

Growth and survival of black spruce in the range-wide provenance study

E. K. MORGENSTERN AND T. J. MULLIN

Faculty of Forestry, University of New Brunswick, Fredericton, N.B., Canada E3B 6C2

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Field experiments of the range-wide black spruce (*Picea mariana* (Mill.) B.S.P.) provenance study were established between 1973 and 1977 through the cooperation of several organizations in the United States and Canada from the Atlantic Coast to Alberta. This study evaluates performance at 11 or 15 years from seed in 29 locations divided into 8 regional clusters of 2 to 10 experiments each. Analytical methods include correlations of height and survival with geographic and climatic variables, analyses of variance, and polynomial regressions followed by contour plotting. Best height was obtained in the Great Lakes States and in other temperate regions, and best survival in Newfoundland and some temperate regions with long growing seasons. Correlations between height and survival were positive and significant only in 10 locations, 8 of which were located in temperate regions. In many locations in boreal regions, correlations with latitude or climatic variables at the place of seed origin and height have opposite signs of correlations with survival, indicating difficulties when simultaneously selecting for good height and high survival in cold climates. Contour plots from the regressions demonstrate a similar trend by showing good pattern overlap of height and survival primarily in mild coastal (Newfoundland) or temperate continental climates (southern Quebec and Ontario, Great Lakes States). There is evidence that provenance differences are still developing and changes in rank are taking place, and therefore additional assessments are required in the future.

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Des essais sur le terrain de diverses populations d'Épinette noire (*Picea mariana* (Mill.) B.S.P.) couvrant l'aire totale de dispersion ont été établis entre 1973 et 1977, grâce à la collaboration de différents organismes américains et canadiens situés de la côte atlantique jusqu'en Alberta. Cette étude évalue le rendement à 11 ou 15 ans de tout ce matériel issu de graines et localisé en 29 lieux de culture répartis en 8 groupes régionaux, comportant chacun 2 à 10 essais. Les méthodes analytiques employées incluent les corrélations de hauteur et de survie, liées aux facteurs géographiques et climatiques, les analyses de variance, les régressions polynomiales et le tracé des contours. La meilleure hauteur origine de la région des Grands Lacs et d'autres régions à climat tempéré d'une part, tandis que le meilleur taux de survie provenait de Terre-Neuve et d'autres régions tempérées caractérisées par des saisons à croissance longue. Les corrélations entre la hauteur et la survie se sont avérées positives et significatives en 10 lieux de culture seulement dont 8 situés en régions tempérées. En plusieurs endroits des régions boréales, les corrélations entre la latitude ou les facteurs climatiques du lieu d'origine des graines et la hauteur étaient en opposition avec celles reliées aux taux de survie, illustrant ainsi les difficultés inhérentes qui apparaissent lorsqu'on sélectionne en même temps une bonne hauteur et un fort taux de survie en climats froids. Le tracé des contours issu des calculs de régression illustre aussi une tendance similaire en montrant un bon chevauchement entre la hauteur et la survie pour des climats doux et côtiers (Terre-Neuve) ou pour des climats continentaux tempérés (Québec méridional, Ontario et les Grands Lacs). Il est certain que les différences entre ces provenances évoluent encore et que les changements dans leur classement s'opèrent aussi de sorte que des évaluations additionnelles sont encore nécessaires pour l'avenir.

[Traduit par la revue]

Introduction

Knowledge of genetic variation patterns of major forest tree species is of fundamental importance in silviculture (Stern and Roche 1974; Nienstaedt 1979). Seed zones based on these patterns may be used to control the distribution of seed and planting stock to assure good growth and survival, and information on variation within and among seed zones or breeding regions helps to plan selection and testing and identifies superior provenances. In Canada, much progress has been made in provenance research during the last 30 years and positive effects on forest management have been obtained (Ying and Morgenstern 1988).

Although genetic variation of the major species has been well explored, there is concern that initial results are not sufficient. There has been much discussion about juvenile-mature correlations, but this subject relates primarily to progeny tests. Progeny testing usually involves native populations that are tested within their region of origin so that general adaptability may be assumed (Rehfeldt 1984). In contrast, provenance testing includes long-distance move-

ment of populations, and the degree of adaptation to the new environment is unknown. Problems may not arise for several decades, but many of the oldest experiments suggest substantial changes in performance halfway through the rotation period, either as a result of the periodic occurrence of extreme climatic events or the slowly accumulating differences in survival related to maladaptation (Wiedemann 1930; Dietrichson 1964; Timofeev 1974; Campbell 1974; Silen 1978).

In this paper we discuss overall trends and patterns of variation in a series of cooperative provenance experiments of black spruce (*Picea mariana* (Mill.) B.S.P.) based on range-wide sampling and testing. Several cooperators have already reported results from their own sets of regional experiments (Corriveau 1982; Fowler and Park 1982; Bihun and Carter 1983; Merrill *et al.* 1984; Nienstaedt 1984; Boyle 1985; Morgenstern *et al.* 1987; Park and Fowler 1988; Beaulieu *et al.* 1989). Using a variety of analytical methods, they have explored relationships with geographic origin, variation patterns, provenance movement, and seed and

breeding zones. It would be superfluous to duplicate such analyses. Instead, the objective of the present study is to examine the correlation of height and survival. Since volume production per unit area depends upon growth and survival at rotation age, both traits must be measured in long-term experiments to obtain meaningful results.

Literature review

General principles

In the Northern Hemisphere, climatic differences between seasons are pronounced and the physiology of native tree species is synchronized with seasonal cycles of temperature, moisture, and day length. Many experiments have shown that the rise of temperature in spring triggers initiation of growth while the formation of buds and cessation of growth in autumn is primarily controlled by day length (Wareing 1956; Withrow 1959; Steiner 1979; Worrall 1983). Other important developmental events are proleptic and sylleptic free growth (Cannell and Johnstone 1978; von Wühlisch and Muhs 1986) occurring in mid or late summer, primarily as a consequence of optimum conditions for growth in young seedlings (Pollard and Logan 1974, 1976). All of these responses can be observed regularly in greenhouse or nursery environments and related to geographic and climatic parameters of the places of seed origin. Usually clear trends appear, and since the physiological traits measured are adaptive, it is possible to interpret the results as evidence for natural selection (Stern and Roche 1974).

It is usually assumed that local populations are broadly adapted to their ecological niche, including the fluctuation of climate from year to year. However, when provenance experiments are conducted (particularly with exotic species), populations may be moved considerable distances from their place of origin. It has been generally observed that movement northward at the same elevation or from high elevations in the south to low elevations in the north increases height growth compared with local provenances, provided that the movement is not so excessive as to delay cessation of growth to the point that plants are exposed to the risk of frost damage and eventually mortality (Dietrichson 1969). Such northward movements have been best documented in the Scandinavian countries where considerable growth increases have been achieved (Langlet 1963). However the contrasting requirements for good growth (long photoperiod) and survival (adequate length of growing season) have been noted by many researchers (e.g., Dietrichson 1964; Namkoong 1967; Morgenstern and Roche 1969; Lindgren *et al.* 1976). A balance between growth and survival or hardiness must be achieved that may sometimes favour the local provenance, in spite of earlier results to the contrary (Timofeev 1974).

Differences among provenances in survival usually appear gradually over time and therefore require a long test period, i.e., field experiments (Campbell 1974). It is a common experience that obvious trends such as clinal variation in phenology and growth observed in nursery experiments no longer exist when the same material is observed in the field (Boyle 1985). There are several reasons for this:

(1) Field experiments extend over a broader range of environments than nursery or greenhouse environments; physical and biological environments have increased in complexity but the control of them has diminished (Snaydon 1980; Rehfeldt 1984). Large provenance-

environment interactions may be observed. Initially there are also confounding effects, such as transplant shock and grass competition, that may influence performance for several years after planting, but provenance differences may emerge strongly at about 15 years of age (Namkoong *et al.* 1972).

- (2) The long-term nature of the experiments will lead to a better appraisal of genetic variation. Provenance performance may not be strongly related to geographic origin when genetic processes other than natural selection play an important role. Conceivably, seed collected range wide may include population samples that are not completely comparable, for example, when all populations have not flowered equally well and therefore different degrees of inbreeding exist or when there is a more permanent difference in population structure and mating system. An example is found in black spruce material of this study when stored seed samples were subjected to isoenzyme analysis. In each case the level of inbreeding (measured as outcrossing rate) was positively related to height growth at 15 years of age in the field (Dr. T. Boyle, personal communication). Therefore, within a narrow north-south range (say 2 to 3° of latitude) such effects could surpass the influence of geographic origin. Similarly, in *Pinus resinosa* Ait., there was no difference among progenies from inbreeding and outcrossing at the germination stage, but a significant 8% depression in height growth was found at 9 years of age in the field (Fowler 1965; Holst and Fowler 1975).
- (3) A more complete assessment of productivity is possible. A full evaluation requires measurements of not only height but also diameter growth, disease resistance, volume production, stem and wood quality, and long-term survival. In many experiments survival was of great significance since it controlled stocking, but large survival differences did not appear until about halfway through the rotation (Rubner 1960; Wakeley and Bercaw 1965; Timofeev 1974; Silen 1978; Eriksson *et al.* 1980; Long 1980; Sluder 1980; Giertych and Oleksyn 1981; Schober *et al.* 1983; Oleksyn and Giertych 1984; Lantz 1986; Fowler *et al.* 1988).

Provenance variation in black spruce

Black spruce is a major species of the pulp and paper industry primarily in eastern and central Canada and the Great Lakes States of the United States. It is the most important reforestation species from Manitoba to the Atlantic Coast in Canada (Smyth and Brownright 1986).

Provenance research was initially concerned with germination, phenology, height growth, lignification, and winter damage. Up to 4 years from seed, variation in populations from the central parts of the range was clinal (Dietrichson 1969; Morgenstern 1969). In range-wide material, experiments in Ontario determined a similar variation pattern (Morgenstern 1978a). Experiments in Newfoundland based primarily on native populations indicated a relationship to the forest regions of the island, and the variation pattern was termed ecotypic (Khalil 1973).

In field experiments up to 15 years from seed, results have been similar, but often general trends have not been as clear. In Newfoundland, at age 10 range-wide experiments revealed weak south-north and east-west trends in height (Khalil 1986). At 15 years, the native populations demonstrated a

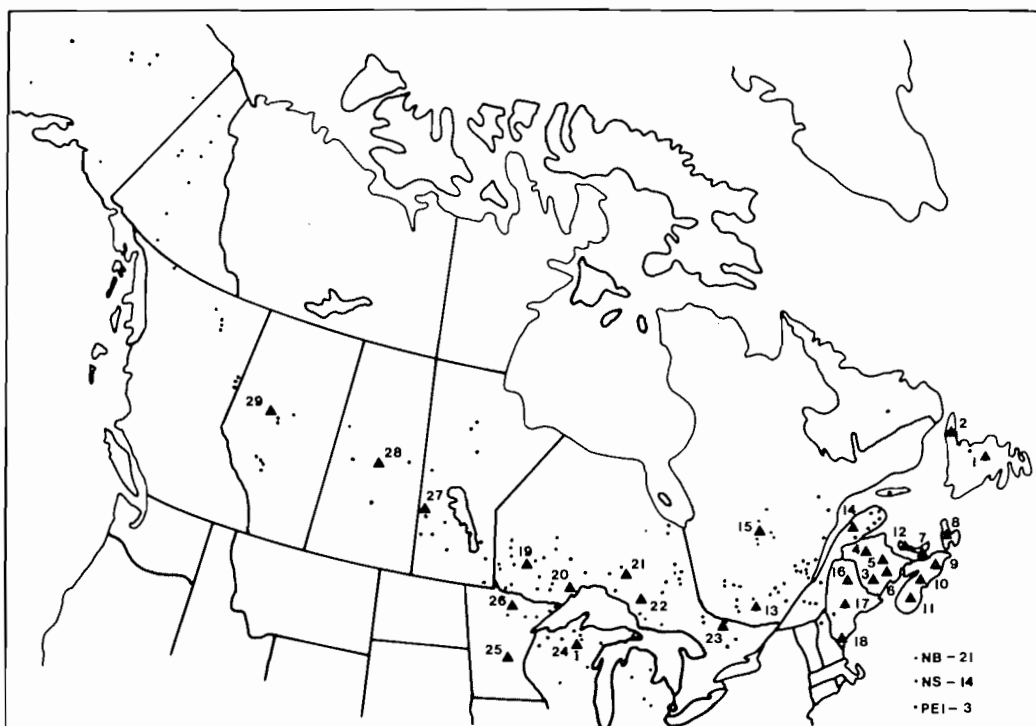


FIG. 1. Geographic distribution of provenances (dots) sampled across the range of black spruce in Canada and the United States, and location of test plantations (triangles). Numbers in the right corner are numbers of provenances included from the three Maritime Provinces.

clinal pattern when tested in the more protected central part of the Island but an ecotypic pattern in the harsher environments of the Northern and Avalon Peninsulas (Hall 1986). In the Maritime Provinces, Quebec, and Ontario, the clinal pattern discovered in nursery experiments was still evident in some locations in the field but not in others, and each experiment varied in the degree to which differences in height and survival were expressed and correlated with geographic and climatic variables. Several broadly adapted provenances were discovered that performed well over a range of environments, but considerable changes in rank were still taking place (Corriveau 1982; Fowler and Park 1982; Boyle 1985; Morgenstern *et al.* 1987; Park and Fowler 1988; Beaulieu *et al.* 1989). In the Great Lakes States experiments, correlations with geographic and climatic variables declined with age and early selection was not considered promising (Merrill *et al.* 1984; Nienstaedt 1984).

Background, materials, and methods

Background

The range-wide black spruce provenance study was planned and initiated by Forestry Canada (formerly the Canadian Forestry Service) in 1967 and seed collections were made by various cooperating organizations in the 1967–1970 period. Initially, collections sampled 202 stands (provenances) with 15 trees each (Selkirk 1974); 16 additional stands were added at a later stage by some cooperators (Morgenstern and Villeneuve 1987). Stand origin ranged latitudinally from 41°N (Connecticut) to 67°N (Alaska) and longitudinally from 53°W (Newfoundland) to 156°W (Alaska) (Fig. 1). While planting stock was being produced in nurseries, several physiological and other short-term experiments were conducted (Pollard and Logan 1974, 1976; Morgenstern 1978a).

Thirty-four field experiments were established across the species range between 1973 and 1977: Newfoundland, 3; Maritime Provinces, 10; Maine, 3; Quebec, 6; Ontario, 5; Great Lakes States, 3; Prairie Provinces, 3; and Alaska, 1 (Morgenstern and Kokocinski 1976; Keable 1978; Morgenstern 1978b; Klein and Nanka 1982).

In 1985, at 15 years from seed (11 years in two experiments in Maine), an overall evaluation was begun of the 29 experiments that were in good condition at that time. All except one had been visited during the previous 5 years or were inspected in 1985 to obtain information on the general conditions of the plantations (health, vigor, insects, and diseases) and on related ecological factors as an aid to the interpretation of results. Measurements provided by individual cooperators constitute the basis for the present report (Morgenstern and Villeneuve 1987).

Methods

Ideally, field experiments would best reflect long-term trends if measurements had been repeated over several decades (as for *Pinus sylvestris* L. in Sweden, see Campbell 1974; Eriksson *et al.* 1980) and if the causes of mortality could be identified (e.g., frost, insects, fungi). None of these conditions existed here, and we had to use data from one assessment. The data were received as means of height and percent survival of each provenance at each location. Percentages were transformed by arcsin before analyses (Steel and Torrie 1980).

The experiments were originally designed and established by 10 cooperators, each of which requested seed from other members of the group. As a rule, each cooperator included all of his own provenances and decreasing numbers of provenance in more distant regions, but usually including extreme southern or northern provenances. This unbalanced design

TABLE 1. Description of provenance sample, test environments, and plantations

Cluster No. (no. of locations)	Area studied	No. and range of provenances	Region ^a	Description of environments		Plantation development; problems observed; mean height of tallest provenance in best location ^c
				(growing season ^b ; soil type; moisture; fertility)		
I(2)	Nfld.	64-72; Nfld.-Man.	Boreal B.28a, B.29	156-163 days; stony medium to fine or silty sands under organic matter of moderate depth, well podzolized; fresh; medium fertility	Good; light mortality from root rot; 219 cm	
II(10)	N.B., P.E.I., N.S.	50-99; Nfld.-Alaska	Acadian A.3, A.7; Great Lakes L.6	175-195 days; extremely variable, ranging from fresh, fertile, loamy sands (old fields) or loams (hardwood sites) to coarse sands with thick organic matter; low moisture; low fertility	Variable; heavy competition by ericaceous vegetation in some locations; 411 cm	
III(3)	Maine	50-114; Conn.-B.C.	Cool temperate, wet	175-195 days; sandy old fields and sandy loam, podzolized; dry to fresh; medium fertility	Some grass competition, root rot; 356 cm	
IV(2)	E. Que.	90; Nfld.-Y.K.	Boreal B.2, B.16	145-160 days; medium to coarse sand, strongly podzolized (both sites disturbed by bulldozing, burning or farming); adequate moisture; moderate fertility	Reasonable growth; some winter drying where much of humus removed; 269 cm	
V(2)	Ottawa R.	56-88; Nfld.-Y.K.	Great Lakes L.4c, L.4b	180 days; medium to coarse sand; dry to moist; medium fertility.	Slow establishment due to competition with grasses, sedges, birches; 348 cm	
VI(4)	N. Ont.	56-64; Nfld.-Y.K.	Boreal B.7, B.8, B.11	158-166 days; silty clays, silty loams, and medium to fine sands; dry to fresh; medium to high fertility	Slow establishment on heavy soils due to grass competition; root rot; 279 cm	
VII(3)	Wis., Minn.	49-108; Conn.-Alaska	Cool temperate, moist	180-190 days; sandy loam, silt loams, and medium to fine sands (old fields); dry to fresh; medium to high fertility	Location 24 replanted in new area after 1976 drought, generally good growth; weevil damage; 535 cm	
VIII(3)	Man., Sask., Alta.	30-49; Nfld.-Alaska	Boreal B.18a	150-165 days; organic materials over loam or clay loam; weakly calcareous; dry to moist; seasonal drought expected in location 28; medium to high fertility	Grass competition common; damage and mortality due to root rot, weevil, and late frost; 298 cm	

^aForest region and section number within each region (Rowe 1972) or climatic description (Daniel *et al.* 1979).

^bBased on the average number of days with mean temperature of 5.6°C and above.

^cFull names of insects or fungus diseases listed: white pine weevil (*Pissodes strobi* Peck.); shoe-string root rot (*Armillaria mellea* (Vahl ex Fr.) Kumm.) and possibly other species within this genus (see Whitney 1988).

precluded a joint two-way analysis of variance for provenance and location of all experiments. Consequently, the total sample of 29 experiments was divided for analysis into eight regional groups or clusters, with adjacent clusters sharing more of the same provenances than distant clusters. This arrangement was checked by cluster analysis using the methods of Ward and Average Linkage (SAS Institute Inc. 1985a) and led to one modification, i.e., the grouping together of one Quebec and one Ontario experiment in the Great Lakes - St. Lawrence Forest Region (Rowe 1972). Even then the number of provenances planted at different locations within a cluster was not identical. A description of clusters including test environments and range of provenances included is given in Table 1 and a map of provenance origin and test locations in Fig. 1. The number of replications ranged from 3 in Ontario and Alberta to 9 in Maine and the number of trees per plot, from 4 in Maine and Minnesota to 25 in Ontario.

To obtain correlations of provenance mean height and survival with geographic and climatic variables, climatic data of the places of seed origin were compiled from summaries and maps published by the United States Weather Bureau and the Canadian Meteorological Service, using interpolation where necessary (Visher 1954; Chapman and Brown 1966; van Groenewoud 1983). All temperature-related variables were based on 5.6°C (42°F). The following analyses were computed:

- (1) for each location, simple linear correlations among height, survival percent, and latitude, longitude, elevation, summer precipitation, date of the last spring frost, length of the frost-free period, growing degree-days, date of start of the growing season, and length of the growing season
- (2) for each cluster, analyses of variance of height and survival, which (similar to a randomized complete-block design) provided mean squares for locations, provenances, and error (Steel and Torrie 1980). The location \times provenance interaction is included in the error and was not separately estimated because of the differences in plot sizes and numbers of replications among and within clusters
- (3) for each cluster, polynomial regressions resulted in response surfaces depicted as contour plots, using either latitude or length of growing season of provenance origin and test location as independent variables, and total height or percent survival (transformed) as dependent variables. The model (SAS Institute Inc. 1985a) is

$$Z_{ij} = \beta_0 + \beta_1 x_i + \beta_2 y_j + \beta_3 x_i^2 + \beta_4 y_j^2 + \beta_5 x_i y_j + e$$

where

Z_{ij} is the height or survival of the j th provenance at the i th location

x_i is the latitude (or growing season) of the i th location

y_j is the latitude (or growing season) of the j th provenance

β_0 is the intercept of the model

β_1 is the linear effect of location latitude

β_2 is the linear effect of provenance latitude

β_3 is the quadratic effect of the location latitude (or growing season)

β_4 is the quadratic effect of provenance latitude (or growing season)

β_5 is the interaction of provenance and location

e is the residual error of fitting individual observations to the response surface

The choice of latitude and length of growing season as independent variables was based on the correlation analyses that showed that these were most often correlated with height and survival. Physiologically, height is an expression of vigour and survival indicates adaptation to the growing season of the test location.

This analysis and subsequent contour plotting are useful to determine the range of suitable provenances and test locations for best height growth and survival. When the contour plots of height and survival of the same cluster are depicted side by side, the degree of overlap can be seen, i.e., to what extent the fastest growing provenances survive well.

The computations were made using the SAS procedure RSREG and GCONTOUR (SAS Institute Inc. 1985a, 1985b). The output consists of the usual regression parameters, including regression coefficients (β_0 to β_5), coefficients of determination (r^2), and a solution for the optimum response. Eigenvalues and eigenvectors from the matrix of quadratic parameter estimates are printed from this solution: if the eigenvalues are all negative, the solution is a maximum; if they have mixed signs, the solution is a saddle point (SAS Institute Inc. 1985a). The plot from a maximum solution may show a concentration of highest values in the middle of the grid (i.e., the region covered by experiments) with circular or elliptical configuration, but the estimated maximum can also lie outside of this region (Cochrane and Cox 1957) and then the plot appears on one side. A saddle-point solution shows concentrations of high values at the extreme left and right sides of the grid. The associated eigenvectors indicate the direction of the axes of these surfaces. Further explanations of the procedure and interpretation are given by Kung and Clausen (1984), and examples of the surfaces discussed are given under results.

For comparisons of climate at the various test locations, we relied on the classifications of Rowe (1972) in Canada and Holdridge (Daniel *et al.* 1979) in the United States. Accordingly, all test locations in Newfoundland, eastern Quebec, northern Ontario, and the Prairie Provinces are situated in boreal climates and all locations further south, in temperate climates. Rowe's *Forest Regions of Canada* are not based on climate directly but on the presence of dominant species at the climax stage of forest succession. Nevertheless, there is a close relationship with climate: comparisons of isotherms (Chapman and Brown 1966) suggest that the southern boundary of the Boreal Forest Region is roughly where the mean frost-free period is about 100 days long, or where a mean daily temperature of 10°C occurs less than 120 times a year (Walter 1973).

Results

General performance

Table 2 summarizes mean height and survival for each of the locations and clusters, showing that the smallest trees were found at location 5, Bartibog, New Brunswick (93 cm), and the tallest at location 24, Rhinelander, Wisconsin (470 cm). Best height growth was obtained in cluster VII, Great Lakes States (342 cm), best survival in cluster I,

TABLE 2. Location and cluster means for height and survival and correlations (*r*) of these responses

Cluster No.	Location No.	Location	Mean height (cm)		Mean survival (%)		<i>r</i>
			Location	Cluster	Location	Cluster	
I	1	Millertown, Nfld.	179	184	84	87	0.08
	2	Roddickton, Nfld.	189		90		-0.05
II	3	Acadia F.E.S., N.B.	258	241	90	84	0.41**
	4	Black Brook, N.B.	379		80		0.27*
	5	Bartibog River, N.B.	93		81		0.12
	6	Sabbies Brook, N.B.	143		80		0.04
	7	Dromore, P.E.I.	308		90		0.12
	8	Cape Breton Highlds., N.S.	168		90		0.40**
	9	Pleasant Valley, N.S.	315		78		0.37**
	10	Stanley, N.S.	185		83		0.10
	11	E. Dalhousie, N.S.	312		79		0.19
	12	E. Bideford, P.E.I.	253		91		-0.14
III ^a	16	Telos, Maine	282	281	80	73	0.60**
	17	Dover-Foxcroft, Maine	246		64		0.71**
	18	Alfred, Maine	315		75		-0.38**
IV	14	Lac St-Ignace, Que.	220	200	69	77	0.18
	15	Chibougamau, Que.	179		86		0.07
V	13	Mont-Laurier, Que.	294	282	89	81	0.20
	23	Chalk River, Ont.	270		72		-0.14
VI	19	Dryden, Ont.	224	208	63	57	-0.07
	20	Thunder Bay, Ont.	198		49		-0.04
	21	Geraldton, Ont.	224		52		0.31*
	22	Chapleau, Ont.	187		63		0.07
VII	24	Rhineland, Wis.	470	342	91	67	-0.00
	25	Rosemount, Minn.	271		60		0.42**
	26	Blackberry, Minn.	285		49		0.62**
VIII	27	Mafeking, Man.	193	202	80	75	0.35*
	28	Snowden, Sask.	243		75		-0.04
	29	Reno, Alta.	169		72		-0.05

NOTE: *, 5% significance level; **, 1% significance level.

^aFor the purpose of this comparison, height values at locations 16 and 17 have been extrapolated to age 15 by multiplying by 15/11.

Newfoundland (87%), poorest growth in cluster IV, eastern Quebec (200 cm), and poorest survival in cluster VI, northern Ontario (57%).

When individual provenance performance is examined in each cluster, good combinations of height and survival are found occasionally that are in conflict with general trends. This aspect will not be pursued further; it is much better handled by individual cooperators (e.g., Park and Fowler 1988).

Correlations

There were statistically significant correlations between height and survival at 11 locations; only one of these bears a negative sign (Table 2).

Numerous correlations existed between height and geographic and climatic variables (Table 3): latitude of provenance origin was most frequently significant (19 locations), followed by degree-days (16), start of the growing season (14), length of the growing season (12), longitude (12), summer precipitation (10), and frost-free period (10). All correlations between height and latitude (including those which were not significant) were negative. This indicates superior height growth of more southerly provenances at each planting site.

Significant correlations between survival and geographic and climatic variables (Table 4) were not quite as frequent as for height. Length of growing season was most promi-

nent (significant at 11 locations), then latitude, longitude, frost-free period and degree-days (each 10), summer precipitation and date of the last spring frost (each 9), and start of the growing season (7). Of the 11 significant correlations with length of the growing season, 9 were negative and 2 positive. This indicates a trend opposite to that for height: in the majority of test locations survival declined with increasing length of the growing season of the place of seed origin.

Analyses of variance

The analyses of variance of height and survival by clusters (Table 5) determined significant differences at the 1 or 5% level among all locations. Provenance differences were not significant for height in the Great Lakes States and the Prairie Provinces, and for survival in Newfoundland, the Maritime Provinces, Maine, the Ottawa River area, and the Great Lakes States. Since the error component included the provenance-location interaction, this simple analysis was relatively insensitive. There were statistically significant differences among provenances at individual locations within some of these clusters shown by the more detailed analyses of individual cooperators (Boyle 1985; Park and Fowler 1988; Beaulieu *et al.* 1989).

Variance component analysis revealed that locations and error contributed the largest percentage to total variance and the provenances the smallest, but the provenance compo-

TABLE 3. Correlation between provenance mean height and geographic and climatic variables, by clusters and locations

Cluster	Location	Correlation coefficient (<i>r</i>) for variable								
		Lat.	Long.	Elev.	Summer precipitation	Last spring frost	Frost-free period	Degree-days	Start of growing season	Length of growing season
I	1	-0.24*	0.06	-0.06	-0.11	-0.13	0.07	0.24*	-0.36**	0.21
	2	-0.14	0.10	0.03	-0.00	-0.08	-0.07	0.15	-0.30*	0.06
II	3	-0.67**	-0.46**	-0.27**	0.35**	-0.27**	0.36**	0.52**	-0.50**	0.50**
	4	-0.37**	0.08	-0.13	-0.03	-0.20	0.12	0.33**	-0.36**	0.28*
	5	-0.22	-0.13	-0.13	0.01	0.05	-0.02	0.09	-0.12	0.06
	6	-0.03	-0.03	0.07	0.35**	0.15	-0.17	-0.10	0.07	-0.09
	7	-0.35**	-0.43**	-0.47**	-0.09	-0.20	0.22	0.18	-0.09	0.22
	8	-0.68**	-0.84**	-0.52**	0.66**	-0.17	0.42**	0.28**	-0.07	0.41**
	9	-0.27*	-0.09	-0.28*	0.03	-0.16	0.11	0.25*	-0.24*	0.17
	10	-0.06	0.35**	0.04	-0.26*	-0.05	-0.08	0.28*	-0.32**	0.08
	11	-0.23*	0.09	-0.04	-0.17	-0.13	0.10	0.20	-0.22	0.20
	12	-0.41**	-0.24	-0.21	0.14	-0.15	0.24	0.27	-0.19	0.29*
III	16	-0.66**	-0.41**	-0.13	0.51**	-0.45**	0.46**	0.52**	-0.27*	0.37**
	17	-0.78**	-0.51**	-0.24*	0.58**	-0.52**	0.58**	0.64**	-0.38**	0.53**
IV	18	-0.01	0.14	0.11	-0.55**	0.03	-0.11	0.10	-0.18	0.06
	14	-0.30**	-0.29**	-0.12	0.11	-0.05	0.10	0.09	-0.12	0.11
V	15	-0.24*	0.16	0.05	0.00	-0.10	0.08	0.29**	-0.35**	0.17
	13	-0.30**	0.25*	0.15	-0.05	-0.10	0.07	0.31**	-0.36**	0.17
VI	23	-0.53**	-0.22	-0.11	0.30*	-0.33*	0.46**	0.46**	-0.27*	0.39**
	19	-0.35**	-0.15	0.29*	0.19	-0.13	0.23	0.22	-0.05	0.14
VII	20	-0.00	0.07	0.29*	-0.13	-0.08	0.09	-0.01	0.00	0.00
	21	-0.10	0.21	0.26	-0.03	-0.22	0.17	0.18	-0.14	0.14
	22	-0.02	0.27*	0.25	0.00	-0.03	-0.08	0.13	0.01	-0.06
VIII	24	-0.21	-0.22	-0.27	0.07	-0.11	0.20	0.26	-0.23	0.32*
	25	-0.68**	-0.59**	-0.10	0.30**	-0.13	0.29**	0.40**	-0.38**	0.48**
VIII	26	-0.63**	-0.44**	0.00	0.15	-0.19	0.30**	0.56**	-0.54**	0.55**
	27	-0.25	-0.11	-0.08	0.06	-0.21	0.30*	0.36*	-0.14	0.16
	28	-0.44**	-0.05	0.07	0.16	-0.38*	0.37*	0.66**	-0.45**	0.47**
	29	-0.60**	-0.44*	-0.12	0.41*	-0.33	0.45*	0.54**	-0.32	0.48*

NOTE: *, 5% significance level; **, 1% significance level.

ment was substantial, up to 32% for height and 34% for survival (Table 5).

Regression analyses and contour plotting

Results from the regression analyses are given in Table 6 where height and survival of the clusters are grouped together for the two independent variables, latitude and length of growing season. For latitude, values of r^2 exceeding 0.50 were found only in Maine, the Great Lakes States, and the Prairie Provinces. The contour plots depicted mostly saddle-point solutions, with higher values of height and survival to the right and left sides of the grid. There was a maximum solution for survival in the Maritime Provinces and for both traits in the Great Lakes States and the Prairie Provinces. However, when the plots were superimposed, meaningful overlap was found only in Newfoundland and a partial overlap in Maine and northern Ontario. In the Great Lakes States there were no significant differences among provenances for height and survival (Table 5), and although there was overlap, the contour plots showed relatively little variation with latitude of origin. Two examples of contour plots are shown (Fig. 2): height and survival for the Prairie Provinces in relation to latitude, illustrating a maximum solution, and height and survival in Maine in relation to length of growing season, depicting a saddle-point solution. In both cases there was only a small zone of overlap of the highest values when the response surfaces were superimposed, implying that selecting simulta-

neously for good height and survival at this stage would be difficult.

Discussion

In this study several individual quantitative methods have been used to analyze variation, but the integration of all methods is needed to interpret the pattern and relate it to climate and other factors of the environment of the test locations. This interpretation is not easy since there are no simple ecological gradients across the range, but it is possible to discover certain trends that will have a bearing on provenance movement and selection.

In Newfoundland (cluster I), height growth was slow but survival was higher than in any other cluster (Table 2). The climate is boreal, but with moderate winters, cool summers, and mean fall frost dates later than in parts of the adjacent temperate Acadian Forest Region (Chapman and Brown 1966; Rowe 1972). The long autumn has helped to avoid frost damage and to increase survival.

Differences among provenances in height were significant, but survival remained undifferentiated (Table 5), which explains the absence of significant height-survival correlations (Table 2). In the regressions, the r^2 values were low and all solutions depicted saddle points (Table 6). There was some overlap of the contour plots and this means that a large number of provenances that grow well in Newfoundland will also survive well, and therefore survival is really not limiting at this stage. Khalil (1984) has proposed that fast-growing

TABLE 4. Correlation between provenance mean survival and geographic and climatic variables, by clusters and locations

Cluster	Location	Correlation coefficient (<i>r</i>) for variable								
		Lat.	Long.	Elev.	Summer precipitation	Last spring frost	Frost-free period	Degree-days	Start of growing season	Length of growing season
I	1	0.03	-0.14	0.03	0.28*	0.11	-0.12	-0.11	0.08	-0.12
	2	-0.04	-0.14	0.08	0.18	0.30*	-0.26*	-0.23	0.09	-0.12
II	3	-0.47**	-0.52**	-0.17	0.32**	-0.15	0.30**	0.22*	-0.11	0.28**
	4	-0.06	0.11	0.15	-0.11	-0.02	-0.00	0.03	-0.01	0.02
	5	-0.07	-0.17	0.02	0.17	0.02	-0.02	-0.02	0.04	-0.05
	6	0.12	0.12	0.11	0.01	0.09	-0.08	-0.05	0.16	-0.14
	7	0.10	-0.08	-0.15	-0.01	0.09	-0.05	-0.11	0.16	-0.07
	8	-0.40**	-0.49**	-0.12	0.42**	0.08	0.08	0.05	0.08	0.09
	9	0.20	0.06	0.06	0.02	0.15	-0.24*	-0.16	0.17	-0.25*
	10	0.25*	0.22	0.08	-0.06	0.12	-0.17	-0.17	0.07	-0.19
	11	0.05	-0.16	-0.07	-0.07	0.20	-0.05	-0.14	0.21	-0.14
	12	0.01	0.20	0.30*	-0.06	-0.04	0.05	0.03	-0.02	0.07
III	16	-0.43**	-0.36**	-0.08	0.41**	-0.12	0.17	0.10	-0.02	0.09
	17	-0.72**	-0.61**	-0.16	0.63**	-0.31**	0.44**	0.33**	-0.15	0.34**
IV	18	0.01	-0.36**	-0.22	0.41*	0.26	-0.11	-0.43**	0.55**	-0.38**
	14	0.05	-0.17	0.03	0.09	0.25*	-0.24*	-0.27*	0.25*	-0.25*
V	15	0.10	-0.15	0.17	0.10	0.27**	-0.27**	-0.35**	0.26*	-0.30**
	13	0.15	-0.01	0.04	-0.02	0.28**	-0.21	-0.32**	0.27*	-0.25*
VI	23	-0.15	-0.38**	-0.15	0.35*	-0.01	0.00	-0.11	0.06	0.01
	19	0.10	-0.21	-0.03	0.06	0.34**	-0.25*	-0.37**	0.38**	-0.30*
VII	20	0.32*	-0.19	-0.08	0.22	0.32*	-0.40**	-0.47**	0.43**	-0.45**
	21	0.01	0.14	0.12	0.16	-0.04	0.08	0.04	-0.06	0.06
	22	0.25*	-0.29*	0.09	0.06	0.24*	-0.28*	-0.34**	0.39**	-0.39**
	24	0.19	-0.02	0.13	-0.37*	-0.02	0.08	-0.01	0.18	-0.04
VIII	25	-0.36**	-0.34**	0.26*	0.00	0.27**	-0.19	-0.11	0.06	-0.04
	26	-0.39**	-0.32**	0.11	0.03	0.14	-0.06	0.14	-0.10	0.07
	27	0.23	0.13	-0.02	-0.28	0.17	-0.15	-0.14	0.17	-0.28*
	28	0.38**	0.32*	0.16	-0.35	0.40**	-0.37*	-0.34*	0.06	-0.17
	29	0.00	0.19	0.18	-0.07	0.25	-0.28	-0.21	-0.03	-0.04

NOTE: *, 5% significance level; **, 1% significance level.

provenances could come from New Brunswick, Quebec, and Ontario. Because of the Island's unique climate, this may be one of the few boreal areas where such long-distance movements are possible.

In the Maritime Provinces (cluster II), the variation in height growth is clearly related to the diversity of soils at the various locations, but the survival was uniformly high. The summer climate is warmer than in Newfoundland, there is adequate precipitation during the growing season, and temperature extremes are rare (van Groenewoud 1983). Good growth can be expected on better than average sites.

There were positive height-survival correlations at four locations and frequent correlations of both traits with latitude, growing season, and other climatic parameters (Tables 2, 3, 4). Differences among provenances were significant for height but not for survival (Table 5). The regressions had low values of r^2 ; perhaps the provenance differences were not well expressed or the great diversity of results was difficult to fit to the model (Table 6). Since the climate is temperate, survival may not be limiting and southern provenances could be introduced, but Park and Fowler (1988) concluded that little would be gained by such measures.

In Maine (cluster III), climatic conditions are similar to those in the Maritime Provinces (Daniel *et al.* 1979). Although the locations are generally farther south than those in New Brunswick, two of them (16 and 17) are at fairly

high elevations that create cool temperate climates. In locations 17 and 18, survival was only 64 and 75%, owing in part to a lack of snow cover and frost heaving in the first winter after planting (Dr. K. Carter, personal communication). It is possible that location 18 in southern Maine is too dry and too far south for optimum growth of black spruce, since southern outliers of black spruce are usually found in swamps. Location 18 had best height in Maine, but the value was substantially lower than at the better locations in New Brunswick.

There were significant height-survival correlations, which were positive at the two northern locations but negative at the southern location (Table 2). Many other correlations existed with climatic parameters (Tables 3, 4) and provenance heights differed significantly, but not survival (Table 5). The regressions have high values of r^2 , but all response surfaces had saddle-point solutions and there was only partial overlap (Table 6). This is due to the fact that location 16 (Telos), at the northern end of this north-south transect, at the highest elevation and with the shortest growing season, still had the highest survival but only intermediate height (Fig. 2). Owing to these unusual circumstances, good height and survival are difficult to combine.

In eastern Quebec (cluster IV), height growth was poor and survival moderate (Table 2), reflecting the short growing season in boreal regions (Chapman and Brown 1966) and an average or below-average soil quality (Table 1). Con-

TABLE 5. Results from analysis of variance of height and percent survival, giving mean square (MS) with significance and percentages of the variance components (% VC)

Cluster	Source	df	Height		Survival	
			MS	% VC	MS	% VC
I	Location	1	4 405**	23	0.3027**	35
	Provenance	58	335**	32	0.0100	6
	Error	58	139	45	0.0083	59
II	Location	9	292 634**	94	0.2889**	34
	Provenance	38	1 893**	2	0.0141	0
	Error	342	346	4	0.0137	66
III	Location	2	18 735**	51	0.1411**	26
	Provenance	26	982*	12	0.0144	3
	Error	52	494	37	0.0130	71
IV	Location	1	64 448**	52	1.7675**	60
	Provenance	84	1 001**	22	0.0187**	13
	Error	84	373	26	0.0094	27
V	Location	1	19 980**	33	0.2022**	13
	Provenance	30	1 784**	28	0.0383	4
	Error	30	742	39	0.0351	83
VI	Location	3	17 414**	52	0.2535**	18
	Provenance	44	612**	12	0.0351**	13
	Error	132	272	36	0.0201	69
VII	Location	2	445 618**	88	4.2011**	71
	Provenance	45	1 174	0	0.0406	1
	Error	90	1 252	12	0.0355	28
VIII	Location	2	17 804**	75	0.0851**	19
	Provenance	12	581	4	0.0429**	34
	Error	24	368	21	0.0134	47

NOTE: *, 5% significance level; **, 1% significance level.

ditions here are less favourable than in any other cluster previously discussed.

There were no significant height-survival correlations in eastern Quebec, but a number of correlations existed with latitude and climatic parameters (Table 2-4). Significant differences among provenances were found for both height and survival (Table 5). The saddle-point solutions of the response surfaces showed no overlap (Table 6). This is apparently an area where good height and survival cannot be combined, except when growing local provenances.

The Ottawa River area (cluster V) is again farther south, and growth and survival are fair (Table 2). This is part of the Great Lakes - St. Lawrence Forest Region (Rowe 1972) where the climate is temperate. A higher soil quality would have resulted in increased growth.

There were no significant height-survival correlations in the Ottawa River area, but some correlations of these two traits with latitude and growing season (Tables 2-4). Provenance differences were significant for height but not survival (Table 5). Although all regressions had response surfaces with saddle-point solutions and relatively low r^2 values (Table 6), there was some overlap for both latitude and growing season as independent variables. Although the correlations gave no indication of this, the regressions reflected the possibility of combining selection for the two traits. Here again, the best solution might be to grow local provenances or provenances from the same region and rarely provenances from farther south since southern populations tend to be small, isolated, and inbred (Morgenstern 1972).

The four locations in northern Ontario (cluster VI) are situated in cold, boreal regions (Chapman and Brown 1966; Rowe 1972), and growth is substantially lower than in the temperate regions to the south (Table 2). Survival was lower than in any other cluster (57%). Experience with the establishment of plantations in that area suggests that high survival is not easily achieved here. In this continental climate, temperatures are high at the time of planting in May before substantial root growth occurs. In addition, short summers may lead to frost damage in late summer or early autumn, hence less growth and possibly lower survival.

A significant and positive correlation between height and survival was found only at one location, Geraldton, which is also one of the more productive sites with good growth (Table 2). Survival was more often correlated with geographic and climatic parameters than height, and significant provenance differences existed for both traits (Tables 3-5). In the regressions, r^2 values were intermediate in size (0.13-0.45), and there were saddle-point solutions and partial overlap of the contour plots when latitude was the independent variable (Table 6). The safest procedure in northern Ontario would be to grow native provenances from the same region, but short-distance movements from one boreal region to the next may be possible.

In the Great Lakes States (cluster VII) we find the greatest height but relatively low survival (Table 2). Climates are similar to the Great Lakes - St. Lawrence Forest Region in adjacent Canada in the two northern locations (Rhinelander, Wis., and Blackberry, Minn.), but in the southern location

TABLE 6. Summary of regression analyses of height and survival based on latitude and length of growing season as independent variables, and characteristics of the response surfaces

Cluster	Trait	Latitude			Growing Season		
		Total r^2	Solution	Contour plot ^a	Total r^2	Solution	Contour plot ^a
I	Height	0.18	Saddle point	Overlap	0.22	Saddle point	Overlap
	Survival	0.36	Saddle point		0.24	Saddle point	
II	Height	0.13	Saddle point	No overlap	0.13	Saddle point	Partial overlap
	Survival	0.11	Maximum		0.03	Maximum	
III	Height	0.87	Saddle point	Partial overlap	0.78	Saddle point	No overlap
	Survival	0.52	Saddle point		0.25	Saddle point	
IV	Height	0.43	Saddle point	No overlap	0.40	Saddle point	No overlap
	Survival	0.48	Saddle point		0.49	Saddle point	
V	Height	0.26	Saddle point	Overlap	0.16	Saddle point	Overlap
	Survival	0.22	Saddle point		0.20	Saddle point	
VI	Height	0.45	Saddle point	Partial overlap	0.43	Saddle point	No overlap
	Survival	0.18	Saddle point		0.13	Saddle point	
VII	Height	0.83	Maximum	Good overlap	0.41	Saddle point	Overlap
	Survival	0.67	Maximum		0.12	Saddle point	
VIII	Height	0.67	Maximum	No overlap	0.64	Maximum	Partial overlap
	Survival	0.18	Maximum		0.12	Saddle point	

^aRefers to the overlap of highest values plotted for height and survival in the contour plots.

(Rosemount, Minn.) they are somewhat warmer and drier (Daniel *et al.* 1979). The long growing season favors height growth, and the large differences in survival among locations may reflect local establishment and maintenance conditions as much as adaptation.

There are significant and positive height-survival correlations at the two Minnesota locations (Table 2). Height is often correlated with geographic and climatic parameters but survival much less frequently (Tables 3, 4), perhaps because climate is not a constraint here. Provenance differences are not significant in the analysis of variance (Table 5). The regressions have high r^2 values, and there is overlap of the contour plots but little curvature in the surfaces reflecting minimal variation. Since this area is relatively far south (44–47°N), provenances from the same region will probably grow best here.

Finally, in the Prairie Provinces (cluster VIII), height growth was again substantially lower than in other regions to the south but survival higher. The three experiments are in the same boreal region (Table 1) with a subhumid climate (Chapman and Brown 1966).

A positive and significant height-survival correlation was found in the southernmost location at Mafeking, Manitoba (Table 2). Although there are more frequent correlations of height with climatic parameters than of survival (Tables 3, 4), in the analysis of variance provenance differences were significant only for survival (Table 5). In the regressions, r^2 values were high and all but one have maximum solutions, but there was only a small zone of overlap (Fig. 2).

This illustrates again the difficulty of moving the fastest growing southern provenances into this boreal climate, but it may be possible to grow provenances that are one region to the south here, in addition to local provenances.

Several general principles of provenance variation seem to apply. Movement north increases height growth, evidenced by the fact that all height-latitude correlations are negative (19 significant; Table 3). Survival responds differently. In temperate regions it is similar to height, but in boreal regions correlations are positive (19 values, 3 significant; Table 4), suggesting movement south to be beneficial. Both of these phenomena are well known from the Scandinavian literature (Dietrichson 1964; Eriksson *et al.* 1980).

General reasons why these relationships are not always consistent in young field experiments have been discussed in the literature review. One additional complicating factor in this series of experiments is that the geographic and climatic relationships are not simple. Whereas photoperiod is directly related to latitude, temperature is not. Isotherms near the Atlantic Ocean do not follow simple east-west trends but are modified by major air currents, elevation, and the irregular configuration of the Atlantic Coast (Chapman and Brown 1966). In Quebec and Ontario, north-south temperature gradients reflected by isotherms are more regular, but there is a change when going west. The isotherms begin to run southeast-northwest in central Ontario, and the temperate-boreal region boundary follows this trend. In southern Quebec and eastern Ontario, the

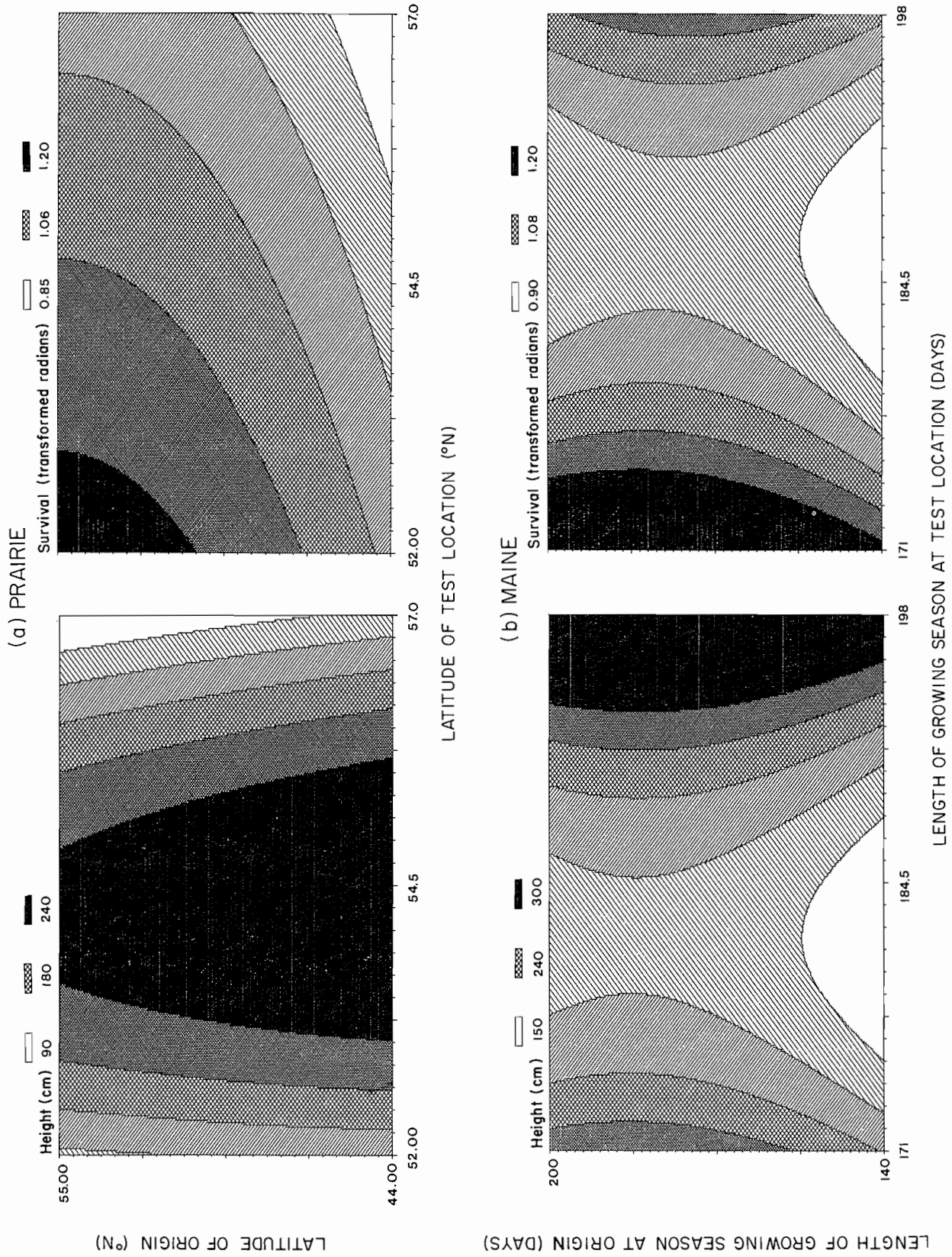


FIG. 2. Contour plot pairs for height (left) and survival (right) response to (a) latitude of provenance origin and test location for the Prairie Provinces and (b) growing season of origin and test location for Maine.

boundary is roughly at 47°N, in northwestern Ontario at 50°N, and in the Prairie Provinces between 51 and 54°N (Rowe 1972). A consequence of this is that test locations at higher latitudes are not necessarily colder. For example, the four test locations in northern Ontario constitute a southeast–northwest transect from 47°57' N (Chapleau) to 49°55' N (Dryden), but the latter location is warmer and closer to the temperate–boreal boundary than the former, and the mean height at Dryden is also substantially greater than at Chapleau (Table 2). A second conclusion to be drawn from this northward shift of boreal climates is that opportunities for northward movement of provenances are greatest in the northernmost areas of the Great Lakes States, in northwestern Ontario, and the Prairie Provinces. Provenances moved from the northern part of the Great Lakes – St. Lawrence Region (46°N) in eastern Canada, which are growing in a climate with a frost-free period of 100 days, may be adapted to a broad zone ranging from the Dryden – Red Lake area in northwestern Ontario (50°N) to central Saskatchewan (53°N) where the frost-free period is the same. However, the experiments considered here must be observed for at least 20 more years to verify this point. Their continued protection and maintenance is therefore important.

One important aspect of provenance selection not discussed here is climatic change. If predictions about the greenhouse effect become true, large areas of forests in North America will become drier and warmer and there will be a shift of southern species in a northeasterly direction (Harrington 1987; Roberts 1989). The effect on black spruce will be that the conclusions in this report have been too conservative and that greater northward movements are possible. Long-term experiments like those discussed here will have an important function in the measurement of the greenhouse effect.

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