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Provenance variation in early growth and development of *Picea mariana* (Mill) B.S.P.

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Studia Forestalia Suecica
No. 187 · 1992

ISSN 0039-3150
ISBN 91-576-4582-5

Abstract

Ståhl, E.G. & Persson, B. 1991. Provenance variation in early growth and development of *Picea mariana* (Mill) B.S.P. *Studia Forestalia Suecica 187*. 17pp. ISSN 0039-3150, ISBN 91-576-4591-4.

Provenance variation in Picea mariana (Mill) B.S.P. (Black spruce) seedlings was studied to provide recommendations for introducing the species into Scandinavia. Provenances were analysed in a series of tests covering root and shoot development, and mineral nutrient (N, P and K) content. The studies were carried out as greenhouse tests, as nursery trials, as cold tolerance tests in growth chambers and by destructive sampling. The performance of Black spruce was compared with that of Norway spruce.

Black spruce seed sources exhibited large clinal variation for most of the properties evaluated. Compared with northwestern seed sources, southeastern sources were taller, exhibited later bud flushing and bud set, showed a lower degree of lignification and a lower dry matter content in autumn, had a higher incidence of winter-damaged seedlings and a higher shoot: root ratio. Within the eastern region, east of 100°W, provenance variation was characterized using cluster analysis. Provenances orginating around latitudes 47–51°N and west of longitudes 65°W were tallest, whereas southeastern provenances produced most dry matter. Norway spruce exhibited a developmental phenology and biomass properties similar to Black spruce orginating at latitudes between 50 and 60°N. However, Norway spruce had thicker roots and stems and was more susceptible to spring frosts following bud flushing.

Key words: Picea mariana, clinal variation, phenology, shoot : root ratio.

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Contents

MS. received 15 May 1991
MS. accepted 30 January 1992

016.34 Tofters tryckeri ab, Östervåla 1992

Introduction

In Sweden, there are severe reforestation problems in frost-prone and wet areas. The native Norway spruce (*Picea abies* (L). Karst.) often suffers from spring frost damage, which reduces its vitality and growth. Surviving trees commonly develop multiple stems and ramnicorns caused by loss of leaders. Black spruce (*Picea mariana* (Mill.) B.S.P.) has been suggested as an alternative (Alriksson, 1987). Being a pioneer species, Black spruce is free from many of the weaknesses of Norway spruce, e.g., it is less prone to spring frost injury and does not exhibit any marked growth retardation after planting. According to Heimburger (1983), Black spruce is adapted to living in swamps and has developed the ability to extract water from a soil solution of high osmotic pressure.

Black spruce is native throughout much of Canada, Alaska and the northeastern part of the USA. It occupies both wet sites (e.g. bogs) and well-drained areas. Consequently, native Black spruce provenances show substantial differences in terms of their adaptation to climatic conditions. In eastern Canada, Black spruce is planted on a large scale, mainly owing to its rapid juvenile growth, good wood properties, resistance to spruce budworm and superior hardiness (Smyth & Brownright, 1986).

Extensive studies have been made on Black spruce grown in Canada. A bibliography of the species was presented by Shoup & Nairn (1969). Provenance variation within the species has been treated by Morgenstern (1969*a*, 1969*b*, 1978), Morgenstern & Mullin (1990), Segaran (1978), Fowler & Park (1982), Bihun & Carter (1981), Khalil (1975, 1984), Nienstaedt (1984) and Park & Fowler (1988) in Canada and USA and in Norway by Dietrichson (1969), Kaasen & Dietrichson (1987) and Brække (1990). In general, provenance variation is large and mainly clinal, mostly reflecting variation in photoperiod and spring temperatures. In the eastern part of the species's range, the variation has been described as ecotypic (Khalil, 1975). There also seems to be considerable within-provenance variation between stands, according to Fowler & Mullin (1977), although no systematic differences between upland and lowland ecotypes have been found. By contrast, Prevost & Bolghari (1990) found differences in rooting ability between an upland and a lowland seed source, indicating two distinct ecotypes.

When studying population structure using allozyme frequencies, Boyle & Morgenstern (1985) found a low degree of population differentiation, short genetic distances that were not correlated with geographical distances and no indication of significant neighbourhood structure. Yeh et al. (1986) found 6 per cent of the genetic variation to be between populations, when studying allozyme variation among Newfoundland black spruce provenances. Heritability levels for height growth and dry weight have been reported to be high (Mullin, 1985), but a significant interaction with nitrogen level was also found, which was ascribed to differences in the degree of expression of genetic variation. Khalil (1985) reported heritabilities of wood characters to be high. He also found clinal variation in these characters and identified populations with superior pulping qualities.

Pollard & Logan (1974) and Logan & Pollard (1975) determined the amount of free growth of the same provenance at different ages, while Colombo (1986) compared the effect of shoot pruning and winter injuries on the amount of free growth.

In Norway, after studying the same seed sources as Morgenstern (1969*a*, 1969*b*), Dietrichson (1969) concluded that the provenance pattern was clinal with regard to winter damage as well as "yield". In Finland, Lähde et al. (1984) did not find any significant differences between eastern and western seed sources and Black spruce was not superior to other species. In Sweden, Black spruce provenance studies have been established and preliminary recommendations made for the northern (Rosvall, 1986) and southern (Persson & Ganered, 1981; Ståhl & Persson, 1987) parts of the country. However, there is a lack of knowledge regarding the morphological and physiological differences existing between provenances when grown under Swedish conditions. Furthermore, there was a need to establish more trials with the species in southern and central Sweden.

The objectives of this study are as follows:

1. To describe the differences in seedling morphology and phenology existing between provenances of Black spruce.
2. To compare Black spruce with Norway spruce.
3. To elucidate the juvenile characters of value in identifying superior provenances of Black spruce.

Material and methods

A total of 33 Black spruce provenances was tested. Five Norway spruce seed sources were also included (Table 1, Fig. 1). The properties assessed are described in Table 2. (Note that the term "winter da-

Table 1. *Origin of seed sources*

Alta = Alberta
BC = British Columbia
NB = New Brunswick
NS = Nova Scotia
PEI – Prince Edward Island
YT = Yukon Territories

Alsk = Alaska
Man = Manitoba
NFld = New Foundland
Ont = Ontario
Que = Quebec
Wis = Wisconsin

Seed source no.	Region	Locality	Lat°	Long	Alt m a.s.l.
Picea mariana					
01	NF	Sandy Brook, Badger	48°47'	56°07'W	245
101	NFld	Skippins Ridge	49°45'	59°16'W	150
103	NFld	Goose Bay	53°17'	60°25'W	10
05	PEI	Farmington, Kings co.	46°23'	62°29'W	25
04	NS	Chiqnecta, Cumberland co.	45°30'	64°28'W	45
09	NB	Acadia Forest Exp. Station	45°59'	66°14'W	45
11	NB	Acadia Forest Exp. Station	46°02'	66°14'W	55
13	Que	Matapedia co.	47°55'	66°55'W	470
100	Que	N Baie Comeau	50°20'	68°40'W	250
15	Que	Grandes Piles co Laviolette	47°02'	72°53'W	75
14	Que	St Zenon co. Berthier	46°30'	73°45'W	460
102	Que	NE Chibougamau	50°10'	73°55'W	375
17	Ont	Site Region 4E, mix	46°30'-48°00'	79°30'W-84°30'W	300-365
18	Ont	Site Region 3E, mix	48°00'-50°05'	79°30'W-85°20'W	300-335
32	Ont	Kapuskasing	49°00'	80°00'W	230
20	Ont	Site Region 4W, mix	48°00'-49°00'	87°15'W-93°50'W	300-335
22	Ont	Site Region 4S, mix	49°30'-50°30'	87°15'W-95°10'W	380-460
23	Wis	Sec 30 T38 NR 12E Forest co.	45°44'	89°04'W	460
24	Wis	Sec 1 T42 NR 4W Ashland co.	46°12'	90°47'W	300-460
29	Wis	Sec 9 T38 NR 3E	45°	90°W	-
28	Man	NW Angel Forest reserv	49°17'	96°18'W	350
25	Man	Pulp river	51°48'	100°12'W	275
26	Man	Birch river	52°23'	101°07'W	320
104	Alta	Loon lake	56°35'	115°20'W	580
30	Alta	Whitecourt	53°45'	115°43'W	760
105	BC	Tsoo Creek	59°10'	123°20'W	350
33	BC	Racing river	58°54'	129°09'W	1000
34	YT	Milepost 132	61°38'	130°15'W	1000
31	YT	Carmacks	62°22'	136°25'W	760
39	YT	Eagle Plains, Artic Circle	66°30'	136°33'W	650
35	YT	N Klondyke River	64°03'	138°37'W	610
38	Alsk	Fairbanks	64°51'	147°52'W	133
36	Alsk	Bonanza Creek	64°17'	148°17'W	335
37	Alsk	Bonanza Creek	64°47'	148°18'W	470
Picea abies					
71	Seed orchard	Sollerö frost, W county			
72	Seed orchard	Saleby, R county			
73	Seed orchard	Ljung, R county			
74	White Russia	Vitebsk, Lepel	54°52'	28°40'E	
75	Latvia	Rezekne	56°30'	27°26'E	

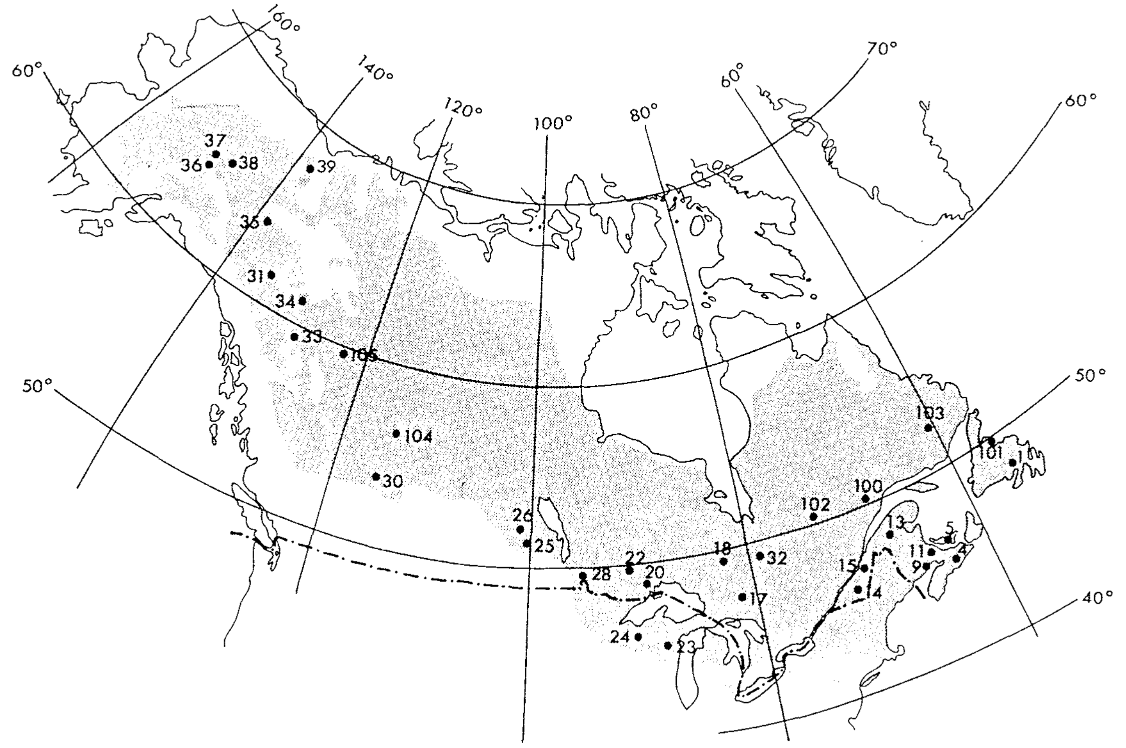

Fig. 1. Distribution of Black spruce and origin of Black spruce provenances studied.

mage" is used to denote an injury between the last autumn assessment and the first spring assessment, inflicting losses of more than one-fifth of the total needle amount.)

In Fig. 2 the relationship between different tests is outlined. Seeds were sown in 72-ml Panth containers (AB Panth Produkter, Sweden) in April 1985 at the Seedling Research Station at Garpenberg (60°15'N, 16°15'E, 180 m a.s.l.) The seedlings were transferred to an outdoor holding area in June 1985, where they also were stored during winter. In September 1985 and in May 1986 two nursery tests were planted at Älvbacka (60°15'N, 16°01'E, 110 m a.s.l.). In May 1986, seedlings were transplanted using 600-ml Combicell containers (Silvesco AB, Sweden) that were kept at the outdoor holding area. The experimental design of different studies is outlined in Table 3.

Phenological studies

Growth cessation and bud set were assessed on seedlings at the outdoor holding area in autumn 1985 (*PHEN* 1 where 1 refers to the first growing season). Stages of bud flushing, shoot elongation and bud set were recorded for transplanted seedlings at the outdoor holding area during 1986 (*PHEN* 2) and 1987 (*PHEN* 3). Phenology was studied on autumn-planted seedlings in nursery tests at Älvbacka from spring 1986 to spring 1988 (*AUT* 2 - *AUT* 4), and on spring-planted seedlings in a nursery test during spring 1987 (*SPR* 3).

Freezing tests

Cold tolerance during bud flushing was evaluated twice using a freezing test (down to -5°C) in a growth chamber during flushing in spring 1986 (*FREEZ*). The material used had been kept in cold storage during winter.

Biomass proportions and nutrient analysis

Fresh and dry weights of shoots and roots, as well as root length, were determined on seedlings stored at the outdoor holding area in early October 1985 (*BIOM* 1). Corresponding tests were made during August and October 1986 (*BIOM* 2) and October 1987 (*BIOM* 3) on seedlings that had been transplanted to Combicell containers during 1986. By comparing the results from the two successive tests in 1986, we were able to determine how dry matter proportions changed during winter hardening. In the tests

Table 2. *Properties assessed in the study*

Property	Study	Units/ classes	Abbre- vation	Comments
Height	all	mm	*H*	
Shoot elongation	all	mm	*SE*	
Early shoot	*PHEN* age 1–2	%	*S%*	Leader length in early June as percentage of annual height increment
Bud flushing	*PHEN* age 2–3 *AUT* age 2–3	0–8	*BF*	0 = no bud swelling (rest) to 8 = fully developed (Krutzsch, 1973)
Bud set	*PHEN* age 2–3 *AUT* age 2–3	0–2 0–4	*BS*	0 = no bud, 1 = indication of bud 2 = bud formed (3 = large bud formed 4 = new bud burst)
Lignification	*PHEN* age 3	1–3	*LI*	1 = fully lignified, 2 = 0–20 mm green shoot 3 = more than 20 mm green shoot
Winter damage	*PHEN* age 3	No	*WD*	No. seedlings (n = 25) with winter damage
Frost damage	*FREEZ*	%	*FD*	Percentage seedlings killed or sustaining shoot damage in response freezing to (−5°C)
Total fresh weight	*BIOM* age 1–3	g	*TFW*	Total fresh weight of seedling
Total dry weight	*BIOM* age 1–3	g	*TDW*	Total dry weight of seedling
Above ground fresh weight	*BIOM* age 1–3	g	*AFW*	Fresh weight of seedling above root collar
Above ground dry weight	*BIOM* age 1–3	g	*ADW*	Dry weight of seedling above root collar
Branch fresh weight	*BIOM* age 3	g	*BFW*	Fresh weight of branches and attached needles of seedling
Branch dry weight	*BIOM* age 3	g	*BDW*	Dry weight of branches and attached needles of seedling
Stem fresh weight	*BIOM* age 3	g	*SFW*	Fresh weight above ground once branches and attached needles had been removed
Stem dry weight	*BIOM* age 3	g	*SDW*	Dry weight above ground once branches and attached needles had been removed
Root fresh weight	*BIOM* age 1–3	g	*RFW*	Fresh weight of roots
Root dry weight	*BIOM* age 1–3	g	*RDW*	Dry weight of roots
Root length	*BIOM* age 1–3	m	*RL*	Total length of roots
Dry matter content	*BIOM* age 1–3	%	*CDW*	$\frac{\text{Dry weight above ground} \cdot 100}{\text{Fresh weight above ground}}$
Diameter at root collar	*BIOM* age 3	mm	*DRC*	Mean value of two assessments of root collar diameter
Diameter at H/2	*BIOM* age 3	mm	*D50*	Mean value of two assessments of diameter at H/2
N content	*BIOM* age 1–2	%	*N*	N content (%) of needles
P content	*BIOM* age 1–2	%	*P*	P content (%) of needles
K content	*BIOM* age 1–2	%	*K*	K content (%) of needles

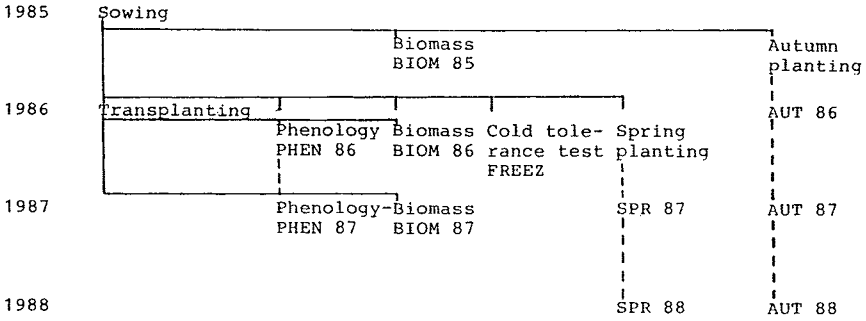

Fig. 2. Relations between different tests. Dashed lines show two repeated assessments of the same seedlings.

Table 3. *Experimental design. Total number of seedlings, number of seed sources, number of replications, number of seedlings in seed source, and replication and design within replications for each study*

Study	Total no. of seedlings	No. of seed sources	No. of replications	No. of seedlings in seed source and replication	Design within replication
PHEN age 1	768	32	2	12	Six-tree rows
PHEN age 2–3	1320	33	8	5	Five-tree rows
AUT age 2–4	800	32	5	5	Single-tree plots
SPR age 3	850	34	5	5	Single-tree plots
FREEZ	1260	35	36	1	Single-tree plots
BIOM age 1	465	31	1	15	Five-tree rows
BIOM age 2–3	420	28	3	5	Five-tree rows
BIOM age 4	330	33	2	5	Five-tree rows

made in 1986 analyses of nutrient content (N, P and K) were also performed. The nutrient analyses were limited to a sample of provenances.

Statistical methods

All calculations, except for partial correlations, were based on provenances means. Thus it was possible to compare results from different tests.

Correlations between the different properties were studied at two levels: The provenance level, by means of product-moment correlation, and the individual plant level, where provenance variation was eliminated by means of partial correlations according to a procedure applied by Ståhl (1984). Provenance was treated as indicator variable ($p10 = 1$ if provenance number is 10 and $p10 = 0$ if not, etc.) and was included in a multiple regression analysis according to the model, $y = x\ \Sigma p + \varepsilon$ where y and x are the parameters correlated, Σp are the indicator variables of provenance and ε is the random error. Partial correlation was calculated as $SS/(SS+SSE)$, where ss and sse are sums of squares of parameter x and error, respectively.

To group provenances into larger units based on their performance, cluster analyses were made. Two fundamentally different clustering methods were used; average linkage and nearest centroid sorting (Anderberg, 1973). Average linkage is an hierarchical method, which successively merges entities into nested clusters on the basis of the average distance between pairwise combinations of observations from different entities. Nearest centroid sorting is a non-hierarchical procedure, in which the observations are assigned to initially selected cluster seeds forming temporary clusters. Clusters are formed after iterative replacement until a stable configuration is achieved. The number of clusters in the models presented was determined to give a geographically logical subdivision. A comparison of the models given by the two methods shows how stable the clusters are. Geographical variation was further studied using stepwise regression analysis. The following model was used:

$$Y = b_0 + b_1(\text{lat-}\overline{\text{lat}}) + b_2(\text{long-}\overline{\text{long}}) + b_3(\text{lat-}\overline{\text{lat}})^2 + b_4(\text{long-}\overline{\text{long}})^2 + b_5(\text{lat-}\overline{\text{lat}})(\text{long-}\overline{\text{long}}) + \varepsilon,$$

where Y = performance of the dependent variable,
lat, long = latitudinal and longitudinal origin of the provenance,
$\overline{\text{lat}}, \overline{\text{long}}$ = mean latitude and longitude (nearest degree),
b_0 - b_5 = regression coefficients,
ε = random error.

Only independent variables whose coefficients were significant at the 5 per cent level were included in the functions. The regression functions were presented graphically as contour plots using a response surface model (Kung & Clausen, 1984).

The analyses were made using the SAS statistical package for personal computers (SAS Institute Inc., 1987).

Results

Correlations between various properties, based on provenance mean values and calculated for a number of studies, are presented in Table 4. Partial correlations, excluding provenance variation, are presented in Table 5 for phenological variables in the autumn planting study and in Table 6 for dry weights, dry matter and nutrient contents in the biomass study of 1986.

To generalize the results for the provenances studied, nearest-centroid cluster analysis was carried out using 15 phenological variables and 27 provenances (Table 7a). A separation into eight clusters yielded the division presented in Fig. 3. The results of a cluster analysis using average linkage method and based on the same material are presented in Table 7b and Fig. 4.

Cluster classes 1, 5 and 8 in the nearest-centroid cluster analysis are situated east of longitude 105°W. The same region is included in classes 1 and 3 in the cluster analysis using the average linkage method.

Table 4. *Correlations between different variables based on provenance mean values*

	H PHEN age 3	*H AUT* age 4	*SE SPR* age 4	*BF PHEN* age 3	*BF SPR* age 3	*BS AUT* age 2	*LI PHEN* age 3	*WD SPR* age 3	*FD FREEZ* age 2	*N BIOM* age 2	*K BIOM* age 2	*TDW BIOM* age 1
HAUT age 4	.87***											
SESPR age 4	.69***	.78***										
BFPHEN age 3	-.80***	-.82***	-.68***									
BFSPR age 3	-.72***	-.83***	-.54**	.89***								
BSAUT age 2	.84***	-.85***	-.64***	.94***	.90***							
LIPHEN age 3	.76***	.80***	.64***	-.90***	-.89***	-.92***						
WDSPR age 3	.59***	.64***	.37	-.72***	-.87***	-.75***	.77***					
FDFREEZ	.46***	.33	.07	-.40*	-.46*	-.36	.41*	.52**				
NBIOM age 2	-.73***	-.65**	-.29	.58**	.60**	.68**	-.67***	-.51**	-.27			
KBIOM age 2	.64***	.73***	.60**	-.91***	-.80***	-.87***	.78***	.70***	.27	-.52**		
TDW BIOM age 1	.56**	.47	.29	-.53*	-.48*	-.33	-.54**	.41*	.61**	-.44	.45	
CDW BIOM age 1	-.66***	-.70	-.48*	.86***	.79***	.81	-.77***	-.70***	-.58**	.59**	-.83***	-.49*

Table 5. *Product-moment (above diagonal) and partial correlation (below diagonal) matrix for bud flushing and bud set 1986-88 for the autumn planting in nursery beds. (AUT86-AUT88)*

	BF AUT age 2	*BS AUT* age 2	*BF AUT* age 3	*BS AUT* age 3	*BF AUT* age 4	*BS AUT* age 4
BF AUT age 2	1	0.802***	0.776***	0.609**	-0.483*	0.197
BS AUT age 2	-0.096	1	0.921***	0.811**	-0.314	0.399*
BF AUT age 3	0.083	0.008	1	0.828***	0.203	0.448*
BS AUT age 3	0.096	0.136**	-0.055	1	0.076	0.690***
BF AUT age 4	0.060	0.048	0.078	0.037	1	0.257
BS AUT age 4	-0.147	-0.059	0.005	0.158***	0.107*	1

Table 6. *Product-moment (above diagonal) and partial correlation (below diagonal) matrices for dry weights, dry matter contents, and nutrient (N, P and K) contents in the biomass study of 1986 (BIOM86)*

	ADW	*RDW*	*ADW/ RDW*	*CDW*	*N*	*P*	*K*	*N/K*
ADW	1	0.168	0.931***	-0.795*	-0.964***	-0.660	0.922**	0.930**
RDW	0.780***	1	0.198	0.263	-0.198	0.258	0.301	0.258
ADW/ RDW	0.207*	-0.372***	1	-0.884**	-0.890**	0.732*	0.803*	0.826*
CDW	0.062	0.082	0.099	1	0.728*	-0.533*	-0.716*	-0.712*
N	-0.384***	0.403**	0.042	0.068	1	0.717	-0.940***	-0.955***
P	-0.337**	-0.363**	0.029	-0.02	0.761**	1	-0.631	-0.682
K	-0.051	0.07	-0.048	0.013	-0.004	-0.013	1	0.996
N/K	0.194*	0.263**	-0.102	-0.002	-0.622**	-0.481**	0.736**	1

Table 7a. *Cluster analysis. Nearest-centroid cluster method using 8 clusters*

Cluster no.	Seed sources
6	39
7	35, 36
3	5, 30, 31, 104, 105
1	1, 14, 25, 26, 101, 103
5	20, 32, 100, 102
8	13, 15, 17, 18, 22, 23, 28
2	4, 24
4	11

Table 7b. *Cluster analysis. Average linkage method*

Cluster no.	Seed sources	Separated at average distance between clusters
6	39	2.5
5	35, 36	1.25
(2+3+4	4, 24, 11, 14, 26, 103, 5, 30, 31, 104, 105)	0.75
4	5, 30, 31, 104, 105	0.65
3	11, 14, 26, 103	0.55
2	4, 24	0.55
1	1, 101, 18, 20, 100, 102, 32, 13, 15, 17, 23, 25, 22, 28	remaining at 0.50

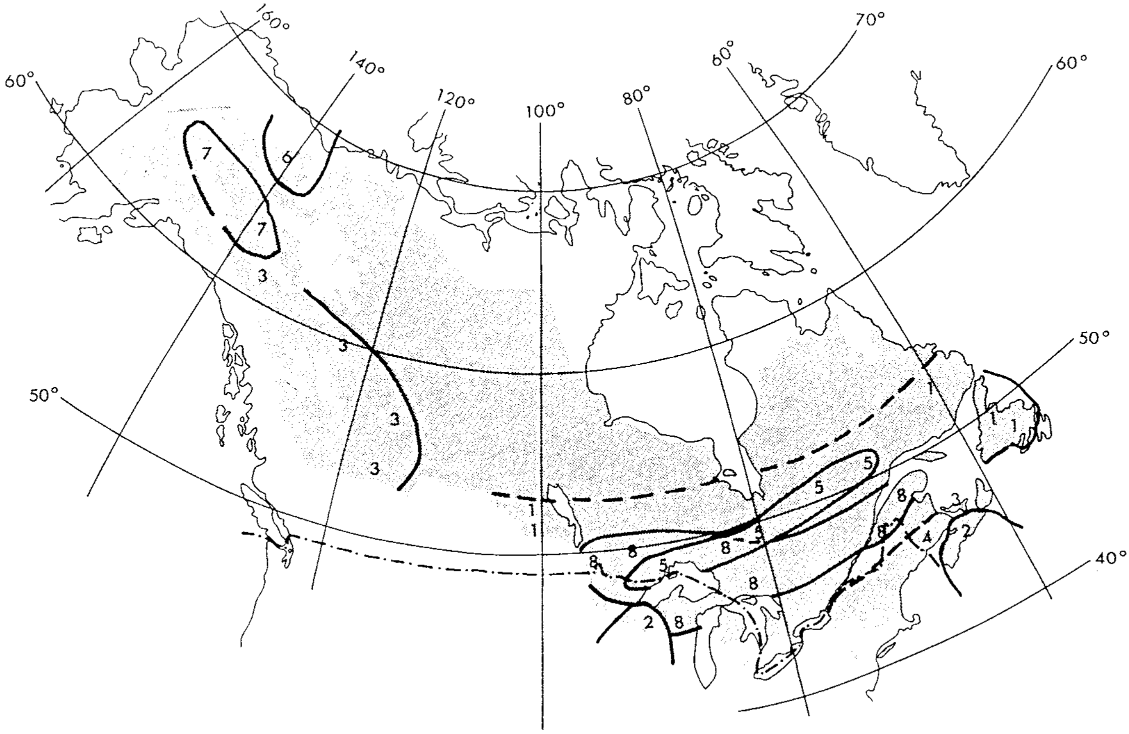

Fig. 3. Twenty seven Black spruce provenances separated into 8 cluster classes using nearest-centroid cluster analysis for 15 phenological variables.

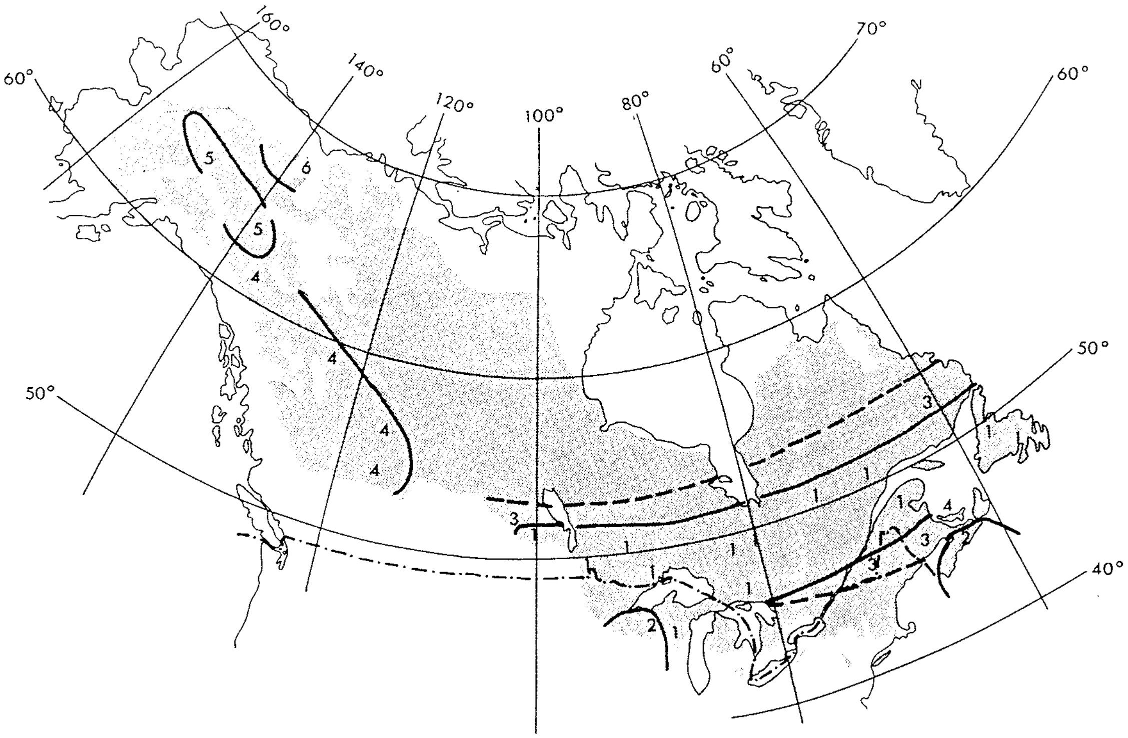

Fig. 4. Twenty seven Black spruce provenances separated into 6 cluster classes using average-linkage cluster analysis for 15 phenological variables.

The results of regressions analyses treating that region are presented using the height at age four years of the spring-planted seedlings in the nursery test (*H SPR* 4) as the dependent variable (Table 8: Function 1, Fig. 5). A similar pattern of variation was found for shoot elongations (*SE SPR* 4, Table 8: Function 2, Fig. 6).

Table 8. *Functions describing clinal variation of eastern Black spruce provenances*

Provenances orginating east of longitude 105°W (cluster classes 1, 5 and 8):

$HSPR4 = 658+1.84\ (\text{long-}79)-8.13\ (\text{lat-}49)^2-0.779\ (\text{lat-}49)\ (\text{long-}79)$

$r^2 = 0.75$ (1)

$SESPR4 = 244+0.811\ (\text{long-}79)-4.59\ (\text{lat-}49)^2-0.672\ (\text{lat-}49)\ (\text{long-}79)$

$r^2 = 0.75$ (2)

$BFSPR4 = 1.75+0.298\ (\text{lat-}49)-0.0181\ (\text{long-}79)$

$r^2 = 0.75$ (3)

Provenances originating at latitudes 67°N to 51°N and east of longitude 100°W (cluster classes 5 and 8):

$HSPR4 = 667+21.0\ (\text{lat-}49)-1.16\ (\text{lat-}49)\ (\text{long-}81)_1$

$r^2 = 0.72$ (4)

$ADWBIOM1 = 727-57.8\ (\text{lat-}49)+10.9\ (\text{lat-}49)\ (\text{lat-}81)_1$

$r^2 = 0.40$ (5)

lat = latitude (°N), long = longitude (°W), dependent variables according to Table 2

When time of bud flushing for two-year-old seedlings in the spring-planted nursery test (BF SPR 3) was used as the dependent variable, a different pattern emerged (Table 8: Function 3, Fig. 7). This divergent pattern was also found for other variables related to bud burst, bud set and lignification, i.e. *BF SPR* 4, *BS PHEN* 2, *BS PHEN* 3, and *LI PHEN* 3.

When the analysed area was limited to cluster classes 4 and 5 in the nearest centroid cluster analysis, which is equivalent to cluster class 1 of the average linkage method excluding seed sources 1, 23 and 101, i.e. the central part of the eastern region, a significant positive relationship was found between latitudinal origin of the seed source, on the one hand and height (*H SPR* 4, Table 8: Function 4, Fig. 8), and shoot elongation (*SE SPR* 4) on the other.

For many biomass properties, more complex patterns are shown. For aboveground dry weight (*ADWM* 1, Table 8; Function 5, Fig. 9), for instance, seedlings from eastern and southern areas, as well as western and northern seedlings, perform best.

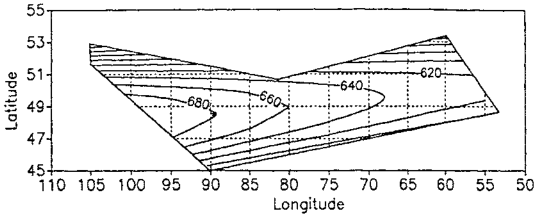

Fig. 5. Height of 4-year-old, spring-planted seedlings in a nursery test (*H SPR88*) as function of latitude and altitude. The analysis is confined to Black spruce provenances originating east of longitude 105°W (cluster classes 1, 5 and 8). The function applied is function 1 in Table 8.

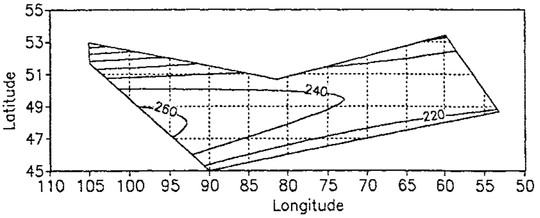

Fig. 6. Shoot elongation for 4-year-old, spring-planted seedlings in nursery test (*SE SPR4*) as provenances originating east of longitude 105°W (cluster classes 1, 5 and 8). The function applied is function 2 in Table 8.

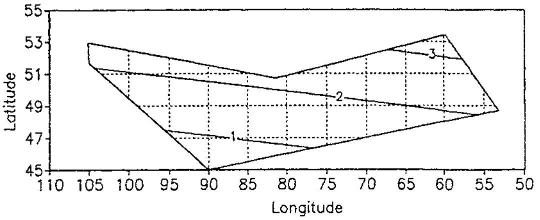

Fig. 7. Calculated bud flushing stage for 3-year-old, spring-planted seedlings in nursery test (*BF SPR87*) for Black spruce provenances originating east of long. 105°W (cluster classes 1, 5 and 8). Function 3.

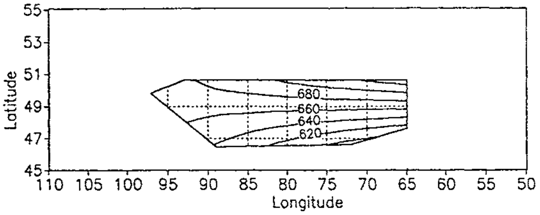

Fig. 8. Height of 4-year-old, spring-planted seedling in a nursery test (*H SPR4*) for Black spruce originating at latitudes 47°N to 51°N and east of longitude. 100°W (cluster classes 5 and 8). Function 4.

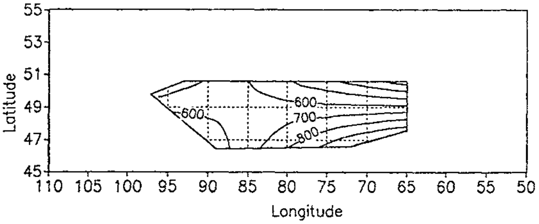

Fig. 9. Above-ground dry weight for first-year containerized seedlings (*ADW BIOM85*) of Black spruce originating at latitudes 47°N to 51°N and east of longitude 100°W (cluster classes 5 and 8). Function 5.

Discussion

Provenance variation in Black spruce

In a study covering the major part of the Black spruce range, the results will naturally depend on where the study is performed. Some provenances are poorly adapted to local environmental conditions. In our study the seed was transferred to another continent, which could result in differences in performance compared with Canadian studies. In terms of latitude, a majority of the seed sources had been transferred more than 10° northwards, exposing them to photoperiodic conditions to which they are not adapted. Like many other coniferous species with a wide latitudinal distribution, Black spruce shows a large amount of clinal variation with regard to properties associated with climatic adaptation (Tables 9a, 9b). Trees orginating from northwestern seed sources exhibited early budbreak, shoot elongation in June and July, an early bud set, a low shoot : root ratio and a high level of lignification in autumn. They did not reach a high dry-matter content by early autumn.

Trees orginating from northwestern seed sources, and grown in the nursery, were generally short, and comparatively few trees showed signs of winter damage during the first few years. Although eastern

Table 9a. *Mean values for 8 clusters of variables used in the nearest-centroid cluster method, together with mean values for 2 White Russian provenances (74, 75) and mean value for all Norway spruce seed sources (70–75)*

Variable	Unit classes	Black spruce cluster No.								Norway spruce	
		6	7	3	1	5	8	2	4	74,75	70–75
H9PHEN age 3	mm	258	359	440	533	498	583	523	527	451	436
HSPR age 4	mm	169	415	520	574	662	645	578	479	483	494
SEPHEN age 2	mm	88	117	159	178	170	184	177	151	110	106
SEPHEN age 3	mm	93	142	159	191	182	187	108	174	195	186
SESPR age 3	mm	65	114	150	157	168	163	115	119	158	158
SESPR age 4	mm	30	129	183	198	252	232	207	135	158	160
BFPHEN age 3	1–8	6.0	6.3	4.5	3.8	3.4	3.2	3.0	3.2	3.5	3.7
BFSPR age 3	1–8	5.2	4.1	3.3	2.5	1.6	1.3	0.8	0.5	3.1	3.1
BFSPR age 4	1–8	1.8	3.4	3.7	4.0	3.2	3.1	2.1	2.0	3.2	3.3
S%PHEN age 2	%	100	96	80	76	68	74	72	74	83	83
BSPHEN age 2	1–2.4	2.0	2.0	0.8	0.1	0.2	0.1	0.0	0.9	2.2	2.2
BSPHEN age 3	1–3	3.0	3.0	2.3	2.1	1.9	2.0	1.8	1.5	2.5	2.5
LIPHEN age 2	1–3	1.0	1.0	1.7	2.3	2.5	2.5	2.9	2.6	1.8	1.8
WDSPR age 3	%	0.0	4.0	24.0	32.4	32.8	50.8	72.0	76.0	8.0	12.0
FDFREEZ	%	25	37	33	44	37	55	78	81	81	87

Table 9b. *Mean values for 8 clusters of variables not used in cluster analysis, together with means for 2 White Russian provenances (74, 75) and mean value for all Norway spruce seed sources (70–75)*

Variable	Unit classes	Black spruce cluster No.								Norway spruce	
		6	7	3	1	5	8	2	4	74,75	70–75
RDW age 3	g	1.3	2.9	3.1	3.7	3.0	4.3	4.8	2.1	3.4	3.2
ADW age 3	g	3.4	7.9	9.9	14.1	10.3	18.2	17.0	8.1	12.1	12.7
ADW/ *RDW* age 3		2.5	2.7	3.2	3.8	3.4	4.3	3.6	3.8	3.5	3.9
CDW age 1	%	39	43	36[a]	34[a]	35[a]	34	32	31	35	37
RDW/ *RL* age 1	g/m	0.019	0.023	0.019[a]	0.018[a]	0.022[a]	0.022	0.022	0.021	0.035	0.034
BDW/ *SDW* age 3		1.12	1.34	1.50	1.66	1.33	1.49	1.75	2.23	1.38	1.26
DRC/ *D50* age 3		0.65	0.64	0.63	0.59	0.61	0.59	0.60	0.60	0.69	0.72

[a] Seed source 100 to 105 not included in clusters.

provenances grew tall and produced substantial amounts of dry matter, winter damage was frequent. These results are in accordance with similar studies in Norway and Canada (Dietrichson, 1969; Morgenstern, 1978; Khalil, 1984; Bihun & Carter 1981 among others). In spring 1988, however, trees orginating from northern seed sources (especially provenance 39) had many frost-damaged buds and showed no shoot elongation. Whether this damage occurred during late autumn or early spring has yet to be determined. It is important to note, however, that under some weather conditions characteristics associated with a northern provenance can be detrimental, even if late spring frosts are not a consideration.

The differences in shoot : root ratio at the end of the growing season are large (Table 9b). As discussed by Cannell & Willett (1976) these differences may well be temporary and reflect the extent to which shoot growth is adapted to climate at the site where provenances are grown. Nevertheless a high shoot : root ratio at the beginning of a growing season can be detrimental in conditions with early summer drought.

No obvious patterns of variation were detected for seed sources east of long. 102°W. The relationships between geographical and climatic factors in this region are not simple. Morgenstern & Mullin (1989) compared Scandinavian and Canadian conditions and found temperature gradients to be more modified and complex in Canada. This would probably be reflected in a complex adaptive pattern in the primary analyses (cf. Bihun & Carter, 1981).

Although cluster analyses are generally used to measure the degree of similarity between provenances, in this study they were used with a dual purpose: 1) to delineate provenance variation and 2) to facilitate regression analysis within regions defined by the clusters. As pointed out by Read (1980), a cluster analysis based on seedling measurements should be looked upon as a first attempt to describe provenance variation, at least when considering a large territory of diverse environments. The two cluster analyses, when limited to phenological properties and growth capacity, revealed a similar and geographically logical pattern (Figs. 3 and 4.) In the eastern part of Canada, a central region was surrounded by a border cluster. Furthermore, a number of random populations emerged. The analyses also revealed three clusters west of long. 100°W.

Regression analyses within clusters 1 and 3 of the average linkage method (Figs. 5, 6 and 7) indicated that the northeastern populations are similar in that they have an early bud flush, whereas bud flushing in the southwestern population, i.e. from Wisconsin, occurs late. Intermediate provenances from around 47-51°N and west of long. 65°W were tallest. For the central area, formed by cluster 1 and excluding provenances 1, 23 and 101 (Figs. 8 and 9), the sources originating north of latitude 49°N were tallest, while the southeastern sources showed the highest dry matter production. These seemingly contradictory results may be explained in terms of adaptation to local weather conditions.

The southeastern and maritime provenances are adapted to a long spring, i.e. frost remains a risk long after the first increases in temperature. Northern provenances, on the other hand, are adapted to a short spring, i.e. the frost incidence remains low once the temperature sum reaches a certain level. Thus, although the southern provenances can take advantage of favourable weather conditions to put on additional growth increment, inclement weather during autumn can lead to insufficient lignification–and thus to winter damage. Furthermore, the southern provenances are inclined to produce free growth for a longer period than northern provenances (cf. Pollard & Logan, 1974). Consequently, if one were to look south of the region containing provenances flushing too early, and north of the region containing provenances flushing too late, it should be possible to locate an area with a suitable seed source with respect to flushing phenology.

The correlations based on provenance mean values (Table 4) indicate that:

- Tall provenances flush and set buds late, and have a low nitrogen content but a high potassium content; their biomassproduction is high and drymatter content in autumn is low.
- Early flushing and bud-setting provenances lignify their shoots early in autumn and have a low risk with regard to winter damage. They have a high nitrogen content and a low potassium content. Similar results have been found for Black spruce (Dietrichson, 1969) and White spruce (Dietrichson, 1971) in Norway. Their biomass production is low and the dry-matter content in autumn is high.
- Provenances incurring winter damage are also at risk of being damaged by frost in spring. They have a low nitrogen content, a high potassium content and a low dry-matter content in autumn.
- Frost-damaged provenances are late-flushing (cf. Dormling, 1982; see Colombo, 1986 for contradictory results) their biomass production is high, and they have a low dry-matter content during autumn.

It is worth noting that the amount of frost damage in the cold tolerance tests appeared to be related more to dry-matter production and seedling vigour than to the time of flushing during spring. This may have been an effect of the test method used. The cold tolerance was tested in growth chambers, in which the temperature was kept constant by increased air circulation by fans. Therefore, the injuries caused could have increased for the large seedlings suffering the combined effects of desiccation and cooling. Smaller seedlings, being sheltered, would in part avoid this effect.

When evaluating the correlation matrix, one should bear in mind that there is a large amount of variation between provenances. Although one finds a negative relationship when examining all black spruce provenances, the relationship obtained when comparing neighbouring provenances could be positive. For example, although there was a negative correlation between total height and bud-flushing, i.e, a tendency for early-flushing provenances to be short (Table 6), this relationship is not found among the provenances in the eastern part of Canada (cf. Figs. 5 and 7).

Within provenances (Table 5) the tall seedlings flush and set buds late. However, the year-to-year correlations in bud flush are low and non-significant, indicating strong random influence or limited variation. By contrast, the correlations for bud set are positive and significant from year to year. Seedlings showing little shoot elongation, and those with early bud set, are comparatively well lignified in autumn.

Large seedlings have large amounts of stem biomass, root biomass and needle and branch biomass (Table 6). The dry-matter content in autumn is higher in large seedlings, probably because the dry-matter content of needles is higher than that of branches, stem or root. Large seedlings have a low content of N and P, but a high K/N quotient.

In comparison to correlations based on provenance values, partial correlations on individual values show two major differences: year-to-year correlations in bud flushing are low, and not significant, and the relationship between dry-matter content and seedling size is positive. The low correlations in bud flush from year to year indicate that bud flush may not be a suitable character for individual tree selection in poorly adapted sources. Although bud flush is under genetic control, flushing in individual seedlings may be delayed as a consequence of minor injuries during the cold period, which may explain the low correlations. The positive and significant correlations between dry-matter content and biomass in three-year-old seedlings is probably method-related, attributable to the fact that dry-matter content estimates were based on the whole seedling above the root collar. Because the dry-matter of needles is often higher than that of branches or stem, and since needles make up a larger proportion of the total biomass in large trees than in small ones, the dry-matter content might appear to be positively related to seedling size (Hultén, H., pers. comm.).

Norway spruce and Black spruce compared

The Norway spruce material used in this project is not representative of its entire range, and any comparison between the two species should take this fact into account. The five Norway spruce seed sources are all to be used in southern and central Sweden, south of 60°N. Seed sources 74 and 75 are of White Russian origin. These two provenances should be suitable as reference material. In a study of Norway spruce in the Maritimes region of Canada, Fowler & Coles (1980) recommended White Russian provenances for use in northern New Brunswick and the Great Lakes region.

Tables 9a and 9b compare the two species in terms of a number of properties. With only a few exceptions, the differences between Norway spruce and Black spruce were small. The Norway spruce seed sources used in this study produced trees with developmental characteristics similar to those of the Black spruce originating between 50° and 60°N. Their phenological and biomass properties were also similar.

There are differences between the two species, however. The roots of Norway spruce are thicker than those of Black spruce. Root thickness was estimated indirectly on this basis of the root dry-weight/total root length ratio (*RD/WRLBIOM* 1 in Table 9b). The difference was not only substantial in the first-year estimates, but was also evident in 3-year-old seedlings. These results were confirmed by observations at transplanting. Roots of first-year seedlings of Black spruce did not completely penetrate the lower parts of the pot, whereas those of Norway spruce did so. This difference in root thickness should be borne in mind by nurserymen dealing with both species. Prevost & Bolghari (1990) reported that bulk densities exceeding 1.05 g cm^{-3} restricted root growth of black spruce, and found interactions between bulk density and seed origin. Upland seed sources developed better roots than lowland seed sources.

There were also differences between the species in terms of their susceptibility to spring frost. The proportion of seedlings that were damaged in the cold tolerance test was higher for Norway spruce than for any of the Black spruce provenances. Interestingly, this dissimilarity was not the result of differences in bud-flushing date. Thus, it appears as if Black spruce can tolerate lower temperatures during its elongation phase. Unfortunately, there have not been any hard spring or summer frosts since the nursery tests were established. Therefore, it was not possible to confirm the results of the cold tolerance tests in this study.

The frequency of winter damage was higher for Black spruce than for Norway spruce. Black spruce has been shown to be more susceptible than Norway spruce to winter desiccation (Christersson & von Fircks, 1988, 1989). Generally, one can assume that Black spruce is prone to suffer from drought injury because of its high shoot : root ratio (Table 9). However, the impact of shoot : root ratio on winter desiccation may be overstimated, because when the soil is frozen during winter, water uptake is blocked, which makes it difficult for the root to supply the shoots with water. Winter damage is often a consequence of delayed and insufficient hardening the previous autumn. Bud set and lignification of Black spruce were very late, especially for southern provenances (Table 9a). This was probably an effect of the long northward transfer to Sweden (cf. Dietrichson, 1969.) Correspondingly, when comparing black and Norway spruce in the Maritimes region in Canada, Fowler & Coles (1980) found that Norway spruce was more susceptible to winter damage than Black spruce, probably because the growth rhythm of the former was out of phase with the environment. The fact that growth cessation and hardening of the provenances transferred far northwards occurred relatively late in our study, could be related to an extended period of free growth which occurs in younger years (Pollard & Logan, 1974; Logan & Pollard, 1985). Free growth can also be an effect of early winter damage (Colombo, 1986). As a result, winter-damaged seedlings could be exposed to renewed climatically induced damage.

With regard to stem and branch properties, the main difference between the species was that Black spruce was more slender, and this difference became apparent as early as the seedling stage (D50/DRC 3 in Table 9b). In terms of other biomass properties, Norway spruce differed from southeastern seed sources of Black spruce, whereas only minor differences were found when comparing seed sources from similar latitudes.

Implications for silviculture

The primary value of these results will be realized when formulating future seed-source recommendations. The results should also provide useful guidelines when reforestation with Black spruce is being considered. The poor root development, thin roots, and long shoot elongation period of Black spruce may be a source of problems in the nursery. The inability to penetrate the container quickly under unfavourable conditions may necessitate that cultural methods be modified. Planting barerooted seedlings, which are two or three years old and thus have a shorter shoot elongation period than first-year seedlings, could help to reduce winter injury. Alternatively, a long- night treatment could be used. The high shoot : root ratios of southern provenances suggest that Black spruce may require a container different in size from that used for Norway spruce. A similar level of shoot : root ratio was, however, reduced for second-generation *Abies procera* (Noble fir) when grown in Denmark (Larsen, 1985).

As pointed out by Nienstaedt (1984) the potential for drawing correct conclusions in young provenance trials regarding future production is reduced in cases where there are large differences between provenances in the amount of free growth.

Although seed-source recommendations for Black spruce cannot be developed on the basis of the results presented here, some conclusions can be drawn:

1. Winter damage, mainly to provenances originating south of 49°N, represents a serious problem. Although these provenances have a superior growth capacity, their shoot elongation period may be too long, at least in areas prone to early autumn frost. The results of cold tolerance tests during spring indicate that these provenances are also injured by spring frost.

2. In comparison with Norway spruce, sources of Black spruce originating north of 49°N are more frost-hardy during the shoot elongation period. In this respect, Black spruce has a considerable advantage over Norway spruce.

3. For eastern seed sources originating north of 49°N, planting should probably be limited to 2-year-old or older seedlings to minimize winter damage. Alternatively, a long-night treatment could be used. Western seed sources originating north of 50°N are probably a safer choice north of latitude 60°N in Sweden. Rosvall (1986) made similar recommendations.

4. Although the winter damage sustained by young Black spruce appeared to be severe, it need not al-

ways have deleterious effects on future development. In two separate studies evaluating the effects of winter damage on shoot elongation (Ståhl & Persson, unpublished), bud set was delayed by about 2 weeks in injured seedlings. (A similar delay was reported for pruned *Salix pentandra* by Junttila & Kaurin (1990)). Height increment was not markedly affected when injury was limited to the previous year's leader. Seedlings sustaining bud damage or damage affecting more than the previous year's leader, exhibited reduced height increment. After one year of favourable weather, height losses had been compensated for, and the only remaining signs of injury were twin or multiple leaders.

Black spruce may eventually become an important species in frost-prone areas of Sweden. Althought the species seems to be free from problems associated with roe deer (*Capreolus capreolus* L.) and elk (*Alces alces* L.) grazing, there is a risk of damage if seed choice is based exclusively on the aim of obtaining superior height growth. Similary, the use of one-year-old seedlings entails a high risk of winter damage.

In the present state of our knowledge, Black spruce should only be recommended for planting on sites where experience shows that other species will not be successful.

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Edited by J.G.K.Flower-Ellis