7 Phenology and Performance of Mountain Birch Provenances in Transplant Gardens: Latitudinal, Altitudinal and Oceanity–Continentality Gradients

J.A. Ovaska, J. Nilsen, F.E. Wielgolaski, H. Kauhanen, R. Partanen,
S. Neuvonen, L. Kapari, O. Skre and K. Laine

7.1 Introduction

Phenology is the study of timing of annually recurring events in plants, especially in relation to year-to-year variation in environmental factors. In forestry, it has been known for many years that transplantation of coniferous tree provenances between southern and northern latitudes has a considerable impact on both phenology and productivity of the trees (Hagem 1931; Kalela 1938; Heikinheimo 1949; Magnesen 1992; Beuker 1994). It has, for instance, been observed that bud break and flowering occur earliest in trees of the northernmost origin when grown under uniform conditions in a transplant garden (Reader 1982; Beuker 1994). They also end growth earliest in autumn (Morgenstern 1996). Generally, the photoperiod has been found to be the dominant factor in determining the cessation of growth in northern plants (Partanen and Beuker 1999). The long-continuing growth of southern provenances planted further north has often caused a weak hardening of the shoots by the end of the summer, which has resulted in frost damage during winter and spring.

Transplantation experiments are often used in determining the degree of ecotypic differentiation among different provenances of a tree species. In a transplantation experiment, seedlings or micropropagated saplings of different provenances are transferred to given environmental conditions and their responses are then determined. When the provenances are grown under uniform conditions for comparative ecophysiological research, all the observed phenotypic differences among the provenances are due to differences in their genotypes – provided that the transplants of different provenances have been treated in the same way before and during transplantation. These different responses may be used to estimate the degree of ecotypic differentiation within a tree species. On the other hand, when the same provenance or geno-

Ecological Studies, Vol. 180
F.E. Wielgolaski (Ed.), P.S. Karlsson, S. Neuvonen, D. Thannheiser (Ed. Board)
Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests

type is grown in varying habitats and its response to different environmental conditions then determined, a knowledge of phenotypic plasticity of a provenance or genotype is obtained.

In the present study, populations of *Betula pubescens*, and mainly of mountain birch (ssp. *czerepanovii*) of southern and northern, as well as of oceanic and more continental origin and from various elevations, were transferred to different transplant gardens north of the Arctic Circle. These transplant gardens are situated in an oceanity–continentality gradient and at different altitudes in northwestern Fennoscandia and northeastern Finland (Fig. 7.1). Different provenances were grown in the transplant gardens for 10 years or more. The aim of the present study is to determine the differences in survival and in the phenological and growth responses among different birch provenances under varying environmental conditions and compare the results with earlier findings.

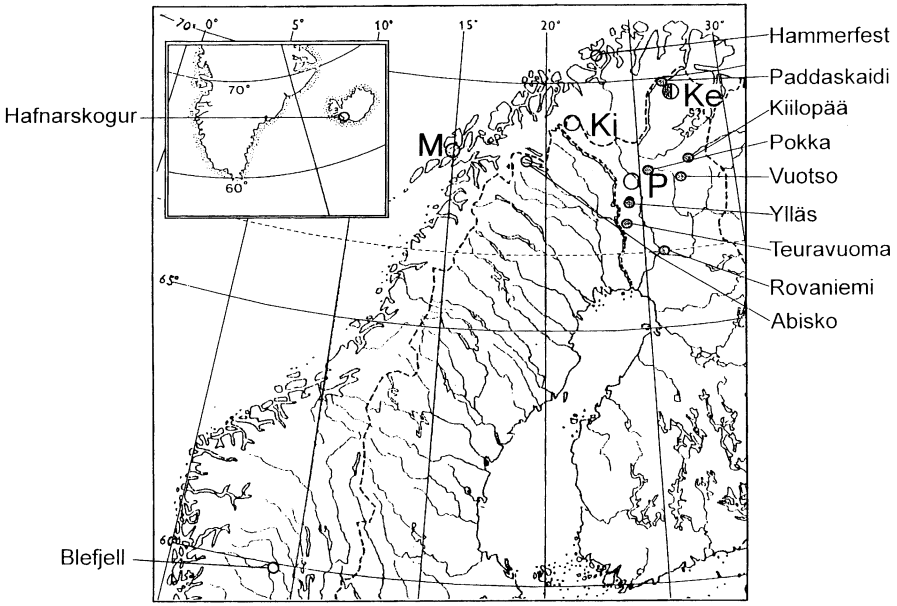

Fig. 7.1. Map showing the location of five transplant gardens and the origin of seedling progenies (provenances) used in the study. Transplantation sites are marked with *large dots*, *M* Melbu (10 m a.s.l., in coastal area), *Ki* Kilpisjärvi (510 m a.s.l., just below altitudinal tree line), *P* Pallasjärvi (320 m a.s.l., far below altitudinal forest line) and *Ke* Kevo (low-elevation garden: 100 m a.s.l., at river valley; high-elevation garden: 280 m a.s.l., at forest line). *Open dots* Provenances grown in Melbu, Kilpisjärvi and Pallasjärvi gardens, *filled dots* provenances grown in Kevo gardens, *half-filled dots* the provenance is grown both in the three former and two latter gardens

7.2 Material and Methods

Results from five transplant gardens (Fig. 7.1) are reviewed in the present study and compared with the results of older studies. Only the high-elevation garden near the Kevo Subarctic Reasearch Station is characterized by relatively nutrient-rich soil. More details of the sites are given in the enclosed CD.

The age of the birches used in the study varied among the transplant gardens. In the Kevo gardens, the seeds were germinated in 1974 and the saplings were planted in 1977, while the material for the Melbu, Kilpisjärvi and Pallasjärvi gardens (Fig. 7.1) was germinated in 1991 and planted in 1992. The mother trees for the Kevo gardens came from different latitudes and altitudes in northern Finland, and the plants in the other transplant gardens originated from southern and northern Norway, northern Sweden and Finland, and from Iceland (see Fig. 7.1; more details in the enclosed CD).

Differences among the provenances at the five transplant gardens were recorded for plant survival, time of leafing (bud burst), foliage senescence (autumnal coloration) and leaf fall. Total height and diameter measurements of the study trees are measured annually, but only data for certain years are given here. More detailed growth measurements will be presented elsewhere (see also, e.g., Chap. 4 and the enclosed CD for more details).

7.3 Results and Discussion

7.3.1 Transplantation Stress and Seedling Survival

When considering the phenological and growth responses of different provenances to the prevailing environmental conditions after transplantation, we often find features typical of each provenance. These characteristics are usually signs of ecotypic differentiation to the original habitat of a provenance and are thus the result of genotypic adaptation. However, a given provenance may be exposed to heavy environmental stress after transplantation due to, e.g. a remote latitudinal distance, an altitudinal difference or a great oceanity–continentality change between its original habitat and the transplantation site. Hence, it is sometimes difficult to distinguish whether the phenological and growth responses of transplants are genotypic adaptations characteristic of a plant in its original habitat or whether they are just phenotypic adjustments in response to transplantation procedure. On the other hand, however, if there are clear differences in seedling survival among the provenances it may be concluded that some provenances are suffering more from transplantation than others. Long-distance latitudinal transfer has been observed to have a negative impact on many tree species (e.g.

Carter 1996) and the same is obvious also in birch (Eriksson and Jonsson 1986).

In terms of the survival of seedlings grown in the Melbu, Kilpisjärvi and Pallasjärvi transplantation sites (see Fig. 7.1), it was clear that the seedlings of the southernmost provenance (Blefjell) suffered most from the transplantation to northern areas (Fig. 7.2). Moreover, the other relatively southern provenance (Hafnarskogur) had a very low survival rate in the Kilpisjärvi site, while it survived well in the more oceanic Melbu site at approximately the same latitudinal location. The birches from southern Greenland (Narssarssuaq) at first (1994) showed relatively good survival in Melbu, but in 2002 they had the lowest survival value. The oceanic Melbu provenance had a high mortality in the Kilpisjärvi site, however, it survived in the more continental site in Pallasjärvi. Survival in both the most oceanic Melbu and most continental Pallasjärvi sites was approximately equally good. The reduced survival of all provenances in Kilpisjärvi was most probably caused by a combination of severe high-altitude conditions and damage by herbivores (willow grouse and hare in winter, *Epirrita* larvae in summer; Rauni Partanen, pers. observ.). With regard to the Kevo gardens, the southernmost provenance (Rovaniemi) had clearly visible injuries (frost or drought damage), which were especially common in the patches of a very dry and sandy soil in the lower garden. This suggests that, in addition to the stress caused by a long-distance transfer of a provenance from its original habitat, edaphic factors in a new environment may play an important role in the susceptibility of a given provenance to damage after transplantation.

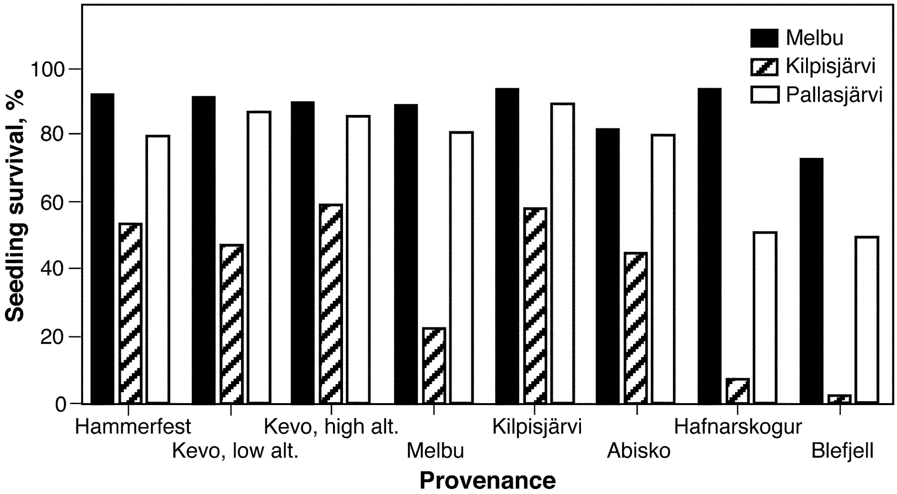

Fig. 7.2. Seedling survival 2 years after planting for different provenances in Melbu, Kilpisjärvi and Pallasjärvi transplantation sites. Note that the low survival in Kilpisjärvi was partly caused by damage from herbivores

7.3.2 Spring Phenology (Bud Burst)

According to e.g. Myking and Heide (1995) and Myking (1997, 1999), when *B. pubescens* ecotypes were growing under uniform environmental conditions, southern, coastal and high-altitude ecotypes had later bud burst than northern, inland and low-altitude ones. This means that the thermal sum requirement for bud burst is higher in the former than in the latter. With regard to the Melbu, Kilpisjärvi and Pallasjärvi transplantation sites, the mean date for bud burst was, indeed, later in the southernmost provenances (Blefjell and Hafnarskogur) than in the provenances originating from farther north (Table 7.1). The longer observation series (1994–2002) from Melbu confirmed that the relative date of bud burst of each provenance was consistent over years (Table 7.1), despite the large annual variation (up to 3 weeks) in actual dates of bud burst. The oceanic Melbu provenance showed later bud burst in all the transplantation sites than the more continental Abisko and Kilpisjärvi provenances of approximately the same latitudinal origin. However, another oceanic provenance (Hammerfest) came into leaf earlier than, e.g., the more continental Kevo provenances, but on the other hand, it was the northernmost of all the provenances, and there might be some kind of compromise in its response to these opposite trends (oceanity vs. northernness). In mountain birch, the timing of bud burst is genetically determined and is related to the length of the growth period in its natural habitat (Sulkinoja and Valanne 1987). Generally, *Betula* needs a chilling period of less than 10–12 °C for bud break, and this requirement decreases significantly with increasing latitude of origin (Myking and Heide 1995), but increases with oceanity (Leinonen 1996; Myking 1999). Normally, the chilling period needed in birch for the start of new activity in spring is long enough all over Fennoscandia, and Myking and Heide (1995) conclude that there is little risk of a chilling deficit in birch under Scandinavian winter conditions, even with a climatic warming of 7–8 °C. The timing of bud burst is dependent on temperature sum in spring, and the threshold value of temperature sum for bud burst varies among birch provenances (Sulkinoja and Valanne 1987; Billington and Pellham 1991).

In contrast to the results obtained from the Melbu, Kilpisjärvi and Pallasjärvi sites, the southernmost provenance (Rovaniemi) in the Kevo transplant sites showed slightly earlier bud burst than the more northern ones (Fig. 7.3). In contrast, some of the higher-elevation provenances (Ylläs and Kiilopää) had delayed bud burst compared to the lower-elevation ones of approximately the same latitudinal origin. These results are in accordance with the results of Sulkinoja and Valanne (1987) who also found that mountain birch provenances from northern Lapland required greater thermal sum for bud break than those from southern Lapland – the same was observed for high-altitude provenances compared to low-altitude ones. The reason for the later bud break in the more northern and higher-elevation provenances in

Table 7.1. Mean date of bud burst for each provenance in Melbu, Kilpisjärvi and Pallasjärvi transplantation sites in 1994, as well as relative date of bud burst and relative senescence timing index in Melbu from 1994 to 2002

			Transplant Garden						
	Latitude N	Altitude (m a.s.l.)	Melbu Mean date of bud burst in 1994		Kilpisjärvi	Pallasjärvi	Melbu Relative date of bud burst[a]		Melbu
Provenance				SE				SE[b]	RSTI[c]
Hammerfest	70°39'	70	17 May	0.27	18 June	09 June	–2.7	0.38	–1.0
Kevo, low alt.	69°46'	95	20 May	0.81	23 June	10 June	–0.4	0.13	–0.7
Kevo, high alt.	69°46'	280	18 May	0.40	20 June	10 June	–1.4	0.23	–1.6
Utsjoki, Paddaskaidi	69°56'	330	19 May	0.39	N.D.	N.D	–0.9	0.22	–2.7
Melbu	68°31'	40	21 May	0.52	27 June	13 June	1.6	0.40	0.8
Kilpisjärvi	69°04'	510	19 May	0.19	19 June	10 June	–0.3	0.20	–2.2
Abisko	68°22'	360	19 May	0.43	20 June	11 June	–0.9	0.31	–0.3
Hafnarskogur	64°31'	20	22 May	0.51	13 July	14 June	1.7	0.30	2.6
Narssarssuaq	61°10'	70	21 May	0.49	N.D.	N.D.	1.7	0.30	2.4
Blefjell	59°47'	750	23 May	0.50	20 July	15 June	1.7	0.43	2.7

N.D., No data

[a] The difference (days) from the annual average over all provenances from 1994 to 2002

[b] Based on interannual variation

[c] Relative senescence timing index 1994–2002 (see CD for explanation)

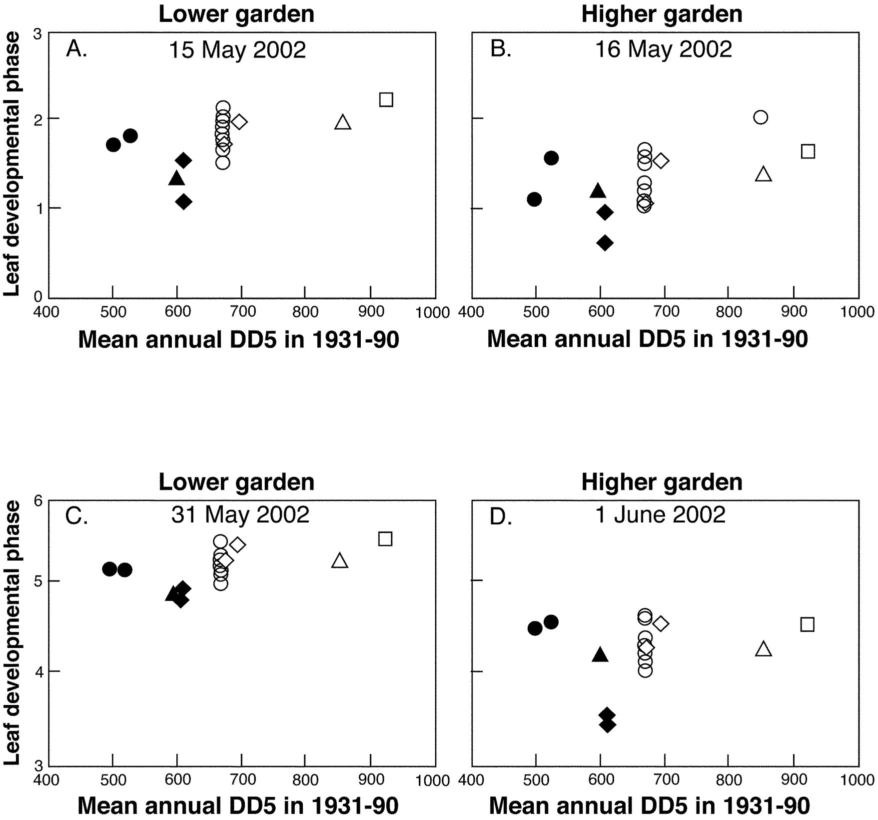

Fig. 7.3. Mean phase of bud burst and leaf development for different provenances in Kevo low-elevation and high-elevation garden at two different observation dates. The *horizontal axis* shows the estimated annual thermal sum (degree days over the base +5 °C; $\mathrm{DD5} = \sum_{n=1}^{n}(t_m - 5)$, where DD5 is the accumulated temperature sum, n is the total number of days with a mean temperature higher than threshold, and t_m is the mean temperature of the nth day) of the original habitat of each provenance. Leaf developmental phase was determined using an index from 0 (dormant bud) to 6 (leaf blade open and petiole clearly discernible). Each *dot* represents a mean value for a progeny. *Symbols with the same shape* represent provenances of approximately the same latitude (*square* 66°30′–67° N, *triangle* 67°15′–67°45′ N, *diamond* 68°–68°30′ N, *circle* 69°30′–70° N); *open symbols* represent low- or moderate-elevation and *filled symbols* high-elevation (tree-line) provenances

northeastern Fennoscandia is probably the greater influence of *B. nana* genes in these provenances as a result of introgressive hybridization (Sulkinoja and Valanne 1987; Myking 1999). Moreover, Senn et al. (1992) observed that short and small-leaved mountain birches had later bud burst than taller and bigger-leaved birches. This also suggests the greater influence of *B. nana* in the former. Indeed, the Kiilopää provenance, which had late bud burst, had clearly smaller leaves than the other provenances. Bud burst occurred slightly later in trees growing in the higher garden than in those growing in the lower garden due to the delayed attainment of the threshold value for thermal sum to bud break.

Phenology is an important tool in studies of climate change as historically documented by phenological data (Linkosalo 2000; Wielgolaski and Inouye 2003), and it can be used to demonstrate the regional/geographical differences in global change impacts (Høgda et al. 2002; Kozlov and Berlina 2002). However, it would be premature to present a predictive model of (mountain) birch bud burst under different climatic scenarios over the whole of Fennoscandia. In fact, Karlsson et al. (2003) analysed mountain birch phenology (bud break) in Abisko (1956–2002) and Kevo (1981–2002), and found that different models showed the best performance with Abisko vs. Kevo data: a simple degree-day accumulation model based on daily mean temperatures resulted in the best predictions in Kevo, while a more complex model was best in Abisko. Furthermore, there seem to be differences in the threshold temperatures for degree-day accumulation in birch studies from different areas (cf. Wielgolaski 1999; Karlsson et al. 2003), and the importance of other factors like air humidity and precipitation for the timing of bud break (see Wielgolaski 2001) in northernmost Fennoscandia is poorly understood. Therefore, studies in transplant gardens like those presented in this chapter, also clearly demonstrate how important the genetic background and local adaptations are in controlling birch phenology and growth (see also Chap. 5).

7.3.3 Autumn Phenology

With respect to leaf senescence and leaf fall of birch seedlings in the Melbu and Pallasjärvi transplantation sites in the second year after planting, the southernmost provenances (Blefjell and Hafnarskogur) showed delayed leaf yellowing and fall compared to the more northern ones (Fig. 7.4). A follow-up monitoring (1994–2002) in Melbu verified the consistency in the order of leaf senescence among different provenances (Table 7.1: RSTI). These results are in accordance with earlier results obtained from phytotron studies using northern and southern mountain birch provenances (Nilsen and Wielgolaski 2001). In addition, the oceanic Melbu provenance had later foliage senescence than the more continental provenances of approximately the same latitudinal origin. The high-altitude provenances (Paddaskaidi, Kevo high-altitude and

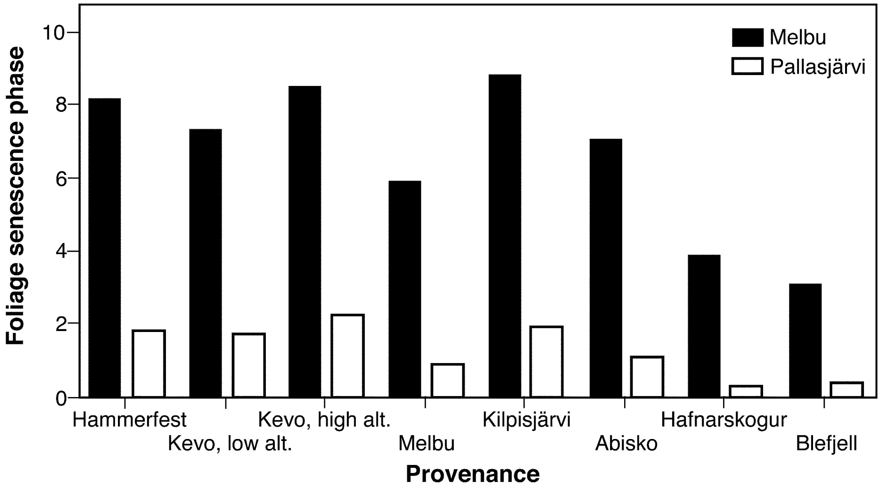

Fig. 7.4. Mean phase of foliage senescence (autumnal coloration) and abscission for different provenances in Melbu and Pallasjärvi transplantation sites on 10 September 1994. Determination of autumnal coloration and fall of leaves was made using the following scale: *0* all leaves green; *1* first signs of yellowing; *2* less than 25 % of the leaves yellow; *3* 26–50 % of the leaves yellow; *4* 51–75 % of the leaves yellow; *5* 76–99 % of the leaves yellow; *6* all leaves yellow; *7* <50 % of the leaves fallen; *8* 51–75 % of the leaves fallen; *9* 76–99 % of the leaves fallen; *10* all leaves fallen

Kilpisjärvi) had earlier leaf yellowing and leaf fall than the lower-altitude provenances. These results clearly indicate that there are genetic differences among latitudinal and altitudinal ecotypes of mountain birch in the timing of autumnal coloration and leaf fall, and that these differences are related to the length of the growing season in their natural habitats (cf. Sulkinoja and Valanne 1987). At the oceanic Melbu transplantation site, foliage senescence and leaf fall were much earlier than in the more continental Pallasjärvi site. Since bud burst also took place earlier at the Melbu site than in the Pallasjärvi site (Table 7.1), the difference in the timing of leaf yellowing and leaf fall between the sites might be partially caused by the genetically determined length of the growth period in different provenances.

In general, also in Kevo transplant gardens, the southernmost low-altitude provenances showed a delay in foliage senescence, while the foliage of the northernmost high-altitude provenances turned yellow early (Fig. 7.5). There was a nice correlation between the foliage senescence index (chlorophyll disruption rate) and the thermal sum of the original habitat of a provenance, showing that the greater the mean maximum thermal sum of the habitat, the more delayed the senescence process is (Fig. 7.5). Together with the results obtained from the bud burst observations (Fig. 7.3), these results suggest that the low-altitude provenances from southern Lapland are genetically adapted

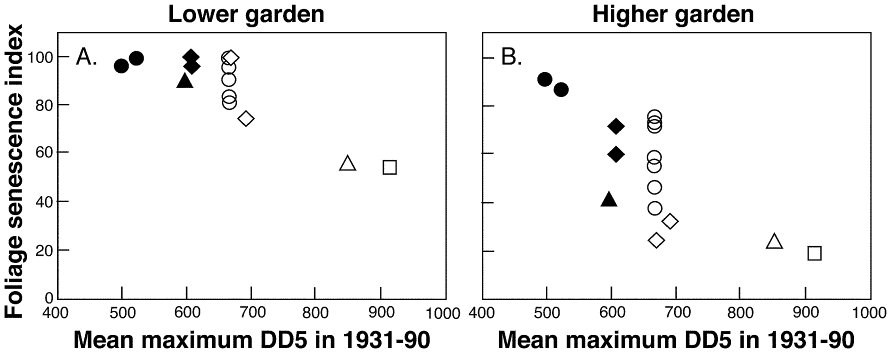

Fig. 7.5. Foliage senescence index (%) for provenances in the Kevo low-elevation and high-elevation garden in mid-September 2000, as a function of the estimated thermal sum of the original habitat of each provenance. Senescence index was determined by estimating visually the yellowing rate of the leaves and the rate of leaf fall. The senescence index is a relative measure of chlorophyll disrupted (0–100 %) in foliage at the observation date. Each *dot* represents a mean value for a progeny. See legend to Fig. 7.3 for the explanation of symbols

to a longer growth period than the more northern and higher-altitude provenances (Sulkinoja and Valanne 1987). Surprisingly, senescence of foliage took place earlier in the lower garden than in the higher garden, although it was expected to occur earlier under high-altitude conditions due to more rapid lowering of temperature in autumn. The delayed senescence of foliage in the higher garden compared to that in the lower garden was most probably due to the more favourable soil conditions in the former. In accordance with this, Nilsen and Wielgolaski (2001) found in their phytotron studies with southern and northern mountain birch provenances that fertilization greatly delayed the leaf senescence process in mountain birch seedlings, and this was seen especially in northern provenances. The results presented here also suggest that, in addition to the strong influence of temperature and light conditions on the phenology of mountain birch, edaphic factors (soil fertility and soil moisture) also play an important role in determining these phenomena.

7.3.4 Growth Forms and Growth Rates

Mountain birch is typically bush-like in shape; this polycormic birch type is widely distributed and concentrated in the continental part of the Fennoscandian subarctic region (Hämet-Ahti 1963). Clearly distinguishable from the polycormic birch type is the more maritime monocormic mountain birch (Kallio and Mäkinen 1978), which normally also grows under better nutrient conditions (Wielgolaski and Nilsen 2001; see also Chaps. 1 and 12). In northernmost Finland this birch type usually occurs at a high elevation (cf. Paddaskaidi provenance), where it forms a sparse, park-like tree-line forest. On the other hand, the monocormic birch type is also found in some places at the sea coast where it may form a very dense population. There is still one birch type which clearly differs from the former ones; it may have a few-meters-long trunk which creeps close to the ground. This creeping or procumbent birch type (*B. pubescens* ssp. *czerepanovii* var. *appressa*; Kallio and Mäkinen 1978) was described first in the Kiilopää area in eastern central Lapland (cf. Kiilopää provenance). It is adapted to grow at very high altitudes and the creeping mode of growth may be an adaptation to the windy and cold winter climate; it is protected against wind and cold by just a thin layer of snow due to its procumbent habit. However, the growth form of the half-sibling offspring in the Kevo transplant gardens is not always identical to that of its mother tree, suggesting that the growth form may not be strictly the outcome of ecotypic differentiation, but partially the result of phenotypic adjustment to the prevailing environmental conditions. Alternatively, the creeping type growing at a high elevation may have hybridized with a polycormic and more upright birch type growing at lower elevations resulting in an intermediate type (Kallio et al. 1983).

In many tree species, growth is retarded after transplantation, irrespective of whether the transfer is directed southwards or northwards from the original habitat of a tree (e.g. Carter 1996). Furthermore, in *B. pubescens* and *B. pendula*, a long-distance transfer from the original habitat causes growth retardation (Eriksson and Jonsson 1986). This was very clearly seen in the southernmost provenances in the Melbu, Kilpisjärvi and Pallasjärvi sites (Fig. 7.6) and to some extent also in Kevo gardens (Fig. 7.7). The slow growth rate of the southernmost provenances was most probably due to transplantation stress caused by the long latitudinal distance between their original habitats and transplantation sites. Eriksson and Jonsson (1986) have concluded that, since a provenance is adapted to a given photoperiod in its natural habitat, transplantation to new photoperiodic conditions may play an important role in this slackening of growth. The shortening of the photoperiod towards the end of the summer has been found to be the key factor in determining the cessation of growth in northern plants (Partanen and Beuker 1999). However, the long-lasting growth of southern provenances transplanted further north often causes a weaker hardening of the shoots by the end of the summer, and hence, they are often exposed to frost damage during winter and spring. Indeed, the southernmost provenance in Kevo gardens had clearly visible injuries, indicating that it was suffering from long-distance transfer from its original habitat. This is probably also one reason for the low survival rate (see Fig. 7.2) of the southern provenances of *B. pubescens* transplanted farther north.

Using reciprocal transplantations with *B. pendula* and *B. pubescens* provenances between two different types of habitats – heath and bog, Davy and Gill

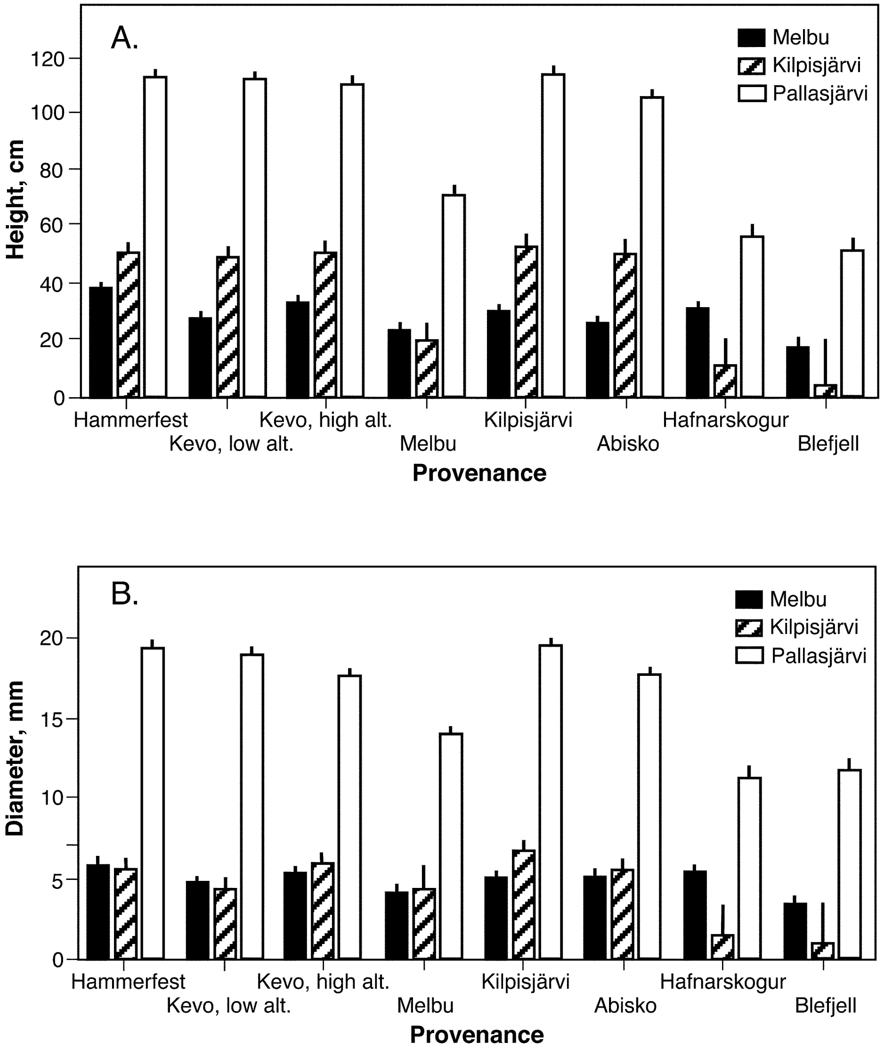

Fig. 7.6. Mean height (cm) and base diameter (mm) for different provenances in Melbu (n=101–129 for each provenance), Kilpisjärvi (n=46–82 for each provenance, except 25–31 for Melbu provenance, and 3–10 for Hafnarskogur and Blefjell provenances) and Pallasjärvi (n=109–123 for each provenance, except 67–70 for Hafnarskogur and Blefjell provenances) in late summer of the second year after planting. The *narrow bars* show SE

(1984) observed that the growth of seedlings was highly dependent on the edaphic factors of the habitat. Fertilization also promotes growth in *B. pubescens* clones (Lappalainen et al. 2000) as well as in mountain birch seedlings (Weih and Karlsson 1999) and older trees in their natural habitats (Sveinbjörnsson et al. 1992) and in transplantation gardens (Ruohomäki et al. 1996). In particular, the Melbu and Kilpisjärvi transplantation sites are relatively

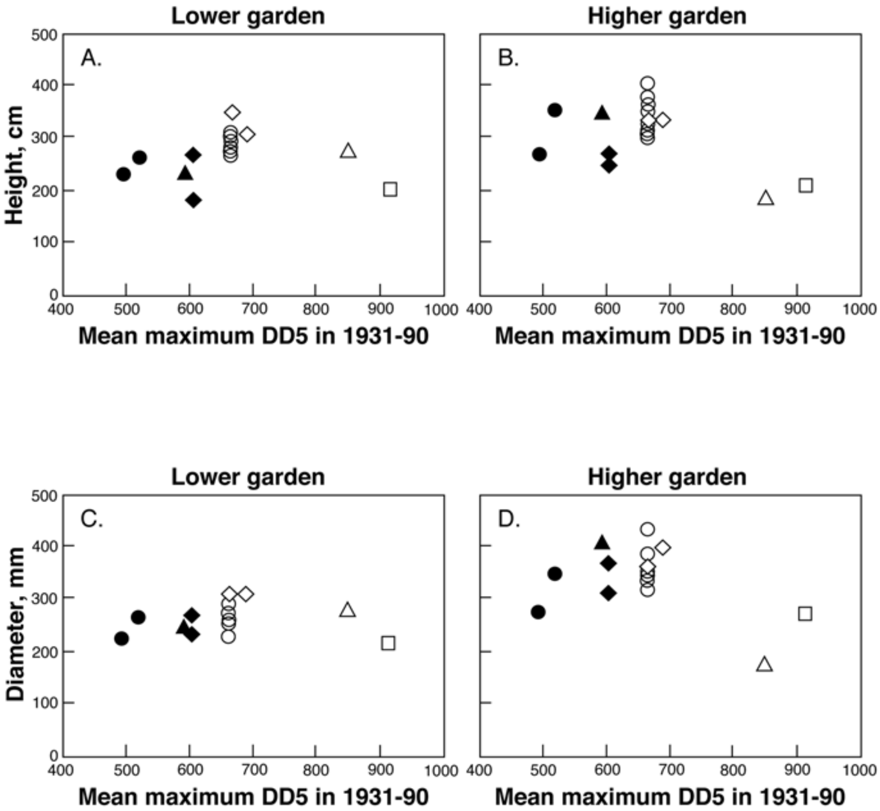

Fig. 7.7. Mean height (cm) and base diameter (mm) for different provenances in the Kevo low-elevation and high-elevation garden in summer 2000, as a function of the estimated thermal sum of the original habitat of each provenance. Each *dot* represents a mean value for a progeny. See legend to Fig. 7.3 for explanation of symbols

nutrient-poor, suggesting that the differences in the growth responses of the seedlings between these sites (Fig. 7.6) were mainly determined by other than edaphic factors. In general, the height growth of the seedlings was less in the oceanic Melbu site than in the more continental Kilpisjärvi and Pallasjärvi sites. Only the southernmost provenances (Blefjell and Hafnarskogur) succeeded markedly better in the Melbu site than in the high-altitude Kilpisjärvi site, and there was no clear difference in the growth of the oceanic Melbu provenance between these two sites. Therefore, highly oceanic conditions seemed to reduce the growth of most provenances compared to more continental conditions. Furthermore, the height of the seedlings in all provenances was markedly greater in the lower-altitude and still more continental Pallasjärvi than in the Kilpisjärvi site. On the other hand, there were no such big differences in the diameter growth of most provenances between the Melbu and Kilpisjärvi sites. The seedlings generally seemed to be more robust under the oceanic conditions than under the more continental and higher-altitude conditions. When considering the growth responses of different provenances between the Kevo transplant gardens, it was obvious that both height and diameter growth of most provenances were increased in the higher garden due to better nutrient and moisture conditions (Fig. 7.7). Only one provenance, having a relatively southern origin, showed a marked reduction in height and diameter growth under high-altitude conditions. Therefore, despite high-altitude conditions, many lower-latitude and lower-altitude provenances were able to benefit from the better soil conditions. Hence, edaphic factors may be as important as climatic factors in determining the performance of northern *B. pubescens* trees.

Ruel and Ayres (1996) observed that when the seedlings of *B. papyrifera* were transplanted to a higher elevation their root-to-shoot ratio increased and hence, the growth of the shoot was retarded. Seedlings are thus able to adjust to cold and nutrient-poor conditions by allocating more resources to root growth. In the present study, there might also be differences in the relative allocation of resources to root growth between different sites. In particular, the soil conditions of the Kevo gardens differed markedly from each other, the lower garden having much poorer soil than the higher garden. Therefore, it might be that the retarded shoot growth of the saplings grown in the lower garden compared to the growth of the saplings in the higher garden was partially due to relatively greater root growth at the expense of shoot growth in the former.

Using a reciprocal transplantation procedure, Weih and Karlsson (1999) showed that there are genetically determined differences in the growth rates and in the reaction norms of the growth between mountain birch ecotypes of different altitudinal origin. Seedlings belonging to a lower-altitude population were able to benefit from temperature rise and the addition of fertilizer by accelerating growth, but seedlings belonging to higher-altitude population experienced no such impact on growth. Higher-altitude seedlings had greater growth rates at low temperatures and higher leaf nitrogen concentration than lower-altitude seedlings (see also Chap. 5). High leaf nitrogen concentration is often an indication of a high leaf photosynthetic rate (e.g. Karlsson 1991). Weih and Karlsson (1999) concluded that the great efficiency of nitrogen metabolism and photosynthesis are adaptations to the short growing season of high-altitude habitats. With respect to provenances grown in the Kevo transplant gardens, Ovaska (1988) found that the saplings of high-altitude provenances (Kiilopää and Paddaskaidi) had greater leaf photosynthetic rates per unit leaf area than those of lower-altitude provenances. Therefore, ecotypic differentiation can also clearly be seen in elevational mountain birch populations in terms of physiological characteristics.

7.4 Conclusions and Future Prospects

The results presented in this chapter suggest that mountain birch provenances are phenotypically plastic in their response to different environmental conditions with the exception of the southernmost provenances which suffered from the long-distance transfer to the north, especially to high-altitude conditions in Kilpisjärvi. Northern and high-altitude provenances showed clearly better seedling growth in Pallasjärvi (warmer growing seasons) than near their site of origin, suggesting that although the northern mountain birches have adapted to harsh growing conditions, they have considerable capacity to respond positively to possible increasing temperatures. However, birch provenances from southern Lapland might have difficulties to adapt to different photoperiods and shorter growing seasons at higher latitudes, with the subsequent increased risks of frost damage. The results presented here also highlight the importance of edaphic factors in determining the phenological and growth responses of mountain birch. Better nutrient and moisture conditions of the soil delay autumnal coloration and improve growth of most mountain birch provenances, and this happens even in low-elevation provenances under high-elevation conditions.

A better understanding of the factors controlling the phenology of birch is urgently needed before we can reliably predict the ecological impacts of climate change on northern birch forests. Linkosalo et al. (2000) stressed that there is increasing evidence that light conditions also play a role in the timing of spring phenology of *Betula* spp. According to Myking (1999), long photoperiods significantly reduce the time to bud burst in partly dormant buds, but not by the normal time of bud burst later in spring. The laboratory experiments by Karlsson et al. (2003) showed that the temperature sum required for bud burst in Abisko and Kevo declined from ca. 250 DD_2 (degree days above the threshold of +2 °C) in January to ca 100 DD_2 in May. The interplay of genetics, photoperiod, temperature, and possibly other environmental factors in determining the actual time of bud break is apparently quite complex. A combination of long-term monitoring, laboratory (and greenhouse) experiments, and transplant experiments at multiple field sites is obviously the most efficient way to test the various phenological models (e.g., Hänninen 1995, 1996; Linkosalo et al. 2000; Karlsson et al. 2003) and to fill the gaps in our understanding of climatic impacts on birch phenology and performance.

References

Beuker E (1994) Adaptation to climatic changes of the timing of bud burst in populations of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. Tree Physiol 14:961–970

Billington HL, Pellham J (1991) Genetic variation in the date of budburst in Scottish birch populations: implications for climate change. Funct Ecol 5:403–409

Carter KK (1996) Provenance tests as indicators of growth response to climate change in 10 north temperate tree species. Can J For Res 26:1089–1095

Davy AJ, Gill JA (1984) Variability due to environment and heredity in birch transplanted between heath and bog. New Phytol 97:489–505

Eriksson G, Jonsson A (1986) A review of the genetics of *Betula*. Scand J For Res 1:421–434

Hagem O (1931) Forsök med vestamerikanske traeslag (German summary). Medd Vestl Forstl Forst 12:1–217

Hämet-Ahti L (1963) Zonation of the mountain birch forests in northernmost Fennoscandia. Ann Bot Soc 'Vanamo' 34:1–127

Hänninen H (1995) Effects of climate change on trees from cool and temperate regions: an ecophysiological approach to modelling of budburst phenology. Can J Bot 73:183–199

Hänninen H (1996) Effects of climate warming on northern trees: testing the frost damage hypothesis with meteorological data from provenance transfer experiments. Scand J For Res 11:17–25

Heikinheimo O (1949) Results of the experiments on the geographical races of spruce and pine (in Finnish with English summary). Comm Inst For Fenn 37:1–44

Høgda KA, Karlsen SR, Solheim I, Tømmervik H, Ramfjord H (2002) The start dates of birch pollen seasons in Fennoscandia studied by NOAA AVHRR NDVI data. In: Proceeding of IGARSS. 24–28 June 2002. Toronto, Ontario, Canada

Kalela A (1938) Zur Synthese der experimentellen Untersuchungen über Klimarassen der Holzarten. Comm Inst For Fenn 26:1–445

Kallio P, Mäkinen Y (1978) Vascular flora of Inari Lapland. 4. Betulaceae. Rep Kevo Subarct Res Stn 14:38–63

Kallio P, Niemi S, Sulkinoja M, Valanne T (1983) The Fennoscandian birch and its evolution in the marginal forest zone. Nordicana 47:101–110

Karlsson PS (1991) Intraspecific variation in photosynthetic light response and photosynthetic nitrogen utilization in the mountain birch, *Betula pubescens* ssp. *tortuosa*. Oikos 60:49–54

Karlsson PS, Bylund H, Neuvonen S, Heino S, Tjus M (2003) Climatic control of budburst in the mountain birch at two areas; consequences of changed climate. Ecography 26:617–625

Kozlov MV, Berlina NG (2002) Decline in length of the summer season on the Kola Peninsula, Russia. Climatic Change 54:387–398

Lappalainen J, Martel J, Lempa K, Wilsey B, Ossipov V (2000) Effects of resource availability on carbon allocation and developmental instability in cloned birch seedlings. Int J Plant Sci 161:119–125

Leinonen I (1996) A simulation model for the annual frost hardiness and freeze damage of Scots pine. Ann Bot 78:687–693

Linkosalo T (2000) Analyses of the spring phenology of boreal trees and its response to climate change. PhD Thesis, University of Helsinki, Department of Forest Ecology Publications 22. Helsinki, Finland

Linkosalo T, Carter TR, Häkkinen R, Hari P (2000) Predicting spring phenology and frost damage risk of Betula spp. under climatic warming: a comparison of two models. Tree Physiol 20:1175–1182

Magnesen S (1992) Injuries on forest trees related to choice of the species and provenances: a literature survey of a one-hundred year epoch in Norwegian forestry. Rep Skogforsk 7:1–46

Morgenstern EK (1996) Environmental influences and geographic variation. In: Morgenstern EK (ed) Geographic variation in forest trees. UBC Press, Vancouver, pp 45–89

Myking T (1997) Dormancy, budburst and impacts of climatic warming in coastal-inland and altitudinal *Betula pendula* and *B. pubescens* ecotypes. In: Lieth H, Schwartz MD (eds) Progress in biometeorology, vol 12. Phenology and seasonal climates I. Backhuys Publ, Leiden, pp 51–66

Myking T (1999) Winter dormancy release and budburst in *Betula pendula* Roth and *B. pubescens* Ehrh. ecotypes. Phyton 39:139–146

Myking T, Heide OM (1995) Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. Tree Physiol 15:697–704

Nilsen J, Wielgolaski FE (2001) Effects of fertilization and watering on morphology in young mountain birch plants of different provenances – a pilot study. In: Wielgolaski FE (ed) Nordic mountain birch ecosystems. Man and biosphere series, vol 27. UNESCO, Paris and Parthenon, New York, pp 71–76

Ovaska J (1988). Hieskoivun (*Betula pubescens* Ehrh.) pohjoisten provenienssien fotosynteettinen adaptaatio. MSc Thesis. University of Turku, Department of Plant Physiology, Turku, 31 pp

Partanen J, Beuker E (1999) Effects of photoperiod and thermal time on the growth rhythm of *Pinus sylvestris* seedlings. Scand J For Res 14:487–497

Reader RJ (1982) Variation in the flowering date of transplanted ericaceous shrubs in relation to their flowering season. J Biogeography 9:397–410

Ruel JJ, Ayres MP (1996) Variation in temperature responses among populations of *Betula papyrifera*. Silva Fenn 30:145–158

Ruohomäki K, Chapin FS III, Haukioja E, Neuvonen S, Suomela J (1996) Delayed inducible resistance in mountain birch in response to fertilization and shade. Ecology 77:2302–2311

Senn J, Hanhimäki S, Haukioja E (1992) Among-tree variation in leaf phenology and morphology and its correlation with insect performance in the mountain birch. Oikos 63:215–222

Sulkinoja M, Valanne T (1987) Leafing and bud size in *Betula* provenances of different latitudes and altitudes. Rep Kevo Subarctic Res Stat 20:27–33

Sveinbjörnsson B, Nordell O, Kauhanen H (1992) Nutrient relations of mountain birch growth at and below elevational tree-line in Swedish Lapland. Funct Ecol 6:213–220

Weih M, Karlsson PS (1999) Growth response of altitudinal ecotypes of mountain birch to temperature and fertilisation. Oecologia 119:16–23

Wielgolaski FE (1999) Starting dates and basic temperatures in phenological observations of plants. Int J Biometeorol 42:158–168

Wielgolaski FE (2001) Phenological modifications in plants by various edaphic factors. Int J Biometeorol 45:196–202

Wielgolaski FE, Nilsen J (2001) Coppicing and growth of various provenances of mountain birch in relation to nutrients and water. In: Wielgolaski FE (ed) Nordic mountain birch ecosystems. Man and biosphere series, vol 27. UNESCO, Paris and Parthenon, New York, pp 77–92

Wielgolaski FE, Inouye DW (2003) High latitude climates. In: Schwartz MD (ed) Phenology: an integrative environmental science. Kluwer, Dordrecht, pp 175–194