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Provenance Variation in Blue Spruce (*Picea pungens*) at Eight Locations in the Northern United States and Canada¹⁾

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Abstract

Blue spruce from 41 stands throughout the natural range were grown at eight locations in the northern United States and Canada. After eight years from seed, height and foliage color were measured at each test site, while data of bud-burst and winter injury were additionally measured at one test site in southern Michigan. The geographic variation patterns were analyzed by regression analysis. Geographic variables accounted for about 70% of the provenance variation in height, bud-burst and winter needle browning, but only about 50% for foliage color. In general, height growth decreased with increasing latitude and elevation, while winter injury declined with increasing latitude. For date of bud-burst, eastern trees were generally earlier than western trees, but the earliest trees were from southwestern Colorado, southern Arizona and New Mexico. The bluest trees originated in northern Arizona and the Colorado-New Mexico border area. Trees from north or south of this area were greener. For height, the degree of provenance differentiation appears to be less for blue spruce than for its Rocky Mountain associates.

Key words: Geographic variation, ecotype, race, adaptation, provenance test.

Zusammenfassung

In den nördlichen USA und in Kanada wurden an 8 Standorten *Picea pungens*-Nachkommenschaften aus 41 Beständen im natürlichen Verbreitungsgebiet der Art angebaut. 8 Jahre nach der Aussaat wurden an jedem Teststandort die Höhe gemessen und die Nadelfarbe bonitiert, während die Daten für den Austrieb und die Frostschäden zusätzlich an einem Standort in Süd-Michigan aufgenommen wurden. Die geographischen Variationsmuster wurden mittels Regressionsanalyse bestimmt. Die geographischen Variablen trugen zu etwa 70% zur Herkunftsvariation bei der Höhe, dem Austrieb und dem Frostschaden und nur zu 50% bei der Nadelfarbe bei. Generell nahm das Höhenwachstum mit zunehmendem Breitengrad und mit zunehmender Höhenlage ab, während die Frostschäden mit der Zunahme des Breitengrades in Beziehung standen. Der Austriebstermin lag bei östlichen Herkünften früher als bei westlichen, aber die am frühesten austreibenden Bäume stammten aus dem südwestlichen Colorado, aus dem südlichen Arizona und aus Neumexiko. Die bläuesten Bäume stammten aus dem nördlichen Arizona und aus dem Grenzgebiet zwischen Colorado und Neumexiko. Bäume nördlich oder südlich dieser Region waren grüner. Für die Höhe erschien der Grad der Herkunfts-differenzierung für

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Picea pungens geringer als für deren Verwandte aus den Rocky Mountains.

Introduction

Blue spruce (*Picea pungens*) is a native of the central and southern Rocky Mountains (Figure 1) where it occurs primarily along streams or the margins of moist meadows. Because of its restrictive habitat it is rarely cut for timber, but it has achieved wide recognition throughout the temperate zone as an outstanding ornamental.

Studies of genetic variation in blue spruce's common associates (Douglas-fir (*Pseudotsuga menziesii*) (REHFELDT, 1979; WRIGHT *et al.*, 1971), ponderosa pine (*Pinus ponderosa*) (WRIGHT *et al.*, 1969; WELLS, 1964a, 1964b), white fir (*Abies concolor*) (WRIGHT *et al.*, 1971), lodgepole pine (*P. contorta*) (REHFELDT, 1983, 1980a), Engelmann spruce (*P. engelmannii*) (BONGARTEN, 1978), and southwestern white pine (*P. strobiformis*) (WRIGHT *et al.*, 1971)) reveal striking differentiation related to geography. The geographic variation patterns in these species show many similarities (e.g. the faster growth and lesser cold hardiness of trees from areas with milder, shorter winters), however, each has its peculiarities revealing different adaptational solutions for survival (REHFELDT, 1984; KING and WRIGHT, 1972). In this paper, the geographic variation of blue spruce, as determined from provenance tests at eight locations, is described and compared with the patterns of its Rocky Mountain associates. The information is also used to identify proper seed sources for blue spruce plantings.

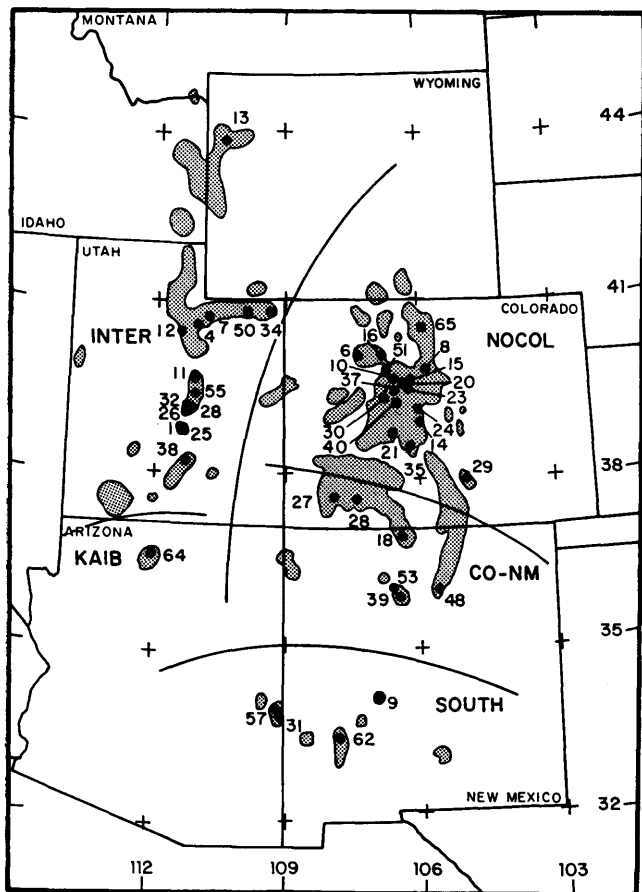


Figure 1. — Native range of blue spruce (from LITTLE, 1971) showing provenances sampled and geographic regions proposed in this paper.

An earlier paper (HANOVER, 1975) describes the nursery results of this study and VAN HAVERBEAK (1984) presents detailed results from the Nebraska installation of this test.

Materials and Methods

Materials

Open pollinated seeds were collected in the fall of 1969 from natural stands throughout the range of blue spruce. Seeds from 41 of these stands were used in the present study; their locations are shown in Figure 1. Each stand was represented, on average, by seed from seven randomly chosen individuals, however, the number ranged from one to seventeen.

The seeds were sown in an East Lansing, Michigan nursery. A randomized complete block design was used with family row plots occurring once in each of four replicates. Each row plot was 1.17 m long and contained 20 seedlings. The distance between plots was 10 cm.

In 1973 3 + 0 stock was used to establish half-sib family test plantations in southern and northern Michigan (Kalamazoo and Chippewa Counties, respectively). Cooperators in the United States and Canada received 2 + 0 seedlings bulked by stand. These were lined out in transplant beds (except in Nebraska where they were potted) until large enough for field planting. Plantations were established at 13 sites. Data from eight plantations having high survival are included in this paper. Two test sites were located in each of Ohio and Michigan and one in each of Pennsylvania, Nebraska, Maine and Quebec (Canada).

Each plantation followed a randomized complete block design of three to ten replications with four tree row plots and a spacing of 1.8 × 2.4 m or 2.4 × 2.4 m. Herbicides and mowing were used as needed to control weeds and grass.

Measurements

Height, foliage color, and survival were measured in all plantations at the end of the 1977 growing season. In addition frost damage was measured at several test locations in spring, 1977 and date of 50% bud-burst, percent of needles browned in winter and percent dead terminals were measured in the Kalamazoo County, Michigan test in spring, 1977.

Foliage color was scored on a scale of 0 = green to 3 = blue for each tree. Plot sums, adjusted for mortality (by extrapolation to four tree plots) were recorded. Date of 50% bud burst was determined by estimating the percent of buds flushed at three day intervals from April 22 to May 6, then interpolating. Frost damage was recorded as percent of buds killed at the Kalamazoo County, Michigan site and by absence or presence at other test locations.

Statistical Analyses

Population differentiation was tested for each trait by analysis of variance. Tree height and foliage color were analyzed over all plantations. Observations consisted of plot means for height and plot sums for color. Before analysis, the data for both traits were transformed to means of zero and variance of one at each test site in order to homogenize variance. The following model of random effects was used to determine population differentiation:

$$Y_{ijk} = \mu + B_j(S_i) + p_k + (pS)_{jk} + e_{ijk} \quad (1)$$

where

Y_{ijk} = plot value for height or foliage color;

μ = the overall mean;

$B_j(S_i)$ = the effect of the j th block in the i th test site;

Table 1. — Analysis of variance and variance components for seventh year height and foliage color over all test sites¹⁾.

Source of Variation	d.f.	Height		Foliage Color	
		Mean Square	Variance	Mean Square	Variance
Blocks/test sites	46	1.197	0.014**	2.036	0.040**
Provenance	40	13.819	0.324****	14.860	0.364****
Provenance x test sites	245	1.298	0.142****	0.855	0.059**
Error	1283	0.524	0.524	0.543	0.543

¹⁾ Data was transformed to mean = 0 and variance = 1 for each test site to homogenize variance. This eliminates test site as a source of variance.

** Statistical significance at 1% level of probability.

**** Statistical significance at 0.01% level of probability.

Table 2. — Analysis of variance and variance components for date of bud-burst, percent of winter needle browning and percent of winter killed terminal buds in the Kalamazoo County, Michigan test plantation.

Source of Variation	d.f.	Bud-burst		Winter browning ^{1/}		Bud-death	
		MS	Var.	MS	Var.	MS	Var.
Block	2	141.904	0.846	0.142	-0.001	5.859	0.088
Provenance	41	145.650	0.549**	4.369	0.291**	3.113	0.352
Family (Prov.)	120	37.936	10.474**	0.433	0.029	2.068	0.601**
Error	313	7.125	7.125	0.349	0.349	0.804	0.804

^{1/} Data transformed by $\sqrt{\% + 1/2}$.

** Statistical significance at the 0.01% level of probability.

P_k = the effect of the k^{th} stand or provenance;
 $(pS)_{ik}$ = the effect of the provenance \times test site interaction;
 e_{ijk} = the residual (provenance \times block (site) effect).

Notice that no test site effect was present since the data were transformed so that all test site means were zero.

For bud-burst, winter needle browning ($\sqrt{\% + 1/2}$), and terminal bud death, which were measured at only one test site, plot values were analyzed using the following model:

$$Y_{ijk} = \mu + B_i + P_j + f(p)_{k(j)} + e_{ijk}$$

where Y_{ijk} = the plot value;

μ = the overall mean;

B_i = the effect of the i^{th} block;

P_j = the effect of the j^{th} provenance;

$f(p)_{k(j)}$ = the effect of families within provenance;

and e_{ijk} = the residual (family \times block effect).

Principal components analysis was used to group the provenances according to their similarities in height, foliage color, date of bud-burst and winter needle damage. The geographic groups discerned from this analysis were compared to the continuous variables, latitude and longitude, in terms of their ability to explain the provenance variation.

The geographic variation patterns of each trait were assessed from a series of linear regression analyses. In the first model, provenance variation was related to latitude and longitude of origin. In the second model, variation was related to geographic region of origin (as determined in the principal components analysis). For all traits, geogra-

phic regions explained more of the provenance variance than latitude and longitude. Therefore, a third model was devised, separately for each trait, that related provenance variation to geographic region and latitude, longitude and elevation within regions. Only those within region terms which were shown to be statistically significant by correlation analysis at the $\alpha = 0.05$ level were incorporated in the third model for a given trait.

Because of the importance of the geographic regions in explaining provenance variation, the provenance \times test site interaction for height and foliage color (from eq. 1) was divided into two components, region \times test site and provenance in regions \times test site to determine if the geographic variation pattern was different from one test site to another.

Results

Analyses of variance

Plantation means ranged from 35 to 73 cm for height, 3.1—7.1 for foliage color and 77—90% for survival at age seven years. The analysis of variance for seventh year height and foliage color appears in Table 1. Since the data were transformed to a variance of one at each test site, the variance components also sum to one.

For height, provenance differences over all test sites were highly significant and accounted for almost a third of the total variation. Provenance \times test site effects were also highly significant but of less importance. Of the provenance variation at any test site 70% was explained by means over all sites and only 30% by deviations at the specific test site. The average provenance effect at a test

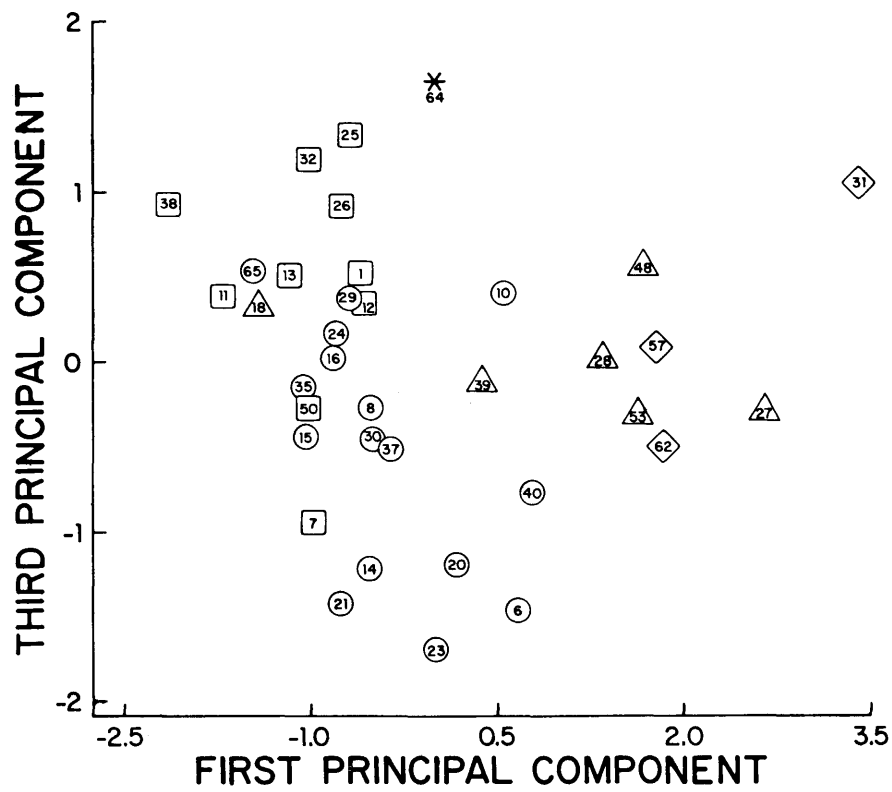
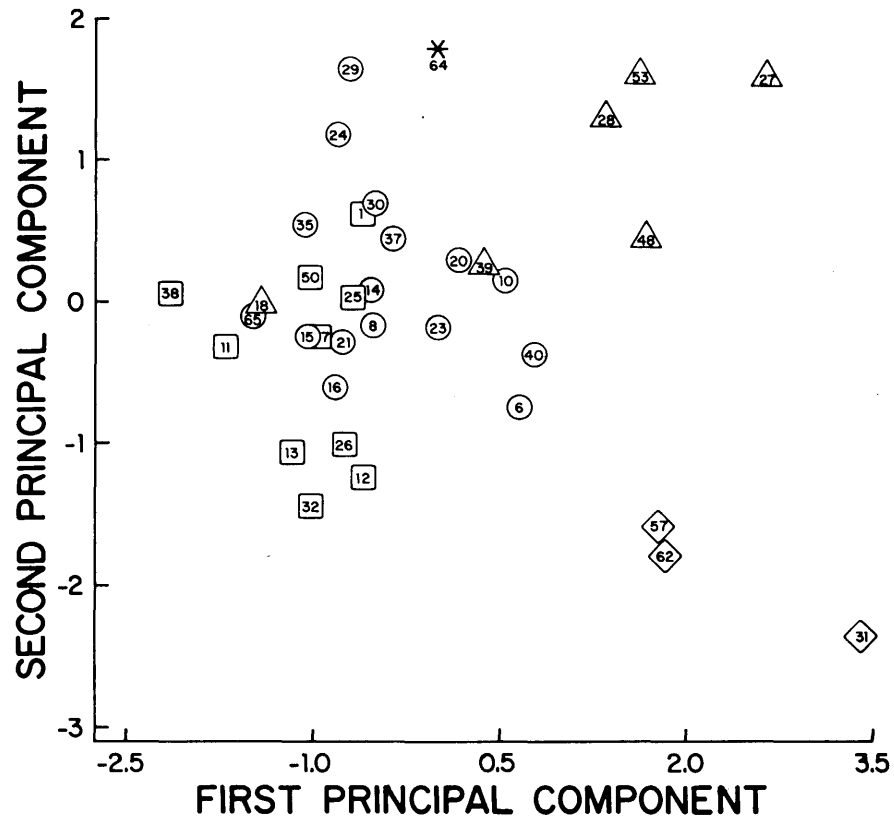


Figure 2. — Plots of provenance values for a) the first and second principal components and b) the first and third principal components. Numbers are provenance designations (see Figure 1). The regions of origin are designated by the following symbols: O = NOCOL; □ = INTER; Δ = CO-NM; ◊ = SOUTH; * = KAIB.

Table 3. — Goodness of fit (R^2) and residual variances ($S_{y \cdot x}$) for regression models relating genetic differentiation to geographic variables.

	MODEL 1		MODEL 2		MODEL 3	
	R^2	$S_{y \cdot x}$	R^2	$S_{y \cdot x}$	R^2	$S_{y \cdot x}$
Height	0.417	0.234	0.556	0.181	0.723	0.121
Foliage Color	0.130	0.323	0.394	0.226	0.474	0.205
Bud-burst	0.403	2.373	0.515	1.872	0.732	1.134
Winter needle browning	0.440	1.731	0.676	0.971	0.676	0.571

site (calculated as the sum of the provenance and provenance \times test site interaction variances) was over 46% of the total variation.

The results for foliage color were similar to those for height. Provenance differences over all sites were highly significant and accounted for over 36% of the total variation. Provenance \times test site interaction was also significant, but of little practical importance; only 14% of the provenance variation at a specific test site was attributable to deviations from the means calculated over all test sites. Average provenance variation at individual test sites was 42% of the total variation at a test site.

Of the traits studied only at the Kalamazoo County, Michigan site (Table 2), highly significant provenance differences were detected for date of spring bud-burst and percent of winter needle browning, but not for percent of dead terminal buds. As with height and foliage color, provenance variation of bud-burst and needle browning was about 40% of the total variation at this one test site.

Principal Components Analysis

Principal components analysis was employed to compare provenances on the basis of all characteristics considered together. Based on plots with the first three principal components (Figure 2), which accounted for over 91 percent of the provenance variation, five geographic regions could be discerned. The four southern provenances (region

SOUTH) clustered together in both plots, and in the plot of the first and second principal components, were entirely separated from the others. With the exception of provenance 18, provenances from northern New Mexico and southern Colorado (CO-NM) also clustered well and were separate from the others in the plot of the first two principal components. Trees from northern Colorado (NOCOL) tended to cluster separately from those from Utah and western Wyoming (INTERmountain), but some overlap is evident. The overlap was not substantial, however. Only provenances 7 and 50 from Utah and provenances 15, 16 and 65 from Colorado overlapped in both principal components plots. Provenance 64 from the KAIBab plateau in northern Arizona had the highest values for the second and third principal components. It lies close to the NOCOL region in the plot of the first and second principal components, but is closer to the INTER region in the plot of the first and third components. For these reasons it is considered to comprise a fifth, separate region.

Patterns of Variation

Provenance variation was first related to latitude and longitude of origin by multiple regression (Table 3). For each trait the model was significant, accounting for over 40% of the provenance variation in height, spring bud-burst and winter needle browning, but only 13% in foliage color. However, model 2, which related provenance variation to region of origin, as defined by principal components analysis, accounted for substantially more of the variation and had less residual (Table 3).

The within region deviations from model 2 were correlated with latitude, longitude and elevation of origin within regions. Those geographic variables having significant correlations (Table 4) were added to model 2 to produce a third and final model unique for each trait. These models accounted for approximately 70% of the provenance variation in height, date of bud-burst and winter needle browning. For foliage color only about 50% of the variation was described by this method (Table 3).

The final models describing variation were quite different for each trait in terms of both (1) the regional (Ta-

Table 4. — Correlations of height, foliage color and bud-burst with latitude, longitude and elevation within some regions¹⁾.

	Region	No. of Provenances	Height	Foliage Color	Date of Bud-burst	Winter Needle Damage
LATITUDE	INTER	12	0.12	0.56*	-0.34	-0.01
	NOCOL	16	0.30	0.58*	0.11	0.39
	CO-NM	6	0.00	0.44	-0.44	0.05
LONGITUDE	INTER	12	0.06	0.37	0.82**	0.21
	NOCOL	16	0.08	-0.34	-0.62**	0.41
	CO-NM	6	0.36	0.69	-0.77*	0.34
ELEVATION	INTER	12	-0.54*	-0.02	-0.14	-0.27
	NOCOL	16	-0.61**	0.11	0.00	-0.22
	CO-NM	6	-0.88*	-0.58	0.46	-0.73

¹⁾ The SOUTH region with only 3 degrees of freedom and the KAIB region with none are not included.

* Significant at 0.05 level of probability.

** Significant at 0.01 level of probability.

Table 5. — Regional means¹⁾.

Region	Height	Foliage Color	Bud-burst	Winter damage
	% of expt. mean	0=green 12=blue	date in April, 1977	% of foliage
SOUTH	120.3 ^a	5.28 ^b	25.8 ^b	5.00 ^a
CO-NM	106.2 ^{ab}	6.83 ^a	26.3 ^b	1.33 ^b
NOCOL	95.7 ^b	5.18 ^b	27.1 ^b	0.38 ^b
INTER	95.6 ^b	4.68 ^b	29.5 ^a	0.90 ^b
KAIB	107.0 ^{ab}	8.20 ^a	30.0 ^a	0.00 ^b

¹⁾ Means having different superscripts differ at the 5% level of probability.

ble 5) (2) the within regional patterns of variation (Table 4). For height, trees from the southern regions were taller than those from farther north, but there was no latitudinal variation within regions. Height variation within regions was significantly related to elevation in the INTER, NOCOL and CO-NM regions, however. In each case height declined as elevation of origin increased.

For foliage color, blueness was greatest in the mid-latitude regions, KAIB and CO-NM, and was less in regions north or south of these (Table 5). There was a slight, but significant trend for foliage blueness to diminish with increasing latitude in the NOCOL and INTER regions (Table 4). Within regions, color did not vary with longitude or elevation of origin. Variation within the SOUTH region deserves special mention. Three of the four provenances in that region had among the lowest scores for foliage blueness while the fourth had the greatest. This condition was primarily responsible for the relatively low R²s for all foliage color models.

Variation in bud-burst was primarily related to longitude. Trees from the two western regions burst bud significantly later than trees from the eastern regions (Table 5). Bud-burst was also related to longitude of origin within regions, but in opposite ways (Table 4). Within the two eastern regions, trees flushed progressively later from west to east. While, in the western, INTER region, the pattern of flushing was the opposite, east to west. The trees earliest to flush were from longitude 107° to 109° W; trees from farther east burst bud a day or two later, while those from farther west burst bud three to four days later. Bud-burst was not related to elevation of origin.

Winter needle damage was similar to height in that both were greatest in the SOUTH region. However, outside this region damage was so slight and sporadic that no variation patterns could be discerned. Colder temperatures are required to observe the true range of variability in cold hardiness.

As previously mentioned, provenance variation in height and foliage color over all test sites was much greater than provenance × test site variation indicating that the geographic variation patterns just described hold more or less at all sites. Nevertheless, provenance × test site variation was significant for both traits. Therefore, the interaction was divided into region × test site and provenances within regions × test site to determine if the large scale geographic variation differed from site to site (Table 6). For height both the region and within region interactions were statistically significant, but most of the interactions was of the within region type and could not be explained. For color, the interaction was primarily of the region × test site type and appears to stem from greater than average

color differentiation at the Maine site and less than average differentiation at the Coshocton, Ohio site. The geographic patterns of height and foliage color, therefore, appear quite similar over test sites.

Discussion

Each of the traits measured had a different geographic pattern of variation. With the exception of height and cold hardiness they are apparently inherited independently and are selected according to different environmental gradients. The variation patterns are similar, in many respects, to those found in other Rocky Mountain conifers, but there are also some interesting dissimilarities.

Among the similarities are (1) the faster growth of trees from southern latitudes than those from northern latitudes, (2) the greater cold hardiness of trees from northern latitudes than those from southern latitudes and (3) the decrease in foliage blueness with increasing latitude (KUNG and WRIGHT, 1972). The trend of decreasing growth rate with increasing elevation within a geographic region has not been detected in provenance tests of other southern Rocky Mountain species, but it has been observed in more precise experiments with northern Rocky Mountain populations of blue spruce associates (*Pseudotsuga menziesii*, *Pinus contorta* and *Pinus ponderosa*) (REHFELDT, 1983, 1980, 1979).

A major difference between blue spruce and its associates which have been provenance tested is that the degree of latitudinal differentiation is considerably less for blue spruce. For example, at eight years blue spruce from southern Arizona and New Mexico averaged 25% taller than blue spruce from northern Colorado, while at the same age the difference in Douglas-fir was over 100% (WRIGHT *et al.*, 1971), and in white fir it was 38% (WRIGHT, LEMMIEN and BRIGHT, 1971). Nursery differences in height were four times greater for ponderosa pine than for blue spruce (WRIGHT *et al.*, 1969). Similar results have been observed in northern Rocky Mountain species (REHFELDT, 1984).

Three reasons can be offered for the lesser differentiation in blue spruce. (1) Selection pressures may be less variable, particularly since the range of environments that blue spruce inhabits is less variable than that of other southern Rocky Mountain conifers. Trees which occur in southern Arizona and New Mexico experience longer growing seasons and milder winters than trees in Colorado and Utah because of their more southerly latitude. For Douglas-fir, ponderosa pine and white fir this difference is accentuated because the southern trees also occur at lower elevations than the northern ones. On the other hand, blue spruce from southern Arizona and New Mexico occur at comparatively high elevations, so the difference in length of growing season and winter temperatures between northern and southern blue spruce is less than for its associated

Table 6. — Analysis of provenance × test site interaction for height and foliage color.

Source of Variation	d. f.	Height		Foliage Color	
		MS	Var.	MS	Var.
Provenances	39	12948	0.293**	14.705	0.353**
Region × test site	28	2.162	0.026**	2.351	0.050**
Prov. (Region) × test site	213	1.280	0.139**	0.694	0.028
Error	1243	0.540	0.540	0.547	0.547

** Significant at 0.01 level of probability.

species. (2) Blue spruce may be more plastic in its response to environmental variations than its associates. REHFELDT (1984, 1983b) has attributed the large differences in the degree of differentiation among northern Rocky Mountain conifers primarily to this cause. WRIGHT (1955) considered the genus *Picea* to be poorly differentiated in general. REHFELDT observed that among the northern Rocky Mountain conifers, Engelmann spruce showed among the least differentiation (pers. comm.). (3) The degree of differentiation is dependent on the test environment. It is possible that the conditions under which the blue spruce were grown did not permit phenotypic differentiation to the same extent that experiments with other southern Rocky Mountain experiments did. This cause is probably not too important since all tests with the southern Rocky Mountain conifers were begun in the same East Lansing, Michigan nursery and were transplanted to several field test sites.

Blue spruce also departs somewhat from the geographic patterns of variation in foliage color observed in its associated species. For Douglas-fir, ponderosa pine, Engelmann spruce and southwestern white-limber pine, the bluest foliage is found in southern Arizona and New Mexico; trees become increasingly green with more northerly origin (BONGARTEN, 1978; KUNG and WRIGHT, 1972). In blue spruce, trees from several of the southernmost stands are exceptionally green. The general latitudinal cline in foliage glaucousness (blueness) is well correlated with the annual amount of solar radiation received, and, as a result, there has been much speculation that glaucousness serves to reduce transpiration or reflect light, thereby reducing leaf temperatures and thwarting photo-destruction of chloroplasts and auxins (REICOSKY and HANOVER, 1978, 1976; WRIGHT *et al.*, 1971; LEVITT, 1980a). However, none of these hypotheses have been proved and the role of surface waxes remains in question, and it is, therefore, impossible to determine if the green color of most blue spruce from the southernmost portions of its range is a result of selection. It seems likely that genetic drift has played a role, however. The conditions for genetic drift, small, isolated populations, are present. And, one stand in this region produced the highest proportion of blue trees of any in the test, a result explainable by genetic drift.

As a third major departure from other tested southern Rocky Mountain species, eastern blue spruce burst bud before western blue spruce, whereas, in the other species, latitudinal trends are the rule (KUNG and WRIGHT, 1972). The physiological mechanisms controlling bud-burst as well as environmental differences may be responsible. Differences in *Picea* seed sources in the time of bud-burst appear to result primarily from differences in the heat sum required for initiation (BURLEY, 1966; pers. obs.); differences in chilling requirements appear to be unimportant (NIENSTADT, 1967). Western trees, flushing later in a common garden, are therefore, though to have greater heat sum requirements for spring shoot flush. This greater requirement may result because (1) a greater heat sum accumulates before a low danger of frost is reached in the west, and/or (2) western trees stand to benefit from early bud-burst, even at the risk of greater injury, more than eastern trees do. (This second cause is exemplified by the early bud-burst of Douglas-fir from areas of extreme summer drought in order to extend an otherwise short effective growing season (CAMPBELL and SAGUNO, 1979)). BAKER'S (1944) summary of western mountain climates indicates that at the mean elevation of blue spruce occurrence, trees from the

western portion of the range (Utah), in fact, have a shorter growing season, with less precipitation than trees from the eastern portion. It does not appear that eastern trees would benefit from early bud burst more than western trees. However, Baker's analysis also indicates that more heating may occur before the last spring frost in the western regions. The evidence is as follows. The mean minimum and maximum temperatures for each month are nearly identical in Colorado and Utah at the mean elevation of blue spruce occurrence. Therefore, we expect, on average, heat sums to accrue at the same rate at both places. But, the average date of the last frost in Colorado is June 15, and in Utah, June 25. Therefore, trees from Utah should experience more heat before the danger of frost has passed and may require a greater heat sum to initiate bud-burst to prevent frost damage. Similar analysis shows that trees from western Colorado, western New Mexico and southern Arizona, which are first to burst bud in a common garden, experience the smallest heat sums before the date of last spring frost in their native environments. The pattern of bud burst seems to parallel, closely, the pattern of heat sum accumulation before the last spring frost, which suggests that the time of bud burst is selected primarily to avoid spring frost damage.

While the variation patterns discerned from provenance testing are useful in extending our knowledge about the processes of evolution, they also have practical value for seed source selection. Results from this test indicate that growth rate, foliage color, time of bud-burst and winter cold hardiness can be improved by seed source selection. However, it may be difficult to select for all traits simultaneously. For example, the fastest growing trees tended to flush early, had green foliage, and suffered more winter damage. On the other hand, about 25% of the provenance variation in height and bud-burst, and 50% of the variation in foliage color were not explained by geographic variables. The existence of this residual, random variation means that specific stands may be found which have the desired combination of traits. In this test, provenance 9, from southern New Mexico, and provenance 27, from southern Colorado, combined excellent growth with extremely high scores for blue foliage. Unfortunately, they were also the earliest to flush and suffered the most spring frost damage. A more intensive search for "ideal" stands might be warranted if the costs of a selective breeding program are not justified.

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Inheritance of Resistance to Races of *Melampsora medusae* in *Populus deltoides*

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Summary

The F_1 progeny of a *Populus deltoides* cross were analysed independently for their reaction to six races of *Melampsora medusae*, which elicited susceptible \times resistant, resistant \times resistant or susceptible \times susceptible reaction in parents depending on the races employed. Resistance was inherited as dominant (3 races), recessive (2 races) or quantitative, additive (1 race) in the clones, and was controlled by a single gene or two genes acting in a complementary or duplicate manner, depending on the race. Modifying factors influenced the degree of susceptibility expressed in certain plants and resulted in a 'slow rusting' effect. Relevance of the results to poplar breeding for leaf rust resistance is discussed.

Key words: Genetics, Leaf rust, *Melampsora medusae*, *Populus deltoides*, Disease Resistance, Slow Rusting.

Zusammenfassung

Die F_1 -Nachkommenschaft einer *Populus deltoides*-Kreuzung wurde unabhängig auf ihre Reaktion auf sechs Rassen von *Melampsora medusae* hin analysiert. Die Analyse zeigte je nach Rasse eine anfällige \times resistente, resistente \times resistente oder anfällige \times anfällige Reaktion bei den Eltern (P_1). Resistenz wird als dominant (in drei Rassen), rezessiv (zwei Rassen) oder additiv auf quantitative Weise (eine Rasse) vererbt und wird von einem oder zwei Genen, die in einer ergänzenden oder verdoppelnden Weise, je nach Rasse, funktionieren, kontrolliert. Modifikationsfaktoren beeinflussten den Grad der Anfälligkeit in bestimmten Pflanzen und resultierten in einem 'slow-rusting' (langsamen Rost)-Effekt. Die Bedeutung dieser Resultate für die Züchtung von Pappeln auf Blattrostresistenz wird diskutiert.

1. Introduction

Leaf rust, caused by *Melampsora medusae* THUM., is an important disease of poplar, and several races of this pa-

thogen have been recognised in Australia (SINGH and HEATHER 1982). An understanding of the inheritance of resistance to different races of the pathogen is essential in devising strategies for management of the disease by breeding and selection. MUHLE LARSEN (1970), following a field analysis of a population of poplar progeny, concluded that resistance to leaf rust, caused by *Melampsora larici-populina* KLEB., may be controlled by a few to several dominant genes.

This paper reports a study of inheritance of resistance to six races of *M. medusae* in a *Populus deltoides* MARSH (2n = 38) cross, assessed on a qualitative scale using detached leaf disks.

2. Materials and Methods

2.1 Origin of Parents

The parents, *P. deltoides* cvs. 60/122 (female) and T-173 (male), are selections from separate Texan provenances (WILLING, R. R., *pers. commun.*). Cv. 60/122 is relatively more susceptible than cv. T-173 to all the races of *M. medusae*.

2.2 Hybridisation

Crosses were performed on bottle grafted branches of cv. 60/122 in a glass house as described by KNOX *et al.* (1972). The branches, bearing unopened female flower buds, were collected from the poplar plantation maintained by the Botany Department, Australian National University, and washed with a jet of tap water. The grafts were made during winter 1982 (mid August) about 3–4 weeks prior to natural flowering in the field. The understocks (rooted for 4 months), consisting of cuttings 30–40 cm long, and 1.5–2.0 cm in diameter, were transplanted into 20 cm pots. Pollen of cv. T-173, collected from plantations at Kempsey, NSW, was dried over silica gel (24 h) and stored in a freezer (–14°C) for 1–2 weeks prior to use. Crosses