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Effects of seed origin latitude on the timing of height growth cessation and field performance of silver birch

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Academic dissertation

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ABSTRACT

The aim of this thesis was to increase our knowledge about the effects of seed origin on the timing of height growth cessation and field performance of silver birch (*Betula pendula* Roth) from different latitudes, with special attention paid to the browsing damage by moose in young birch plantations. The effect of seed origin latitude and sowing time on timing of height growth cessation of first-year seedlings was studied in a greenhouse experiment with seven seed origins (lat. 58º - 67ºN). Variation in critical night length (CNL) for 50 % bud set within two latitudinally distant stands (60º and 67ºN) was studied in three phytotron experiments. Browsing by moose on 5-11-year-old silver birch saplings from latitudinally different seed origins (53º - 67ºN) was studied in a field experiment in southern Finland. Yield and stem quality of 22-year-old silver birch trees of Baltic, Finnish and Russian origin (54º - 63ºN) and the effect of latitudinal seed transfers were studied in two provenance trials at Tuusula, southern and Viitasaari, central Finland. The timing of height growth cessation depended systematically on latitude of seed origin and sowing date. The more northern the seed origin, the earlier the growth cessation and the shorter the growth period. Later sowing dates delayed growth cessation but also shortened the growth period. The mean CNL of the southern ecotype was longer, 6.3 ± 0.2 h (95 % confidence interval), than that of the northern ecotype, 3.1 ± 0.3 h. Within-ecotype variance of the CNL was higher in the northern ecotype (0.484 h^2) than in the southern ecotype (0.150 h^2). Browsing by moose decreased with increasing latitude of seed origin and sapling height. Origins transferred from more southern latitudes were more heavily browsed than the more northern native ones. Southern Finnish seed origins produced the highest volume per unit area in central Finland (lat. 63º11'N). Estonian and north Latvian stand seed origins, and the southern Finnish plus tree origins, were the most productive ones in southern Finland (lat. 60º21'N). The relationship of both survival and stem volume/ha to the latitudinal seed transfer distance was curvilinear. Volume was increased by transferring seed from ca. 2 degrees of latitude from the south. A longer transfer from the south, and transfer from the north, decreased the yield. The proportion of trees with a stem defect increased linearly in relation to the latitudinal seed transfer distance from the south.

Keywords: climatic adaptation, critical night length, moose browsing, provenance, seed transfer, stem quality, yield

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I dedicate this thesis to the memory of my late parents; two warm-hearted and hard-working people of the past generation.

Porvoo, April 2009

Anneli Viherä-Aarnio

LIST OF ORIGINAL ARTICLES

This thesis is based on the following articles, which are referred to by their Roman numerals. All the articles are reprinted by kind permission from the publishers.

I Viherä-Aarnio, A., Häkkinen, R., Partanen, J., Luomajoki, A. & Koski, V. 2005. Effects of seed origin and sowing time on timing of height growth cessation of *Betula pendula* seedlings. Tree Physiology 25:101-108.

II Viherä-Aarnio, A., Häkkinen, R. & Junttila, O. 2006. Critical night length for bud set and its variation in two photoperiodic ecotypes of *Betula pendula*. Tree Physiology 26:1013-1018.

III Viherä-Aarnio, A. & Heikkilä, R. 2006. Effect of the latitude of seed origin on moose (*Alces alces*) browsing on silver birch (*Betula pendula*). Forest Ecology and Management 229:325-332.

IV Viherä-Aarnio, A. & Velling, P. 2008. Seed transfers of silver birch (*Betula pendula*) from the Baltic to Finland - effect on growth and stem quality. Silva Fennica 42(5):735-751.

AUTHOR'S CONTRIBUTION

Paper I: The author was the corresponding author and responsible for writing the manuscript. Viherä-Aarnio planned the experiment together with the co-authors. Viherä-Aarnio also participated in the data collection and analysis as a member of the group. Dr. Häkkinen performed the statistical analysis for the study.

Paper II: The author was the corresponding author and responsible for writing the manuscript. The author participated in planning the experiments, was responsible for doing the observations and measurements and performed part of the statistical analysis.

Paper III: The author was responsible for planning the field trial and planned the measurements of moose browsing together with the co-author. The author was responsible for analyzing the data and for writing the manuscript and acted as the corresponding author.

Paper IV: The author planned the measurements together with the co-author. The author was responsible for statistical analysis and for writing the manuscript and acted as the corresponding author.

CONTENTS

1 INTRODUCTION

1.1 General framework

The climate of the northern boreal zone is characterized by a strong seasonal variation in temperature and light conditions. Trees, as tall phanerophytes, must confront temperature extremes from cold winters to warm summers. In order to survive, they spend the unfavourable winter period in a frost hardy dormant state, and thus, the period of active growth and dormancy alternate in their annual cycle (Weiser 1970, Sarvas 1972, 1974, Fuchigami et al. 1982, Hänninen 1986, 1990).

The timing of the changes from an active growth state to frost hardy dormant state and back is fundamental to the survival of trees. Too early growth onset and dehardening in spring, and too late growth cessation and hardening in the autumn both cause frost damage and poor survival (Heide 1985). On the other hand, delaying the onset of growth in the spring, and ceasing growth at the end of summer too early lead to a poor utilization of the growing season and competitive ability (Heide 1985). Regulatory mechanisms have therefore evolved to synchronize the annual physiological rhythm of trees with the annual climatic cycle.

According to present knowledge, growth onset is mainly regulated by air temperature (Sarvas 1972, Fuchigami et al. 1982, Hänninen 1990), although photoperiod also seems to play a role (Heide 1993ab, Myking and Heide 1995, Häkkinen et al. 1998, Partanen et al. 1998). Cessation of growth, on the other hand, is in first place regulated by photoperiod (Wareing 1956, Vaartaja 1959, Heide 1974, Ekberg et al. 1979, Fuchigami et al. 1982), but modified by other factors, temperature being the most important one (Heide 1974, Fuchigami et al. 1982, Koski and Selkäinaho 1982). The regulation of annual physiological rhythm of trees is based on the interaction of genetic and environmental factors, which determine the timing of the events of the annual cycle in manner that is specific to each species and population (Wareing 1956, Nitsch 1957, Håbjørg 1978, Heide 1974, 1985, 1993ab, Ekberg et al. 1979). Directed by the natural selection, tree populations have adapted to the climatic conditions and the particular combination of temperature and light of their home district (Eriksson and Ekberg 2001).

The regulatory mechanisms of the annual rhythm, as well as the diverse adaptation of tree populations, can be studied experimentally by transferring tree origins to different photoperiodic and temperature conditions and measuring their response. Both short-term growth chamber, greenhouse or nursery experiments in artificial environments, and long-term provenance trials in the field can be used (White et al. 2007).

Forest regeneration with seeds or seedlings from too distant, poorly adapted sources results in poor survival, abiotic and biotic damages and, consequently, losses in yield and quality of the harvest (Kalela 1937, Heikinheimo 1949, Morgenstern 1996, White et al. 2007). Thus, awareness of the different adaptation of tree populations and understanding of the regulating mechanisms of their annual rhythm is a prerequisite for successful forestry.

Global warming and climatic change poses a new threat to trees and forestry (IPCC 2001). In order to make any predictions for the future acclimation and adaptation of trees in changing conditions, we need better understanding of the regulation of their annual physiological rhythm and of its variation both between and within populations.

1.2 Silver birch as a forest tree

Silver birch (*Betula pendula* Roth) has a wide area of distribution in the temperate and cold regions of the Eurasian continent, ranging from the Atlantic Ocean to Lena river in Siberia (Hulten and Fries 1986, Jonsell 2000) and, according to some authors, even as far as to the Pacific Ocean (Hämet-Ahti and Alanko 1987, Hämet-Ahti et al. 1992). It grows throughout almost the whole of Europe, except Iceland, most of the Iberian peninsula and Greece, from 35°N in the south to 69°30'N in the north (Walters 1964). Except the northernmost part of Lapland silver birch grows throughout the whole of Finland (Hämet-Ahti et al. 1992). Birches started their dispersion to northern Europe soon after the end of the last glacial period some 12 000 years ago (Huntley and Birks 1983). Recolonization from refugia came from two main directions, one eastern and one western (Palme et al. 2003) and birches became dominating tree species in Finland during the preboreal era, 10 000 - 8 800 years ago (Kalliola 1973).

Silver birch is a monoecious wind- and cross-pollinating species with, unisexual, small and simple flowers situated in separate male and female catkins (Jonsell 2000). Light and small pollen grains are produced in huge quantities in the hanging male catkins (Kujala 1946, Sarvas 1952) and carried by the wind over long distances, even as far as 2000 km (Hjelmroos 1991). Flowering occurs simultaneously with leafing in spring (Sarvas 1952), flowering times overlapping widely among distant populations (Luomajoki 1999). A chemical self-incompatibility mechanism ensures that seeds usually develop as a result of cross-pollination (Hagman 1971). Silver birch is a prolific seed producer, but there is large interannual variation in the quantity and quality of seed crops. Abundant seed crops are repeated at 2-3 years intervals in southern Finland and with less frequency in the north (Sarvas 1948, 1952, Koski and Tallqvist 1978). The seeds are small and light nutlets with two separate wings and rather good dispersal ability (Sarvas 1948, Nygren 2003). Generation time of silver birch is usually about 10 years in nature, but it can be induced to produce seed as early as at the age of 8 months when kept in greenhouse conditions in continuous day, regulated temperature, increased CO_2 concentrations, fertilization, irrigation and increased air humidity (Longman and Wareing 1959, Holopainen and Pirttilä 1978).

Silver birch is a light-demanding, fast-growing and relatively short-lived species. It is an early successional species, readily colonizing open areas after forest fire and clear-cutting, forming pure stands or admixtures with conifers (Niemistö et al. 2008). It can occupy a wide variety of sites, from fertile mesic sites to poor, dry sites, even in rocks, but does not survive on wet sites, peatlands or poorly aerated and compact clay soils. Together with downy birch (*B. pubescens* Ehrh.), silver birch is the most common broad-leaved tree species in northern Europe and thus important to the biodiversity and to the fertility of forest soils in the northern coniferous zone (Niemistö et al. 2008). It is expected that the significance of birch will increase in the future, being able to benefit more than conifers from predicted global warming (Kellomäki et al. 1996, Talkkari 1998).

Silver birch is appreciated as a valuable raw material in both mechanical and chemical forest industries and as an essential ecological component of a diverse and healthy forest. The growing stock of silver birch in Finland is estimated at 75 million m^3, which corresponds to 3.6 % of the total growing stock of forests in the country (Niemistö et al. 2008). Large-sized birch is mainly used in the plywood and sawmilling industry; the former consuming 1.5-1.8 million m^3 per year on the average during the 2000's. By volume, the most important consumer of birch in Finland is the pulp industry, consuming some 10-12 million m^3 annually in the beginning of the 2000's (Niemistö et al. 2008). However, only about half of supply of birch wood is met from Finnish forests, the rest being imported, mainly from Russia (Finnish

Statistical...2008). The rapid increase in the prices of Russian timber has created an urgent need to increase the supply of birch wood from Finnish forests.

From the silvicultural point of view, the aim of management of birch is to produce high quality large-sized timber for the plywood and sawmilling industries (Niemistö et al. 2008). To achieve this, programmes to cultivate silver birch were initiated in the 1960's (Raulo 1978). The planting of silver birch increased significantly in the 1980's peaking in 1992, when nurseries produced more than 23 million silver birch seedlings (Finnish Statistical...2008). As a result of an extensive breeding program that started in the 1960's, (Raulo and Koski 1977, Viherä-Aarnio 1994), the yield and stem quality of silver birch has been significantly improved (Hagqvist and Hahl 1998). The mass production of improved birch seed in polythene greenhouse seed orchards has become well established practice (Lepistö 1973, Hagqvist 1991, Ahtikoski 2000, Haapanen and Mikola 2008), and successful methods for vegetative propagation by tissue culture have also become available (Simola 1985, Ryynänen and Ryynänen 1986, Viherä-Aarnio and Velling 2001). However, since the 1990's, the planting of silver birch has steadily decreased to 3 million seedlings in 2007 (Finnish Statistical...2008). This decline has mainly been because of the high risk of moose browsing and damage (Heikkilä and Raulo 1987). Avoiding moose damage in young plantations is a prerequisite for successful cultivation of silver birch.

1.3 Height growth cessation, dormancy and hardening

1.3.1 Height growth cessation and bud formation in birch

The height growth of juvenile silver birches follows a free growth pattern (Junttila and Nilsen 1993), i.e. during the elongation of the shoot, internodes lengthen and leaf primordia are formed simultaneously (Pollard and Logan 1976, Kanninen 1990). In fixed or predetermined mode of shoot growth, only the internodes between the leaf primordia lengthen and the number of leaves (or dwarf shoots) in the overwintering buds are fixed (Lanner 1976, Kanninen 1990). In mature silver birches, shoot growth is also partly predetermined (Kennedy and Brown 1984). During growth, cell proliferation and primordia initiation occur at apical meristem, whereas internode elongation occurs in the subapical meristem immediately beneath the apical meristem (Junttila and Nilsen 1993, Welling 2003).

The resting buds of woody plants develop when the cessation of normal internode extension leads to a telescoping of the shoot. In birch, the lack of elongation alone leads directly to the formation of a resting bud, because the overlapping stipules of the unexpanded leaf primordia form the protective bud scales. Thus, birch buds are unextended shoots in which the apical meristem are covered by leaf primordia and brown scales formed from rudimentary leaves, stipules, that overlap them (Wareing and Phillips 1978, Thomas and Vince-Prue 1997). Apical bud, bearing the apical meristem, is formed during embryogenesis, whereas axillary or lateral buds are formed as a function of apical meristem (Welling 2003). The axillary buds develop on the main axis above the leaf primordia on long shoots, but terminally on short shoots (Kalela 1971). The embryonic foliage leaves of silver birch for the next growing season develop in each bud and reach their maximum size in August and September (Rinne et al. 1994). Initiation of the bud scales also takes place in the late summer.

Formation of the terminal bud in birch is followed by the abortion of the shoot tip. This happens through the formation of an abscission layer just above the uppermost axillary bud of the long shoot. The shoot tip drops during late spring or summer and the function of the terminal bud is taken over by the uppermost axillary bud (Romberger 1963). Thus, growth habit of birch is symbodial and monocasic (Kalela 1971).

1.3.2 Regulation of height growth cessation in birch

Cessation of height growth in woody plants is in the first hand regulated by photoperiod (Fuchigami et al. 1982). The influence of the photoperiod on growth and dormancy of woody plants was first shown by Garner and Allard (1923) and later confirmed in numerous studies (e.g. Wareing 1956, Nitsch 1957, Luoranen 2000). The photoperiodic control of vegetative growth is particularly important in species with a free growth pattern, such as juvenile birches (Junttila and Nilsen 1993). They can grow indefinitely under long days but stop growing and set terminal buds under short days (Nitsch 1957, Luoranen 2000). However, height growth cessation is not necessarily followed by dormancy. Height growth may restart if the duration of a short day treatment has been too short or if the seedlings are treated too early after sowing (Luoranen and Rikala 1997, Luoranen 2000). Adult trees are less sensitive to photoperiod (Junttila and Nilsen 1993), and usually stop growth in mid-summer independently of the photoperiod (Junttila 1976).

When the lengthening of night at the end of summer reaches a critical length, growth cessation is triggered. The effect of photoperiod is usually determined by the length of the dark period rather than day length (Nitsch 1957, Howe et al. 1996, Thomas and Vince-Prue 1997), but northern tree populations show a light-dominant response and sensitivity to light intensity and quality as well (Håbjørg 1972b, Junttila and Kaurin 1985, 1990).

The critical night length can be defined in different ways. Eriksson and Ekberg (2001) defined it as the shortest night length at which 50 % of the plants belonging to a genetic entry are induced to form an apical bud. Critical night length can also be defined as the night length that causes cessation of height growth (e.g. Håbjørg 1978). Thus, depending on the definition and method of measurement, slightly differing values for critical night length can be obtained.

In tree species with a wide natural distribution, origins from different latitudes have different critical night lengths that trigger height growth cessation. Northern ecotypes have shorter critical night length than the southern ones (Vaartaja 1959, Håbjørg 1978, Ekberg et al. 1979). Geographical origins that clearly differ as regards their critical night length are commonly called phoperiodic ecotypes (Vaartaja 1954, 1959, Heide 1974, Håbjørg 1978). The existence of photoperiodic ecotypes in forest trees has been shown in many studies (e.g. Sylvén 1940, Pauley and Perry 1954, Vaartaja 1954, 1959, Heide 1974 and Ekberg et al. 1979). For birch, the studies by Atle Håbjørg are classics. He showed the existence of photoperiodic ecotypes in *B. pubescens* (Håbjørg 1972a) and later in *B. pendula* and several other Scandinavian tree species (Håbjørg 1978). The variation in critical night length among individual trees within birch populations is, however, poorly known, although it may largely explain the variation in the timing of growth cessation and development of frost hardiness, which are important adaptive traits.

The night length signal is captured by phytochomes, which are the best known group of light sensing pigments, photoreceptors, in plants (Thomas and Vince-Prue 1997, Eriksson 2000). The phytochromes mainly sense red (λ_{max} 660 nm) and far-red (λ_{max} 730 nm) light, and to some extent also blue light (Batschauer 1998). They exist in two spectrally interchangeable forms: an inactive red light absorbing form (Pr) and active far-red absorbing form (Pfr). During the light period, the Pr form changes to Pfr form. The Pfr form is converted back to Pr by far-red light treatment or in darkness, which is called dark-reversion (Welling 2003). The determining factor is the length of the uninterrupted dark period. When the dark period is long enough, bud set is induced.

The photoperiodic signal is mediated by the phytochromes through complicated signaling pathways, and finally the action of growth regulators (plant hormones) modify the growth and developmental responses of the plant (Eriksson 2000). Gibberellins (GAs) and abscisic acid (ABA) are the most studied plant hormones involved in the regulation of growth and dormancy (Welling 2003). GAs have a central role in regulation of the elongation growth and height growth cessation of woody plants (Junttila et al. 1991, Olsen et al.1995). As a response to long night conditions, biosynthesis of GA_1 is blocked, which hinders cell divisions in subapical meristems and growth ceases (Olsen et al. 1995, 1997, Hansen et al. 1999). ABA on the other hand, has been shown to induce dormancy and accelerate abscission by counteracting the growth-promoting hormones (Welling 2003).

The photoperiodic regulation of growth cessation is modified by several other external and internal factors. Temperature is the most important external factor and can affect the photoperiodic response in many ways. The response to photoperiod may be different in low and high temperatures (Dormling et al. 1968, Håbjørg 1972a, Heide 1974, Li et al. 2002), in constant and fluctuating temperatures (Heide 1974) and in low and high night temperature (Håbjørg 1972a, Heide 1974). According to Koski and Selkäinaho (1982), as well as Koski and Sievänen (1985), the timing of height growth cessation is determined by the interaction of night length and temperature sum of the growth period. Height growth cessation and bud phenology of Norway spruce (*Picea abies* (L.) Karst.) seedlings is also influenced by the temperature during zygotic embryogenesis, i.e. higher temperature during seed development delays growth cessation and bud formation (Kvaalen and Johnsen 2008, Johnsen et al. 2009). This kind of epigenetic memory has not been studied in birch, but there is evidence of the effect of post-zygotic temperatures during seed development on fitness of the progeny in other angiosperms (e.g. Lacey and Herr 2000). Soil water and water stress (Li et al. 2002), air humidity (Håbjørg 1972a) and nutrient availability (Landis et al. 1999, Black-Samuelsson and Eriksson 2002) also affect the growth cessation of tree seedlings. Internal factors including seedling size (Junttila 1976) and physiological stage of development (Hari et al. 1970, Hari 1972, Landis et al. 1999) may also affect the photoperiodic response of seedlings (Luoranen and Rikala 1997, Luoranen 2000, Partanen 2004). The effect of tree age on regulation of height growth cessation is not completely understood. Precise characterization of birch seedling materials related to cessation of height growth and critical night length, between and within populations, is needed in a variety of studies, such as gene mapping of photoperiodism and frost hardening. It is crucial also in nursery production of seedlings for forest cultivation (Luoranen 2000, Luoranen and Rikala 2001).

1.3.3 Dormancy

After growth cessation in autumn, the vegetative buds of trees enter a state of dormancy, which is defined as the temporary suspension of visible growth of any plant structure containing a meristem (Lang et al. 1987). Dormancy usually refers to bud dormancy or bud rest (Hänninen 1986), which is built up in the buds soon after budset. Dormancy prevents untimely budburst during a season that would be unfavourable (Eriksson and Ekberg 2001). The nature and depth of dormancy changes gradually during the autumn and winter, and it is usually divided into three consecutive phases (Sarvas 1974, Hänninen 1986, Lang et al. 1987). The different phases of dormancy, named as para-, endo- and ecodormancy by Lang et al. (1987), are regulated in a complex way by various factors during autumn, winter and spring time.

After their formation, axillary buds are in paradormancy, when the presence of the apical bud prevents their growth (Lang et al. 1987). A few weeks after growth cessation both apical and axillary buds enter endodormancy, in which their growth is prevented by internal physiological factors within the buds themselves, and are incapable of growth even under favourable growth conditions. Thus, the buds of *B. pubescens* are unable to burst from July to October (Welling et al. 2004). When buds are exposed to chilling temperatures, i.e. temperatures between -3 to +10ºC, for a certain time period (Sarvas 1974) they switch from endodormancy to ecodormancy. Ecodormancy, in turn, is maintained by environmental factors, i.e. unfavourable low ambient temperatures, released by temperatures above zero (Fuchigami et al. 1982) and followed by bud burst, when the accumulated temperature exceeds a species specific threshold (Sarvas 1972).

1.3.4 Hardening

Frost hardening starts simultaneously as trees enter dormancy. Cessation of height growth is the first visible component of the frost hardening process and necessary for its further development (Weiser 1970). There is a close relationship between growth cessation and development of frost hardiness (Sakai and Weiser 1973, Junttila 1989, Junttila and Kaurin 1990, Junttila and Skaret 1990). Development of frost hardiness is a multi-phased and sequential process (Weiser 1970, Christersson 1978). The first stage is initiated by a short photoperiod and requires rather high temperatures (Fuchigami et al. 1971). For further development, low and freezing temperatures are needed (Weiser 1970, Howell and Weiser 1970). There is a rapid increase in frost hardiness a few days after the first autumn frost (Howell and Weiser 1970). Finally, exposure to freezing temperatures of -30°C...-50°C are needed for the development of maximum hardiness (Weiser 1970). During winter, birch becomes insensitive to the photoperiod and the overwintering process is mainly regulated by ambient temperature (Welling et al. 2004).

Cold injury can be generated by several conditions, e.g. late spring or early autumn frosts, severe cold in late fall, winter and early spring, frost cracking and winter desiccation (Sakai and Weiser 1973). When temperate zone woody plants are fully hardened, they can survive very low temperatures, even the temperature of liquid nitrogen (-196°C), and frost injury in mid-winter rarely takes place (Sakai and Weiser 1973, Koski 1983, Junttila and Kaurin 1990, Welling et al. 2004). Severe early autumn frosts can cause extensive damage to silver birch seedlings, if frost hardening is delayed. This occurred in nurseries in eastern Finland in September 1993 for example (Kivivuori 1994ab, Luoranen 2000). The proper timing of hardening is, thus, crucial in avoiding of frost injury in the autumn (Junttila and Kaurin 1990).

1.4 Moose as a damage agent in young birch plantations

Moose (*Alces alces* L.) are one of the major causes of damage in young silver birch plantations in Finland (Heikkilä and Raulo 1987, Tomppo and Joensuu 2003). The natural distribution of moose covers the whole country, and its population density has increased drastically since the 1960's. Consequently, the high risk of moose damage is one of the main reasons for the sharp decrease of birch cultivation in Finland in recent years (Tomppo and Joensuu 2003, Finnish Statistical...2008, Niemistö et al. 2008). Moose browse leaves and young twigs of birch and, in striving for these, may break the stems of even tall saplings (Kangas 1949, Löyttyniemi and Lääperi 1988). Damage by moose may reduce the growth or lower timber quality (Lavsund 1987, Heikkilä et al. 1993, Lilja and Heikkilä 1995).

Moose are generalist ruminant herbivores, feeding on several plant species (Cederlund et al. 1980). Birch is an important part of their diet throughout the year, but it is mostly browsed in summer, from June through September, when the leaves and young shoots are eaten (Cederlund et al. 1980, Lavsund 1987, Hjeljord et al. 1990). In winter time the palatability and digestibility of birch is much lower than in summer (Hjeljord et al. 1982, Palo et al. 1985, Hjeljord 1987), but it is still frequently browsed due to its widespread availability (Andersson 1971, Cederlund et al. 1980). Scots pine (*Pinus sylvestris* L.) forms a predominant part of the diet of moose in winter, but aspen (*Populus tremula* L.), rowan (*Sorbus aucuparia* L.) and willows (*Salix* L.) are preferred (Andersson 1971). Selective feeding is related to habitat, forage palatability and relative abundance (Renecker and Shwartz 1998). Selection has also been attributed to nutritional quality (nutrients, carbohydrates, energy) and the availability and size of the food items (Belovsky 1981, Saether and Andersen 1990) and to the avoidance by the moose of deterring secondary substances with antiherbivore activity (Bryant and Kuropat 1980).

Moose usually prefer silver birch to downy birch (Danell et al. 1985) and planted silver birches are preferred to naturally born ones (Heikkilä 1991). Otherwise reports on the selective browsing within a birch species by moose are few. In Scots pine it has been shown, that the intensity of moose browsing in winter is negatively correlated with the latitude of the geographical origin (Niemelä et al. 1989). However, little is known about the browsing preference by moose for silver birch of different origin.

Transferring seed from south to north can be a means to improve yield in forestry (Hagman 1980, Morgenstern 1996). In order to take advantage of the warming up of climate, the use of slightly more southern seed origins has been suggested (Marttila et al. 2005). The effects of seed origin, as well as the effects of seed transfers on the susceptibility of silver birch to moose browsing are poorly understood. It is not known, whether seed transfers increase the risk for moose damage, or whether seed transfer or proper selection of the seed origin could be a means to decrease the risk.

1.5 Geographic variation, provenance research and seed transfers of birch

1.5.1 Basic concepts

The geographic genetic variation observed in any tree species is shaped by the interaction of three main evolutionary forces: natural selection, genetic drift and migration (Hedrick 1983, Endler 1986, White et al. 2007). The most important of these is natural selection, i.e. the tendency for the fittest individuals to survive and leave more offspring to the next generation, whereby a population becomes genetically adapted to the local climatic and edaphic conditions. If environmental gradients exist, populations in distinct localities become differentiated from each other as a result of different selection pressures. Natural selection is not always easy to detect and is sometimes even a subject of misleading interpretations (Endler 1986). Genetic drift occurs as a consequence of drastic reduction in population size, resulting in a haphazard loss of genetic variation and influencing genetic variation both within and between populations. Migration (gene flow) in the form of seed and pollen dispersal reduces genetic differences among populations and thus counteracts the genetic differentiation due to natural selection (Hedrick 1983, White et al. 2007).

In principle, the patterns of genetic geographic variation may be described with two different terms: a cline or an ecotype. A cline is a continuous genetic gradient in a single measurable trait that is associated with an environmental gradient (Langlet 1959, Morgenstern 1996). If environmental gradients vary continuously, clinal patterns of genetic variation are most commonly observed. Clinal variation cannot, however, always be explained merely as an effect of natural selection as shown e.g. in the studies of epigenetic memory of Norway spruce (Kvaalen and Johnsen 2007, Johnsen et al. 2009). An ecotype is a clearly defined ecological unit within a species which is adapted to a particular environment. The ecotype concept was introduced to botanical-genetic discussion by Turesson (1922) based on his studies on the adaptation of perennial herbs to different site conditions. Ecotypes are most likely to develop when environments change abruptly and populations are more isolated from each other (White et al. 2007). The ecotype concept was adopted in studies of photoperiodism in forest trees after differences in critical night length of tree populations from different latitudes were discovered (Vaartaja 1954, 1959). It has been commonly used in literature when comparing origins from distant latitudes adapted to differing photoperiodic conditions, with clearly differing critical night lengths (Håbjørg 1972a, 1978, Heide 1974, Junttila 1976, Li et al. 2002).

The purpose of studying the geographic variation of forest trees is to describe the pattern and amount of variation and to understand the role of evolutionary forces behind the observed patterns. Describing and detecting the statistical patterns of geographic variation provide us with good hypotheses of causality, but finally we should aim at understanding and proving the true causal relationships behind the variation. Knowledge of the geographic variation of tree species is needed to find the best geographical sources of seed for a particular region, for planning seed transfer rules and breeding programs, and for designing gene conservation strategies. Studies of geographic variation should be the first step in genetic research or domestication of any tree species (Morgenstern 1996, White et al. 2007). Climatic change further emphasizes the importance of understanding the differing adaptation of tree populations in different regions (Rehfeldt et al 1999, 2002, Saxe et al. 2000).

Three types of approaches are used to study geographic genetic variation: 1) use of genetic markers measured from material obtained directly from natural stands, 2) use of seeds of different geographic origins sown in artificial environments (growth chamber, greenhouse, nursery), grown for a short time followed by measurement of seedling traits, and 3) use of different origins grown in long-term field experiments that enable measurement of economic traits: yield, stem and wood quality.

Genetic markers are largely neutral to selection pressure and the pattern of variation detected by them usually explains little about the adaptation of populations (Karhu et al. 1996, White et al. 2007). Short-term experiments in artificial, strictly controlled and homogeneous environmental conditions are powerful tools for demonstrating and modeling adaptive variation among provenances. Long-term provenance experiments in the field are, however, required to develop definitive seed transfer rules and to make final decisions about the best provenances for reforestation programs. Although being costly to establish, maintain and measure, long-term field experiments are irreplaceable when testing the performance of provenances across the range of climates, soils and management regimes and when choosing the best provenance for reforestation (White et al. 2007).

"Provenance" is defined as the geographic location of the native population where the plant material originated and "seed source" as the geographic location from which the seed was obtained, regardless of whether or not the parent trees are located in their native population (White et al. 2007). The term "provenance" is commonly used in the international literature, but it is sometimes used also in the meaning of "seed source" as defined above by White et al. (2007). Thus, Hämet-Ahti et al. (1992) in Finland consider it ambiguous and, instead, recommend concepts "*alkuperä*" and "*lisäyslähde*" to be used in Finnish literature. Accordingly, the "seed origin" is used instead of "provenance" in this thesis and in the original papers. A provenance experiment, on the other hand, is a well-established term for an experiment where different provenances are compared at the same site.

1.5.2 Background of silver birch provenance research

Variation within tree species related to geographic origin has been of interest for a long time (Morgenstern 1996). Pioneering work was initiated on Scots pine by du Monceau in 1745-55, repeated by de Vilmorin in 1820-30 and published in 1862 (Langlet 1971, Morgenstern 1996), attracting much attention in all European countries (Langlet 1971). At that time seeds of foreign origin were widely used in forestry, which increased the interest in provenance research (Heikinheimo 1949). Systematic provenance testing of several species in Europe and North America was initiated in the early 1900's (Kalela 1937, White et al. 2007). In Finland, the first extensive provenance experiments with Scots pine and Norway spruce were established in the 1920's. Based on these trials, Kalela (1937) reported the first, early age results, and Heikinheimo (1949) outlined the first seed transfer rules for Scots pine and Norway spruce in Finland. Beuker (1996) utilized the old provenance trials of Scots pine and Norway spruce to elucidate the long-term effect of climate change on forest trees.

Birches were ignored in this early provenance research, because they were undervalued species in forestry at that time. The first progeny trials of birch in the Nordic countries were established in Sweden in the 1940's and thus Johnsson (1951, 1967) was the first to compare birch families of geographically distant origin. Johnsson also pioneered birch provenance research by establishing extensive trials in 1973-74 (Johnsson 1976). Based on these trials, Stener (1997) studied the differences in yield, stem quality and wood density among seed origins, and developed seed transfer rules for birch in Sweden. Erkén's (1972) study based on progeny trials established in northern Sweden in 1947-51 also dealt with seed transfers.

In Finland, extensive progeny trials with silver birch were established in the 1960's in southern and central part of the country as a part of a newly initiated breeding program. Principles for seed transfers were based on the results from these trials (Raulo and Koski 1977, Raulo 1979). Long distance seed transfers from south to north and differences between southern and central Finnish birch families in adaptation were studied by Raulo (1976).

In Norway, Langhammer (1982) compared single tree progenies of birch from open pollination covering a wide number of origins from Norway, Sweden, Finland and Latvia. In Germany, combined progeny and provenance trials, including origins from central Europe, Finland and Sweden, were established in 1976 (Kleinschmit and Otto 1980) and analyzed some 20 years later (Kleinschmit 1998, 2002). Progeny and provenance trials of birch established in Scotland in 1970's and 1980's also included Finnish origins in addition to local Scottish ones (Worrell et al. 2000).

Very few studies have been made concerning the performance of exotic birch origins in Finnish conditions. Velling (1979) reported results on the early survival, phenology and growth of silver birch seedlings of Baltic origin in nursery and field trials. Some Baltic origins were also included in nursery and growth chamber studies of the annual physiological rhythm of silver birch by Koski and Sievänen (1985) and Li et al. (2002, 2003). Studies of mature trees in long-term field trials are, however, missing.

1.5.3 Geographic variation in silver birch

Taxonomically, silver birch populations in northern Europe are divided into two types, the southern main type *B. pendula* var. *pendula* and the northern type *B. pendula* var. *lapponica* (Hämet-Ahti et al. 1992), based on the south to north variation in the morphology of bark, leaves, catkin scales, samara wings, dwarf shoots and the form and stickiness of the buds (Lindquist 1947). The latter type is dominating in northern Finland and northern Sweden (Kallio and Mäkinen 1978).

In adaptive traits, such as the timing of growth cessation in autumn, bud burst in the spring and other events of the annual cycle, clinal variation has been shown within the natural distribution of silver birch in northern Europe (Eriksson and Jonsson 1986 and references therein). Because photoperiod and temperature conditions, as well as the length of the growing season, change more or less gradually from southern to northern latitudes, these clines often follow a latitudinal pattern. Silver birch populations from different latitudes have different critical night lengths that trigger height growth cessation: northern ecotypes having shorter critical night lengths than the southern ones (Håbjørg 1978, Langhammer 1981).

The growth rhythm characteristics studied by Johnsson (1976), e.g. timing of height growth cessation, autumn coloration and defoliation were found to be strongly correlated with seed origin latitude, showing a clinal variation over the total range of latitudes 56º-66ºN. The more northern the seed origin the earlier the autumn coloration and defoliation, irrespective of the place of cultivation, and, in contrast to the relationship between the height and latitude. A negative correlation between the latitude of seed origin and autumn coloration of silver birch seedlings was shown by Velling (1979) in a material from the Baltic countries and Finland (56º-61ºN). Kleinschmit and Otto (1980) noted a clinal variation in growth cessation of one-year-old seedlings of silver birch, with the northerly southern Finnish progenies being the earliest, followed by southern Swedish and Polish progenies, and progenies from Holland being the last. A latitudinal cline in the growth rhythm of open pollinated families of silver birch from northern Europe (57º-67ºN) was reported by Langhammer (1981), the northern origins being the earliest to start and the southern ones the last to cease.

Silver and downy birches of northern origins come into leaf earlier than southern ones and the temperature sum required for initiation of growth in spring is higher for southern than for northern populations (Johnsson 1974). Finnish silver birch origins flushed much earlier than the more southern, local Scottish origins and were prone to spring frost damage in Scotland (Worrell et al. 2000). A longitudinal cline in flushing time of Lithuanian and Polish silver birch origins was shown by Wojda (2004).

Clinal variation in growth of silver birch seedlings was shown by Velling (1979) among provenances from eastern Europe, the Latvian provenances having the greatest growth and the Finnish the smallest. Langhammer (1981) showed a latitudinal cline in annual height growth of open pollinated silver birch families from 57º-67ºN when grown at Ås (59º40'N). Raulo (1976) reported a latitudinal cline for south and central Finnish silver birch progenies planted in northernmost Lapland (69º45'N) with respect to their reforestation value (mean height at age 8 and 10 multiplied by survival). The southern origins are able to reach a bigger total height during the growing season due to their later growth cessation and longer growth period compared to the northern origins (Velling 1979, Langhammer 1981). For the same reason, the southern origins are also more prone to damage by early autumn frosts when transferred northwards, which in turn decreases their growth in more northern test locations. Thus, depending on the direction and distance of seed transfer in relation to the test location, the pattern of height growth usually follows a curvilinear pattern of variation (see review by Eriksson and Jonsson 1986).

The wide and continuous area of distribution, outcrossing breeding system, long-distance dispersal of pollen by wind, wide overlapping of flowering times of distant stands, abundant seed production and good dispersal of seeds all enhance gene flow from one birch population to another, maintaining wide genetic variation within populations and continuous variation among populations (Hamrick et al. 1992, Eriksson et al. 2003).

1.5.4 Effects of seed transfers of silver birch

As a general rule, transferring seed from a provenance evolved in a harsher (colder, drier) environment to a milder one usually results in less growth and yield than the use of a local provenance, while some gain in growth may be expected when moving seed from milder to harsher climates (Rehfeldt et al. 1999, 2002). There is, however, a risk of losses in survival and yield if the transfer is too extreme (White et al 2007).

Current seed transfer guidelines for silver birch in Finland are based on extensive single tree progeny trials established in the 1960's (Raulo 1976, 1979, Raulo and Koski 1977) and later experiences obtained from the field. According to the studies by Raulo and Koski (1977) and Raulo (1979), latitudinal transfer distances of ca. 200 km in southern and central Finland are possible without any systematic effect on mortality, growth or stem quality. Erkén (1972) observed increased mortality in birch progenies when transferred ca. 3 degrees of latitude northwards in northern Sweden, whereas Johnsson (1976) and Stener (1997) found a weak response to seed transfers within a few degrees of latitude in Sweden in either a northwards or southwards direction. A long distance transfer from south Finland to northern Lapland resulted in a drastic decrease in survival and growth of southern and central Finnish origins and revealed a difference in the adaptation of these two groups in extreme northern conditions (Raulo 1976).

In the study by Erkén (1972), silver birch origins that had their origin within ± 1 degree of latitude from the site of the trial were the best with regards to growth, whereas a long transfer from the north (3 degrees of latitude) resulted in reduced growth. According to Stener (1995) a transfer of Finnish birch origins 400-600 km southwards to southern Sweden had negative effects on survival and growth of the trees, and the use of Finnish origins in southern Sweden south of 59ºN was not recommended (Stener and Werner 1997). Even longer transfers southwards were carried out in Germany in the 1970's where southern Finnish birch origins proved to be very slow growing compared to central European ones (Kleinschmit and Otto 1980, Kleinschmit 1998, 2002). Finnish seed origins of silver birch also performed very poorly when transferred to Scotland (Worrell et al. 2000).

It is recommended to use seed of local origin in the prime area of silver birch cultivation in southern and central Finland, which means a transfer distance either northwards or southwards of less than 100 km (Hyvän metsänhoidon... 2006, Niemistö et al. 2008). If there is no local origin available, the transfer distance, measured as temperature sum (degree days), should not exceed 150 d.d. (ca. 150 km). At present, birch cultivation is mainly based on the use of improved seed from seed orchards. The recommended utilization area of seed orchard seed extends 80 d.d northwards and 100-140 d.d. southwards from the mean temperature sum of the original growing sites of the clones in the seed orchard (Niemistö et al. 2008).

In the southern and middle parts of Sweden (south of 61ºN) it is recommended that transfers to the north can be made within 2 degrees of latitude, and in northern Sweden (north of 61ºN) within 1.5 degrees, without any noteworthy effect on growth, quality and mortality (Stener 1997). On the other hand, in the southern and middle parts of Sweden transfers to the south can be made within 3 degrees of latitude and in northern Sweden within 2 degrees.

1.5.5 Need for provenance research

Practically no imported seed origins have been used for the cultivation of birch in Finland. This has been because seed of native origin with high genetic quality has been available in abundance (Hagqvist 1991, Viherä-Aarnio 1994, Haapanen and Mikola 2008). However, there is a need to improve our knowledge about the performance of imported seed origins of birch in Finland. The free trade of forest cultivation material within EU may give rise to efforts to introduce birch seeds or seedlings to Finland from abroad, e.g. from the Baltic countries. Transferring seed from south to north, within certain limits, may offer an opportunity to improve yield (Hagman 1980). The use of slightly more southern seed origins has been suggested as a part of Finland's National Strategy for Adaptation to Climate Change in order to maximize carbon fixation and storage (Marttila et al. 2005). Provenance experiments and seed transfer studies in general are valuable in improving our understanding of the adaptation of trees to changing climatic conditions.

1.6 Aims of the study

The general aim of this thesis is to improve our knowledge about the effects of seed origin on the timing of height growth cessation and the field performance of silver birch from different latitudes, with special attention given to browsing damage by moose in young plantations.

The specific aims of the individual studies included in this thesis were:

I To examine the effect of seed origin and sowing time on the timing of height growth cessation, length of growth period and final height of first-year silver birch seedlings in a naturally changing photoperiod.

II To estimate the critical night length for 50 % bud set and its within-population variation in two photoperiodic ecotypes - a southern and a northern stand - of silver birch.

III To examine the effect of seed origin latitude on the extent and degree of moose browsing of silver birch in field conditions.

IV To compare Baltic and native Finnish seed origins of commercial sized silver birch grown in Finland, and to examine the effects of latitudinal seed transfers on the growth and stem quality of silver birch.

2 MATERIAL AND METHODS

2.1 Seed origins

The effect of seed origin and sowing time on the timing of height growth cessation (**I**) was studied with material consisting of seven stand seed origins from Estonia and Finland ranging in latitudes from 58° to 67°N (Table 1). Critical night length for bud set and its variation (**II**) was studied with seeds from 21 open pollinated mother trees from one southern (Tuusula, 60°N) and one northern (Kittilä, 67°N) Finnish stand. Browsing damage by moose (**III**) was examined with material including 28 stand seed origins from Finland, Sweden, Estonia, Scotland and Russia, ranging in latitude from 53° to 67°N and one controlled crossing. The effects of seed transfer on yield and stem quality (**IV**) were studied with 16 stand and 5 single tree origins from Finland, Baltic countries and Russia, ranging in latitude from 54° to 63°N (Table 1).

Table 1. Seed origins and experiments used in the studies (**I - IV**) of the thesis.

Study	I	II	III	IV
Aim	Timing of height growth cessation	Critical night length for bud set	Moose browsing	Growth and stem quality
Number of origins	7	2	29	21
Range of latitudes	58°10’N - 67°44’N	60°27’N and 67°44’N	53°50’N - 67°44’N	54°30’N - 63°18’N
Type of seed	Stand seed	Single tree progeny from 21 trees/stand	Stand seed (28) Single tree progeny (1)	Stand seed (16) Single tree progeny (5)
Type of experiment	Greenhouse	Phytotron	Field test	Field test
Age of plant material	1st-year seedlings	1st-year seedlings	11-year-old saplings	22-year-old trees
Location of experiment	Loppi	Tromsø	Loppi	Tuusula Viitasaari
Latitude, longitude of experiment	60°37’N, 24°26’N	69°39’N, 18°55’N	60°39’N, 24°22’N	60°21’N, 25°02’N 63°11’N, 26°07’N

2.2 Experiments and measurements

The experiment relating to the timing of height growth cessation (**I**) was conducted in a greenhouse at Haapastensyrjä Tree Breeding Station, Loppi, southern Finland (Table 1). The experiment was carried out under natural light and photoperiod during the growing season. All seven origins were sown eight times at 1-2 -week intervals during the summer, from late May to late July. Origin and sowing time combinations with 12 seedlings in plots were replicated twice. Growth cessation was observed by measuring seedling height twice a week until the height remained constant over three successive measurements. The mean value of the date of growth cessation in the plot was used as the observation in statistical analysis.

The three photoperiodic response experiments for estimating the critical night length (**II**) were carried out in the phytotron of the University of Tromsø, northern Norway (Table 1). Progeny from open pollinated mother trees of both ecotypes (Tuusula and Kittilä) were grown for 4 to 6 weeks in different night length treatments. For Tuusula seedlings, the night lengths used varied from 5 to 8.5 h, and those for Kittilä seedlings from 1 to 4.5 h. The seedlings received high intensity light from incandescent and fluorescent lamps (experiments 1 and 2) or natural daylight (experiment 3) for 12 h each day. This was preceded and followed by low intensity light from incandescent lamps to give the different night length treatments. Bud set was determined indirectly by observing the formation of new leaves at the shoot apex. The number of seedlings with set buds was counted to calculate the percentage of seedlings with set buds for each night length treatment and mother tree. Studies **I** and **II** were carried out with first-year seedlings.

Browsing damage by moose and differences between seed origins (**III**) were studied in a provenance trial located at Loppi (Table 1). Seedling height was measured before (age 5) and after (age 10) moose damage had occurred. At the age of 11 years, every tree was graded for severity and frequency of moose browsing, and the number of browsed branches estimated from a crown sample. Diameter at breast height of all trees and stem diameter at the point of stem breakage of broken trees were measured.

Effects of seed transfers on yield and stem quality (**IV**) was examined in two provenance trials, one at Tuusula, southern Finland and one at Viitasaari, central Finland (Table 1). Measurements were made on 22-year-old trees. Tree height and diameters at 1.3 and 6.0 m were measured and the number of vertical branches and forks per stem were counted. Stem taper and individual tree volume were calculated, and respective volumes/ha were estimated. Relative frequencies (%) of trees with a vertical branch or a forked stem were calculated.

The experiments used in studies **III** and **IV** were established on typical southern and central Finnish clear-cut areas on moist upland forest sites. In both studies, the plot means were used as observations in statistical analysis.

2.3 Statistical analysis

In study **I**, the effects of seed origin and sowing time on time of growth cessation, night length and seedling height at growth cessation and length of growth period were examined with a two-way analysis of variance. Regression models of response variables on seed origin and sowing date were determined, in which the seed origin factor was replaced with the interval scale variable of latitude, and the sowing time factor with the interval scale time variable.

In study **II**, to estimate the critical night length (CNL) for 50 % bud set in the progeny of a particular mother tree, S-shaped regression models of bud set percentages on night length were estimated for each mother tree and experiment. The models were then used to calculate CNL values for each mother tree. A repeated measures mixed model analysis of variance was used to test for the differences in the mean CNL value between ecotypes and experiments. Levene's test was used to compare the within-population variances of the ecotypes. The effect of individual mother trees in the experiments was tested by two-way analyses of variance. The interaction between mother tree and experiment was analyzed with Spearman rank correlation coefficients.

An analysis of covariance was used in study **III** to test for the effects of seed origin latitude and sapling height on moose browsing. Latitude and plot height at age of 5 were used as covariates.

In study **IV**, a linear mixed model analysis was used separately for the two trials to examine the effects of latitude of seed origin on survival, tree height, diameter at breast height, relative stem taper, volume/ha and proportion of trees with a stem defect. Latitude of seed origin and the square of latitude were used as covariates.

The effects of seed transfer distance (latitudinal difference of the seed origin and location of the field trial) on survival, volume/ha and proportion of trees with stem defect were also examined with a linear mixed model analysis. Seed transfer distance and the square of transfer distance were used as covariates.

3 RESULTS

3.1 Timing of height growth cessation of first-year seedlings (I)

3.1.1 Timing of height growth cessation and night length at growth cessation

The timing of height growth cessation varied according to seed origin and sowing time (Fig. 3 in **I**). There was a systematic linear clinal pattern in the timing of growth cessation from southern to northern origins, as well as a linear trend from early to late sowing times. The more northern the origin, the earlier the cessation of growth occurred, and therefore, the shorter the night at growth cessation. Delay in sowing time delayed growth cessation into autumn, and thus increased the night length at the time of growth cessation within each origin.

There was an interaction between seed origin and sowing time, and thus differences in date of growth cessation among seed origins were greater for seedlings sown earlier than for seedlings sown later (Fig. 1). On the other hand, differences in date of growth cessation among sowing times were greatest for seedlings of northern origin and lowest for seedlings of southern origin.

According to the regression model (Equation 1 in **I**), the timing of growth cessation increased by 0.24 days per 1-day delay in sowing date at the mean latitude (63.39°N) and decreased by 2.78 day per 1° (110 km) increase in latitude of seed origin at the mean sowing date (177.75 days). Night length at growth cessation increased by 1.3 min for every 1-day delay in sowing date at the mean latitude and decreased by 15.4 min per every 1° increase in latitude of seed origin at mean sowing date (Equation 2 in **I**).

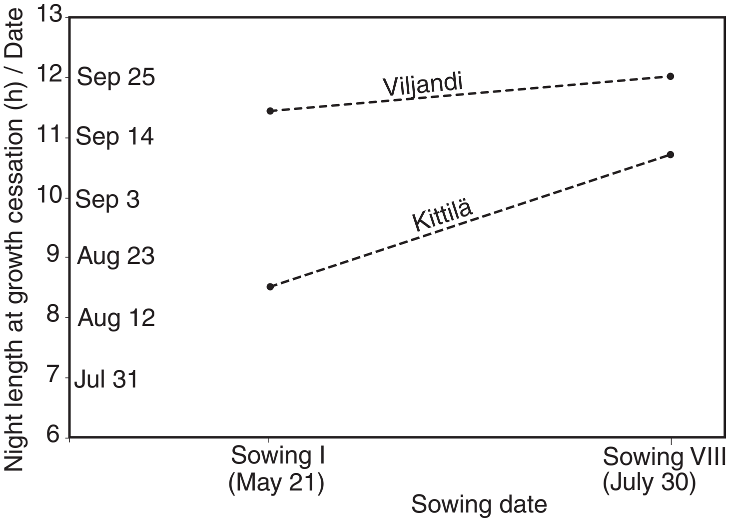

Figure 1. Mean date of growth cessation and associated night length of first-year silver birch seedlings of a southern Viljandi (58°10’N) and a northern Kittilä (67°44’N) origin in relation to sowing date (May 21 and July 30) in a greenhouse experiment at Haapastensyrjä (60°37’N) in a naturally changing photoperiod in study I .

3.1.2 Length of growth period

The total length of the growth period from sowing to growth cessation varied according to the seed origin and sowing time, and there was an interaction between these variables. The observed change in growth period length was systematic: increasingly northerly origins and later sowing times shortened the growth period (Fig. 4 in **I**).

Because of the interaction between origin and sowing date, differences among seed origins in length of growth period were largest within the earliest sowings and decreased as sowing date advanced (Fig. 2). On the other hand, differences between sowing times in the length of growth period were the largest for seedlings of southern origin.

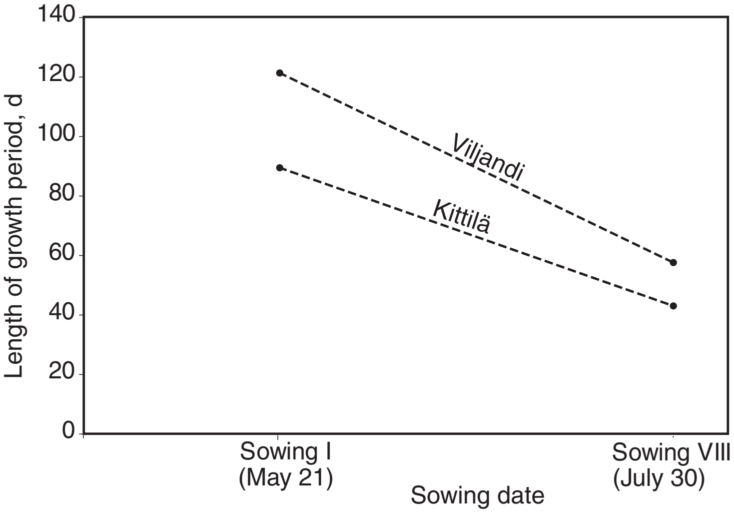

Figure 2. Mean length of growth period from sowing to growth cessation of first-year silver birch seedlings of a southern Viljandi (58°10’N) and a northern Kittilä (67°44’N) origin in relation to sowing date (May 21 and July 30) in a greenhouse experiment at Haapastensyrjä (60°37’N) in a naturally changing photoperiod in study I.

The growth period shortened by 0.76 days for every 1-day delay in sowing date at the mean latitude and shortened by 2.78 days for every 1° increase in latitude of seed origin at the mean sowing date (Equation 3 in I).

3.1.3 Final height of the seedlings

The final heights of seedlings at the end of the experiment varied according to the seed origin and sowing time, and there was an interaction between seed origin and sowing time. Final height of the seedlings decreased as a curvilinear function of sowing time, and southern origin seedlings were always taller than northern origin seedlings (Fig. 5 in **I**). The differences in final height between seed origins decreased with increasing sowing time.

3.1.4 Regression models

The second-order regression models (Eq. 1, 2, 3 and 4 in **I**) with sowing time and the latitude of seed origin as independent variables explained the variation in timing of growth cessation, night length at growth cessation, length of growth period and final height of the seedlings with high precision ($R^2 = 0.92 - 0.97$). Unlike the other response variables, the dependence of seedling final height on sowing time (Eq. 4 in **I**) was strongly curvilinear (Fig. 5 in **I**).

3.2 Critical night length for bud set of first-year seedlings (II)

3.2.1 Critical night length for 50 % bud set

In the photoperiodic response experiments, the mean percentage of seedlings with a set terminal bud was lowest in the shortest night length treatments and increased sharply with night length (Fig. 1 in **II**). Ecotypic differences were evident and consistent in all experiments: seedlings of the northern ecotype set bud with nights of shorter length than seedlings of the southern ecotype.

The mean critical night length value (CNL) for the Tuusula ecotype, calculated over all three experiments, was 6.3 ± 0.2 h (95 % confidence interval) and that for the Kittilä ecotype 3.1 ± 0.3 h (Table 2 in **II**).

There was a significant but small interaction between ecotype and experiment (Figure 3 in **II**). The difference in CNL values between the Tuusula and Kittilä ecotypes was the same (2.9 h) in Experiments 1 and 2, but was higher (3.8 h) in Experiment 3 (Table 2 in **II**). However, the CNL value for the southern Tuusula ecotype was higher than for the northern Kittilä ecotype in all experiments. In Experiment 1, in which the period of exposure to the night length treatments was the shortest, CNL values for both the Tuusula and Kittilä ecotypes were higher than in Experiments 2 and 3 (Figures 2 and 3 in **II**).

3.2.2 Variation in critical night length within ecotypes

Within-ecotype variances of CNL were systematically higher for the northern Kittilä ecotype than for the southern Tuusula ecotype in all three experiments (Table 2 in **II**). The pooled variance of the CNL value for the Kittilä ecotype was 0.484 h^2 and that for the Tuusula ecotype 0.150 h^2.

The mean CNL value for the progeny of individual mother trees calculated over the three experiments varied between 5.5 and 6.7 h for the Tuusula ecotype and between 1.8 and 4.0 h for the Kittilä ecotype (**II**). Mean CNLs of mother trees differed significantly in Tuusula, but not in Kittilä. However, the ranking of CNL values for mother trees within both ecotypes differed between experiments, especially within the Kittilä ecotype, where the ranking was quite irregular. The Spearman rank correlation coefficients of the mother tree CNL values between experiments were not statistically significant.

3.3 Effects of seed origin latitude on moose browsing (III)

At the age of 5 years, when no browsing had occurred in the field trial, the average height of the birch saplings was 1.4 m. The average height of the origins varied between 1.0 and 1.7 m, and the height of individual saplings between 0.3 and 3.5 m (Table 2 and Fig. 2 in **III**). At the age of 10 years, the saplings with no stem breakage had reached an average height of 3.8 m.

The average proportion of trees browsed by moose (BT) in different seed origins varied between 6 and 86 % (Table 3 in **III**). The origins brought to Finland from more southern latitudes (southern Estonia, southern Sweden, Scotland, Russia) had the highest mean BT value, whereas origins from central parts of Finland (i.e. transferred some two degrees latitude southward) had the lowest mean BT value (Fig. 3 in **III**). BT decreased with increasing seed origin latitude and sapling height (Table 4 in **III**). According to the analysis of covariance model (Equation (1), Table 4 in **III**), the proportion of browsed trees decreased by 7.3 percentage units per 1° increase (≈110 km) in seed origin latitude at the mean latitude (61.2°N) and mean sapling height (1.4 m).

The proportion of trees with stem breakage (TSB) averaged between 2 and 64 % and the proportion of repeatedly browsed trees (RBT) between 0 and 48 % among origins (Table 3 in **III**). The highest average TSB and RBT values were associated with seed origins from southern Estonia, southern Sweden, Scotland and Russia and the lowest values with the central Finnish origins (Fig. 4 and 5 in **III**), a similar pattern as shown for average BT values. TSB and RBT also decreased with increasing latitude and sapling height (Table 4 in **III**). TSB decreased by 4.9 and RBT by 2.5 percentage units per 1° increase (≈110 km) in seed origin latitude at the mean latitude (61.2°N) and the mean sapling height (1.4 m). The number of browsed branches in the browsed trees (NBB) also decreased with increasing seed origin latitude. There was a significant positive correlation between BT and NBB, i.e. in origins with a high proportion of browsed trees, individual trees were also more heavily browsed.

3.4 Seed transfer of silver birch from the Baltic countries to Finland (IV)

3.4.1 Effects of seed origin on survival, growth and stem quality

In both field trials, Viitasaari and Tuusula, significant differences were detected among the seed origins in survival, height, breast height diameter, relative stem taper, volume/ha and proportion of trees with a vertical branch or a forked stem at the age of 22 years (Figs. 2-5 in **IV**).

At the Viitasaari trial, the average survival of the seed origins varied from 30 to 65 % (Table 2 in **IV**). The origins from Lithuania and southern Latvia had the lowest and southern and central Finnish origins the highest survival (Fig. 2a in **IV**). At the Tuusula trial, the average survival of the origins ranged from 58 to 87 %. Origins from northern Latvia, southern Estonia and southern Finland had the highest survival (Fig. 2b in **IV**). At the Viitasaari trial, where all the origins had been transferred from the south to the north, survival increased linearly with increasing seed origin latitude, whereas at the Tuusula trial, the relationship was curvilinear.

At the Viitasaari trial, the average stem volume of the seed origins varied from 47 m^3/ha to 140 m^3/ha (Table 2 in **IV**), and the southern Finnish stand and plus tree origins had the highest stem volume values. At the Tuusula trial, the average stem volume of the seed origins ranged from 74 to 194 m^3/ha, and northern Latvian, southern Estonian and some of the southern Finnish plus tree origins had the highest volume. The relationship between stem volume and seed origin latitude was curvilinear at both field trials (Fig. 4 in **IV**).

The average proportion of trees with stem defect varied from 27 to 79 % among seed origins at the Viitasaari trial and from 34 to 78 % at the Tuusula trial (Table 2 in **IV**). In both trials, the proportion of trees with stem defect decreased linearly with increasing seed origin latitude (Fig. 5 in **IV**).

3.4.2 Effects of latitudinal seed transfer distance on survival, growth and stem quality

The latitudinal seed transfer distance had a significant effect on survival, stem volume and proportion of trees with stem defect (Table 3 in **IV**).

Seed origin survival showed a curvilinear relationship to the latitudinal seed transfer distance (Table 4 and Figure 6 in **IV**). The trial had a significant effect on the survival (Table 3 in **IV**). The highest survival was attained with the local seed origin or transferring seed from no more than 2 degrees of latitude (ca. 220 km) from the south, whereas longer transfer distances decreased survival. A transfer of northern seed origins southwards also resulted in decreased survival (Fig. 6 in **IV**).

Stem volume also showed a curvilinear relationship to seed transfer distance (Table 4 and Figure 7 in **IV**). The trial and the transfer distance had significant effects on stem volume (Table 3 in **IV**). In addition, there was a weak but significant interaction between the trial and the square of the seed transfer distance, i.e. the seed transfer distance response differed between the two trials (Table 4 in **IV**). According to the model, the highest stem volume would be attained by transfer distance of ca. 2 degrees of latitude from the south, whereas longer transfer distances from the south as well as transfers from the north would decrease the yield.

The proportion of trees with stem defect increased linearly in relation to seed transfer distance from the south (Table 4 and Figure 8 in **IV**), i.e. the longer the transfer from the south, the higher the proportion of trees with stem defect. According to the model, the proportion of trees with stem defect increases by ca. 3 % when the seed transfer distance from the south increases by 1 degree of latitude.

4 DISCUSSION

4.1 Timing of height growth cessation

The pattern of height development and timing of height growth cessation of first-year silver birch seedlings depended on the latitude of seed origin and sowing time (Fig. 2 and Fig. 3 in **I**). Significant differences in the timing of height growth cessation were detected among the silver birch seed origins from different latitudes, and the pattern of variation was a latitudinal cline, with northern origins ceasing growth earlier and at shorter night lengths than the southern origins. These results are in accordance with those found from earlier nursery and common garden experiments (Clausen 1968, Sharik and Barnes 1976, Velling 1979). They are also in accordance with growth chamber studies showing differentiation between tree populations in response to photoperiod and critical night length that induces growth cessation, northern populations having shorter critical night lengths than the southern ones (Håbjørg 1972a, 1978, Heide 1974). Since photoperiodic conditions change gradually with latitude, clinal latitudinal variation in photoperiodic response is likely to exist (Langlet 1959, White et al. 2007). Continuous variation is maintained by effective gene flow and the continuous distribution of silver birch in northern Europe (Hjelmroos 1991, Hamrick et al. 1992, Eriksson et al. 2003).

Within each seed origin, the timing of seedling growth cessation varied according to sowing date, i.e. a delay in sowing date delayed height growth cessation in all origins (Fig. 3 in **I**). Thus, no unambiguous night length at growth cessation could be determined for a particular seed origin. This is in accordance with the findings of Luoranen and Rikala (2001), who reported that later sowing times caused poorer height growth and later growth cessation of silver birch seedlings in a nursery experiment. In addition, there was an interaction between the seed origin and sowing time, i.e. the origins responded differently to the delay of sowing in the present study.

The growth and development of first-year nursery seedlings can be divided into three main phases: the establishment, rapid growth and hardening phase, and the effects of environmental factors on seedling performance vary according to phase (Landis et al. 1999). Thus, the response to long night signal may also differ in each phase (Luoranen 2000), which is in accordance with results of this study.

In experimental design used in this study (**I**) seeds were sown at different times during the summer to obtain seedlings at different developmental stages that were then subjected to lengthening nights at the end of summer. The later the sowing time, the higher the number of days needed from the day of receiving the critical night length till the cessation of height growth; the critical night lengths for different origins were determined according to Håbjørg (1978). Seedlings from early sowings were in a rapid growth phase and rather tall when receiving the critical night length signal and capable in responding to it, whereas seedlings from late sowings were small, having hardly reached the establishment phase and were therefore slower to respond to the critical night length.

As found in our study, a delay in sowing time has been shown to delay growth cessation of first-year silver birch seedlings in the studies by Koski and Selkäinaho (1982), Koski and Sievänen (1985) and Partanen (2004). These authors concluded that the timing of growth cessation was determined by the joint effect of night length and accumulated temperature sum: the higher the temperature sum, the shorter the night length required to induce growth cessation. A similar interaction between night length and accumulated temperature was observed in this study (Table 2 and Fig. 3. in **I**). In this kind of experimental designs, the developmental phase of first-year seedlings has been described with the temperature sum accumulated during the growth period. It is however unclear, whether the temperature sum model of the developmental phase of first-year seedlings is valid for older trees, and whether this kind of joint effect between the night length and temperature sum as reported here and in the earlier studies (Koski and Selkäinaho 1982, Koski and Sievänen 1985, Partanen 2004) holds true for older trees. Thus, the effect of tree age on the regulation of growth cessation needs thorough examination. Further, the joint effect of night length and temperature sum at the time of growth cessation does not reveal the physiological regulatory mechanism that induces growth cessation a few weeks earlier.

Shortening the photoperiod, i.e. lengthening night has been shown to be the primary signal inducing tree growth cessation (Garner and Allard 1923, Wareing 1956, Nitsch 1957, Luoranen 2000). This is especially so in tree species having a free growth pattern, such as juvenile birches (Junttila and Nilsen 1993), but the response to it can be modified by several factors. Temperature is the most important external factor, but soil moisture and nutrient conditions, and air humidity may also have a modifying effect (Håbjørg 1972a, Heide 1974, Li et al. 2002).

Internal factors may also modify seedling response to photoperiod. Sensitivity to night length has been shown to increase with seedling development (Koski and Selkäinaho 1982, Koski and Sievänen 1985, Partanen 2004). This relationship may be interpreted in two ways. First, the critical night length varies in relation to the stage of seedling development as suggested by Koski and Selkäinaho (1982) and Ekberg et al. (1979). Alternatively, the critical night length itself remains constant, but the speed of response to it varies with the developmental stage of seedlings. According to Junttila (1976), the rate of response to short day treatment of *Salix caprea* L. and *S. pentandra* L. depended on seedling size, with small seedlings being slow to respond to short days, and the time from the start of short-day treatment to apical growth cessation decreasing with increasing initial seedling size. As trees mature, sensitivity to photoperiod decreases, and endogenous conditions are suggested to become increasingly important in regulating growth cessation (Junttila and Nilsen 1993, Thomas and Vince-Prue 1997). Adult trees usually stop height growth in midsummer, independently of the photoperiod (Junttila 1976). However, in general the role of seedling and tree age in the regulation of growth cessation is poorly understood.

The final height of seedlings decreased curvilinearly with sowing time (Figure 5 in **I**), although the length of the growth period decreased linearly (Fig. 4 in **I**). Growth of seedlings sown at different times is determined by both light conditions and the length of growth period. Seedlings from the first three sowing dates began their development during lengthening days, whereas seedlings from later sowing dates faced shortening day from the beginning (Fig. 1 in **I**). The rate of shoot elongation increases rapidly with increasing photoperiod above the critical day length for shoot elongation (Junttila and Nilsen 1993). Thus, the curvilinearity in the relationship between height and sowing date was most pronounced in the seedlings of southern origins, which were grown during long days and confronted their critical night length later than the more northern origins.

In conclusion, the results from this study showed that height growth cessation of silver birch seedlings in the year of sowing is controlled by the interaction between night length and stage of seedling development, and varies with seed origin. The use of a single value of a night length parameter is insufficient to characterize the height growth cessation of birch seedlings of differing origins: the stage of seedling development also needs to be taken into account. The order of latitudinally different origins in the timing of growth cessation, however, remains the same.

4.2 Critical night length for bud set

Variation in the critical night length (CNL) for 50 % bud set of two photoperiodic ecotypes (two latitudinally distant stands) of silver birch was studied in study **II**. Significant differences were detected in CNL between the ecotypes as well as in within-ecotypes variances of CNL (Table 2 and Fig. 3 in **II**). Several earlier studies have also demonstrated differentiation between distant populations regarding critical night length (Håbjørg 1972a, 1978, Heide 1974, Ekberg et al.1979). Although the mean CNL of the ecotypes differed between experiments in our study, and although there was a slight interaction between ecotype and experiment (Figure 3 in **II**), the difference in CNL between the ecotypes remained quite constant. The mean CNL values could be estimated precisely. i.e. the confidence intervals of the means were narrow (Table 2 and Fig. 2 in **II**). The interaction between ecotype and experiment might be due to the sensitivity of northern populations to light quality (Håbjørg 1972a, Junttila and Kaurin 1990, Clapham et al. 1998). Thus, the seedlings of Kittilä (67°44’N) origin may have benefited from the northern light conditions at Tromsø (69°39’N) in Experiment 3, in which the seedlings were grown in natural light for 12 h.

The mean CNL values estimated in study **II** were a little lower than those reported by Håbjørg (1978). This can be attributed to differences in experimental conditions and methods for determining CNL. The CNL values presented by Håbjørg (1978) were based on height growth cessation. Longer nights are probably required for complete cessation of apical growth than for 50 % bud set, on attainment of which half of the seedlings may still be growing.

The date at which the mean CNL was reached in local light regimes at Tuusula and Kittilä is July 23 and July 25, respectively (**II**). Growth cessation of northern ecotypes occurs in the middle of August according to Junttila and Nilsen (1993). Thus, the dates for CNL estimated in study **II** seem realistic, considering that 1-3 weeks is usually needed from the time that the CNL is achieved to the time that growth ceases (Junttila et al. 2003). When the confidence intervals of the CNL values were converted to calendar dates (Figure 2 in **II**), the broader intervals of the northern Kittilä ecotype were no more apparent. This is because the night length changes faster at higher latitudes.

The mean CNL of both ecotypes was significantly longer in Experiment 1 than in Experiments 2 and 3 (Table 2 in **II**). This difference may be related to the period of exposure to the night length treatments, which was shortest in Experiment 1. Over a shorter treatment period, a longer night length is probably needed to reach the same frequency of bud set as in treatments of longer duration.

The within-ecotype variance of CNL was higher in the northern Kittilä ecotype (0.484 h^2) than in the southern Tuusula ecotype (0.150 h^2) (Table 2 in **II**). The within-ecotype variation of CNL in birch has not been reported previously. Dormling (1979) reported a narrower amplitude in CNL for bud set in northern than in southern origins of *Picea abies*, which is contradictory to our results. A hypothesis has been presented that populations near the edge of a species distribution possess less genetic variation than other populations (Tigerstedt 1973). Although the hypothesis was not supported by the results of Norway spruce (Tigerstedt 1973), in fact, the Kittilä silver birch stand used in study **II** has been shown to contain less isoenzyme variation than southern Finnish birch populations (Rusanen et al. 2003). Neutral molecular markers such as isoenzymes, are not, however, necessarily good predictors of quantitative, adaptive traits such as timing of bud set (Karhu et al. 1996).

The mean CNL values of individual mother trees were calculated over the three experiments. These values varied between 5.5 and 6.7 h (1.2 h) in the Tuusula population and between 1.8 and 4 h (2.2 h) in the Kittilä population, i.e. the tree level amplitude in CNL was wider in the northern population. But again, when converted into corresponding calendar dates, the range was narrower in the north than in the south. At Tuusula, the dates ranged between July 10 and July 28 and at Kittilä between July 19 and July 29.

One aim in study **II** was to determine whether individual mother trees differ significantly regarding their CNL and whether trees with significantly shorter or longer CNL existed in either of the ecotypes. In terms of timing of growth cessation these could be regarded as “early” or “late” types. In the southern ecotype, some support for this hypothesis was found. Trees with the shortest and the longest CNL differed significantly from each other on the average, but the trees had, however, a different ranking in the three experiments. In the northern ecotype, no significant differences among trees were detected, and their ranking between the experiments was even more irregular than in the southern ecotype.

4.3 Effects of seed origin latitude on moose browsing on silver birch

Seed origin latitude and sapling height both had a significant effect on the extent and degree of browsing by moose (**III**). The proportion of trees browsed decreased with increasing seed origin latitude (Table 4 and Fig. 3 in **III**). The number of browsed branches per browsed tree was also highest among trees of southern origin and decreased significantly with increasing latitude, irrespective of the sapling height. There was a positive correlation between the proportion of browsed trees and the number of browsed branches per browsed tree. Thus, there was clearly selective browsing among geographical origins and preference for southern origins.

Differences in the degree of moose browsing among the origins are probably related to differences in the annual physiological rhythm of the trees, especially regarding the timing of growth cessation and subsequent hardening. Birch populations from different latitudes are adapted to the local seasonal variation of their home sites by means of their annual rhythm. Birches from northern latitudes cease their height growth earlier than the southern origins, as shown in study **I** and in several previous studies (Clausen 1968, Sharik and Barnes 1976, Velling 1979). In the greenhouse experiment of study **I** carried out in natural day length at Loppi, the same location as the field trial in study **III**, seedlings of Viljandi (58ºN) origin stopped their height growth two weeks later than seedlings of Viitasaari (63ºN) and one month later than seedlings from Kittilä (67ºN). The more southern the origin, the longer the foliage remains green in the autumn (Velling 1979). Thus, the moose probably preferred the southern origin trees, because they were still green and leafy compared to the northern ones.

Birch is an important part in the diet of moose throughout the year, but it is mostly browsed in summer, from June to September, when leaves and young shoots are eaten (Cederlund et al. 1980, Bergström and Hjeljord 1987, Lavsund 1987, Hjeljord et al. 1990). In winter time, birch remains to be eaten because of its wide availability (Andersson 1971, Cederlund et al. 1980), although its palatability and digestibility in winter is low (Hjeljord et al. 1982, Palo et al. 1985, Hjeljord 1987).

Seasonal variation has been shown in the digestibility of birch twigs related to the contents of crude protein, cell walls (neutral detergent fibre) and phenolic compounds (Eastman 1983, Palo et al. 1985). Organic matter digestibility and crude protein contents are lowest in winter twigs, whereas the proportion of hydrophilic phenols and cell walls (cellulose, hemicellulose and lignin) is highest. Both phenolic substances and high fibre content decrease the digestibility of birch twigs (Palo 1985, Palo et al. 1985, 1992). It has also been suggested that during the time of rapid tree growth, the production of deterring substances is low, but as growth ceases more resources are allocated to the production of defence substances (Bryant et al. 1983, Palo et al. 1985, 1992). Thus, the differences in timing of growth cessation and switch from the active growth to leafless state, and subsequent seasonal changes in digestibility, including fibre content and secondary metabolites, are suggested to explain the differences in palatability and browsing between seed origins observed in study **III**.

Moose prefer planted silver birches to the naturally born ones (Heikkilä 1991), and silver birch is usually preferred to downy birch (Danell et al. 1985). Reports on selective browsing within a birch species by moose are few. Jia et al. (1992) presented some evidence of selective browsing by moose among silver birch clones, but did not report its relation to the geographical origin or phenology of the clones. No consistent latitudinal trend was detected in palatability of silver birch origins to mountain hare (*Lepus timidus* L.) by Rousi et al. (1989), and no preference by voles (*Microtus* Schrank) for southern silver birch origins or 1-year-old seedlings with delayed winter-hardening by Rousi (1988). Phenology may, however, play a different role in relation to the palatability of birch saplings to voles, hares and moose, because they feed on differing parts of the plants and at differing times of the year. There are significant physiological differences among these mammalian herbivores, and the resistance of birch to browsing by different animals may be based on different factors.

The proportion of trees with stem breakage also decreased significantly with increasing seed origin latitude (Table 4 and Fig. 4 in **III**). This further emphasizes the importance of seed origin selection in forestry practice, because stem breakage is regarded as a severe type of moose damage. Stem breakage usually leads to crookedness as well as wood discoloration and decay within the main stem (Heikkilä et al. 1993, Lilja and Heikkilä 1995). However, the ability of birch to recover regarding growth is considered good (Kangas 1949, Heikkilä and Raulo 1987, Heikkilä et al. 1993).

4.4 Seed transfers of silver birch

Results on the yield and stem quality of Baltic seed origins of silver birch at commercial size grown in Finland are reported for the first time in study **IV**. Study **IV** is also the first one in Finland in which the effect of seed transfers on performance of silver birch was examined in provenance trials established with population seed samples. Current seed transfer principles of birch in Finland are based on progeny trials of single tree progenies (Raulo 1976, 1979, Raulo and Koski 1977).

Wide variation in survival, yield and stem quality among the silver birch origins ranging in latitudes from 54ºN to 63ºN was detected (Table 2 in **IV**). The survival of different origins reported in study **IV** was much higher than that reported by Velling (1979) for seedlings of exactly the same origins, but the general pattern of variation in these two studies was similar (Fig. 2 in **IV**). At Viitasaari, the more southern the origin, the lower the survival. At Tuusula, survival showed a curvilinear relationship to latitude. In addition to the most southern origins, the central Finnish Pielavesi origin, transferred southwards by ca. 3 degrees of latitude, also showed low survival. This is probably due to its weaker growth and, consequently, poor ability to compete with weeds. The same reason for low survival of northern origins when transferred south has been suggested also by Johnsson (1976) and Stener (1995) in Sweden.

The highest stem volume values were achieved by origins from more southern areas, i.e. at Viitasaari by southern Finnish stand and plus tree origins, and at Tuusula by the north Latvian Alūksne and Estonian origins (Fig. 4 in **IV**). At Tuusula, the north Latvian Alūksne and Estonian Viljandi origins manifested high growth potential, their yield by far exceeded that of the local origin and that reported by Niemistö (1997) for cultivated silver birch stands on similar sites and of similar age in southern and central Finland. However, it should be noted that the southern Finnish plus trees origins were also among the best regarding yield (Fig. 4 in **IV**). The better yield of more southern birch origins, is probably due to their longer growth period compared to the local ones, as shown by Velling (1979). Due to their longer critical night length (Håbjørg 1972a, 1978) trees of southern origin continue their growth later than tree of northern origin. Rate of shoot elongation increases rapidly with increasing photoperiod above the critical daylength for shoot elongation (Junttila and Nilsen 1993). Thus, when transferred northwards the southern origins are transferred to longer day conditions, which may further increase their growth potential, because the prevailing day length during their growth period in summer in the north is much longer than in the south, as discussed in study **I**.

Forks and vertical branches, observed in study **IV**, are generally caused by the death of the leader shoot followed by development of a new leader from sub-apical buds. Trees of more southern origin were found to be more likely to have stem defects. This may be explained by their longer growth period and delayed hardening, which makes them more susceptible to frost resulting in forking, vertical branches and bushy growth (Raulo 1976). Stem defects can also be caused by moose browsing when the trees are young. As shown in study **III**, silver birches transferred from more southern latitudes (southern Estonia, southern Sweden, Scotland, Russia) to Finland were more heavily browsed by moose than the more northern, native ones.

Producing high-quality timber for the plywood and joinery industry is an important goal of growing birch in Finland (Niemistö et al. 2008). The value of birch as a raw material for veneer is determined first of all by the size of the logs, but also by stem taper and incidence of defects (Heiskanen 1966, Kärkkäinen 1986). There are great differences in the price for saw and plywood logs and pulpwood, and between logs of different quality (Heräjärvi and Verkasalo 2002, Velling et al. 2002).

Results of study **IV** showed that stem volume/ha was greater for origins that had been transferred northwards by ca. 2 degrees of latitude, whereas longer transfers resulted in decreased yield. Thus, in the most southern part of Finland some improvement in yield could be achieved by using Estonian or northern Latvian origins. Although some of the transferred origins did very well, the mean increase predicted by the model was not very high. At the Tuusula trial the increase was about 10 m^3/ha in 22 years compared to the local origin (Table 4 and Fig. 7 in **IV**). Furthermore, this increase might come at the expense of reduced stem quality and increased risk of moose damage as shown in study **III**. The use of the Baltic material is clearly not suitable for central Finland, shown by the results from the Viitasaari trial (63ºN). According to Raulo and Koski (1977) and Raulo (1979) seed transfers of ca. 200 km from the south to north or vice versa within southern and central Finland did not have any systematic effect on mortality, growth or stem quality of silver birch. Mortality of silver birch progenies increased when transferred ca. 3 degrees of latitudes northwards in northern Sweden (Erkén 1972), but on the other hand, Johnsson (1976) and Stener (1997) found only a weak response to seed transfers when made within a few degrees of latitude in Sweden in either northwards or southwards direction. According to the current Swedish seed transfer recommendations, transfer northwards in the southern and middle parts of Sweden (south of latitude 61ºN) can be made within 2 degrees of latitude and in northern Sweden (north of latitude 61ºN) within 1.5 degrees, without any noteworthy effect on growth, quality and mortality (Stener 1997). In the light of the results from our study **IV,** the prevailing Finnish seed transfer rules for birch (max. 150 km northwards or southwards) appear appropriate.

Rehfeldt et al. (1999, 2002) found, like in our study, a curvilinear response to seed transfers on their studies of *Pinus* L. species, and showed that natural populations tend to occupy suboptimal environments, and grow optimally when planted in a harsher climate outside their native climates. In both Scots pine and Norway spruce in Finland, higher yield was obtained by using seed of more southern origins according to the seed transfer rules outlined by Heikinheimo (1949). For Scots pine, transfer distances exceeding 200 kilometres were not advised and nowadays even more strict recommendations are applied (Hyvän metsänhoidon... 2006). Transfer distances of 200-300 km (ca. 2-3 latitudes) northwards in South and Central Finland are deemed safe and even advantageous for Norway spruce (Heikinheimo 1949, Hagman 1980). The seed transfer distances for birch found in study **IV** indicate that birch is not as flexible as Norway spruce.

In study **IV**, transfers from north to south could only be examined with quite a restricted material at the Tuusula trial, where origins from southern and central Finland had been transferred southwards and the longest transfer distance was 3 degrees of latitude. The long transfer from central Finland (63ºN) to the southernmost part of the country (60ºN) considerably reduced the mean volume compared to the mean value predicted by the model for the local origin (Figure 7 in **IV**). According to the model, even shorter transfer distances (1-2 degrees) from the north have a negative effect on volume, which contradicts the results of Raulo and Koski (1977) and Raulo (1979) in Finland and Stener (1997) in Sweden. The negative effect of long (3 degrees of latitude or more) southward transfer on survival and growth of silver birch has been shown in several studies (Erkén 1972, Stener 1995, Kleinschmit and Otto 1980, Kleinschmit 1998, 2002).

For Norway spruce and Scots pine, long southward transfer distances have been shown to increase the yield of northern origins (Beuker 1996). This has been considered to indicate of the positive effects of climate warming on growth of conifers in the boreal zone. The transfer southward means a transfer to warmer climate, but at the same time, a transfer to short day conditions. Since cessation of height growth of silver birch is in the first hand regulated by photoperiod, trees of northern origin having shorter critical night lengths (Håbjørg 1972a, 1978 and study **II**) would be induced to cease height growth earlier as a result of southward transfer. In Scots pine and Norway spruce, the shoot elongation is a predetermined process and cessation of height growth takes place regardless of the photoperiod (Lanner 1976, Beuker 1996). Thus, the response of birch to climate warming cannot be deduced from southward transfer experiments equally well as for conifers due to the differing regulation of growth cessation. It has, however, been predicted that birch will benefit from global warming and lengthening growing season (Kellomäki et al. 1996, Talkkari 1998). The growth of birch will also probably benefit from increasing CO_2 concentrations (Riikonen et al. 2004). On the other hand, there are other effects of climate change that may be harmful to birch. These include damage caused by increasing O_3 concentrations and exposure (Oksanen 2005), changes in snow cover and soil temperatures (Aphalo et al. 2006), disturbances in dormancy development and release, higher risk for frost damage (Linkosalo et al. 2000) and emergence of new pests and pathogens (Niemelä and Veteli 2005, Jalkanen et al. 2007, Nuorteva and Nuorteva 2007).

Although latitudinal seed transfer distance had a significant effect on survival, stem volume/ha and stem quality of silver birch (Table 3 in **IV**), the coefficients of determination for seed transfer distance in the model remained rather low (Eq. 2 and Table 4 in **IV**). Other factors than latitude must therefore be involved in determining the variation in growth performance among birch origins. One of them could be differences in adaptation among Latvian birch populations even at the same latitude, due to climatic difference between the coastal and inland areas of Latvia (Laivinš and Melecis 2003). The possible epigenetic effects, as shown in Norway spruce (Kvaalen and Johnsen 2007), due to differing temperature conditions in different years of seed development may also cause an extra source of unexplained variation among the origins. There was also wide variation within the origins among the different blocks in the trial, seen as the variation of small dots in Figures 2-5 in study **IV**. This variation is probably explained by varying site factors between and within the blocks, because silver birch is quite sensitive to soil factors, like nutrition, moisture and physical structure (Sutinen et al. 2002, Niemistö et al. 2008). Thus, the seed transfer models presented in study **IV** could probably be improved by including variables describing the soil conditions at the trial sites and variables describing temperature and continentality of the home sites of the origins.

5 CONCLUSIONS

The general aim of the thesis was to improve the knowledge about the effects of seed origin on the timing of height growth cessation and the field performance of silver birch from different latitudes, with special attention to browsing damage by moose in young plantations. The following main conclusions can be summed up based on the studies **I-IV:**

Silver birch seedlings displayed clinal pattern of variation in the timing of height growth cessation in relation to the seed origin latitude in a naturally changing photoperiod. The more northern the origin, the earlier the cessation of growth occurred and, consequently, the shorter the growth period and the smaller the final height of the seedlings. Delay in sowing time delayed growth cessation of all origins. The critical night length for bud set was shorter in the northern population than in the southern one, but the within population variation in CNL was higher in the north.

Browsing by moose on silver birch saplings decreased with increasing latitude of seed origin and sapling height. The origins transferred to Finland from more southern latitudes were more frequently and more heavily browsed than the more northern native ones, whereas origins transferred some two degrees latitude southwards had the lowest values of browsed trees. The different timing of growth cessation and consequent changes in the nutritive value and palatability of birch to moose are suggested to explain the differences in browsing by moose on silver birch origins from different latitudes.

The yield and stem quality of commercially sized silver birches varied significantly in relation to the seed origin latitude and the latitudinal seed transfer distance. The dependence of stem volume/ha to seed transfer distance was curvilinear. Yield could be increased by a transfer of no more than two degrees of latitude from the south, but longer transfers from the south, as well as transfers from the north decreased the yield. Optimal yield was achieved by seed transfer from the south, because the more southern origins could utilize the growing season better than the local origins due to their later growth cessation. However, the proportion of trees with a vertical branch or a forked stem increased linearly in relation to the seed transfer distance from the south, probably due to increasing susceptibility to damage by early autumn frosts.

The results of this study emphasize the proper synchronization of the annual physiological rhythm of different silver birch origins with the annual climatic cycle, which should be taken into account when selecting seed origins for forest cultivation.

6 IMPLICATIONS FOR RESEARCH AND FORESTRY PRACTICE

The size of silver birch seedlings produced in nurseries can be controlled by changing the sowing time, temperature and photoperiod. The results of this study concerning the differential growth rhythm and systematic clinal variation in the timing of growth cessation of the different origins, as well as the interaction of seed origin and sowing time, can be utilized to produce seedlings of a particular size from different origins. Within each seed origin, the sowing time is essential to achieve the proper timing of height growth cessation and subsequent hardening. In addition, the natural photoperiod of the nursery location should be taken into account.

Results concerning the regulation of height growth cessation of seedlings of the sowing year cannot be directly applied to older trees. More studies are needed to elucidate the importance of seedling and tree age in the regulation of height growth cessation, including the interaction with photoperiod, temperature and other regulating factors. This holds true for the regulation of other events of the annual cycle as well. Such information will be needed to be able to predict how trees of different ages will be able to acclimate to changing climatic conditions.

The differing adaptation of distant ecotypes to the photoperiodic regime of their home location was evident at the population level. A higher within-population variation in critical night length was detected in the northern population, but the reason for this remains unresolved. It is unclear, whether photoperiod and other characteristics of light could have different roles in regulation of growth cessation in different birch populations. No clear evidence was obtained of the existence of trees with systematically short or long critical night length. The within-population variation in critical night length, thus, deserves more detailed studies in order to understand, what is the significance of tree-level variation in critical night length on physiological acclimation of the trees as well as on long-term genetic adaptation of birch populations. More studies at the tree level are also needed to find out the relationship between critical night length and timing of growth cessation measured in controlled conditions and in the field.

The higher frequency of moose browsing of the imported southern seed origins suggests that the variation in moose browsing among the seed origins is related to differences in their annual rhythm, especially the timing of growth cessation, leaf discoloration and abscission, and related changes in digestibility and palatability. The relationship between the annual rhythm of silver birch and susceptibility to moose browsing deserves further examination. It also remains to be determined if the higher risk of moose damage to planted silver birches, as shown earlier by Heikkilä (1991), is due to their longer growth period and possible transfer effect within the country. A thorough examination of the clone constitution and utilization areas of silver birch seed orchards in Finland is thus recommended. Taking the differences in autumn phenology into consideration and transferring seed origins from the north to the south could be an option to help decrease the risk of browsing. This, however, would solve only a part of the browsing problem, as birch is browsed throughout the year. Silver birch plantations are usually small and, when situated within coniferous forests, subject to very intense browsing. However, the possible epigenetic effects of producing birch seed in polythene greenhouses, i.e. in higher temperatures, or the effects of nursery production of birch seedlings, cannot be ignored either.

In southernmost Finland, the yield of silver birch could be increased by seed transfer from the northern Baltic, keeping in mind that there is variation among the Baltic origins, as well. However, transfer northwards from the south would increase the risk of moose browsing and decrease the stem quality. Baltic material is not suitable for central parts of the country. Furthermore seed transfers from abroad are not needed because genetically improved seed of native origin can be produced in abundance in seed orchards. The results from this study support the prevailing seed transfer rules for silver birch stand seed material. However, the material used in this study was rather limited, especially concerning transfers from north to south. The effects of seed transfers on silver birch deserve studies with more extensive materials.

Southward seed transfers in provenance trials have successfully been used to elucidate the effect of climate warming on conifers in Finland. Although transfer southwards is a transfer to both a warmer climate and to short day conditions, conifers of northern origin have been shown to benefit from the transfer. According to the results presented here, although based on a limited material, transfers southwards considerably decrease the yield of silver birch. The northern origins seemed to be suffering instead of benefiting from transfer southwards. This is probably due to the strict photoperiodic regulation of growth cessation of juvenile birches. Thus, the effects of climate warming on birch cannot be deduced from southward transfer experiments equally well as for conifers because of the differing role of photoperiod in the regulation of growth cessation of these species. Nevertheless, provenance trials are valuable tools to study the differing climatic adaptation of tree populations, e.g. timing of the events of their annual physiological cycle and their regulation by external and internal factors.

REFERENCES

Ahtikoski, A. 2000. The profitability of Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth) next-generation seed orchards in Finland. Academic dissertation. University of Helsinki. 148 p. + 41 app.

Andersson, E. 1971. Havaintoja hirven talvisesta ravinnonkäytöstä ja vuorokausirytmistä. Summary: Observations on the winter food and diurnal rhythm of the moose (*Alces alces*). Suomen Riista 23:105-118.

Aphalo, P.J., Lahti, M., Lehto, T., Repo, T., Rummukainen, A., Mannerkoski, H. & Finér, L. 2006. Responses of silver birch saplings to low soil temperature. Silva Fennica 40(3):429-442.

Batschauer, A. 1998. Photoreceptors of higher plants. Planta 206:479-492.

Belovsky, G.E. 1981. Food plant selection by a generalist herbivore: the moose. Ecology 62(4):1020-1030.

Bergström, R. & Hjeljord, O. 1987. Moose and vegetation interactions in Northwestern Europe and Poland. Swedish Wildlife Research Supplement 1:213-228.

Beuker, E. 1996. Implications of climate adaptability in provenance trials with Scots pine and Norway spruce in Finland for the possible effects of climate warming. Academic dissertation. University of Joensuu, Faculty of Forestry. 33 p. + 5 original papers.

Black- Samuelsson, S. & Eriksson, G. 2002. Effects of nitrogen stress on adaptive genetic variation in *Acer platanoides* L. and *Betula pendula* Roth. Forest Genetics 9(1):71-86.

Bryant, J.P. & Kuropat, P.J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Annual Review of Ecology and Systematics 11:261-285.

—, Chapin III, F.S. & Klein, D.R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357-368.

Cederlund, G., Ljungqvist, H., Markgren, G. & Stålfelt, F. 1980. Foods of moose and roe-deer at Grimsö in Central Sweden. Results of rumen content analysis. Swedish Wildlife Research 11(4):169-247.

Christersson, L. 1978. The influence of photoperiod and temperature on the development of frost hardiness in seedlings of *Pinus silvestris* and *Picea abies*. Physiologia Plantarum 44:288-294.

Clapham, D.H., Dormling, I., Ekberg, I., Eriksson, G., Qamaruddin, M. & Vince-Prue, D. 1998. Latitudinal cline of requirement for far-red light for the photoperiodic control of budset and extension growth in *Picea abies* (Norway spruce). Physiologia Plantarum 102:71-78.

Clausen, E.K. 1968. Variation in height growth and growth cessation of 55 yellow birch seed sources. In: Proceedings of Eighth Lake States Forest Tree Improvement Conference. Madison, WI, September 12-13, 1967. USDA Forest Service, Research Paper NC-23. p. 1-4.

Danell, K., Huss-Danell, K. & Bergström, R. 1985. Interactions between browsing moose and two species of birch in Sweden. Ecology 66(6):1867-1878.

Dormling, I. 1979. Influence of light intensity and temperature on photoperiodic response of Norway spruce provenances. IUFRO Norway spruce meeting, S 2.03.11-S 2.02.11, Bucharest. p. 398-408.

—, Gustafsson, Å. & von Wettstein, D. 1968. The experimental control of the life cycle in *Picea abies* (L.) Karst. I. Some basic experiments on the vegetative cycle. Silvae Genetica 17:44-64.

Eastman, D.S. 1983. Seasonal changes in crude protein and lignin of ten common forage species of moose in North-Central British Columbia. Alces 19:36-70.

Ekberg, I., Eriksson, G. & Dormling, I. 1979. Photoperiodic reactions in conifer species. Holarctic Ecology 2:255-263.

Endler, J.A. 1986. Natural selection in the wild. Monographs in population biology 21. Princeton University Press, Princeton, New Jersey. 336 p.

Eriksson, G. & Ekberg, I. 2001. An introduction to forest genetics. SLU Repro, Uppsala, Sweden. 166 p.

— & Jonsson, A. 1986. A review of the genetics of *Betula*. Scandinavian Journal of Forest Research 1:421-434.

—, Black-Samuelsson, A., Jensen, M., Myking, T., Rusanen, M., Skrøppa, T., Vakkari, P. & Westergaard, L. 2003. Genetic variability in two tree species, *Acer platanoides* L. and *Betula pendula* Roth, with contrasting life-history traits. Scandinavian Journal of Forest Research 18:320-331.

Eriksson, M.E. 2000. The role of phytochrome A and gibberellins in growth under long and short day conditions. Studies of hybrid aspen. Doctoral thesis. Swedish University of of

Agricultural Sciences, Umeå. Acta Universitatis Agriculturae Sueciae, Silvestria 164. 55 p. + 6 original papers.

Erkén, T. 1972. Planterad björk i mellersta och övre Norrland. Summary: Results of progeny trials with birch in Middle and Upper Norrland. Sveriges Skogsvårdsförbunds Tidskrift 70:435-465.

Finnish Statistical Yearbook of Forestry 2008. Finnish Forest Research Institute. Official Statistics of Finland. Agriculture, forestry and fishery 2008. 458 p.

Fuchigami, L.H., Weiser, C.J. Evert, D.R. 1971. Induction of cold acclimation in *Cornus stolonifera* Michx. Plant Physiology 47:98-103.

—, Weiser, C.J., Kobayashi, K., Timmis, R. & Gusta, L.V. 1982. A degree growth stage (°GS) model and cold acclimation in temperate woody plants. In: Li, P.H. & Sakai, A. (eds.). Plant cold hardiness and freezing stress. Academic Press, New York. p. 93-116.

Garner, W.W. & Allard, H.A. 1923. Further studies in photoperiodism, the response of the plant to relative length of day and night. Journal of Agricultural Research 23:871-920.

Haapanen, M. & Mikola, J. 2008. Metsänjalostus 2050 - pitkän aikavälin metsänjalostusohjelma [Forest Tree Breeding 2050 - a long-term tree breeding program]. http://www.metla.fi/julkaisut/workingpapers/2008/mwp071.htm.

Håbjørg, A. 1972a. Effects of photoperiod and temperature on growth and development of three latitudinal and three altitudinal populations of *Betula pubescens* Ehrh. Meldinger fra Norges Landbrukshøgskole 51(2):1-27.

— 1972b. Effects of light quality, light intensity and night temperature on growth and development of three latitudinal populations of *Betula pubescens* Ehrh. Meldinger fra Norges Landbrukshøgskole 51(26):1-17.

— 1978. Photoperiodic ecotypes in Scandinavian trees and shrubs. Meldinger fra Norges Landbrukshøgskole 57(33):1-20.

Hagman, M. 1971. On self- and cross-incompatibility shown by *Betula verrucosa* Ehrh. and *Betula pubescens* Ehrh. Communicationes Instituti Forestalis Fenniae 73(6):1-125.

— 1980. Experiences with Norway spruce provenances in Finland. Silva Fennica 14(1):32-39.

Hagqvist, R. 1991. Jalostetun koivunsiemenen tuotanto ja saatavuus. Summary: Production of genetically improved birch seed and micropropagated seedlings. Foundation for Forest Tree Breeding in Finland. Year Book 1991. p. 12-17, 31.

— & Hahl, J. 1998. Rauduskoivun siemenviljelysten jalostushyöty Etelä- ja Keski-Suomessa. Summary: Genetic gain provided by seed orchards of Silver birch in Southern and Central Finland. Reports from the Foundation for Forest Tree Breeding 13. 32 p.

Häkkinen, R., Linkosalo, T. & Hari, P. 1998. Effects of dormancy and environmental factors on timing of bud burst in *Betula pendula*. Tree Physiology 18:707-712.

Hämet-Ahti, L. & Alanko, P. 1987. Suomessa viljellyistä koivulajeista [The cultivated birch species and cultivars grown in Finland]. Sorbifolia 18(4):161-170.

—, Palmén, A., Alanko, P. & Tigerstedt, P.M.A. 1992. Suomen puu- ja pensaskasvio [Woody flora of Finland]. 2. edition. Publications of the Finnish Dendrological Society 6:1-373. Yliopistopaino, Helsinki.

Hamrick, J.L., Godt, M.J.W. & Sherman-Broyles, S.L. 1992. Factors influencing levels of genetic diversity in woody plant species. New Forests 6:95-124.

Hänninen, H. 1986. Metsäpuiden vuosirytmitutkimuksen käsitteistä ja teorioista. Summary: Conceptual remarks about the study of the annual rhythm of forest trees. Silva Fennica 20(1):9-22.

— 1990. Modelling bud dormancy release in trees from cool and temperate regions. Acta Forestalia Fennica 213. 47 p.

Hansen, E., Olsen, J.E. & Junttila, O. 1999. Gibberellins and subapical cell divisions in relation to bud set and bud break in *Salix pentandra*. Journal of Plant Growth Regulation 18:167-170.

Hari, P. 1972. Physiological stage of development in biological models of growth and maturation. Annales Botanici Fennici 9:107-115.

—, Leikola, M. & Räsänen, P. 1970. A dynamic model of the daily height increment of plants. Annales Botanici Fennici 7:375-378.

Hedrick, P.W. 1983. Genetics of populations. Science Books International, Boston. 629 p.

Heide, O.M. 1974. Growth and dormancy in Norway spruce ecotypes (*Picea abies*). I. Interaction of photoperiod and temperature. Physiologia Plantarum 30:1-12.

— 1985. Physiological aspects of climatic adaptation in plants with special reference to high-latitude environments. In: Kaurin, Å., Junttila, O. & Nilsen, J. (eds.). Plant production in the north. Norwegian University Press, Tromsø. p. 1-22.

— 1993a. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. Physiologia Plantarum 88:531-540.

— 1993b. Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. Physiologia Plantarum 89:187-191.

Heikinheimo, O. 1949. Tuloksia kuusen ja männyn maantieteellisillä roduilla suoritetuista kokeista. Summary: Results of experiments on the geographical races of spruce and pine. Communicationes Instituti Forestalis Fenniae 37(2):1-44.

Heikkilä, R. 1991. Moose browsing in a Scots pine plantation mixed with deciduous tree species. Acta Forestalia Fennica 224. 13 p.

— & Raulo, J. 1987. Hirvituhot vuosina 1976-77 istutetuissa rauduskoivun taimikoissa. Abstract: Moose damage in plantations of *Betula pendula* established in 1976-77. Metsäntutkimuslaitoksen Tiedonantoja 261. 16 p.

—, Lilja, A. & Härkönen, S. 1993. Rauduskoivuntaimien toipuminen latvan katkeamisen jälkeen. Summary: Recovery of young *Betula pendula* trees after stem breakage. Folia Forestalia 809. 10 p.

Heiskanen, V. 1966. Tutkimuksia koivujen vikaisuuksista, niiden vaikutuksesta sorvaustulokseen sekä niiden huomioonottamisesta laatuluokituksessa. Summary: Studies on the defects of birch, their influence on the quality and quantity on the rotary veneer, and their consideration in veneer birch grading. Acta Forestalia Fennica 80(3):1-128.

Heräjärvi, H. & Verkasalo, E. 2002. Timber grade distribution and relative stumpage value of mature Finnish *Betula pendula* and *B. pubescens* when applying different bucking principles. Forest Products Journal 52(7/8):40-51.

Hjeljord, O. 1987. Research on moose nutrition in the Nordic countries. Swedish Wildlife Research, Supplement 1:389-397.

—, Sundstøl, F. & Haagenrud, H. 1982. The nutritional value of browse to moose. Journal of Wildlife Management 46(2):333-343.

—, Hövik, N. & Pedersen, H.B. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. Holarctic Ecology 13:281-292.

Hjelmroos, M. 1991. Evidence of long-distance transport of *Betula* pollen. Grana 30:215-228.

Holopainen, L. & Pirttilä, V. 1978. Kukittamishuoneen varusteet ja käyttö. Summary: The equipment in and use of the flower induction hall. The Foundation for Forest Tree Breeding in Finland. Information 1(1978). 4 p.

Howe, G.T., Gardner, G., Hackett, W.P. & Furnier, G.R. 1996. Phytochrome control of short-day-induced bud set in black cottonwood. Physiologia Plantarum 97:95-103.

Howell, G.S. & Weiser, C.J. 1970. The environmental control of cold acclimation in apple. Plant Physiology 45:390-394.

Hulten, E. & Fries, M. 1986. Atlas of North European vascular plants north of the Tropic of Cancer I. Koeltz Scientific Books, Königstein. 498 p.

Huntley, B. & Birks, H.J.B. 1983. An atlas of past and present pollen maps for Europe: 0-13,000 years ago. Cambridge University Press, Cambridge.

Hyvän metsänhoidon suositukset [Recommendations for good silviculture]. 2006. Metsäkustannus Oy, Helsinki. 100 p.

IPCC (Intergovernmental Panel of Climate Change). 2001. Climate Change 2001: The Scientific Basis. http://www.ipcc.ch/ipccreports/tar/wg1/index.htm.

Jalkanen, R., Büttner, C. & von Bargen, S. 2007. Cherry leaf roll virus abundant on *Betula pubescens* in Finland. Silva Fennica 41(4):755-762.

Jia, J., Niemelä, P., Rousi, M. & Härkönen, S. 1997. Selective browsing of moose (*Alces alces*) on birch (*Betula pendula*) clones. Scandinavian Journal of Forest Research 12:33-40.

Johnsen, Ø., Kvaalen, H., Yakovlev, I., Dæhlen, O.G., Fossdal, C.G. & Skrøppa, T. 2009. An epigenetic memory from time of embryo development affects climatic adaptation in Norway spruce. In: Gusta, L., Wisniewski, M. & Tanino, K. (eds.). Plant cold hardiness: From laboratory to the field. CAB International. p. 99-107 (in press).

Johnsson, H. 1951. Avkommeprövning av björk - preliminära resultat från unga försöksplanteringar. Summary: Progeny tests in birch - preliminary results from young experiments. Svensk Papperstidning 54:379-393, 412-426.

— 1967. Avkommeprövning av björk [Progeny testing of birch]. Föreningen Skogsträdsförädling. Årsbok 1966:90-135. (In Swedish).

— 1974. Genetic characteristics of *Betula verrucosa* Ehrh. and *B. pubescens* Ehrh. Annales Forestales (Anali za sumarstvo) 6/4:91-133 + 28 Figs.

— 1976. Syd- och nordförflyttning av björkprovenienser. Summary: South- and north dislocation of birch provenances. Föreningen Skogsträdsförädling och Institutet för Skogsförbättring. Årsbok 1976:48-61.

Jonsell, B. (ed.) 2000. Flora Nordica. Volume 1. Lycopodiaceae to Polygonaceae. The Bergius Foundation, the Royal Swedish Academy of Sciences, Stockholm. 344 p.

Junttila, O. 1976. Apical growth cessation and shoot tip abscission in *Salix*. Physiologia Plantarum 38:278-286.

— 1989. Physiological responses to low temperature. Annales des Sciences Forestieres (Suppl.) 46:604S-613S.

— & Kaurin, Å. 1985. Climatic control of apical growth cessation in latitudinal ecotypes of *Salix pentandra* L. In: Kaurin, Å., Junttila, O. & Nilsen, J. (eds.). Plant production in the north. Norwegian University Press, Tromsø. p. 83-91.

— & Kaurin, Å. 1990. Environmental control of cold acclimation in *Salix pentandra*. Scandinavian Journal of Forest Research 5:195-204.

— & Skaret, G. 1990. Growth and survival of seedlings of various *Picea* species under northern climatic conditions. Results from phytotron and field experiments. Scadinavian Journal of Forest Research 5:69-81.

—, Jensen, E. & Ernstsen, A. 1991. Effects of prohexadione (BX-112) and gibberellins on shoot growth in seedlings of *Salix pentandra*. Physiologia Plantarum 83:17-21.

— & Nilsen, J. 1993. Growth and development of northern forest trees as affected by temperature and light. In: Alden, J., Mastrantonio, J.L. & Ødum, S. (eds.). Forest development in cold climates. Plenum Press, New York. p. 43-57.

—, Nilsen, J. & Igeland, B. 2003. Effect of temperature on the induction of bud dormancy in ecotypes of *Betula pubescens* and *Betula pendula*. Scandinavian Journal of Forest Research 18:208-217.

Kalela, A. 1937. Zur Synthese der experimentellen Untersuchungen über Klimarassen der Holzarten. Communicationes Instituti Forestalis Fenniae 26(1):1-445.

Kalela, A. 1971. Kasviorganologia [Plant organology]. 3. edition. Kustannusosakeyhtiö Otava, Helsinki. 180 p.

Kallio, P. & Mäkinen, Y. 1978. Vascular flora of Inari Lapland. 4. Betulaceae. Reports from Kevo Subarctic Research Station 14:38-63.

Kalliola, R. 1973. Suomen kasvimaantiede [Plant geography of Finland]. Werner Söderström Osakeyhtiö, Porvoo. 308 p.

Kangas, E. 1949. Hirven metsässä aikaan saamat tuhot ja niiden metsätaloudellinen merkitys. Summary: On the damage to the forests caused by moose, and its significance in the economy of the forests. Suomen Riista 4:62-90.

Kanninen, M. 1990. Havupuiden pituuskasvu [Height growth of conifers]. Silva Carelica 16:183-206.

Karhu, A., Hurme, P., Karjalainen, M., Karvonen, P., Kärkkäinen, K., Neale, D., Savolainen, O. 1996. Do molecular markers reflect patterns of differentiation in adaptive traits of conifers? Theoretical and Applied Genetics 93:215-221.

Kärkkäinen, M. 1986. Koivuvaneritukkien ja -runkojen arvosuhteet. Abstract: Value relations of birch veneer logs and stems. Silva Fennica 20(1):45:57.

Kvaalen, H. & Johnsen, Ø. 2007. Timing of bud set in *Picea abies* is regulated by a memory of temperature during zygotic and somatic embryogenesis. New Phytologist 177:49-59.

Kellomäki, S., Väisänen, H. & Strandman, H. 1996. Response of the boreal forest ecosystem to climatic change and its silvicultural implications: modelling. In: Roos, J. (ed.). The Finnish Research Programme on Climate Change. Final Report. Publications of the Academy of Finland 4/96. Edita, Helsinki. p. 252-253.

Kennedy, D. & Brown, I.R. 1984. Crown development and shoot growth in *Betula pendula* Roth and its implications for forestry and arboriculture. Arboricultural Journal 8:245-257.

Kivivuori, U. 1994a. Koivuntaimet kärsivät viime syksyn pakkasista [Birch seedlings suffered from frosts last autumn]. Metsälehti 1994(13)

— 1994b. Itä-Suomen koivuntaimikoissa miljoonatuhot [Severe damages in eastern Finnish birch plantations]. Metsälehti 1994(17):11.

Kleinschmit, J. 1998. Die Birke - Standortansprüche und Möglichkeiten der züchterischen Verbesserung. Summary: The birches - site requirements and breeding. Forst und Holz 53(4):99-104.

— 2002. Konsequenzen aus der Birkenzüchtung für die forstliche Praxis - eine Bilanz nach 35 Berufsjahren. Summary: Consequences from birch breeding for practical forestry - a balance after 35 professional years. Forst und Holz 57(15/16):470-475.

— & Otto, H.-J. 1980. Prüfung von Birkenherkünften und Einzelbäumen sowie Züchtung mit Birke. Der Forst- und Holzwirt 35(5):81-90.

Koski, V. 1983. Puiden vuosirytmi ja pakkasenkestävyys. Summary: The annual rhythm and frost resistance in forest trees. Oulanka Reports 4:34-37.

— & Tallqvist, R. 1978. Tuloksia monivuotisista kukinnan ja siemensadon mittauksista metsäpuilla. Summary: Results of long-time measurements of the quantity of flowering and seed crop of forest trees. Folia Forestalia 364. 60 p.

— & Selkäinaho, J. 1982. Experiments on the joint effect of heat sum and photoperiod on seedlings of *Betula pendula*. Communicationes Instituti Forestalis Fenniae 105:1-34.

— & Sievänen, R. 1985. Timing of growth cessation in relation to the variations in the growing season. In: Tigerstedt, P.M.A., Puttonen, P. & Koski, V. (eds.). Crop physiology of forest trees. Helsinki University Press, Helsinki, Finland. p. 167-193.

Kujala, V. 1946. Koivututkimuksia. Summary: Some recent data on birches. Communicationes Instituti Forestalis Fenniae 34(1):1-36.

Laivinš, M. & Melecis, V. 2003. Bio-geographical interpretation of climate data in Latvia: multidimensional analysis. Acta Universitatis Latviensis. Earth and Environment Sciences 654:7-22.

Landis, T.D., Tinus, R.W. & Barnett, J.P. 1999. The container tree nursery manual. Vol. 6. Seedling propagation. Agriculture handbook 674. USDA Forest Service, Washington, DC. 166 p.

Lang, G.A., Early, J.D., Martin, G.C. & Darnell, R.L. 1987. Endo-, para-, and ecodormancy: physiological terminology and classification for dormancy research. HortScience 22(3):371-377.

Langhammer, A. 1981. Breddegradsøkotyper an lavlandsbjørk (*Betula verrucosa* Ehrh.). Summary: Latitudinal ecotypes of silver birch (*Betula verrucosa* Ehrh.). Meldinger fra Norges Landbrukshøgskole 60(1):1-12.

— 1982. Vekststudier på hengebjörk (*Betula verrucosa* Ehrh.) i Norge. Summary: Growth studies on silver birch (*Betula verrucosa* Ehrh.) in Norway. Meldinger fra Norges Landbrukshøgskole 61(23):1-43.

Langlet, O. 1959. A cline or not a cline - a question of Scots pine. Silvaea Genetica 8:13-22.

— 1971. Two hundred years genecology. Taxon 20(5/6):653-722.

Lanner, R.M. 1976. Patterns of shoot development in *Pinus* and their relationship to growth potential. In: Cannell, M.G.R. & Last, F. (eds.). Tree physiology and yield improvement. Academic Press, London. p. 223-243.

Lacey, E.P. & Herr, D. 2000. Parental effects in *Plantago lanceolata* L. III Measuring parental temperature effects in the field. Evolution 54(4):1207-1217.

Lavsund, S. 1987. Moose relationships to forestry in Finland, Norway and Sweden. Swedish Wildlife Research, Supplement 1:229-244.

Lepistö, M. 1973. Accelerated birch breeding - in plastic greenhouses. The Forestry Chronicle 49(4):172-173.

Li, C., Puhakainen, T., Welling, A., Viherä-Aarnio, A., Ernstsen, A., Junttila, O., Heino, P. & Palva, T. 2002. Cold acclimation in silver birch (*Betula pendula*). Development of freezing tolerance in different tissues and climatic ecotypes. Physiologia Plantarum 116:478-488.

—, Viherä-Aarnio, A., Puhakainen, T., Junttila, O., Heino, P. & Palva, T. 2003. Ecotype-dependent control of growth, dormancy and freezing tolerance under seasonal changes in *Betula pendula* Roth. Trees 17:127-132.

Lilja, A. & Heikkilä, R. 1995. Discoloration of birch trees after wounding or breakage. In: Aamlid, D. (ed.). Forest Pathology Research in the Nordic Countries 1994. Aktuelt fra Skogforsk 4(95):30-32.

Lindquist, B. 1947. On the variation in Scandinavian *Betula verrucosa* Ehrh. with some notes on the *Betula* series Verrucosae Sukacz. Svensk Botanisk Tidskrift 41:45-80.

Linkosalo, T., Carter, T.R., Häkkinen, R. & Hari, P. 2000. Predicting spring phenology and frost damage risk of *Betula* spp. under climatic warming: a comparison of two models. Tree Physiology 20:1175-1182.

Longman, K.A. & Wareing, P.F. 1959. Early induction of flowering in birch seedlings. Nature 184:2037-2038.

Löyttyniemi, K. & Lääperi, A. 1988. Hirvi ja metsätalous. Summary: Moose in Finnish Forestry. University of Helsinki. Department of Agricultural and Forest Zoology. Reports 13. 56 p.

Luomajoki, A. 1999. Differences in the climatic adaptation of silver birch (*Betula pendula*) and downy birch (*B. pubescens*) in Finland based on male flowering phenology. Acta Forestalia Fennica 263. 35 p.

Luoranen, J. 2000. Control of growth and frost hardening of silver birch container seedlings: growth retardants, short day treatment and summer planting. Academic dissertation. The Finnish Forest Research Institute, research Papers 777. 167 p.

— & Rikala, R. 1997. Growth regulation and cold hardening of silver birch seedlings with short-day treatment. Tree Planters' Notes 48(3/4):65-71.

— & Rikala, R. 2001. Kylvöajankohdan vaikutus koivun paakkutaimien kasvun päättymiseen ja maastomenestymiseen [Effect of sowing time on growth cessation and field performance of birch container seedlings]. Metsäntutkimuslaitoksen tiedonantoja 813:76-81.

Marttila, V., Granholm, H., Laanikari, J., Yrjölä, T., Aalto, A., Heikinheimo, P., Honkatukia, J., Järvinen, H., Liski, J., Merivirta, R. & Paunio, M. 2005. Ilmastonmuutoksen kansallinen sopeutumisstrategia. Abstract: Finland's National Strategy for Adaptation to Climate Change. Publications of the Ministry of Agriculture and Forestry 1/2005. 276 p.

Morgenstern, E.K. 1996. Geographic variation in forest trees: Genetic basis and application of knowledge in silviculture. UBC Press, Vancouver, Canada. 209 p.

Myking, T. & Heide, O.M. 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. Tree Physiology 15:697-704.

Niemelä, P., Hagman, M. & Lehtilä, K. 1989. Relationship between *Pinus sylvestris* L. origin and browsing preference by moose in Finland. Scandinavian Journal of Forest Research 4:239-246.

— & Veteli, T. 2005. Ilmastonmuutoksen vaikutukset metsätuhoihin ja -tauteihin boreaalisen vyöhykkeen metsissä [Effects of climate change on forest damages and diseases in boreal forest zone]. In: Riikonen, J. & Vapaavuori, E. (eds.). Ilmasto muuttuu - mukautuvatko metsät [Climate changes - do the forests acclimate]. Metsäntutkimuslaitoksen tiedonantoja 944: 92-98.

Niemistö, P. 1997. Ensiharvennuksen ajankohdan ja voimakkuuden vaikutus istutetun rauduskoivikon kasvuun ja tuotokseen [Effects of the timing and intensity of the first thinning on growth and yield of planted silver birch]. Metsätieteen aikakauskirja – Folia Forestalia 4/1997:439-454.

—, Viherä-Aarnio, A., Velling, P., Heräjärvi, H. & Verkasalo, E. (eds.) 2008. Koivun kasvatus ja käyttö [Management and utilization of birch]. Metsäkustannus, Helsinki. 254 p.

Nitsch, J.P. 1957. Photoperiodism in woody plants. Proceedings of the American Society for Horticultural Science 70:526-544.

Nuorteva, M. & Nuorteva, H. 2007. Hävinneeksi luokitellun koivutuholaisen, pulskamailapistiäisen massaesiintymä Ylämaalla. [Mass occurrence of European birch sawfly (*Arge bullata*), earlier defined as extint, at Ylämaa]. Metsätieteen aikakauskirja 3/2007:313-316.

Nygren, M. 2003. Metsäpuiden siemenopas [Seed guide of forest trees]. Metsäntutkimuslaitoksen tiedonantoja 882. Gummerus Kirjapaino Oy, Jyväskylä. 144 p.

Oksanen, E. 2005. Ilmastonmuutoksen biologiset vaikutusmekanismit metsäpuilla. [Biological impact mechanisms of climate change on forest trees]. In: Riikonen, J. & Vapaavuori, E. (eds.). Ilmasto muuttuu - mukautuvatko metsät [Climate changes - do the forests acclimate]. Metsäntutkimuslaitoksen tiedonantoja 944: 41-51.

Olsen, J.E., Junttila, O. & Moritz, T. 1995. A localised decrease of GA_1 in shoot tips of *Salix pentandra* seedlings precedes cessation of shoot elongation under short photoperiod. Physiologia Plantarum 95:627-632.

—, Junttila, O., Nilsen, J., Eriksson, M.E., Martinussen, I., Olsson, O., Sandberg, G. & Moritz, T. 1997. Ectopic expression of oat phytochrome A in hybrid aspen changes critical daylength for growth and prevents cold acclimatization. The Plant Journal 12(6):1339-1350.

Palmé, A.E., Su, Q., Rautenberg, A., Manni, F. & Lascoux, M. 2003. Postglacial recolonization and cpDNA variation of silver birch, *Betula pendula*. Molecular Ecology 12:201-212.

Palo, R.T. 1985. Chemical defence in birch: inhibition of digestibility in ruminants by phenolic extracts. Oecologia 68:10-14.

—, Sunnerheim, K. & Theander, O. 1985. Seasonal variation in phenols, crude protein and cell wall content of birch (*Betula pendula* Roth) in relation to ruminant in vitro digestibility. Oecologia 65:314-318.

—, Bergström, R., Danell, K. 1992. Digestibility, distribution of phenols, and fiber at different twig diameters of birch in winter. Implication for browsers. Oikos 65:450-454.

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.

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

Pauley, S.S. & Perry, T.O. 1954. Ecotypic variation of the photoperiodic response in *Populus*. Journal of the Arnold Arboretum 35:167-188.

Pollard, D.F.W. & Logan, K.T. 1976. Inherent variation in "free" growth in relation to numbers of needles produced by provenances of *Picea mariana*. In: Cannell, M.G.R. & Last, F. (eds.). Tree physiology and yield improvement. Academic Press, London. p. 245-251.

Raulo, J. 1976. Development of *Betula pendula* Roth progenies in northern Lapland. Communicationes Instituti Forestalis Fenniae 88(4):1-19.

— 1978. Forestation chain for birch (*Betula pendula* Roth) in Finland. Silva Fennica 12(1):17-24.

— 1979. Rauduskoivujälkeläistöjen rungon laatu Etelä- ja Keski-Suomessa. Summary: Stem quality of *Betula pendula* Roth progenies in South and Central Finland. Communicationes Instituti Forestalis Fenniae 97(5):1-39.

— & Koski, V. 1977. Growth of *Betula pendula* Roth progenies in southern and central Finland. Communicationes Instituti Forestalis Fenniae 90(5):1-39.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton, D.A. Jr. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. Ecological Monographs 69(3):375-407.

Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A. & Milyutin, L.I. 2002. Intraspecific responses to climate in *Pinus sylvestris*. Global Change Biology 8:912-929.

Renecker, R.A. & Schwartz, C.C. 1998. Food habits and feeding behavior. In: Franzmann, A.W. & Schwartz, C.C. (eds.). Ecology and Management of North American Moose. p. 403-440.

Riikonen, J., Lindsberg, M.-M., Holopainen, T., Oksanen, E., Lappi, J., Peltonen, P. & Vapaavuori, E. 2004. Silver birch and climate change: variable growth and carbon allocation responses to elevated concentrations of carbon dioxide and ozone. Tree Physiology 24:1227-1237.

Rinne, P., Tuominen, H. & Junttila, O. 1994. Seasonal changes in bud dormancy in relation to bud morphology, water and starch content, and abscisic acid concentration in adult trees of *Betula pubescens*. Tree Physiology 14:549-561.

Romberger, J.A. 1963. Meristems, growth and development in woody plants. An analytical review of anatomical, physiological and morphogenic aspects. U.S. Department of Agriculture, Forest Service. Technical Bulletin No 1293. 214 p.

Rousi, M. 1988. Resistance breeding against voles in birch: possibilities for increasing resistance by provenance transfers. EPPO Bulletin 18:257-263.

—, Tahvanainen, J. & Uotila, I. 1989. Inter- and intraspecific variation in the resistance of winter-dormant birch (*Betula* spp.) against browsing by the mountain hare. Holarctic Ecology 12:187-192.

Rusanen, M., Vakkari, P. & Blom, A. 2003. Genetic structure of *Acer platanoides* and *Betula pendula* in northern Europe. Canadian Journal of Forest Research 33:1110-1115.

Ryynänen, L. & Ryynänen, M. 1986. Propagation of adult curly-birch succeeds with tissue culture. Silva Fennica 20(2):139-147.

Saether, B.-E. & Andersen, R. 1990. Resource limitation in a generalist herbivore, the moose (*Alces alces*): ecological constraints on behavioral decisions. Canadian Journal of Zoology 68(5):993-999.

Sakai, A. & Weiser, C.J. 1973. Freezing resistance of trees in North America with reference to tree regions. Ecology 54(1):118-126.

Sarvas, R. 1948. Tutkimuksia koivun uudistumisesta Etelä-Suomessa. Summary: A research on the regeneration of birch in South Finland. Communicationes Instituti Forestalis Fenniae 35(4):1-91.

— 1952. On the flowering of birch and the quality of seed crop. Communicationes Instituti Forestalis Fenniae 40(7):1-38.

— 1972. Investigations on the annual cycle of development of forest trees. Active period. Communicationes Instituti Forestalis Fenniae 76(3):1-110.

— 1974. Investigations on the annual cycle of development of forest trees. II Autumn dormancy and winter dormancy. Communicationes Instituti Forestalis Fenniae 84(1):1-101.

Saxe, H., Cannell, M.G.R., Johnsen, Ø., Ryan, M.G. & Vourlitis, G. 2001. Tree and forest functioning in response to global warming. Tansley review 123. New Phytologist 149:369-400.

Sharik, T.L. & Barnes, B.V. 1976. Phenology of shoot growth among diverse populations of yellow birch (*Betula alleghaniensis*) and sweet birch (*B. lenta*). Canadian Journal of Botany 54:2122-2129.

Simola, L.K. 1985. Propagation of plantlets from leaf callus of *Betula pendula* f. *purpurea*. Scientia Horticulturae 26(1):77-86.

Stener, L.-G. 1995. Jämförelse mellan björk av finskt och svenskt ursprung i ett försök i södra Sverige. Summary: Comparison of silver birch of Finnish and Swedish origin in a trial in southern Sweden. SkogForsk. Redogörelse 1(1995):1-17.

— 1997. Förflyttning av björkprovenienser i Sverige. Summary: Transfer of birch provenances in Sweden. SkogForsk. Redogörelse 3(1997):1-30.

— & Werner, M. 1997. Skogsodlingsmaterial av björk - Vad finns i dag och vad kommer att finnas i morgon? Summary: Regeneration material for birch - present and future options. SkogForsk. Resultat 6(1997):1-4.

Sutinen, R., Teirilä, A., Pänttäjä, M. & Sutinen, M.-L. 2002. Distribution and diversity of tree species with respect to soil electrical characteristics in Finnish Lapland. Canadian Journal of Forest Research 32:1158-1170.

Sylvén, N. 1940. Lång- och kortdagstyper av de svenska skogsträden. Summary: Long day and short day types of the Swedish forest trees. Svensk Papperstidning 43:317-324, 332-342, 350-354.

Talkkari, A. 1998. The development of forest resources and potential wood yield in Finland under changing climatic conditions. Forest Ecology and Management 106(2/3):97-106.

Thomas, B. & Vince-Prue, D. 1997. Photoperiodism in plants. 2. edition. Academic Press, London. 428 p.

Tigerstedt, P.M.A. 1973. Studies on isozyme variation in marginal and central populations of *Picea abies*. Hereditas 75:47-60.

Tomppo, E. & Joensuu, J. 2003. Hirvieläinten aiheuttamat metsätuhot Etelä-Suomessa Valtakunnan metsien 8. ja 9. inventoinnin mukaan [Damages caused by Cervidae in southern Finland in the 8th and 9th National Forest Inventory]. Metsätieteen aikakauskirja 4/2003:507-535.

Turesson, G. 1922. The species and the variety as ecological units. Hereditas 3:100-113.

Vaartaja, O. 1954. Photoperiodic ecotypes of trees. Canadian Journal of Botany 32:392-399.

— 1959. Evidence of photoperiodic ecotypes in trees. Ecological Monographs 29(2):91-111.

Velling, P. 1979. Erilaisten rauduskoivuprovenienssien alkukehityksestä taimitarhalla ja kenttäkokeessa. Summary: Initial development of different *Betula pendula* Roth provenances in the seedling nursery and in field trials. Folia Forestalia 379:1-14.

—, Viherä-Aarnio, A., Rautanen, J. & Kurttio, O. 2002. Züchtung und Anbau von Birke in Finnland - eine Erfolgsstory? Abstract: Breeding and cultivation of birch in Finland - a story of success? Forst und Holz 57(15/16):459-465.

Viherä-Aarnio, A. 1994. Genetic variation and breeding strategy of birch in Finland. Norwegian Journal of Agricultural Sciences. Supplement No 18:19-26.

— & Velling, P. 2001. Micropropagated silver birches (*Betula pendula*) in the field - performance and clonal differences. Silva Fennica 35(4):385-401.

Walters, S.M. 1964. *Betula*. In: Tutin et al. (ed.) Flora Europaea 1:57-58. Cambridge.

Wareing, P.F. 1956. Photoperiodism in woody plants. Annual Review of Plant Physiology 7:191-214.

— & Phillips, I.D.J. 1978. The control of growth and differentiation in plants. 2. edition. Pergamon Press. 347 p.

Weiser, C.J. 1970. Cold resistance and injury in woody plants. Science 169:1269-1278.

Welling, A. 2003. Overwintering in woody plants: Involvement of ABA and dehydrins. Academic dissertation. University of Helsinki. Dissertationes Biocentri Viikki Universitatis Helsingiensis 19/2003. 59 p. + 4 original papers.

—, Rinne, P., Viherä-Aarnio, A., Kontunen-Soppela, S., Heino, P. & Palva, E.T. 2004. Photoperiod and temperature differentially regulate the expression of two dehydrin genes during overwintering of birch (*Betula pubescens* Ehrh.). Journal of Experimental Botany 55(396):507-516.

White, T.L., Adams, W.T. & Neale, D.B. 2007. Forest genetics. CABI Publishing, Oxfordshire, UK and Cambridge, MA, USA. 682 p.

Wojda, T. 2004. Zmienność wiosennej fenologii polskich i litewskich pochodzeń brzozy brodawkowatej (*Betula pendula* Roth). Abstract: Variability of Polish and Lithuanian birch provenances (*Betula pendula* Roth) in the spring phenology. Sylwan 8:52-60.

Worrell, R., Cundall, E.P., Malcolm, D.C. & Ennos, R.A. 2000. Variation among seed sources of silver birch in Scotland. Forestry 73(5):419-435.