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Juvenile Growth Performance of Local and Exotic Birches in Southern Finland

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Abstract

Adaptation of trees to a mosaic of various edaphic factors and the need to utilize effectively a relatively short growth period is essential for fast growing pioneer species in northern conditions. Growth and survival of birch seedlings and saplings originating from different parts of northern temperate and boreal zone, *Betula resinifera* from Alaska, *B. pendula* from Finland and *B. platyphylla* from Japan, were studied in southern Finland in different growing conditions (pot and field experiments with different nutrient levels). Even though these white birches are supposed to be related taxonomically, we found large differences in their phenology, growth and survival in field conditions. In the autumn *B. resinifera* and *B. pendula* ceased growing earlier than did the more southern *B. platyphylla*. In the field experiments, *B. resinifera* showed poor growth and, contrary to expectations, clearly the poorest survival rate. In the field the mortality of the exotic birches increased gradually during the experiments, but in the outdoor pot experiment virtually all the seedlings of all three birch species survived. This indicates that the edaphic factors characteristic of the study area might have been more crucial for birch survival than the extreme temperatures or other climatic factors. Consequently, to reveal the potential performance of exotic species in new ecological conditions, field tests should be run in parallel with more intensive early tests with potted seedlings.

Key words: *Betula*, edaphic, exotic, fertilisation, growth, white birch

Introduction

In temperate and boreal zones, woody plants undergo an annual cycle of dormancy and growth. In deciduous tree species the timing of autumn bud set and spring bud burst varies clinally along altitudinal and latitudinal gradients (Junttila 1980, Junttila and Kaurin 1990, Howe *et al.* 1995, Myking and Heide 1995, Li *et al.* 2003). In most woody species at high latitudes cessation of the growth in autumn is induced by a short-day period (Junttila 1976, Håbjørg 1978, Junttila and Kaurin 1990, Howe *et al.* 1995, Welling *et al.* 1997), while the spring temperature accumulation determines timing of the bud burst (e.g. Häkkinen *et al.* 1998). Populations of trees are usually well adapted to local climatic conditions through proper timing of active growth (e.g. Junttila and Kaurin 1990, Li *et al.* 2003). Transfers of seed sources towards the north (i.e. high latitude) usually result in progeny with longer growth period and higher growth rate than the local populations (Rosvall *et al.* 1998 and references therein, Li *et al.* 2003). In contrast, tree genotypes moved south from their natural habitats may have lower rates of growth than the local populations mainly because they terminate their growth much earlier than the local genotypes. On the other hand, after transfer to warmer southern locations, the early initiation of growth of the northern provenances may lead to spring frost damage (Junttila and Kaurin 1990, Worrell *et al.* 2000, Li *et al.* 2003).

Birches *(Betula* L.) are widely distributed trees and shrubs throughout the Northern Hemisphere (Dugle 1966, Furlow 1990). The taxonomy of the genus is quite complex (de Jong 1993), and especially confusing are the white birches (subgenus *Betula*), which are variously considered as an aggregation of separate species, subspecies, hybrids or geographic races of a single species (Johnsson 1949, Jansson 1962, Furlow 1990). Several workers (e.g. Dugle 1966, Julkunen-Tiitto *et al.* 1996, Keinänen *et al.* 1999, Saikkonen *et al.* 2003) have noted morphological, ecological and phytochemical similarities between the white birches, *Betula resinifera* Britt. (*B. neolaskana* Sarg., *B. papyrifera* var. *humilis* (Regel) Fern. and Raup), *B. pendula* Roth (*B. verrucosa* Ehrh.) and *B. platyphylla* Suk. var. *japonica* (Miq.) Hara. These three, apparently closely related species, are widely distributed in the northern boreal and temperate zone so that *B. resinifera* occurs in North America, *B. pendula* in western Eurasia and *B. platyphylla* in eastern Eurasia. They are very common and occupy a great variety of habitats (e.g. Furlow 1990, de Jong 1993, Shibuya *et al.* 2000, Tabata 2000). *B. resinifera* inhabits bogs, sandhills and sunny slopes (Dugle 1966). *B. pendula* tolerates poor and wet soil conditions but thrives best on fertile mineral soils (Sarvas 1948, Kujala 1964, Laitinen *et al.* 2002). Also *B. platyphylla* occupies a wide range of habitats with highly variable moisture conditions (Tabata 2000). Thus the habitat requirements

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of the three species are rather similar but it is probable that they are somewhat differentiated in their adaptations to specific climatic and soil conditions of their ranges.

In this study we examine the performance of Alaskan *Betula resinifera*, Finnish *B. pendula* and Japanese *B. platyphylla* in long-term field and 4-year pot and field experiments. We hypothesise that when these closely related birch species are grown in various fertilisation treatments and climatic and edaphic conditions characteristic of southern Finland, adaptation to growth conditions in Alaska, Japan and Finland will be seen through the differences in survival rates and growth performance. This study should shed light on the nature and extent of ecological differentiation of the studied birches. Moreover, it should give information on the possibilities and threats if the geographical transfers of birch material for practical forestry is considered.

Materials and Methods

For these studies seeds of three species of birches, *Betula resinifera*, *B. pendula* and *B. platyphylla* were sowed in 1991 for a long-term field experiment and in 1998 for a pot and short-term field experiment in the vicinity of Punkaharju Forest Research Station (61°48'N, 29°20'E). The seeds of *B. resinifera* were from Alaska (64°52'N, 147°47'W) from 8 mother trees, the seeds of *B. pendula* were from Finland (61°49'N, 29°19'E) from 13 trees, and the seeds of *B. platyphylla* were from Japan (43°15'N, 143°46'E). Number of mother trees of *B. platyphylla* is unknown.

Saplings in long-term field experiment established in 1992

In June 1991, the seeds of the three birch species were germinated in an unheated greenhouse in 0.28l pots (28 plastic pots/container = EK 28) (Rousi *et al.* 1996). In the nursery seedlings were fertilised with 0.1-0.2% solution of Superex9, Superex5 and Superex7, which are commonly used in the nurseries of Punkaharju Forest Research Station (see e.g. Rousi *et al.* 1993, Julkunen *et al.* 1996, Keinänen *et al.* 1999).

For the long-term field experiment a mixed (pine, spruce and birch) forest stand was clear-cut the preceding winter. The two sites used in the experiment (sites 1 and 2) are about 100m apart. The fertility of each site is rather similar but site 2 is clearly moister. At each site four blocks were established. Each block is composed of one random replicate plot of each birch species. The planting distances of the 25 seedlings in each plot were 1 x 2m. Not enough seedlings were available for site 2. Therefore, in block 3 only 18 seedlings of *B. resinifera* and 21 seedlings of *B. platyphylla* were planted. In addition, in block 4 there were no seedlings of *B. platyphylla*. The height and survival of seedlings were measured after the first field growing season, i.e. autumn 1992, and every autumn thereafter until 1998. Final measurements were made in autumn 2002. Neither nutrients nor water were added and weeds were not removed. Hereafter we refer to the young trees from this experiment as saplings.

Seedlings in short-term field and pot experiments established in 1998

In spring of 1998 the seeds from the same sources as used in 1991 were sown in 0.28l pots (EK 28) containing pre-fertilised (N about 10 g/m^2) commercial peat (purchased from VAPO, Finland). For the first year the seedlings were grown in an unheated greenhouse.

In spring of 1999, a total of 2160 1-year-old seedlings were replanted in 3-litre pots. In the pot experiment the growth media consisted of a mixture of sand (25%) and pre-fertilised Vapo peat (75%). The pots were arranged on a grass field outside the greenhouse in three blocks, each containing 60 seedlings in one replicate plot of each treatment (birch species and fertilisation treatments). The distance between the seedlings was 30cm and between replicate blocks 1m. To prevent excessive heating and drying of the roots in summer or freezing during the winter, in the spring of 2000 the pots were dug ca. 20cm into the ground. In 2001 (4th growing season) the pots were placed 50cm from each other in order to avoid shading of the seedlings.

A short-term field experiment was established at the end of June 1999 (2nd growing season) by planting part of the birch seedlings (1475 in total) established in the greenhouse in 1998 for the pot experiment on an old hay field. There were three replicate blocks, each divided into 11 plots (total of 33 plots) for the combinations of four fertilisations and three species (due to lack of seedlings, one treatment (highest fertilisation) was not available for *B. platyphylla*). The distance between blocks was 2m and between the seedlings in a plot 1m. The number of seedlings/plot varied between 13 and 60. In the autumn of 1999 and 2000, to prevent hare and vole feeding during the winter, the seedlings in the field were surrounded by tree-shelter tubes (Tubex, made of polypropylene in the UK). The heights of the tree shelters varied between 60 and 120cm and the diameters between 80 and 120mm, depending on the size of the seedling to be covered. The tubes were removed in the spring.

Fertiliser for seedlings grown in pots was given as a solution (Superex, Kekkilä Yhtiöt, Eurajoki Finland) for the first three years, but in the fourth year granular fertiliser was given as in the field (Kemira Y1) (for fertilisation details, see Table 1). In the field the fertiliser was a granular NPK fertiliser Kemira Y1 (for fertilisation details, see Table 2). The seedlings grown in pots were watered when necessary, but the seedlings in the field were not watered at all.

The base diameters and fresh weights of the seedlings grown in pots were recorded after the 1st, 3rd and 4th growing seasons, but from the seedlings in the field experiment the same measurements were made only after the 4th growing season. Height was measured yearly from both pot and field experiments. In the autumn of 2000 the growth cessation of the seedlings both in pot and short term field experiment was estimated visually (at about three-day intervals from August 15 to September 21) using the growth and lignification of the leader shoot and the colour of the leader shoot scale buds in 15 seedlings in each of the 12 treatments. The following phenological categories were formed: 3 = active growth, 2 = very slow growth, little lignification, green bud, 1 = the leader shoot and bud partly green, clear lignification and 0 = brown shoot and bud, lignified (sturdy) shoot, no growth. Hereafter we refer to these 1- to 4-year-old young trees as seedlings.

Statistical analyses

First, the plot means for height, base diameter and fresh weight were calculated (n = 3-4), because single plants within a plot may be correlated. The Kolmogorov-Smirnov test was used to ascertain the normality of test distributions. Growth, base diameter and biomass data were analysed using GLM univariate

Table 1. Fertilisation schedule for *B. resinifera, B. pendula* and *B. platyphylla* seedlings in the pot experiment in 1998-2001. The sowing date of the seeds, planting times, concentrations of fertilisers (fert. %), N kg/ha and number of fertilisation treatments are also shown. Superex9 contained 19.4% N (7.2% NO_3-N), 5.3% P, 20.0% K, 0.20% Mg; Superex5 contained 10.9% N (9.1% NO_3-N), 4.0% P, 25.3% K, 1.5% Mg; Superex7 contained 0% N, 6.9% P, 31.9% K, 1.0% Mg. To ensure balanced growth and proper winter hardening of the seedlings, the composition of fertiliser was changed in autumn 1998. For the same reason, at the last fertilisation time in 1999 and 2000 the amount of Superex9 was half of the amount given previously. Micronutrients (Fe, Mn, B, Zn, Cu, Mo, Co) were included in all Superex fertilisers. Kemira Y1 contained 10.0% N (3.0% NO_3-N), 7.0% P, 14.0% K, 2.0% Mg. In addition, Kemira Y1 included S, B, Cu, Fe, Mn, Mo, Zn and Se. The nitrogen of the peat used in the growth media is included in the calculations of N kg/ha in years 1998 and 1999.

Seeds sown in 0.28 l pots in May 28, 1998 (greenhouse)			Seedlings planted outside in 3 l pots in May 31-June 4, 1999					
year	1998		1999		2000		2001	
Number of fertilisation treatment	fert. %	N kg/ha	fert. %	N kg/ha	fert. %	N kg/ha		N kg/ha
1	0.05	159	0	0	0	0		0
2	0.1	217	0.05	106	0.17	105		96
3	0.2	334	0.1	136	0.32	198		192
4	0.3	452	0.2	198	0.65	401		384
	Fertil. (Superex)	Time of fertilisation	Fertil. (Superex)	Time of fertil.	Fertil. (Superex)	Time of fertil.	Fertil.	Time of fertil.
	9	June17-July15	9	June 23	9	June7&26	Kemira	June 12
	5	July22-Aug12	9	July7&21	9	July 17	Y1	July 12
	7	Aug19-Sept9	9	Aug 4	9	Aug 7		

Table 2. Fertilisation schedule in 1999-2001 for *B. resinifera, B. pendula* and *B. platyphylla* seedlings and saplings grown in the field. N kg/ha and number of fertilisation treatments are also shown. For the content of Kemira Y1 fertiliser, see Table 1.

Seedlings planted in the field in June 21-22, 1999			
year	1999	2000	2001
Number of fertilisation treatment	N kg/ha		
1	0	0	0
2	10	80	96
3	20	160	192
4	40	320	384
Fertiliser	Time of fertilisation		
Kemira Y1	July 5	June 12, July 10	June 13, July 12

analyses of ANOVA. In yearly comparisons block was kept as random factor. Species, site, fertilisation and age were always kept as fixed factors. The homogeneity of variances was tested using Levene statistic. In some cases, homogeneity of variance was not reached; but even in such cases the residuals were normally distributed (1-sample Kolmogorov-Smirnov test), so analysis of variance was used. Tukey's HSD was used for multiple comparisons. The software used was SPSS 11.0 for Windows.

Results

Growth and survival

In the long-term field experiment, 12-year-old saplings of *B. resinifera, B. pendula* and *B. platyphylla* planted in the forest soil differed in their height growth and survival both within sites and between sites (Fig. 1, Tables 3 and 4). *B. resinifera* was the slowest growing species, the difference from other white birches being evident already in the second year of growth (Tukey's HSD $p < 0.05$ in both experiments) and continued to increase throughout the experiment (species x age

Table 3. ANOVA-table for height growth of birch saplings in the 12-year field experiment. Degrees of freedom for hypothesis (df) and for error terms (df_{err}) are presented.

Factors	df	df_{err}	F	p
Site	1	6	6.989	0.038
Site x Block	6	11	4.211	0.019
Species	2	11	91.679	0.000
Species x Site	2	11	2.994	0.092
Species x Site x Block	11	136	4.465	0.000
Age	8	136	1416.486	0.000
Age x Species	16	136	29.802	0.000
Age x Site	8	136	17.913	0.000
Age x Species x Site	16	136	2.414	0.003

Table 4. Survival rate of birch saplings in the 12-year field experiment.

	Site 1								Site 2							
	Age, years															
	2	3	4	5	6	7	8	12	2	3	4	5	6	7	8	12
Species	Survival, %								Survival, %							
B. resinifera	97	95	85	78	66	50	48	48	91	85	71	69	57	52	46	38
B. pendula	99	98	96	96	95	95	94	94	96	94	94	94	94	94	94	94
B. platyphylla	97	97	92	83	79	77	77	77	99	99	94	93	90	90	90	90

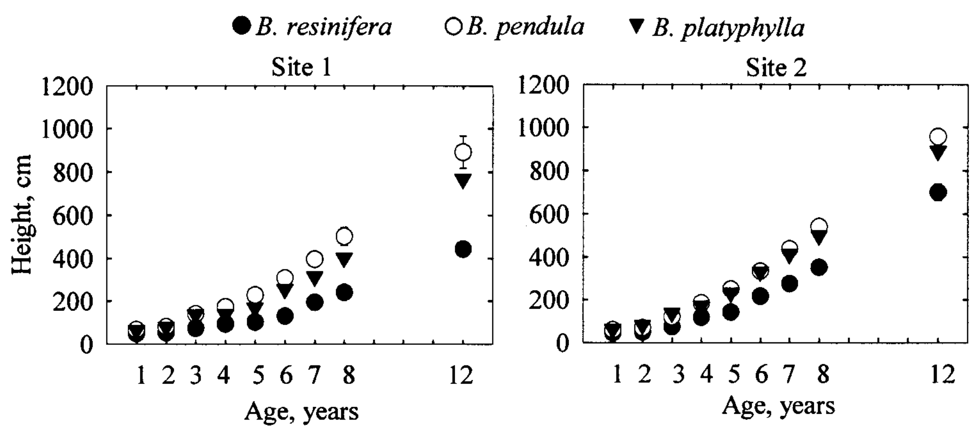

Fig. 1. Height growth of *B. resinifera, B. pendula* and *B. platyphylla* in the 12-year field experiment.

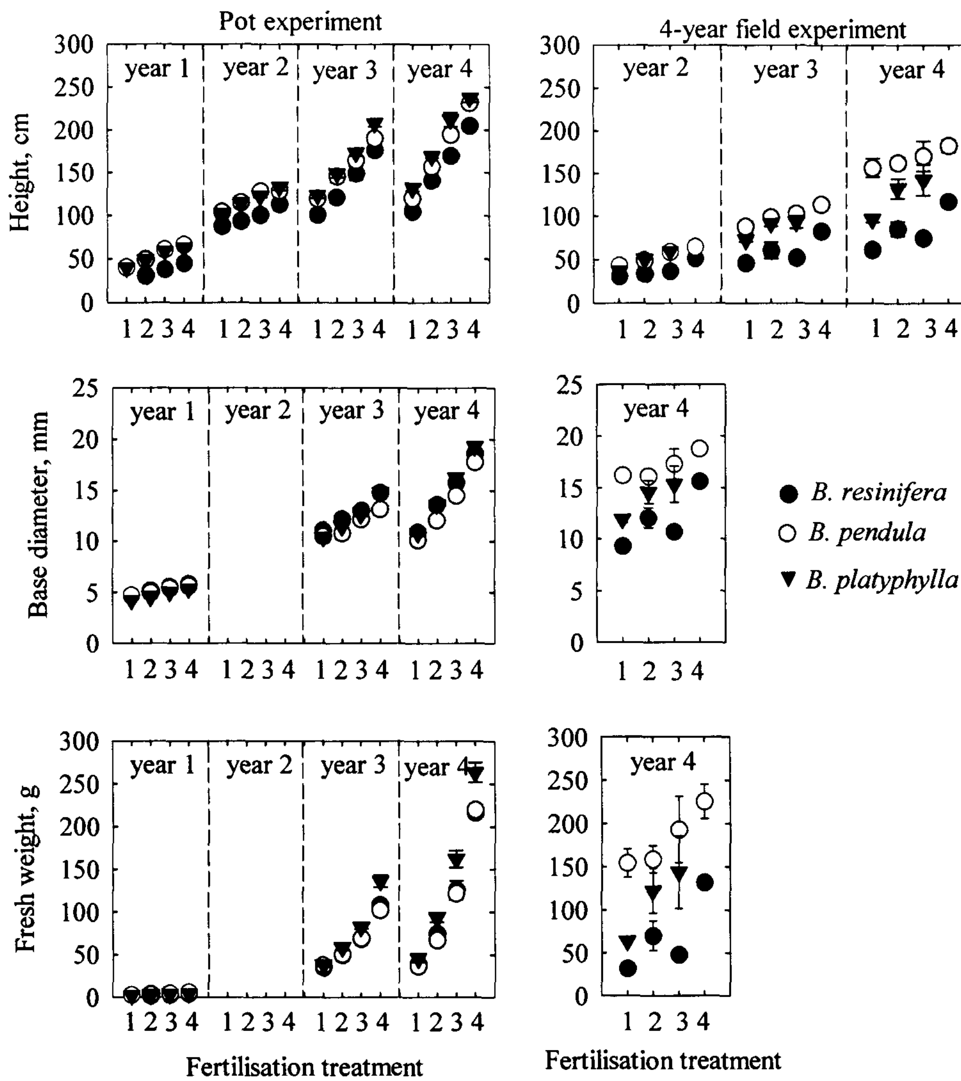

Fig 2. Height, base diameter and above-ground fresh weight of *B. resinifera, B. pendula* and *B. platyphylla* seedlings grown in pots, and 4-year field experiments in different fertilisation treatments. For fertilisation treatments see Tables 1 and 2.

interaction in Table 3, Fig. 1). The relative differences in growth between species were also dependent on the site and age (age x species x site interaction in Table 3, see also Fig. 1). However, there were no statistical differences in growth rate between saplings of *B. pendula* and *B. platyphylla* in any of the yearly comparisons (Tukey's HSD $p > 0.05$, Fig. 1).

The survival of *B. resinifera* saplings showed a steady decrease from the early years of the 12-year experiment (Table 4). The mortality of *B. pendula* and *B. platyphylla* was, on the other hand, dependent on the site. At site 1 the survival rate of *B. platyphylla* decreased rapidly until the seedlings were six years old (Table 4).

The 4-year field experiment also indicated the lowered performance of the exotic birches. Seedlings of *B. resinifera* grew poorly. The seedlings of *B. platyphylla* grew less in height, base diameter and fresh weight than did those of *B. pendula* (Fig. 2, Table 5). Again, the seedlings of *B. resinifera* showed rather low survival rates (75% at the age of 4 years) and *B. pendula* (97%) survived better than *B. platyphylla* (89%) (Table 6).

In the pot experiment, all seedlings of the three birch species survived and the height differences between the species were small but significant (Fig. 2, Table 7). There was also a clear contrast in results between the pot experiment and the 4-year field experiment: compared to *B. pendula* seedlings, the basal diameter of *B. resinifera* seedlings was greater in the pot experiment but smaller in the field experiment. In the field experiment, seedlings of *B. pendula* were clearly heavier than those of *B. resinifera*; but in the pot experiment there was no difference in weight of the two species (Fig. 2).

Effect of fertilisation

In the 4-year field experiment fertilisation increased seedling growth significantly but in general fertilisation had less effect on seedling growth in the field experiment than it had in the pot experiment (Fig. 2, Table 5).

The growth of potted seedlings was strongly accelerated by fertilisation treatments. As expected, without fertilisation, growth slowed down after two growing seasons, being only 20 to 30cm in the 3rd and 4th years. In the highest fertilisation treatment, height growth at the same time was roughly 100cm in all species. In the accumulation of fresh weight the results are roughly the same: during the fourth growing season at the lowest level of fertilisation *B. resinifera* and *B. pendula* seedlings did not add biomass, but at the highest fertilisation their fresh weight more than doubled (Fig. 2). The reaction of *B. platyphylla* seedlings was, however, slightly different (Fig. 2, Table 7).

Growth termination

The winter hardening of 4-year-old seedlings seemed to take place at the same time in the field and in the pots (Figs. 3 and 4). Seedlings of *B. platyphylla* clearly continued to grow longer than the other species. Its shoots and buds were not totally dormant even on September 21. Seedlings of *B. resinifera* seemed to winter-harden slightly earlier than seedlings of *B. pendula*. Fertilisation had no effect on winter hardening in the field, but in pots the less fertilised seedlings winter hardened first; and overall, the higher fertilisations tended to delay the hardening process slightly (Figs. 3 and 4).

Discussion

The seeds of the white birches studied originated from different latitudes and climatic conditions. In Hokkaido, Japan (43°N), where the seeds of the experimental *B. platyphylla* were collected, long humid summers and mild winters prevail whereas Finnish *B. pendula* (61°N) and especially Alaskan *B. resinifera* (64°N) are indigenous in areas with short growing seasons and cold winters. Correct timing of both the release of winter dormancy in spring and growth termination in autumn is essential for these pioneer species in northern conditions. To maximise the growth in highly competitive successional communities a long active period is needed, and tolerance to freezing temperatures must be obtained prior to onset of the early winter. In spring the bud burst of *B. resinifera* is the earliest of the white birches studied and that of *B. platyphylla* the latest (M. Rousi, unpublished results). On the other hand, in autumn *B. resinifera* and *B. pendula* cease their growth much earlier than *B. platyphylla* (Figs. 3 and 4). This agrees with the recent report of Li *et al.* (2003), who found major differences in growth phenology among *B. pendula* ecotypes originating from latitudes between 58° and 68°N. Our results thus confirm the expectation that *B. platyphylla* is adapted to longer growing seasons than the other two white birch species. Consequently, *B. platyphylla* should have better growth potential but also higher risk of severe frost damage at the high latitude of the study area. *B. pendula* had the highest seedling survival in all field experiments, indicating the good overall

Table 5. ANOVA-table for height, base diameter and fresh weight of the birch seedlings grown in the 4-year field experiment. Degrees of freedom for hypothesis (df) and for error terms (df_{err}) are presented.

Dependent	Factors	df	df_{err}	F	p
Height	Species	2	22	63.349	0.000
	Fertilisation	3	22	13.123	0.000
	Species x Fertilisation	5	22	1.227	0.330
	Species x Fertilisation x Block	22	44	5.850	0.000
	Age	2	44	937.275	0.000
	Age x Species	4	44	65.122	0.000
	Age x Fertilisation	6	44	3.508	0.006
	Age x Species x Fertilisation	10	44	1.389	0.217
Base diameter	Species	2		43.385	0.000
	Fertilisation	3		14.309	0.000
	Block	2		4.257	0.029
	Species x Fertilisation	5		2.196	0.095
	Error	20			
Fresh weight	Species	2		35.235831	0.000
	Fertilisation	3		9.7436198	0.000
	Block	2		4.4821565	0.025
	Species x Fertilisation	5		1.1207844	0.381
	Error	20			

Table 6. Survival rate of the birch seedlings grown in different fertilisation treatments (Fertil.) in the 4-year field experiment. For different fertilisation treatments, see Table 2.

		Age, years		
		2	3	4
Species	Fertil.	Survival, %		
B. resinifera	1	99	93	73
	2	100	98	88
	3	99	95	48
	4	100	98	92
B. pendula	1	99	99	99
	2	100	100	100
	3	100	99	98
	4	100	93	90
B. platyphylla	1	98	97	88
	2	99	99	92
	3	100	97	86

Table 7. ANOVA-table for height, base diameter and fresh weight of the birch seedlings in the 4-year pot experiment. Degrees of freedom for hypothesis (df) and for error terms (df_{err}) are presented.

Dependent	Factors	df	df_{err}	*F*	*p*
Height	Species	2	24	77.818	0.000
	Fertilisation	3	24	232.122	0.000
	Species x Fertilisation	6	24	0.336	0.911
	Species x Fertilisation x Block	24	70	3.109	0.000
	Age	3	70	3349.385	0.000
	Age x Species	6	70	6.007	0.000
	Age x Fertilisation	9	70	82.460	0.000
	Age x Species x Fertilisation	17	70	1.091	0.380
Base diameter	Species	2	26	57.701	0.000
	Fertilisation	3	25	902.156	0.000
	Species x Fertilisation	6	26	4.372	0.004
	Species x Fertilisation x Block	24	46	0.895	0.607
	Age	2	46	7523.176	0.000
	Age x Species	4	46	24.813	0.000
	Age x Fertilisation	6	46	172.632	0.000
	Age x Species x Fertilisation	11	46	1.594	0.133
Fresh weight	Species	2	25	26.692	0.000
	Fertilisation	3	25	485.854	0.000
	Species x Fertilisation	6	25	3.367	0.014
	Species x Fertilisation x Block	24	46	2.103	0.015
	Age	2	46	2937.353	0.000
	Age x Species	4	46	21.229	0.000
	Age x Fertilisation	6	46	356.071	0.000
	Age x Species x Fertilisation	11	46	2.438	0.017

adaptation of this species to the abiotic and biotic conditions of the study area where its seeds originated. Contrary to expectations, *B. resinifera* showed clearly lower survival rates than the much more southern *B. platyphylla*, indicating the existence of factors other than climatic ones which cause mortality among seedlings of the introduced birches.

The three field experiments were quite similar with regard to the growth patterns among the tested birch species. In both the 4-year and 12-year field experiments the height growth of the Alaskan *B. resinifera* was always poor, while local *B. pendula* was the fastest growing species (Figs. 1 and 2). The pot experiment, however, provided somewhat different results. There Japanese birch was the fastest growing species at all fertilisation levels, and *B. resinifera* also grew well so that its diameter growth and total biomass accumulation were equal to or better than those of *B.*

pendula (Fig. 2). Significant interactions in the growth and fresh weight accumulation of experimental birches indicate that birch species react differently to environmental variation and the reaction may be different at different ages (significant age x species x site interaction in height growth and significant species x fertilisation x age interaction in fresh weight -Tables 3 and 5). Similar ecological differences were found earlier even between genotypes (families) of the single species, *B. pendula* (Laitinen *et al.* 2002).

Our results from the field experiments show that there are major ecological differences between the white birches studied. However, the fact that in the outdoor pot experiment, where homogenised optimal growing substrate was used, the survival rate and growth of all species were good and were about the same indicates that the reasons for the differential mortality and growth patterns in the field experiment may not be associated with latitudinal or climatic factors. In addition, in spite of regular observations, no major differences in herbivore or pathogen pressure on the foliage were found among these birch species. Thus, local features in soil moisture, nutrient and microbial conditions may have been disadvantageous to the exotic birches. For instance, mycorrhizal-forming fungi, which are essential for proper growth of birches, are usually generalists but host tree-specific reactions cannot be ruled out (see Bruns *et al.* 2002 and references there in). Recently, differences have been found between *B. pendula, B. resinifera* and *B. platyphylla* in susceptibility to pathogenic (Poteri *et al.* 1997) and endophytic fungi (Saikkonen *et al.* 2003) as well as to mammalian herbivores (Rousi *et al.* 1996). This interspecific variation in biotic interactions may be related to documented differences in defensive secondary chemistry among these closely related birch species (Taipale *et al.* 1994, Julkunen-Tiitto *et al.* 1996, Keinänen *et al.* 1999). Whatever the actual mechanisms, the contrasting results from pot and field experiments suggest that the different responses of studied birch species are mainly related to edaphic factors rather than to possible differential adaptations to climatic factors.

In summary, our results indicate that the three birch species studied here can tolerate substantial variation in

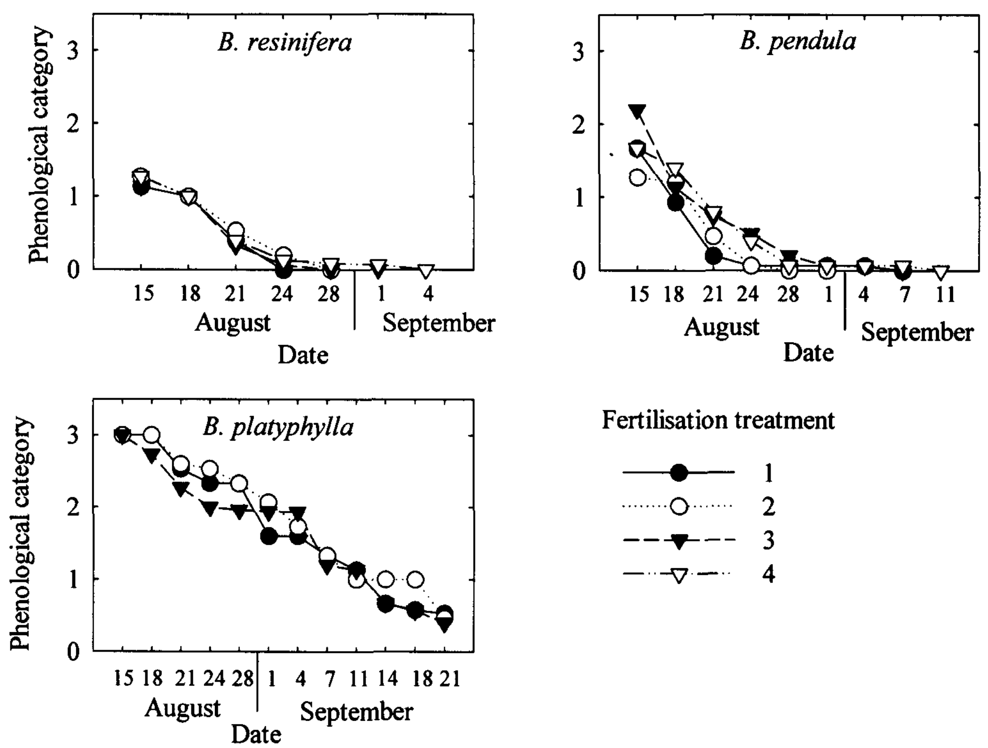

Fig. 3. Growth cessation of seedlings in the 4-year field experiment in the third growing season. At each observation round the seedlings were classified into the following phenological categories: 3 = active growth, 2 = very slow growth, little lignification, green bud, 1 = leader shoot and bud partly green, clear lignification and 0 = brown shoot and bud, lignified (sturdy) shoot, no growth.

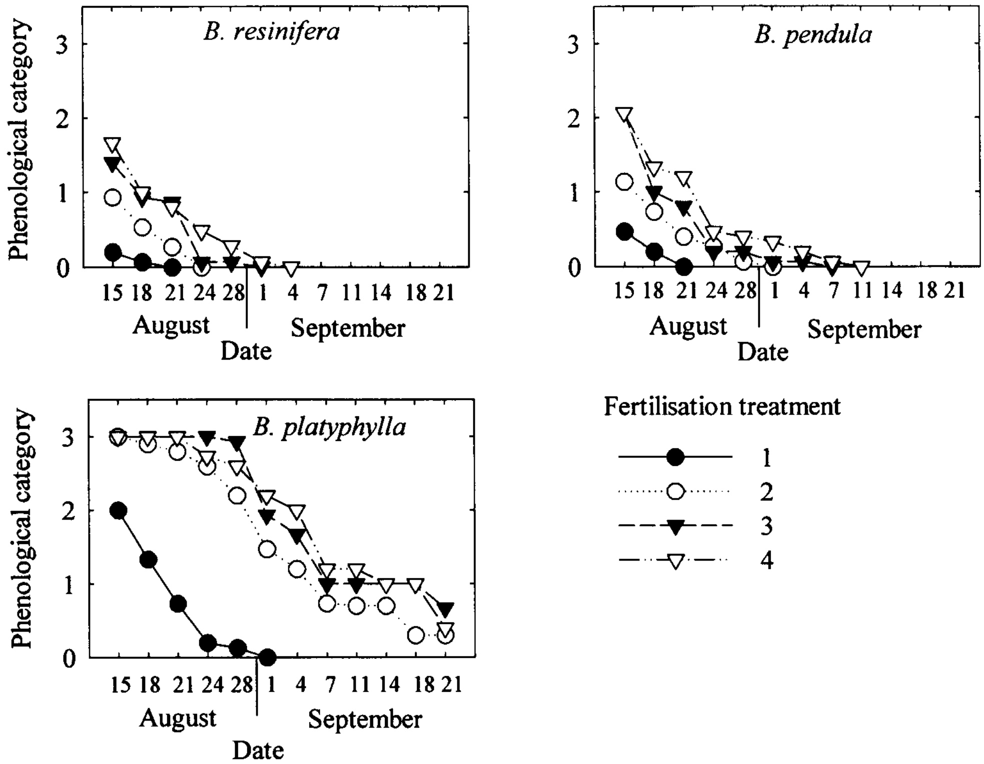

Fig. 4. Growth cessation of birch seedlings in the pot experiment in the third growing season. At each observation round the seedlings were classified into the following stages: 3 = active growth, 2 = very slow growth, little lignification, green bud, 1 = leader shoot and bud partly green, clear lignification and 0 = brown shoot and bud, lignified (sturdy) shoot, no growth.

climatic conditions and in overall soil fertility. High mortality of the exotic species in the field, however, suggests that so far largely unknown edaphic factors and specific biotic interactions in the soil severely restrict the performance of birches introduced outside their natural range. Consequently, to reveal the potential performance of exotic species in new ecological conditions, field tests should be run in parallel with intensive early tests with potted seedlings.

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