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Isozyme Differentiation of Upland and Lowland Picea mariana Stands in Northern Ontario

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Summary

Patterns of allozyme variation among naturally established upland and lowland black spruce *(Picea mariana* (Mill.) B.S.P.) stands were studied from five locations across northern Ontario. Variation in thirteen polymorphic enzyme loci (AAT2, ACO, ALD, GDH, 6PGD1, 6PGD2, LAP1, LAP2, MDH1, MDH2, MDH3, PGI and PGM) was assessed using electrophoretic analysis of gametophytic tissue. The average percentage of polymorphic loci was higher for the five lowland stands (57.3%) compared to the five upland stands (47.5%). In addition, the average heterozygosities of the lowland stands were slightly, but consistently higher (h = 0.23) than those of the upland stands (h = 0.21). Wright's F_{ST} values calculated over all loci indicated that upland stands were further differentiated from each other (F_{ST} = 0.069) than were lowland stands (F_{ST} = 0.048). Similarly, Nei's genetic distances were larger between upland stands than among lowland ones; the average distance between all upland/upland pairings was 0.027 as opposed to 0.016 for all lowland/lowland pairings. These results indicate that the five upland stands were more differentiated than the five lowland stands. Discriminant analysis of genotypic frequencies showed that 70 percent of the black spruce trees were correctly classified into upland and lowland categories. Genetic differences between upland and lowland sites may be related to differential survival of seedlings resulting from selective edaphic effects. The distribution of variation appears to reflect more stringent location-specific selection pressures on upland sites, in contrast to the generally more favorable survival conditions for seedlings on the five lowland sites. The greater heterozygosity in the lowland stands may reflect a need for more vigorous growth in response to greater nutrient stresses on trees after seedling establishment.

Key words: edaphic ecotypes, *Picea mariana*, isoenzyme variation.

Zusammenfassung

In natürlichen Hoch- und Tieflandbeständen von *Picea mariana* (Mill.) B. S. P. and 5 Standorten in Nordontario wurden die Variationsmuster der Allozyme untersucht. Die Variation von 13 Isoenzym-Loci (AAT2, ACO, ALD, GDH, 6PGD1, 6PGD2, LAP1, LAP2, MDH1, MDH2, MDH3, PGI und PGM) wurde mittels Gel-Elektrophorese an Endosperm-Gewebe untersucht. Der durchschnittliche Prozentsatz polymorpher Loci war für die 5 Tieflagenbestände höher (57,3 %) als für die Hochlagenbestände (47,5). Außerdem waren die durchschnittlichen Heterozygotiegrade der Tieflagenstandorte zwar geringfügig, aber beständig, höher (h = 0,23), als die der Hochlagenstandorte (h = 0,21). Wright's F_{ST}-Werte über alle Loci zusammen berechnet, zeigten, daß Hochlandbestände sich mehr voneinander unterschieden (F_{ST} = 0,069) als die Tieflandbestände (F_{ST} = 0,048). Ähnlich waren die genetischen Distanzen nach Nei zwischen Hochlandbeständen größer als zwischen Tieflandbeständen. Der mittlere genetische Abstand zwischen allen Hochland-Hochland-Paarungen war 0,027, gegenüber 0,016 für alle Tiefland-Tiefland-Paarungen. Diese Ergebnisse zeigen, daß die 5 Hochland-Bestände mehr differenziert waren als die 5 Tiefland-Bestände. Eine Diskriminanzanalyse genotypischer Häufigkeiten zeigte, daß 70% der untersuchten *Picea mariana* Bäume korrekt in Hoch- und Tieflandgruppen eingeteilt worden waren. Die genetischen Unterschiede zwischen Hoch- und Tiefland-Standorten können mit den verschiedenen Überlebensraten der Sämlinge, die aus den selektierenden Bodeneffekten resultieren, in Beziehung stehen. Die Variationsmuster scheinen einen stärkeren ortspezifischen Selektionsdruck der Hochlandstandorte, gegenüber den allgemein günstigeren 5 Tieflandstandorten widerzuspiegeln, die den Sämlingen dort generell bessere Überlebensbedingungen bieten. Der höhere Heterozygotie-

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grad der Tieflandbestände könnte die Notwendigkeit eines stärkeren Wachstums in Abhängigkeit vom größeren Nährstoffstress widerspiegeln, der auf die Sämlinge nach der Bestandsgründung einwirkt.

Introduction

Picea mariana (MILL.) B. S. P. (black spruce) occupies a variety of topographical situations, moisture regimes and soil types within the boreal forests of North America. Within a single locality black spruce stands are often growing under markedly different ecological conditions including poorly-drained peat bogs as well as more productive, mineral soils. Although range-wide clinal differentiation is present in this species (MORGENSTERN 1978), ecotypic differentiation corresponding to upland and lowland conditions within a single locality has not been conclusively demonstrated.

Several approaches have been used to investigate the degree of ecotypic differentiation present within black spruce stands growing in specific localities. MORGENSTERN (1969) examined a large number of subpopulations by evaluating germination and growth parameters of seedlings, but his analysis showed only minor components of variation expressed between subpopulations corresponding to upland and lowland origins. FOWLER and MULLIN (1977) demonstrated small but significant differences in seedling survival, as well as some temporary differences in growth rate between seedlings derived from upland black spruce stands sampled from three northern Ontario provenances. However, the authors concluded that their results gave no convincing indication of ecotypic differentiation at the local level.

In a preliminary study (PARKER *et al.* 1983) we noted that black spruce trees sampled from upland and lowland sites from a single locality of northern Ontario were not significantly differentiated from each other either morphologically (phenotypically) or chemically. However, trees from the bog stand were consistently more variable than the upland trees for cone, isozyme and flavonoid characters although they were no more variable for vegetative morphological traits.

Edaphic ecotypes have been demonstrated in other northern coniferous species. Both HABECK (1958) and MUSSELMAN *et al.* (1975) noted differences in survival and morphological and physiological characteristics between upland and lowland stands of *Thuja occidentalis* L. (white cedar). As well, TEICH and HOLST (1974) demonstrated growth differences in the progeny of *Picea glauca* (MOENCH) VOSS (white spruce) sampled from soils of limestone versus granitic origin. In view of these results for other northern coniferous species, it is possible that local ecotypic differences may exist in black spruce for various phenological or physiological traits that have not yet been investigated.

The goal of this study was to examine isoenzyme variation within and between upland and lowland stands of black spruce from several geographic areas across northern Ontario. This procedure was chosen to allow direct comparison, based on one type of genetic evidence, between naturally established trees that had survived local selection pressures under the different edaphic conditions.

Materials and Methods

Naturally established stands of black spruce were sampled from five geographic areas extending across northern Ontario from its western to eastern borders (*Figure 1*). Collection sites were located near the vicinities of Sioux Narrows, Sioux Lookout, Nipigon, Macdiarmid, and Cochrane. At each collection location, two mature black spruce stands were sampled, one growing on an upland well-drained mineral soil, and the second growing on a lowland poorly-drained organic soil. In some cases it was necessary to sample the remnants of formerly large natural stands left after harvesting of adjacent areas. Upland/lowland stand pairs were sampled from one to two km from one another at each of the five locations. However, complete genetic isolation either by exclusion of seeds or pollen between upland and lowland stands at any one site would have been unlikely.

All upland stands were either pure or predominantly black spruce in composition with occasional minor components of white spruce, jack pine (*Pinus banksiana* LAMB.) and rarely, poplar (*Populus tremuloides* MICHX.). Species composition of the lowland sites were generally pure black spruce with an occasional occurrence of tamarack (*Larix laricina* (DU ROI) KOCH) and white cedar. All ten of the stands exhibited evidence of fire origin in soil profiles.

From each of the ten chosen stands, ten black spruce trees were randomly selected subject to their having a minimum of about 20 seed cones present in the upper crown. Descriptive data regarding each of the ten black spruce stands is presented in *Table 1*.

Seeds of individual black spruce trees were extracted following standard procedures (EDWARDS 1981). Before dissection, the seeds were imbibed in growth chambers for approximately 48 hours at 20 degrees. All diploid tissue including embryo and seed coat was removed and discarded prior to homogenization of individual megagametophyte tissue in an extraction buffer (CHELIAK and PITEL 1984). Genotypes of all sampled trees were inferred from the analysis of six megagametophytes per tree.

Isozyme variation in the haploid tissue was assessed by horizontal starch gel electrophoresis using buffers, stains and procedures described by CHELIAK and PITEL (1984). Abbreviations and references to the enzyme systems follow the Enzyme Commission Code (Nomenclature Committee 1979). Usable results were obtained for the enzyme systems aspartate aminotransferase (AAT) (2.6.1.1), glutamate dehydrogenase (GDH) (1.4.1.2), leucine-amino peptidase (LAP) (3.4.11.1) and phosphoglucose isomerase (PGI) (5.3.1.9) when these systems were resolved with a lithium hydroxide gel buffer. As well, consistently scorable results were obtained for the systems phosphoglucomutase (PGM) (2.7.5.1), isocitrate dehydrogenase (IDH) (1.1.1.42), malate dehydrogenase (MDH) (1.1.1.37), 6-phosphogluconate dehydrogenase (6PGD) (1.1.1.44), aldolase (ALD) (4.1.2.13) and aconitase (ACO) (4.2.1.3.) when resolved with a histidine citrate buffer. Several additional attempts were made to obtain isozyme data based on other enzyme systems, but none were consistently scorable for our material.

Allozyme phenotypes of individual trees were scored for all systems, and allelic frequencies were calculated at each locus for each of the ten stands. These data were used to determine average percentages of polymorphic loci and average heterozygosity values per stand. In addition the data were used to derive WRIGHT's (1969) F_{ST}, F_{IT} and F_{IS} statistics and NEI's (1975) genetic distances (Dm) between population pairs.

Isozyme data were coded for subsequent multivariate statistical analyses by translation of each genotype into component vectors. Since the multivariate statistical

methods require the elimination of the correlations present in polynomially distributed traits, each polymorphic enzyme locus was represented by one fewer vector than the number of alleles observed for that locus. Each vector had three possible scores indicating the presence or absence of a particular allele: 1) the homozygous presence of a vector allele was scored as 1, 2) its presence in the heterozygous state was scored as 0.5, and 3) its absence was scored as 0 and indicated the presence of an alternate allele. Coded genotype data of individual trees were then analyzed by 1) discriminant analysis recognizing various permutations of upland, lowland and geographic groupings and 2) principal components analysis. All multivariate analyses were performed using the S.P.S.S. package (Nie *et al.* 1975) on a Vax 11/780 computer at the Lakehead University Computer Centre.

Results

Among the ten enzyme systems examined, fifteen loci provided reliable data. Thirteen of the loci were polymorphic, while IDH and AAT1 were monomorphic over all populations. The average percentage of polymorphic loci *(Table 1)* was higher for the five lowland stands of black spruce (57.3%) compared to the five upland stands (47.5%). Similarly, the average heterozygosities *(Table 1)* of the lowland stands were slightly, but consistently higher ($h = 0.23$) than those of the five upland stands ($h = 0.21$). These results indicate that the sampled lowland stands had greater isoenzyme variation than the upland stands. Unexpectedly, this trend also appeared to correspond to stand age *(Table 1)* where the youngest stands had the greatest levels of variability. A significant negative correlation ($p < 0.05$) existed between stand age and level of variation based on percentage of polymorphic loci ($r = -0.74$), and the correlation based on average heterozygosity ($r = -0.61$) was nearly as strong but not quite significant ($p > 0.05$). To investigate further the relationship of age with isozyme variability, the same correlations were calculated based on data from individual trees. When treated in this way the correlations were much reduced in magnitude, and neither was significant. Thus, it seems likely that the observed correspondence of stand age and isozyme variability resulted from a coincidence of average stand age with stand environment; i. e. the upland stands, which on average had less isozyme variation than the lowland stands, were also on average the older stands.

Wright's F statistics (1969) supported the same trend indicating a slight deficiency of heterozygotes for upland stands ($F_{IT} = 0.046$) and a slight excess for lowland stands ($F_{IT} = -0.065$). The average value of F_{IT} for all populations was -0.009, indicating a negligible heterozygote excess overall. G-tests (Sokal and Rohlf 1981) indicated that genotypic distributions at several loci deviated significantly from Hardy-Weinberg expectations. These deviations are probably attributable to the relatively small sample size.

Wright's F_{ST} values (1969), calculated over all loci, indicated that upland stands were more differentiated from

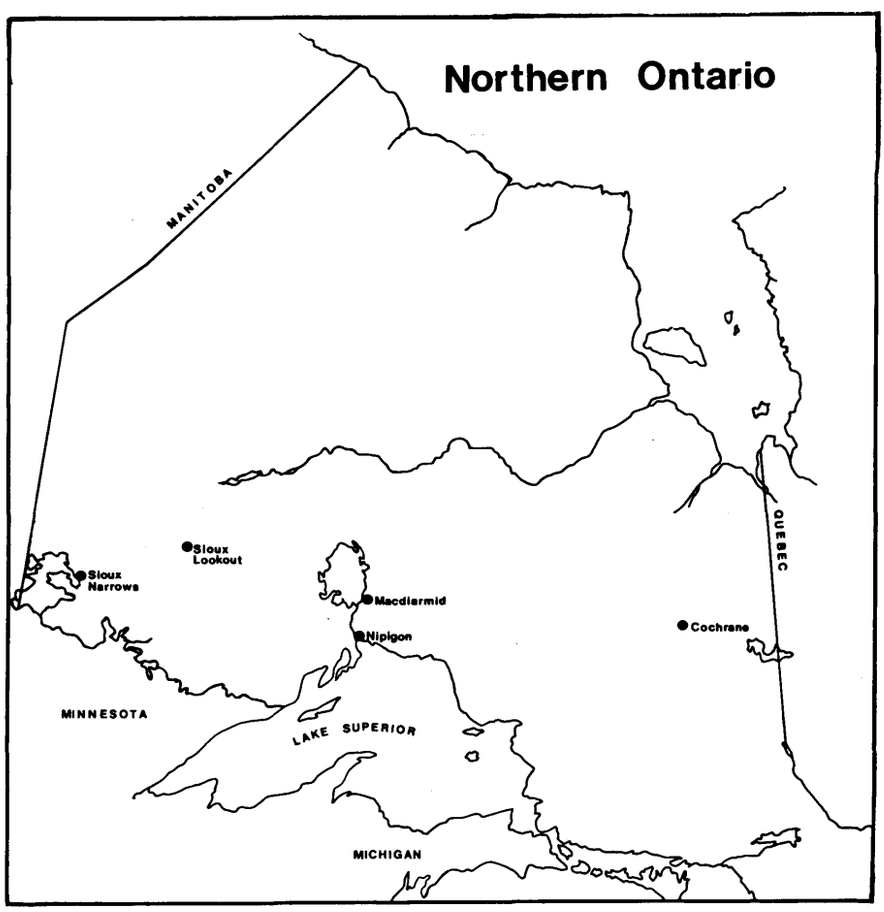

Fig. 1. — Map of northern Ontario showing the locations of the five sampled pairs of upland and lowland stands of *Picea mariana*. See *Table 1* for descriptive details.

Table 1. — Descriptive data for 10 sampled stands of *Picea mariana*. Standard deviations are in parentheses.

STAND LOCATION	STAND TYPE	HEIGHT (m)	DIAMETER (cm)	AGE	STAND DENSITY (trees/ha)	MEAN PERCENT POLYMORPHIC LOCI	MEAN HETERO-ZYGOSITY
Sioux Narrows 49 25 N, 94 8 W	Upland	9.9 (0.94)	11.4 (0.80)	42.8 (6.1)	3300	53.3	0.20
	Lowland	11.3 (0.29)	12.2 (0.61)	42.8 (3.2)	3700	46.7	0.22
Sioux Lookout 50 9 N, 91 45 W	Upland	10.5 (1.18)	10.5 (1.43)	64.4 (10.8)	2300	33.3	0.16
	Lowland	10.5 (1.23)	22.8 (12.0)	42.3 (10.6)	2800	53.3	0.21
Nipigon 48 50 N, 88 35 W	Upland	9.3 (1.27)	14.6 (2.21)	25.3 (2.8)	2800	64.3	0.26
	Lowland	10.6 (1.58)	12.2 (1.65)	43.1 (2.4)	4100	73.3	0.27
Macdiarmid 49 25 N, 88 7 W	Upland	11.4 (0.99)	13.4 (2.11)	52.4 (14.6)	3000	46.7	0.20
	Lowland	9.8 (1.03)	10.4 (1.23)	44.8 (16.2)	2500	46.7	0.22
Cochrane 49 5 N, 80 55 W	Upland	9.1 (0.81)	10.3 (1.34)	63.9 (2.6)	3900	40.0	0.23
	Lowland	10.2 (1.64)	13.3 (1.99)	42.1 (9.8)	4700	66.7	0.25
Mean All Sites	Upland	10.0 (1.04)	12.0 (1.58)	49.8 (7.38)	3060 (594)	47.5 (12.0)	0.21 (0.04)
	Lowland	10.5 (1.15)	14.2 (3.50)	43.0 (8.44)	3560 (909)	57.3 (12.1)	0.23 (0.03)

each other (F_{ST} = 0.069) than were the lowland stands (F_{ST} = 0.048). Similarly, genetic distances (Nei, 1975) were larger among upland stands than among lowland groups *(Figure 2);* the average distance between all upland/upland pairings was 0.027 as opposed to 0.016 for all lowland/lowland pairings. These results indicate that the five upland stands were more differentiated than the five lowland stands. Average genetic distance between each of the five upland and lowland black spruce stands was an intermediate value (0.020).

Discriminant analysis of the entire data set treated as ten individual populations showed little distinction among the ten stands (results not shown). Most of the observed discrimination was attributable to the first function which accounted for 43.8% of the total variation, but only 48 percent of the trees were correctly classified by the predicted discriminant groupings. However, 59 percent of the upland cases were correctly classified by the discriminant function in comparison with 40 percent correct classifications for lowland individuals. Cochrane was the most distinct population, while Nipigon, Sioux Lookout and Sioux Narrows were slightly less so; Macdiarmid was the least easily distinguished.

Discriminant analysis of the data set with upland/lowland stand pairs pooled by geographic location *(Figure 3)* showed a clearer, although still overlapping, separation of the five groups. Again, the first function is mainly responsible for the variation (58.1%). Concordance of actual groups with predicted groups was somewhat greater at 56.4 percent.

Two additional dicriminant analyses were completed, first for all five upland stands, and second for all five lowland stands. With the exception of Macdiarmid, the five upland stands clustered in more condensed and distinct groups *(Figure 4)* than did the five lowland stands *(Figure 5).* The initial upland discriminant function encompassed 62.7 percent of total variation, while the second accounted for 27.6 percent. In comparison, the lowland functions represented 68.4 percent and 15.5 percent of total variation, respectively. The percentage of cases correctly classified into the actual groups by the analysis was 72.2 percent for upland and 76.0 percent for lowland data. The upland value would have been substantially higher (ca. 81%) without the influence of the upland Macdiarmid stand which appeared to respresent two separate groups when trees were plotted as scattergrams. The more di-

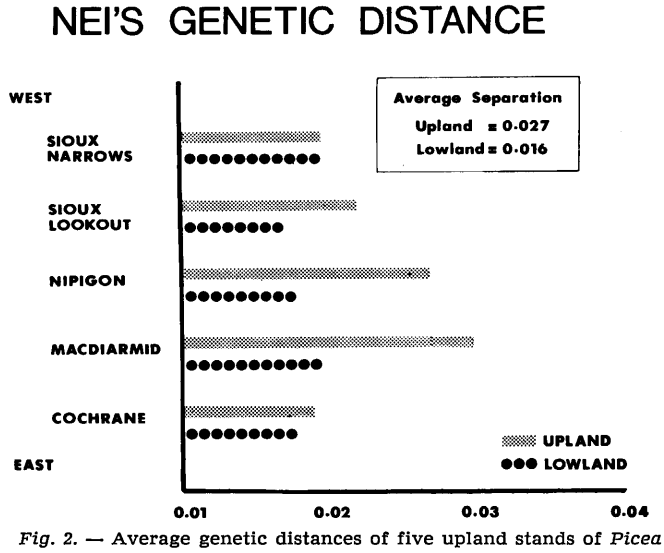

Fig. 2. — Average genetic distances of five upland stands of *Picea mariana* from the other upland stands and average genetic distances of five lowland stands from the other lowland stands.

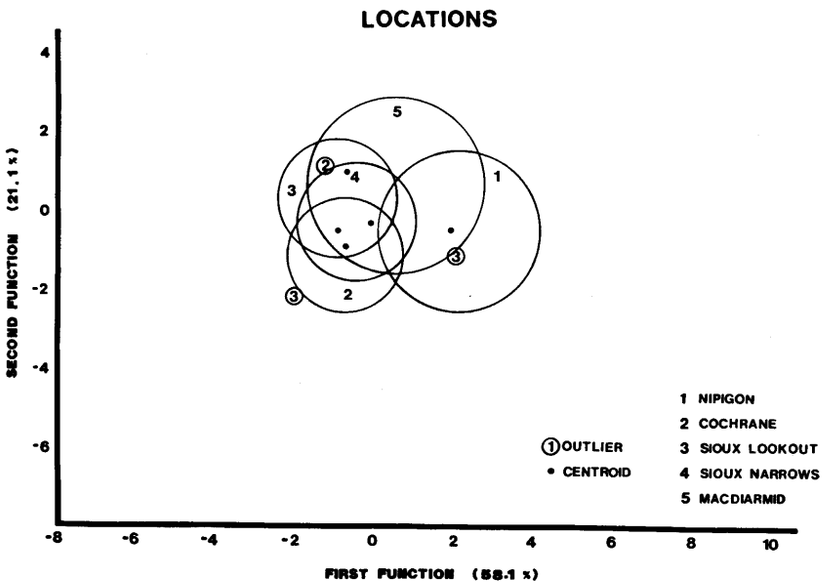

Fig. 3. — Scattergram of pooled upland and lowland stands of *Picea mariana* from five locations in northern Ontario based on discriminant analysis of genotype frequencies. Circles represent boundaries confining individual trees; outlying individuals and group centroids are also indicated.

versified character of this stand might have resulted from the necessity of sampling the remnants of a natural stand around the periphery of a small cutover area.

Finally, data from all five sites were pooled into upland and lowland groups and compared by discriminant analysis. Agreement between actual and predicted groups was 70.2 percent. The histogram *(Figure 6)* shows upland and lowland trees as two overlapping distributions which are slightly skewed in opposing directions. Upland and lowland centroids differed by one unit, and the lowland distribution was somewhat wider than that of the upland.

Principal components analysis yielded components that individually accounted for only minor proportions of the total variation; the first, or largest factor represented only fourteen percent of the total variance. As well, simple correlation results indicated that relationships among variables were generally nonsignificant. These results indicate that the variation present in the enzyme data set cannot be condensed into a few common dimensions. This observation is in contrast to the results of our earlier multivariate analyses of cone, twig and needle characteres (Parker *et al.* 1983) of black spruce and suggests that the scored alleles are not functionally interrelated to any great extent.

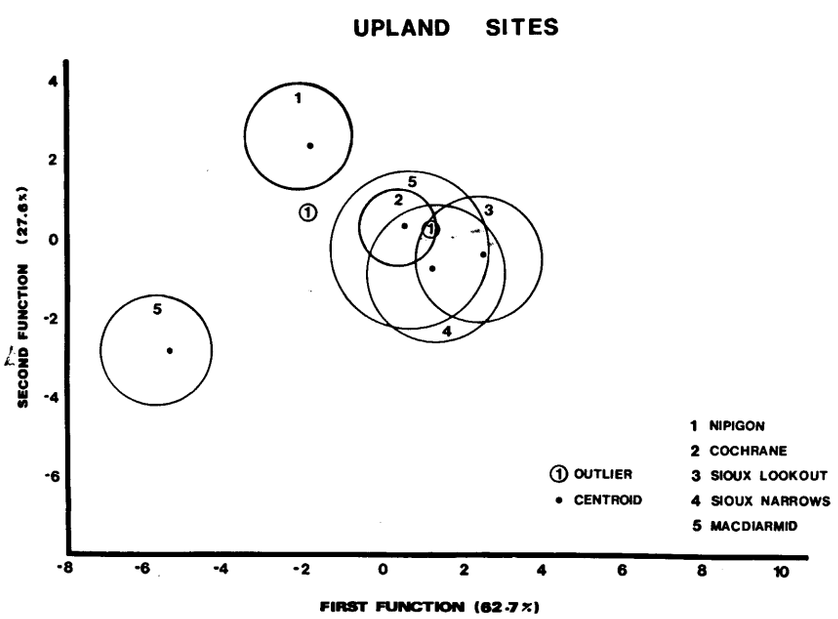

Fig. 4. — Scattergram of five upland stands of *Picea mariana* sampled from five locations in northern Ontario based on discriminant analysis of genotype frequencies. Circles represent boundaries confining individual trees; outlying individuals and group centroids are also indicated.

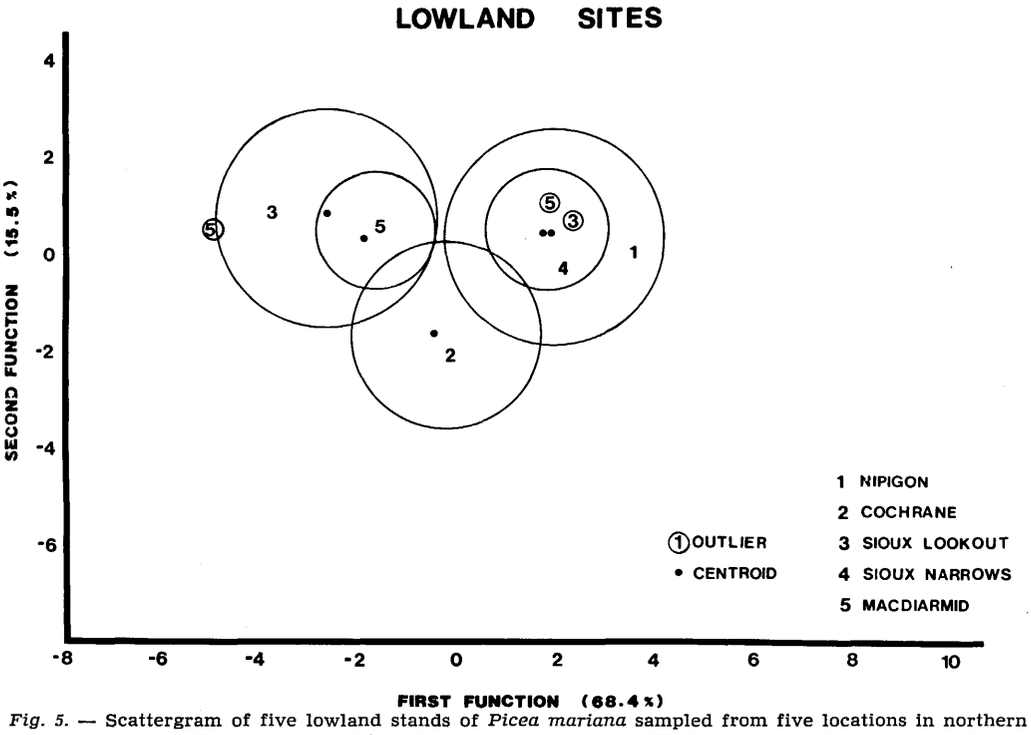

Fig. 5. — Scattergram of five lowland stands of *Picea mariana* sampled from five locations in northern Ontario based on discriminant analysis of genotype frequencies. Circles represent boundaries confining individual trees; outlying individuals and group centroids are also indicated.

Discussion

Although the extent of local gene flow in black spruce has not yet been established, the evidence from other tree species indicates that mating is generally restricted to near neighbors (Shen *et al.* 1981, Müller-Starck 1979, Levin and Kerster 1974) and that local differentiation is possible. Since environmental differences between upland and lowland sites would be expected to give rise to variation in selection pressures, the existence of local edaphic ecotypes of black spruce associated with upland and lowland habitats would be predicted. Contrary to expectations, earlier studies have revealed little or no distinction between local stands situated on these two site types (Morgenstern 1969, Fowler and Mullin 1977, Parker *et al.* 1983). Isozyme data presented here *(Fig. 6)* demonstrate that elements of the variation distinguish about 70 percent of the sampled black spruce trees from upland and lowland stands across a wide geographic range in northern Ontario. In spite of this distinction provided by the isozyme data, only 52 percent of the open-pollinated progeny from one of the sampled upland/lowland stand pairs (Nipigon) was classified correctly by discriminant analysis of morphological variation after one season's growth (Lee 1984).

An association between environmental heterogeneity and genetic polymorphism has been demontrated several times for other plant species, most notably in the wind-

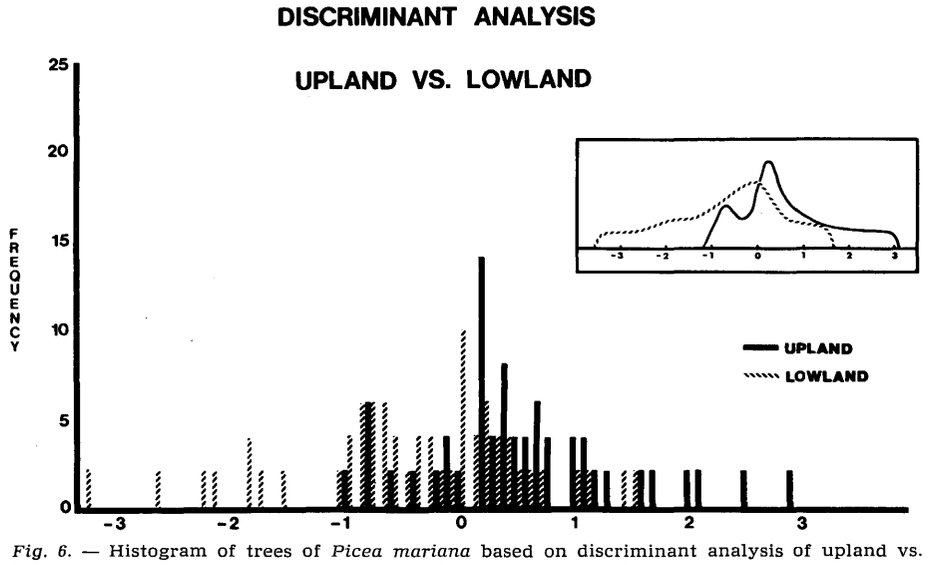

Fig. 6. — Histogram of trees of *Picea mariana* based on discriminant analysis of upland vs. lowland genotype frequencies. For this analysis upland trees from all five sites were pooled into one group and lowland trees from all sites were pooled into a second group. Group centroids are indicated.

pollinated, slender wild oat (*Avena barbata* L.) (CLEGG and ALLARD 1972). These authors found a strong correlation between increased polymorphism and local moisture regime. Similar microhabitat differentiation, especially with regard to soil moisture levels, has been demonstrated in various additional species (HABEK 1958, HAMRICK and ALLARD 1972, SCHAAL 1975, TURKINGTON and HARPER 1979, HAMRICK *et al.* 1979a, 1979b).

The percentages of polymorphic loci and calculated heterozygosities reported in this study demonstrate a trend towards greater variability in individual and pooled lowland populations of black spruce compared to upland populations. These results are in agreement with our earlier observations based on morphological and chemical variation (PARKER *et al.* 1983) for one additional upland/lowland stand pair of black spruce.

Differences in soil and moisture conditions and in vegetation characteristics of upland and lowland black spruce sites undoubtedly lead to different selection pressures at these two environmental extremes. A significant amount of differential selection presumably occurs during seedling establishment.

THOMAS and WEIN (1982) have shown that the small seed size and shallow rooting characteristic of black spruce limit seedling survival in drier areas. Radicle growth after germination is too slow to keep up with the downward dessication of surface soil during subsequent dry periods. Also, success of black spruce seedlings has been found to be consistently higher on wet peatlands (HEINSELMAN 1957, RICHARDSON 1970, JOHNSTON 1971, and HAAVISTO 1979) compared to success on drier areas (Richardson 1979). Generally, these findings indicate a more favorable environment for establishment of greater range of seedling genotypes on lowland sites. Thus, the higher levels of isozyme variability noted in this study for lowland populations may be the result of more stringent selection pressures exerted on seedlings during periods of establishment on upland sites.

While selection pressures may be less stringent to some degree at the seedling stage on lowland sites, they certainly do not remain so throughout the life cycle of black spruce. Lowland black spruce sites are typified by deep, often sterile, accumulations of peat. Low temperatures, high moisture levels and acidic conditions inhibit absorption of oxygen, water and nutrients (LARSEN 1982). Once established, growth conditions for black spruce trees are more optimal on upland sites in the center of its range (FOWELLS 1965) including northern Ontario where our sample stands were located.

An alternate explanation for higher observed levels of heterozygosity in mature lowland and black spruce stands relates to heterozygote advantage in stressful or fluctuating environments (JOHNSON 1976). Because the lowland sites are more stressful than the upland sites and tend to inhibit growth of mature trees, levels of heterozygosity generally higher than those present on upland sites would be predicted if the greater variability resulted in a growth advantage under these circiumstances. Evidence for this hypothesis from work done on other conifer species is conflicting for the most part (MITTON and GRANT 1980, KNOWLES and GRANT 1981, MITTON *et al.* 1981). LEDIG *et al.* (1983) noted a positive relationship between growth differences and levels of heterozygosity for stands of pitch pine (*Pinus rigida* MILL.) sampled from the most variable environments and in the densest stands where competition could be assumed to be the highest. However, they indicate that levels of heterozygosity may simply be an indication of the levels of inbreeding present in the population. Thus, the positive relationship of enhanced growth to heterozygosity results from decreased growth in growth in homozygous individuals caused by deleterious recessive alleles rather than from enhanced growth due to greater homeostasis in heterozygous individuals, Although this explanation cannot be discounted for the differences reported here, it is difficult to conceive of differences in the breeding systems of the parents that would consistently lead to greater inbreeding in upland stands. If higher levels of inbreeding exist in upland areas, it seems more likely they are attributable to stand continuity. Upland stands had a greater mix of tree species and generally lower stand densities (*Table 1*) than the lowland stands.

The calculated genetic distances and results of discriminant analysis reported here for black spruce indicate that upland stands are more distinct with respect to one another than are lowland stands. Various factors may be responsible for population differentiation over different geographic regions such as limited gene flow, differences in breeding system, genetic drift and differential selection parameters. It seems likely that most of the differentiation observed between upland stands is related to selection differences since each of the five sampled stands was situated in a different forest section type (ROWE 1972). Comparable, although weaker, differentiation was reported for pitch pine by GURIES and LEDIG (1982) who observed correlations between allozyme variation and several climatic variables. Apparently, the lowland stands of black spruce that we sampled were less distinct than the upland stands from the same five locations since the specific selection pressures resulting from different geographic locations had less severe effects in the lowland stands. This explanation also is consistent with the higher levels of isozyme variation observed in the lowland stands. Thus, the genotypes of black spruce trees from upland stands represent a more restricted subset of the regional gene pool than do those of the lowland stands.

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Genetics of wood characters of black spruce (Picea mariana (Mill.) B.S.P.) in Newfoundland, Canada

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Summary

The variation and relative control of genotype and environment over 11 wood characters in black spruce *(Picea mariana* (Mill.) B.S.P.) were studied to identify populations with superior pulping qualities. A four- and three-level cluster sampling scheme was adopted and the statistical and genetic analyses comprised analyses of variance, Bonferroni t-tests, repeatability calculations and multiple regressions.

Trees, discs and populations rank from highest to lowest as sources of variation in most characters. Within trees, the trend varies with character. There are weak north-south trends in relative densities, alcohol-benzene and sodium hydroxide solubilities and fibre length and wall thickness. Regression analyses of the squares of longitude and altitude show a negative and a positive influence respectively on sodium hydroxide solubility. Temperature and precipitation appear most frequently in different combinations in other regression equations. Repeatability values are good estimates of heritabilities. All characters except fibre wall thickness have high heritability ($R \geqslant 0.30$). The environmental factors studied have a significant influence on the non-genotypic portion of variation in all characters except fibre and lumen diameters (tangential section) and alcohol-benzene solubility. Populations 11, 16 and 19—23 have superior pulping qualities.

Key words: Heritability, Hierarchical analyses of variance, Multiple regression analyses, Step-wise multiple regression analyses, Genotypic variation, Environmental variation.

Résumé

Les tendances dans la variabilité générale et le conôle relatif du génotype et du milieu de 11 caractéristiques du