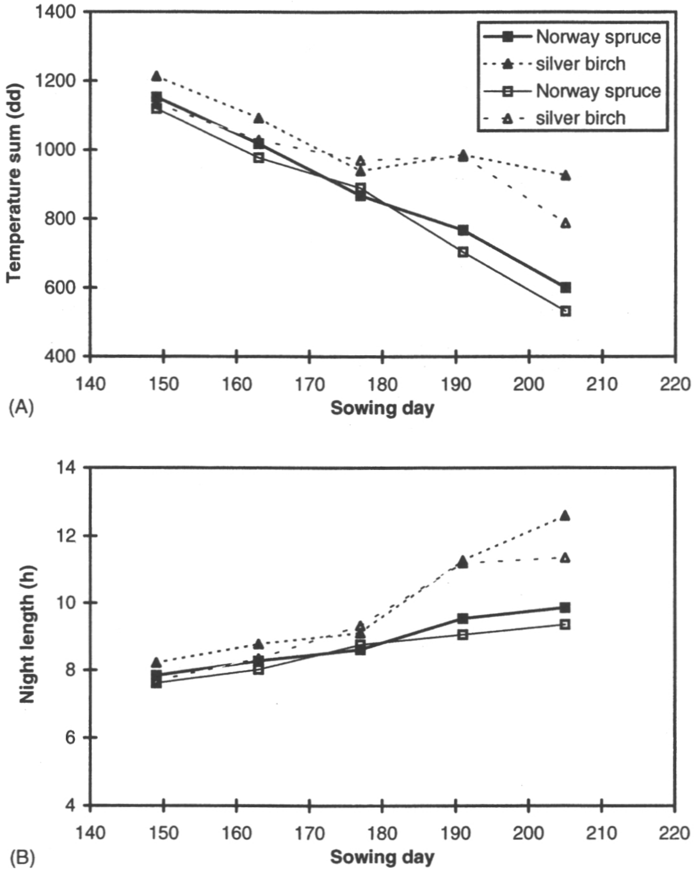

Fig. 4. Effect of sowing time (number of days from the beginning of the year) on temperature sum (A) and night length (B) required for average terminal bud formation (closed symbols) and height growth cessation (open symbols) of Norway spruce and silver birch seedlings in the first growing season. Pooled data over all origins.

development (estimated with temperature sum or, equivalently, with age of the seedlings) changed the critical night length of growth cessation more with silver birch than with Norway spruce.

For Norway spruce, latitude and average annual temperature sum of the original growing sites of the origins were strongly correlated ($r = -0.98$). Accordingly, either one of them alone can be used to predict the variation in the properties (= predicted night lengths at fixed temperature sums and the slopes) of the fitted growth cessation lines of origins. The linear regressions of the predicted night lengths of the fitted growth cessation lines at fixed temperature sums (700, 800 and 900 dd) using latitude or annual temperature sum as predictor were all highly significant ($P < 0.001$) (Table 5). In all three cases, both predictors accounted for 93–96% of the variability. Accordingly, both latitude and average temperature sum of the original growing site of the origin had an effect on the critical night length of growth cessation of Norway spruce seedlings in experimental conditions. The seedlings from northern origins generally ceased their growth earlier (i.e. with shorter critical night length and with smaller temperature sum) than the seedlings from southern origins (Fig. 1). The slopes of the growth cessation lines were slightly more dependent on the latitude ($P < 0.001$) than on the corresponding annual temperature sum ($P = 0.001$).

Table 5
Linear regression analysis of the predicted night lengths at fixed temperature sums and the slopes of the fitted growth cessation lines of Norway spruce seedlings in the first growing season using latitude and average annual temperature sum of the original growing sites of the origins as predictors

Dependent	Predictor	*P*-value	R^2
Night length at 700 dd	Latitude	<0.001	0.95
Night length at 700 dd	Temperature sum	<0.001	0.93
Night length at 800 dd	Latitude	<0.001	0.95
Night length at 800 dd	Temperature sum	<0.001	0.93
Night length at 900 dd	Latitude	<0.001	0.96
Night length at 900 dd	Temperature sum	<0.001	0.93
Slope	Latitude	<0.001	0.92
Slope	Temperature sum	0.001	0.85

Table 6
Linear regression analysis of the predicted night lengths at fixed temperature sums and the slopes of the fitted growth cessation lines of silver birch seedlings in the first growing season using latitude and average annual temperature sum of the original growing sites of the origins as predictors

Dependent	Predictor	*P*-value	R^2
Night length at 900 dd	Latitude	0.035	0.62
Night length at 900 dd	Temperature sum	0.032	0.64
Night length at 950 dd	Latitude	0.041	0.60
Night length at 950 dd	Temperature sum	0.037	0.61
Night length at 1000 dd	Latitude	0.053	0.56
Night length at 1000 dd	Temperature sum	0.048	0.58
Slope	Latitude	0.287	0.22
Slope	Temperature sum	0.289	0.22

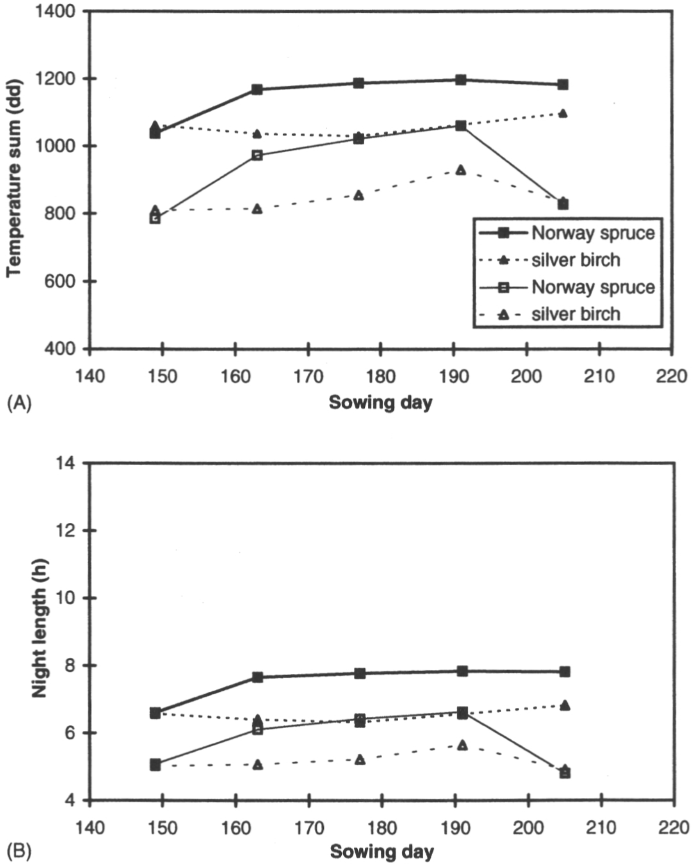

Fig. 5. As Fig. 4, but in the second growing season.

The latitude of the original growing sites of the origins accounted for 92% of the variability and the temperature sum for 85% of the variability (Table 5).

For silver birch, latitude and average annual temperature sum of the original growing sites of the origins were also strongly correlated ($r = -0.99$). The linear regressions of the predicted night lengths of the fitted growth cessation lines at fixed temperature sums (900, 950 and 1000 dd) using latitude or annual temperature sum as predictor were significant ($P \leq 0.05$) (Table 6). The dependence was, however, not so strong as in the case of Norway spruce. In all three cases, both predictors accounted for 56–64% of the variability. The difference in the timing of growth cessation between northern and southern origins was smaller in the case of silver birch than in the case of Norway spruce (Figs. 1 and 2). The slopes of the growth cessation lines, unlike in the case of Norway spruce, were not dependent on the latitude or annual temperature sum of the original growing sites of the origins ($P > 0.1$), which both accounted for only 22% of the variability (Table 6).

In the first growing season both the average formation of the terminal buds and the height growth cessation over all Norway spruce origins occurred with smaller temperature sum accumulation and shorter night length than the corresponding phenomena of the silver birch seedlings (Fig. 4). This difference was clearest in the fourth and the fifth sowings. In the second growing season, however, it was the silver birch seedlings that had the smaller temperature sum accumulation and shorter night length requirements (Fig. 5).

Both in Norway spruce and in silver birch in the first growing season, the differences of temperature sum and night length required for the formation of the terminal buds over all origins between different sowing dates were highly significant ($P < 0.001$) (Fig. 4). In the second growing season, however, these differences were not significant ($P > 0.1$) (Fig. 5). In other words, sowing time did not affect the timing of the terminal bud formation of either Norway spruce or silver birch seedlings in the second growing season. In both species in the first growing season, the differences of temperature sum and night length required for the height growth cessation between different sowing dates were highly significant ($P < 0.001$) (Fig. 4). In the second growing season, unlike in the case of formation of the terminal buds, these differences were also slightly significant ($P < 0.05$) (Fig. 5).

4. Discussion

Sowing time had an effect on the timing of growth cessation of Norway spruce and silver birch seedlings in the first growing season. In first sowings, growing periods were longer and critical night lengths shorter than in later sowings. This is in accordance with earlier studies (Koski and Selkäinaho, 1982; Koski and Sievänen, 1985; Partanen and Beuker, 1999). In addition to the length of the growing periods, also the total height growth of the seedlings varied among sowing dates. Because the daily temperature sum accumulation in the experiment was kept constant, it is likely that the seedlings from different sowing dates were at different stages of development at given calendar dates (night lengths) before the height growth ceased. Accordingly, the results suggest that the variation in the timing of growth cessation in the first growing season was explained jointly by night length and stage of development of the seedlings, the latter estimated with the temperature sum accumulation or, equivalently, with the age of the seedlings.

Using constant 15 and 20 °C temperatures Koski and Selkäinaho (1982) detected that the growing periods of seedlings in the same sowings were longer in 15 °C than in 20 °C temperature conditions. A possible explanation for this is that the development of the seedlings was faster in 20 °C than in 15 °C temperature conditions. In earlier studies differences have also been found in the timing of growth cessation between experimental years (Koski and Selkäinaho, 1982; Partanen and Beuker, 1999). The existence of this year-to-year variation suggests that, in addition to photoperiod and temperature, other environmental factors like nutrition and light intensity have an additional effect on the timing of growth cessation.

In the present study both Norway spruce and silver birch origins displayed a latitudinal variation. Compared to southern origins, the growth cessation of the seedlings from northern origins generally occurred earlier. Correspondingly, the average final height of the seedlings from northern origins remained smaller. The presence of latitudinally oriented ecotypes has been demonstrated in several tree species (Pauley and Perry, 1954; Vaartaja, 1951, 1954, 1959; Dormling et al., 1968; Håbjørg, 1972).

Short day treatment is commonly used in nurseries to stop the growth and to start the hardening of the seedlings. In this study the growth cessation lines were more gently sloping for Norway spruce origins than for silver birch origins. This sensitivity of Norway spruce to increasing night length during the first growing season has been detected earlier, e.g. by Vaartaja (1951), and makes it possible to stop the growth of Norway spruce seedlings by lengthening the night artificially (Rosvall-Åhnebrink, 1977, 1980, 1982, 1990; Dormling and Lundkvist, 1983).

The height growth of silver birch seedlings can be stopped by using short day treatment after the seedlings have reached a certain stage of development. An appropriate time to start short day treatment is when about two-thirds of the average annual temperature sum (threshold 5 °C) of the original growing site of the origin has been accumulated (Koski and Sievänen, 1985; Luoranen, 2000). Consequently, in central Finland the height growth of local silver birch can be stopped effectively with an 8 h short day treatment lasting for 2 to 3 weeks started at the earliest in July (Luoranen and Rikala, 1997; Luoranen, 2000). In the present study in the fourth and the fifth sowings, the height growth of silver birch seedlings occurred when the night length was already between 11 and 12 h. In these late sowings, the two-thirds of the average annual temperature sum (threshold 5 °C) of the original growing site of the origins had not been accumulated. Accordingly in late sowings, the night length over 11 h seemed to be the factor that forced the seedlings to cease their growth in spite of low temperature sum accumulation.

Unlike in the first growing season, the sowing date did not affect the timing of the formation of the terminal buds in the second growing season either in Norway spruce ($P > 0.1$) or in silver birch ($P > 0.1$) seedlings (Fig. 5). The sowing date, however, slightly affected the timing of height growth cessation in the second growing season both in Norway spruce ($P < 0.05$) and in silver birch ($P < 0.01$) seedlings. Koski and Sievänen (1985) did not find a correlation between the sowing date and the timing of growth cessation in the following growing season for Norway spruce and silver birch seedlings.

In conclusion, in the present study the growth of the seedlings from different sowing dates did not cease with the same critical night length, and the height of the seedlings also varied between sowing dates. The photoperiodic regulation of height growth cessation in the sowing year was dependent on the stage of seedling development estimated with the temperature sum accumulation or, equivalently, with the age of the seedlings. On the other hand, in similar photoperiodic conditions the height growth cessation was dependent on the latitude of the origin. Information about the effect of sowing time and the effect of photoperiodic conditions on the height growth and the growth cessation of the seedlings from different origins is needed when seedlings are produced in nurseries for forest cultivation.

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