

Glen B. Dunsworth¹

and

Bruce P. Dancik

Department of Forest Science
University of Alberta
Edmonton, Canada T6G 2G6

Seedling Variation among Alberta Populations of White Spruce (*Picea glauca* (Moench) Voss) in Controlled Environments²

Abstract

Seedlings of 27 sources of white spruce (*Picea glauca* (Moench) Voss) were used to investigate the nature and amount of genetic variability of white spruce in Alberta. Seedlings were grown in containers for two growing seasons, in a factorial design, under two controlled environment regimes simulating northern and southern Alberta forest conditions. Of 12 characters measured, only total and top relative dry matter and number of branches were found to have significant among-source variation. Northern Alberta sources had significantly higher total and top relative dry matter than all other sources tested in both environments. Sources from central and north-central Alberta had significantly more branches than all other sources tested.

Relative dry matter increased continuously with latitude and elevation of the source. Number of branches exhibited a grouped pattern of variation. It is possible that the patterns of variability illustrated in this study could have developed from the retreat and reestablishment of white spruce in central and north-central Alberta during the late post-glacial period.

Introduction

White spruce (*Picea glauca* (Moench) Voss), one of the most widely distributed conifers in North America, grows naturally on a variety of sites throughout the boreal forest of Canada and the northern United States (Nienstaedt 1957, Nienstaedt and Teich 1972, Nienstaedt 1968). Rangewide studies have suggested clinal patterns of genetic variation in several characters (Miksche 1968, Wilkinson *et al.* 1971, Khalil 1974). While there have been studies of genetic variation and differentiation in British Columbia (Roche 1969) and Ontario (Teich and Holst 1974, Teich *et al.* 1975), there have been no similar studies in Alberta.

The objectives of this study were to determine (1) the amount of variability of selected seedling characters among populations of *P. glauca* in Alberta, and (2) any patterns of variability with respect to environmental parameters.

Methods and Materials

Controlled environment chambers were employed to simulate natural environments. Twenty-seven sources of white spruce seed, selected from the Alberta Forest Service seed bank to provide altitudinal and latitudinal gradients (Fig. 1a), were planted in

¹Present address: Woodlands Division, MacMillan Bloedel Limited, 65 Front Street, Nanaimo, B.C. V9R 5H9.

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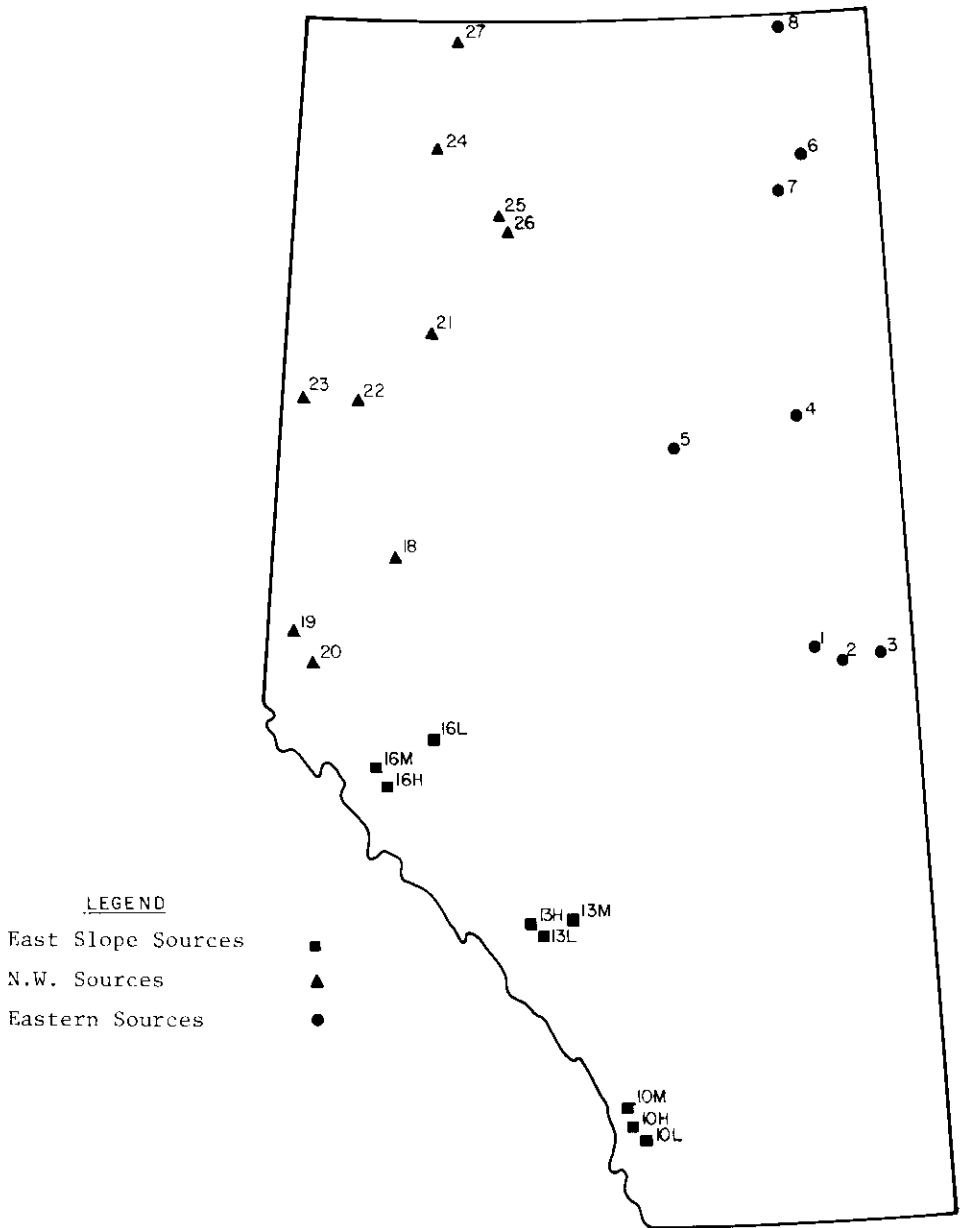


Figure 1. Source maps displaying the 27 white spruce populations used in this study (1a) and Duncan's Multiple Range Test results for total relative dry matter in the (1b) top relative dry matter (1c) and number of branches (1d) in the southern environment (dark squares are significant ($P \leq 0.05$) different from dark circles).

a factorial design in each of two growth chambers and grown for two simulated growing seasons. The factorial design of this experiment consisted of two environments with three replicates per environment, and six seedlings per population in each replicate. Analyses were carried out using replicate means for a given character. Missing values were accounted for in the analysis of variance using a weighted average approach.

The twenty-seven sources were grown in Spencer Lemaire (Ferdinand) containers throughout the study period. The initial soil medium was pure peat. Regular watering, approximately twice a week, began four weeks after seeding. The seedlings were fertilized biweekly with nutrient solution (approximately 1 litre per tray of 112 p.p.m. N, 69 p.p.m. P, 156 p.p.m. K). Six weeks before the end of each growing season, regular waterings were reduced to once a week or whatever was just sufficient to keep the seedlings from wilting. At this time, a hardening-off solution of 32.87 g of 10-52-10 (N-P-K) in 40 litres of water was used biweekly in place of the regular nutrient solution until the end of the growing season.

The two growing seasons used as test treatments simulated the photoperiod, day-night temperature, and relative humidity of northern and southern Alberta growing seasons. Simulations were based on data from Ft. Smith, N.W.T., and Pincher Creek, Alberta, meteorological stations (List 1966, Anonymous 1968, Anonymous 1971). Conditions were altered every two weeks to simulate the progression of growing seasons (Dunsworth 1977).

During both growing seasons, individual height measurements were carried out biweekly. Between growing seasons the seedlings in each environment were subjected to 10 weeks of 4°C day-night temperatures (with some supplementary lighting) as a treatment to break dormancy (Nienstaedt 1966, 1967). At the end of the second growing season, final height, diameter at first internode, and number of branches were taken. The seedlings then were destructively sampled to determine total fresh weight, total dry weight, top fresh weight, top dry weight, fresh weight root-to-shoot ratio, dry weight root-to-shoot ratio, top dry weight to top fresh weight ratio (top relative dry matter), and total dry weight to total fresh weight ratio (total relative dry matter). The latter two measures are estimators of succulence or the degree to which the plant has withdrawn water from its tissues during the hardening process. Langlet (1959, 1967) has indicated that dry matter percentage (relative dry matter) is well correlated with length of growing season and latitude of the provenance for Scots pine in Sweden. Relative dry matter indicates the plants' adaptation to temperature and day length of the native habitat of the provenance.

The analyses of the data were carried out in two sections:

1. First season results:
 - a) analysis of variance (ANOVA) of final first season heights;
 - b) correlation analyses of first season heights on environmental parameters (latitude, longitude, elevation, and latitudes adjusted for elevation (Wiersma 1964)).
2. Final results:
 - a) ANOVA of second season height growth and all final measurements;
 - b) correlation analysis of measurements showing statistical significance ($P \leq .05$) among sources within treatments using environmental parameters as independent variables;
 - c) Duncan's Multiple Range Test of measurements showing ANOVA statistical significance ($P \leq .05$) among sources within treatments;
 - d) principal components analysis using all final measurements.

First Season Results

Analysis of variance of seedling heights at the end of the first growing season indicated a significant ($P \leq 0.001$) difference between treatments (simulated northern and southern environments). However, no significant differences could be detected among sources within treatments. There were no significant correlations of first season final heights on latitude, longitude, elevation, and converted latitudes in either growth regime.

Analysis of growth at biweekly intervals (expressed as a percentage of first season final height) using analysis of variance indicated that significant ($P \leq 0.001$) differences existed among biweekly growth periods in both environments. However, no significant differences were evident among sources within either environment.

Second Season Results

Analysis of variance of all final measurements indicated that there were significant ($P \leq 0.05$) differences among sources with respect to three measures: total relative dry matter or the ratio of total dry weight to total fresh weight, top relative dry matter or the ratio of top dry weight to top fresh weight, and number of branches per individual (Dunsworth 1977). Correlation analysis of the above characters with respect to environmental parameters indicated that these were also the only variables with any significant ($P \leq 0.10$) correlations (Table 1; Dunsworth 1977).

TABLE 1. Summary table of correlations of total and top relative dry matter and number of branches versus latitude, elevation, and converted latitude of the source (27 sources of white spruce grown in simulated northern and southern Alberta environments).

		Latitude	Elevation	Converted Latitude
Top Relative Dry Matter	SE	0.54***	-0.65***	-0.49***
	NE	0.09	-0.41	-0.67***
Top Relative Dry Matter	SE	0.64***	-0.62***	-0.25
	NE	0.35*	-0.47**	-0.34*
Number of Branches	SE	0.04	0.12	-0.50***
	NE	-0.04	-0.10	-0.19

SE—Southern Environment
NE—Northern Environment

* $P < 0.10$

** $P < 0.01$

*** $P < 0.001$

Analysis of all final measurements indicated that three principal components accounted for a significant (eigenvalues ≤ 1.0 ; Isenbrands and Crow 1975) proportion of the variation among sources within either environment. In the northern and southern environments, ordering of principal components was the same. The first principal component was essentially an overall size component, the second a root-to-shoot ratio component, and the third a relative dry matter (hardiness) component. Within the northern and southern environments, the first two principal components accounted for 84.5 and 86.4 percent, respectively, of the inter-source variation.

The 27 white spruce sources tested have coefficients of variation (C.V.) for total and top relative dry matter ranging from 5.8-8.0 percent (Dunsworth 1977). The greatest amount of variability existed in total relative dry matter. The poor performing high elevation sources (10H, 13H, 16M, 16H) tended to have larger than average coefficients of variation (ranging from 4-18 percent).

With respect to number of branches, the 27 white spruce sources had coefficients of variation of 20.4 and 23.8 percent, respectively, in the northern and southern environment. Thus, numbers of branches appear to have greater standard deviations relative to their means than do total and top relative dry matter. Although these different variables were measured in different ways, it appears that greater variability exists among the white spruce sources for number of branches than for total or top relative dry matter.

The correlative trends between environmental parameters and total and top relative dry matter differed only slightly between environments. Both tended to decrease with increasing elevation and increase with increasing latitude of the source (Figs. 2, 3, 4, 5). These consistent relationships were not evident with number of branches (Table 1).

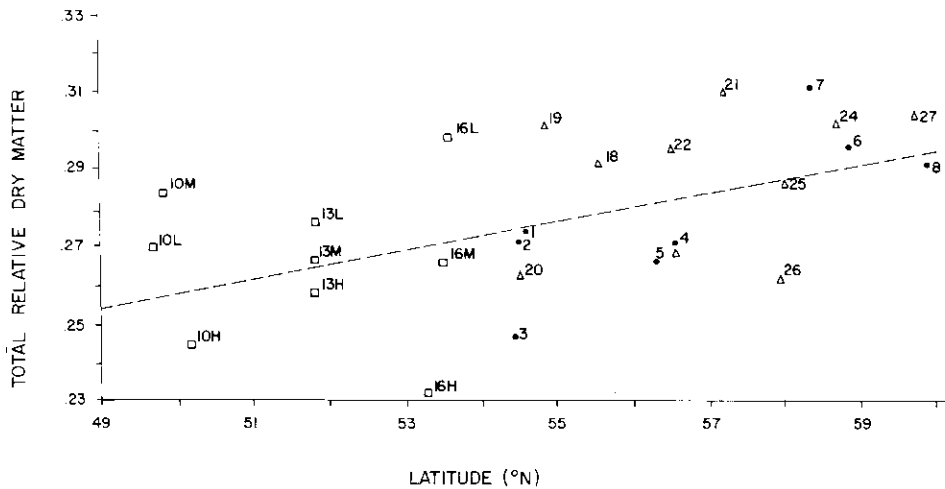


Figure 2. Relationship of total relative dry matter and latitude of 27 white spruce sources grown in a simulated southern Alberta environment ($r = 0.537$, $y = 0.074 + 0.0037 x$).

Analysis by Duncan's Multiple Range Test of total and top relative dry matter, as well as number of branches, showed some significant ($P \leq 0.05$) groupings of sources in both environments (Figures 1b, 1c, 1d).

Total and Top Relative Dry Matter

In general, relative dry matter measure (hardiness) tended to increase in both environments as latitude of the source increased. The relationships in the southern-type environment were more significant than the same relationships in the northern-type environment.

Relative dry matter of all sources tended to decrease with increasing elevation. The plants in the southern environment tended to have more significant relationships with elevation than those in the northern environment. This elevational relationship appears to contradict the latitudinal relationship previously discussed. One would logically assume that higher elevation sites would be climatically similar to higher latitude sites. Thus, the trends with respect to latitude and elevation would be expected to parallel each other. One possible explanation for the apparent anomaly reported herein is that the photoperiodic change caused by displacement in latitude may be more influential than displacements in elevation when considering relative dry matter (hardiness). This

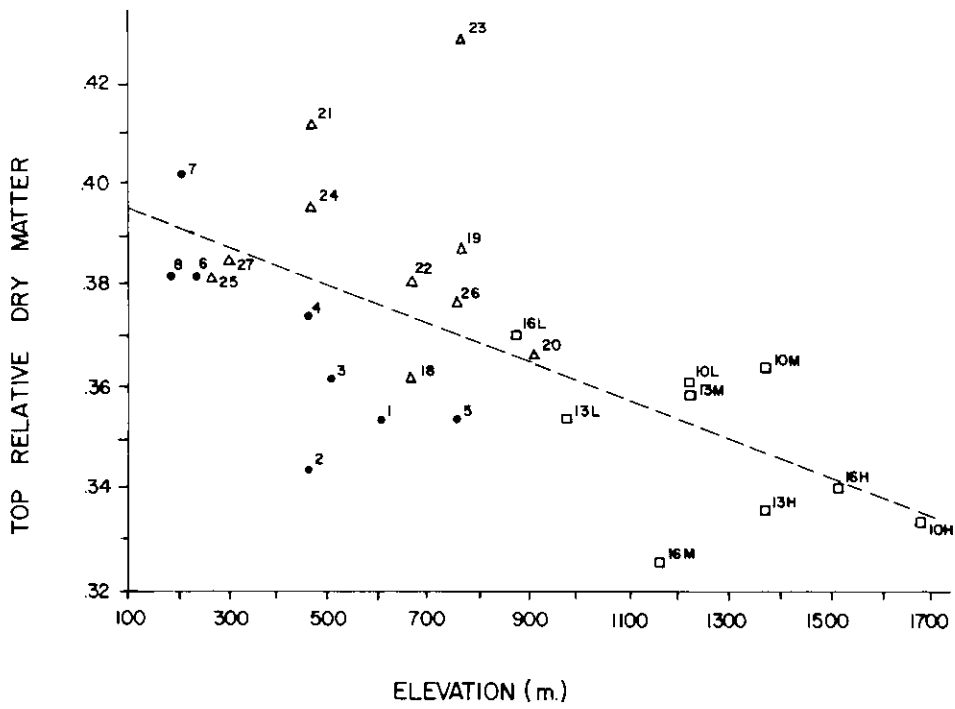


Figure 3. Relationship of top relative dry matter and latitude of 27 white spruce sources grown in a simulated southern Alberta environment ($r = 0.644$, $y = 0.085 + 0.0052 x$).

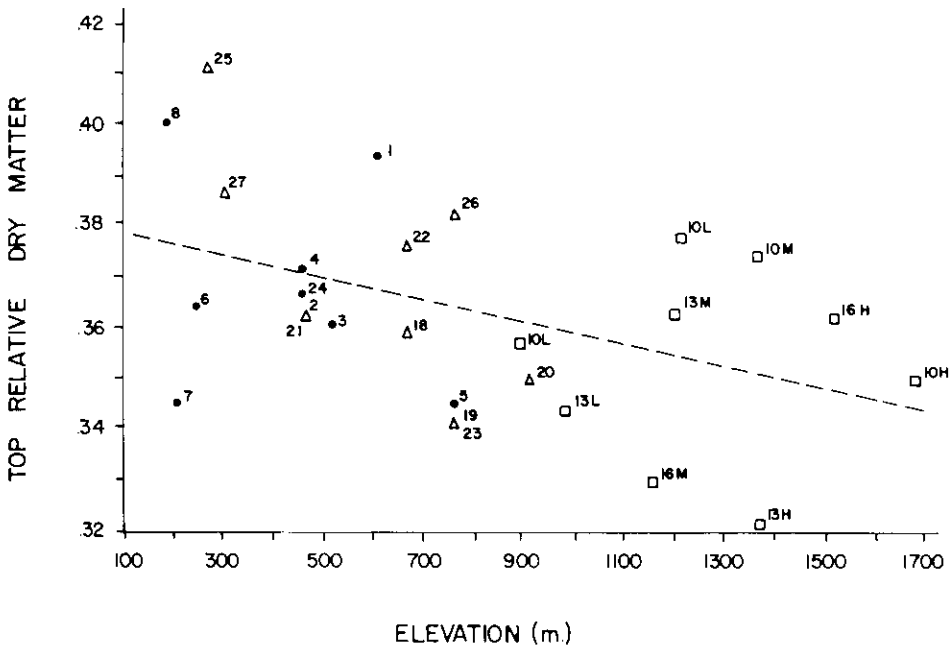


Figure 4. Relationship of top relative dry matter and elevation of 27 white spruce sources grown in a simulated northern Alberta environment ($r = 0.496$, $y = 0.38 - 0.00002 x$).

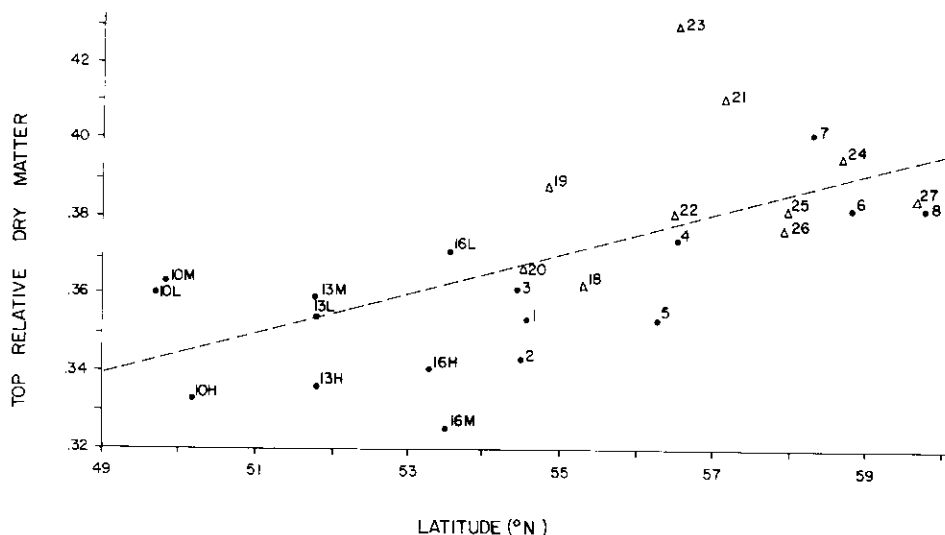


Figure 5. Relationship of top relative dry matter and elevation of 27 white spruce sources grown in a simulated southern Alberta environment ($r = -0.618$, $y = 0.396 + 0.000035 x$).

conjecture, together with the fact that there is a very strong inverse relationship between latitude and elevation of the sources used in this study ($r = -0.871$, $P \leq 0.001$), would lead one to believe that the elevation trends probably confirm the strong influence of latitude of the source on relative dry matter. (Also see Figs. 1b, 1c).

In all but one case (total relative dry matter in the northern environment), northern sources have significantly higher total and top relative dry matter than do southern sources. In the exceptional case, total relative dry matter in the northern environment, a number of northeastern sources and two extreme southern sources have significantly higher relative dry matter than any of the other sources.

In general, considering only total relative dry matter rankings, those sources with high rankings in the simulated northern environment tended to have much lower rankings when grown in the simulated southern environment. Only three sources (numbers 8, 21, and 22) of the top 10 in the simulated northern environment remained in the top 10 in the southern environment. Of these, only one (source 8) remained in the group with the significantly highest total relative dry matter values. With respect to top relative dry matter, those sources which performed best in the northern environment tended to perform poorly in the southern environment. However, this change in performance was not nearly as evident as it was in the total relative dry matter measures. Five of the top 10 sources (numbers 8, 22, 24, 25, and 27) from the northern environment remained in the top 10 in the southern environment. Of these, four sources (numbers 8, 24, 25, and 27) remained in the group with the significantly highest top relative dry matter.

The poorest performers with respect to both total and top relative dry matter in both environments were high elevation sources (numbers 10H, 13H, 16M, and 16H). These sources remained in the bottom 10 in all cases and tended to have greater than average variability.

Number of Branches

Among-population differences in number of branches tended not to be as significant as total or top relative dry matter, nor was the pattern of variability as well defined. Specifically, when considering all sources, number of branches showed a significant ($P \leq .05$) correlation only in the southern environment with respect to converted latitudes. Number of branches for the northwestern sources were significantly ($P \leq .05$) correlated with latitude of the source, but only in the southern environment. In both environments the number of branches on the eastern sources was significantly ($P \leq .05$) correlated with latitude of the source. These results indicate that a weak but noticeable trend exists for number of branches to decrease as latitude of the source increases, particularly under simulated southern Alberta conditions.

The pattern of variability with respect to number of branches and latitude can be further illustrated by the results of Duncan's Multiple Range Test. Source maps of significantly different groups of sources from either environment indicated that a group in the central and north-central region of the province tended to have significantly higher numbers of branches than sources to the north or south of this area (Fig. 1d).

In terms of rankings it generally appears that sources which perform well under northern environmental conditions (i.e., those with high numbers of branches) perform as well or better under southern environmental conditions. Six of the top 10 sources under northern environmental conditions (sources 1, 2, 3, 5, 16L, and 19) remained in the top 10 in the southern environment. However, only two sources (sources 1 and 15) remained in the group with a significantly greater ($P \leq .05$) number of branches. Both northern and southern sources (i.e., sources 8, 10M, 13L, and 21) were consistently poor performers in both environments.

Although there appears to be a weak tendency for number of branches to decrease as one moves from the central portion of the province northward, the more significant relationship appears to be the greater number of branches exhibited by sources in the central and north-central region of the province relative to all others tested. This group of "high branch number sources" appears to be similar to the zone found by Hellum (1971) for seed weight of a number of Alberta sources of white spruce. Hellum's "central zone" extended from 53° to 57° N latitude. In the present study the "central zone" extends from about 53° - 58° N latitude.

Conclusions

If one can assume, as Langlet (1967) has, that autumnal relative dry matter essentially reflects winter hardiness, it appears that the northern Alberta sources of white spruce tend to be more hardy than any of the other sources tested. The hardiness of northern sources may well be explained by the strong relationship between relative dry matter and latitude of the source. Changes in latitude correspond to changes in photoperiod. Lavee (1973) hypothesized that photoperiod is the most important environmental trigger involved in the initiation of dormancy. The initiation of dormancy and the subsequent increase in dry matter are two of a number of processes involved in a plant's preparation for winter. If photoperiod is a major trigger in these processes, northern sources (adapted to the longer days of the northern growing season) when grown in a southern environment should receive their trigger to harden off earlier than southern sources. Thus, by autumn, northern sources should have greater relative dry matter and more hardiness

than the southern sources. Conversely, southern sources in a northern environment will receive their short photoperiod trigger later than northern sources. Consequently, northern sources would again tend to be hardy earlier than southern sources.

The low and considerably variable relative dry matter of the high elevation, east-slope sources may be explained by a unique set of selective forces at work at these high elevations. These sites tend to have a greater seasonal variability in environmental conditions. Severe drought conditions during the growing season, stress due to exposure, poorly developed soils, and occurrence of warm temperatures for short periods during winter prevail on these higher elevation sites. It is feasible that these factors, as selective forces, have had a greater influence on the survival of white spruce at higher elevations than has winter hardiness. The reduction in selective importance of winter hardiness may have led to lower and more variable autumn dry matter than for spruce from lower elevations.

The pattern of variation in number of branches is not similar to that of total or top relative dry matter and does not show similar, significant relationships with any environmental parameters. However, the preponderance of sources with more branches in the central and north-central region of the province appears similar to the pattern of variation in seed weight which Hellum (1971) illustrated. Possibly, the selective forces which have acted to shape the pattern of variation for seed weight may be similar to those which shaped the pattern of variation for number of branches.

Grassland likely expanded into the area formerly occupied by forests of central Alberta during Hypsithermal Interval, approximately 5000 to 8000 years ago, when the climate became warmer and drier (Hansen 1949, 1952; Moss 1952, 1955). During this period, boreal species may have been eliminated from central Alberta and only persisted in the cooler and moister east-slope and northern regions of the province (Raup 1934, 1935; Moss 1952; Deevey and Flint 1967; Lichti-Federovich 1970; Ritchie 1976). Separation of these two boreal zones may have continued for 2000-3000 years. Such isolation may have permitted genetic differentiation, yielding two genetically distinct groups of white spruce near the end of the Hypsithermal. As the climate became cooler and moister, the boreal species became reestablished on the extended grassland region, which may have been a zone of genetic mixing between the two previously isolated groups of white spruce.

Selective forces acting on white spruce during the period of reestablishment would tend to favor different characteristics than those favored under the more normal late-successional situation. Lighter spruce seed would probably have a competitive advantage in this reestablishment, since they would expectedly disperse farther, and could become established more quickly at greater distances than would heavy seed. Relatively open sites, which would likely have been prevalent in the region of reestablishment during the post-Hypsithermal period, would likely have favored individuals with more branches and fuller crowns, since they would probably be more photosynthetically efficient.

Total and top relative dry matter, on the other hand, exhibit continuous variation with no noticeable discontinuities in the northcentral region. It may be possible that during the separation of the boreal zones, selection for plants able to become frost hardy (i.e., high relative dry matter) early in the growing season continued in the two groups. It is also feasible that during and since the post-Hypsithermal period this same

selective force has persisted. If this hypothesis is correct, then the outcome would likely have been a continuous pattern of variation in autumn dry matter relative to latitude. Thus, it may have been possible for a variety of selective forces, acting on a number of characters, to shape the differing patterns of variation illustrated in this study.

Acknowledgments

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