



Introduction of ponderosa pine and Douglas-fir to Argentina

Using quantitative traits for retrospective identification and prospective selection of provenances

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Abstract. Patterns of shoot elongation of 2-yr seedlings from native North American populations of ponderosa pine and Douglas-fir were compared to those of Argentine land races originating from unknown provenances. The comparisons were conducted in Moscow, Idaho (USA), and suggested that the ponderosa pine land race was descended from a California provenance at low or middle elevations but that the growth potential of the land race was only mediocre in comparison to eight native populations. The Douglas-fir land race exhibited a relatively high growth potential in comparison to 19 native provenances and undoubtedly originated from a mild coastal environment. The results provide concrete recommendations for upgrading the growth potential of the Argentine land races by importing germ plasm of specific provenances.

Key words: afforestation, land races, provenance selection, reforestation, shoot elongation, tree introduction

Introduction

Remarkably fast growth and high levels of productivity typify Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Laws.) from unknown provenances that were introduced early in the Twentieth Century to Victoria Island (latitude, 41°S) in Nahuel Huapi Lake of northwest Patagonia, Argentina. The performance of these trees prompted planting programs in Patagonia using wind-pollinated seeds collected from the original introductions (Unpublished Victoria Island Nursery Records, National Park Administration, Argentina). The introduced species now appear to be especially suited to the ecotone between the steppe

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and *Nothofagus* spp. forests in northwest Patagonia (40° to 48°S). This ecotone occupies a narrow strip of land about 40 km in width within the rain shadow of the Andes. At present, the Forest Genetics Unit of the National Institute for Agricultural Technology of Argentina is exploring the potential of using them to augment wood production.

This paper deals with the retrospective identification of the provenance of the original introductions so that additional selections of prospectively higher growth potential can be made from populations in western North America. Although molecular techniques are frequently employed to determine either or both phylogenetic relationships and parentage, the present studies use quantitative traits because of their suitability for estimating genetic variances in growth potentials and other adaptive traits (Yang et al. 1996) and, therefore, for assessing adaptation and responses to selection (Lynch 1966). Throughout this paper, the term 'provenance' is used to designate a geographic location; 'population' refers to the individuals at that location and their wind-pollinated descendants. Because the trees originally introduced to Argentina have passed through one generation in their foreign environment, they represent fledgling land races.

Common sense dictates that when introducing tree species into foreign environments, success requires the foreign climate to approximate that of the native. In northwest Patagonia, the climate is relatively mild, with a mean annual temperature of about 8 °C, mean temperature in the coldest month of -2 °C, mean temperature in the warmest month of 23 °C, and precipitation in the forest-steppe ecotone between 500 and 800 mm (De Fina 1972; Bustos and Rocchi 1993). Climate data for western North America (National Oceanic and Atmospheric Association 1994; Environment Canada 1994) show that analogues to these climates recur sporadically within the ponderosa pine and Douglas-fir distributions of North America.

Materials and methods

Wind-pollinated seeds have been routinely collected for afforestation from the land races growing in Argentina. A sample of these seeds was imported to the United States where they were grown along with North American populations (Tables 1 and 2) in designed experiments conducted at Moscow, Idaho (latitude, 46.7°N; longitude, 117°W; elevation, 685m) that allowed the land races and native populations to be compared according to the patterns of shoot elongation.

Morphological characteristics of the mature trees originally introduced to Argentina demonstrate that the ponderosa land race was var. *ponderosa* while that of the Douglas-fir land race was of var. *menziesii*. Consequently,

Table 1. Name and geographic location of ponderosa pine provenances, mean (v_{il}) values for the first principal component, and Euclidean distances (D) from the Argentine land race.

code	race ¹	provenance	latitude (°E)	longitude (°W)	elevation (m)	v_{il}	D
7	NP	Hoodoo Creek, Idaho	48.05	116.83	700	1.36	2.66
2	P	Siskiyou Mountains, Oregon	42.17	123.67	600	1.28	2.49
1	P	Willamette Valley, Oregon	44.25	122.67	200	1.23	2.72
6	NP	Pend O'rielle River, Idaho	48.41	117.30	630	0.88	2.26
5	A	Thomason Creek, Idaho	48.30	117.65	580	0.70	2.13
3	NP	Argentine land race	–	–	–	–1.07	0.00
8	NP	Three Mile, Idaho	44.98	116.22	1340	–1.13	1.35
9	NP	Bitterroot River, Montana	46.48	114.20	1225	–1.63	1.32
4	P	Truckee, California	39.33	120.08	1900	–1.74	0.98

¹NP, North Plateau; P, Pacific; A, Argentine land race

the ponderosa pine land race was tested against eight native populations of var. *ponderosa* (Table 1), three of the Pacific race (see Conkle and Critchfield 1988) and four of North Plateau race. Of the latter, three (numbers 5, 6, and 7, Table 1) were Idaho populations that had demonstrated a high growth potential in tests conducted previously in North America (see Rehfeldt 1991, 1993). The Douglas-fir land race was compared against 19 populations (Table 2): 13 of var. *menziesii* from moderately low elevations in coastal locations, three from the British Columbia transition between the coastal and interior (var. *glauca*) varieties, and three of the interior variety. One of the coastal populations (number 5, Table 2) was a mixture of four promising full-sib families from British Columbia's coastal breeding program. Seeds of the land races and many of the provenances were obtained from reforestation coffers and thereby represent bulked collections of an unknown number of maternal trees.

The experimental procedures paralleled those used frequently (e.g., Rehfeldt 1991, 1993) for studying genetic variation in conifers in western North America. Seedlings were grown in plastic containers (740 cm³) arranged in a randomized complete block design with three blocks that provided a maximum of 27 seedlings for each population and land race. The seedlings were grown for 2 yrs in a shadehouse (50% shade) under optimal moisture and fertilizer. Shoot elongation of each seedling during yr 2 was measured at frequent intervals (approximately 7 days for ponderosa pine and 10 days for Douglas-fir) and was modeled with a modified logistic function (Rehfeldt and Wykoff 1981). Eleven measurements were available for ponderosa pine while 12 were available for Douglas-fir.

Table 2. Name and geographic location of Douglas-fir provenances, mean (v_{il}) value for the first principal component, and Euclidean distances (D) from the Argentine land race.

code	variety ¹	provenance	latitude (°E)	longitude (°W)	elevation (m)	v_{il}	D
5	C	Coastal British Columbia breeding zone	–	–	–	1.78	1.40
14	C	Rockport, Washington	48.50	121.62	150	1.63	1.38
16	C	Granite Falls, Washington	48.00	121.90	150	1.19	1.31
17	C	Raymond, Washington	46.70	123.62	150	1.11	1.32
11	C	Olympia, Washington	47.03	123.08	140	0.69	0.78
6	A	Argentine land race	–	–	–	0.47	0.00
13	C	Clearwater, Washington	47.65	124.10	450	0.40	1.84
8	C	Lacomb, Oregon	44.58	22.70	276	0.38	0.63
7	C	Eddyville, Oregon	44.67	123.75	50	0.31	1.25
9	C	North Bend, Washington	47.52	121.90	235	0.14	0.82
15	C	Quilcene, Washington	47.82	122.90	100	0.08	0.89
10	C	Cathlamet, Washington	46.18	123.37	40	0.04	1.19
18	C	Skamakawa, Washington	46.35	123.43	250	–0.19	1.27
12	C	Stevenson, Washington	45.65	121.92	150	–0.25	1.11
3	T	D’arcy, British Columbia	50.55	122.50	270	–0.39	1.22
4	T	Nahatlatch, British Columbia	49.98	121.48	305	–0.62	1.61
2	T	Lonesome Lake, British Columbia	52.22	125.70	475	–0.95	1.43
19	I	Priest River Experimental Forest, Idaho	48.33	116.83	790	–1.03	2.26
1	I	Shuswap Lake, British Columbia	51.00	119.63	830	–1.57	2.66
20	I	O’Hara Creek, Idaho	46.00	115.50	1000	–3.28	4.13

¹C, coastal; T, transition; I, interior.

The logistic functions were used to estimate the (1) start of shoot elongation, the day on which 5 mm of elongation had occurred; (2) initiation of rapid elongation, the day on which 20 mm of elongation had occurred; (3) cessation of elongation, the day on which all but 5 mm of elongation had occurred; (4) duration of elongation, the number of days between initiation and cessation; (5) rate of elongation, the amount of elongation per day over the period during which 20% to 80% of the annual elongation had occurred; and (6) total elongation. Additional variables included 2-yr height and the residual from

the regression of 2-yr height on 1-yr height. The last variable quantifies 2-yr growth after the effects of autocorrelation of previous height measurements are removed and, therefore, maternal effects such as seed weight are eliminated. For ponderosa pine, each tree also was scored according to the color (bright green or blue-green) of the succulent 2-yr shoot, a variable that has been effectively used to distinguish geographic races (Wells 1964; Read 1980).

Principal component analyses using the correlation matrix were made to reduce the number of dimensions according to which comparisons were to be made. Analyses of variance under a model of random effects were made to determine for which of the principal components populations differed significantly. The degree of similarity of each population to the Argentine land race was assessed by (1) determining if population means for each principal component fell within the confidence interval ($\alpha = 0.05$) of the land race, and (2) calculating a Euclidian distance between a population and the land race as:

$$D = \left[\sum (v_{ij} - v_{Aj})^2 \right]^{1/2}$$

where v_{ij} is the score of population i for principal component j , and v_{Aj} is the component j mean for the Argentine land race. All statistical analyses used the algorithms of SAS (1996).

Results

In accord with the rich literature describing geographic variation among provenances of ponderosa pine (e.g., Squillace and Silen 1962; Wells 1964) and Douglas-fir (e.g., Munger and Morris 1936), the populations tested in this study exhibited much different patterns of shoot elongation (Figures 1 and 2). Quite fortuitously, the patterns displayed by the Argentine land races were intermediate.

Analyses of variance detected differences among populations ($\alpha \leq 0.05$) of both species for the first four principal components. For ponderosa pine, eigenvalues of these four components sequentially accounted for 51, 21, 14, and 10% of the total variance and thereby accounted for 96% of the variance within the system of 9 variables. For Douglas-fir, the first four accounted for 52, 25, 19 and 3% of the total variance, respectively, and thereby accounted for essentially all of the variance within the system of eight variables.

Eigenvectors for the first two principal components were of remarkably similar composition in the two analyses. The first principal component represented innate growth potential, with variables contributing to a large stature

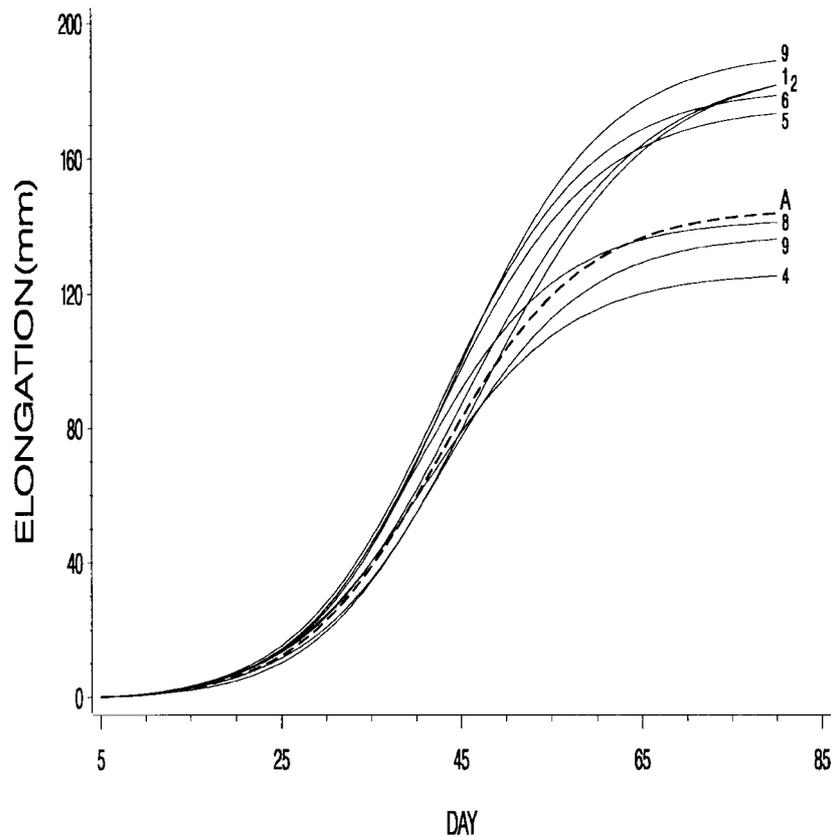


Figure 1. Modeled shoot elongation of 9 ponderosa pine populations. Hash line (–) is the Argentine land race (A). Days are numbered consecutively after March 25. Population numbers are aligned with provenance codes of Table 1.

(amount, cessation, duration, and rate of shoot elongation; 2-yr height; and the residual from the regression of 2-yr height on first year height) receiving strong positive weights. The second component was controlled primarily by the initiation and start of shoot elongation. Although the fourth component for ponderosa pine primarily reflected stem color, the control of principal components other than the first two was otherwise obscure.

Only one ponderosa pine population, Truckee (Table 1), did not differ significantly from the Argentine land race for any of the principal components. Euclidean distances, moreover, also indicated that Truckee was the most similar to the land race (Table 1). Because both the Truckee provenance and the land race had low growth potentials, the populations that were the most dissimilar to the land race were those with the highest growth potentials, regardless of geographic origin. In addition, about 50% of trees from both

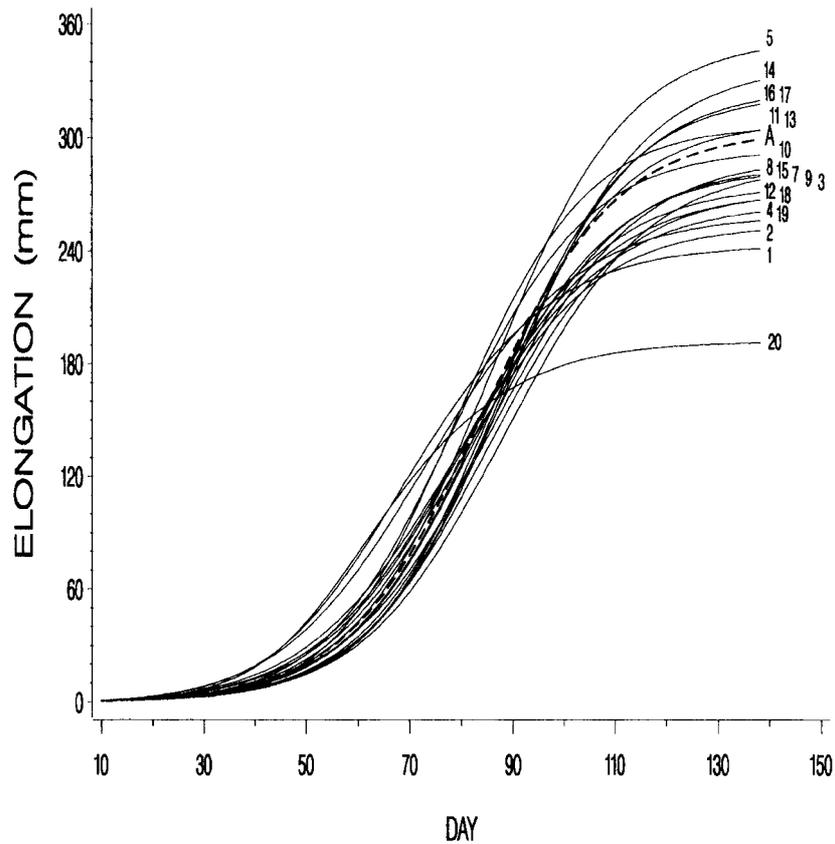


Figure 2. Modeled shoot elongation of 20 Douglas-fir populations. Hash line (—) is the Argentine land race. Days are numbered consecutively after March 25. Population numbers are aligned with provenance codes of Table 2.

Truckee and the land race had blue-green succulent shoots, whereas other populations had <20%.

For Douglas-fir, all native populations differed significantly from the Argentine land race for one or more of the principal components. The distance measures suggested that the land race was most similar with populations from moderately low elevations in either the coastal ranges of Oregon (Lacomb, Table 2) or from the Puget Sound (Quilcene, Olympia, North Bend) of Washington. Although the growth potential of the land race was higher than that of most of the provenances tested, it was inferior to the genotypes being produced in the first generation of British Columbia's coastal breeding program (Figure 2).

Discussion

The different patterns of shoot elongation displayed by populations of both species reflect variation not only in growth potential but also in environmental adaptations. Shoot elongation is the most conspicuous event in an annual sequence that begins with dehardening in the spring; includes shoot elongation, leaf expansion, bud development, diameter growth, and lignification; and concludes with cold acclimation. As described by Dietrichson (1964), this sequence has been molded to fit a general temperature regime. In the mountains of western North America where ponderosa pine and Douglas-fir grow naturally, a general climatic gradient occurs from maritime to continental on which is superimposed steep altitudinal gradients whereby temperatures decrease by 6 °C across 1000 m of elevation (Rosenberg 1974). This complex of climatic gradients can thus provide powerful evolutionary forces. Patterns of shoot elongation in young trees are viewed as a key to understanding adaptive differences among populations of these montane species (see Rehfeldt 1991, 1993).

Our comparisons thus involve adaptive traits. Therefore, even though the use of quantitative traits in plant systematics is well founded (Fisher 1936), one must recognize that microevolution resulting from a single generation of selection in the climate of Patagonia could produce genotypes atypical of native populations. Nonetheless, results from such comparisons can provide an assessment of genetic similarities among populations from which practical conclusions can be drawn.

Shoot elongation in the ponderosa pine land race occurred at a slow rate and ceased early (Figure 1), and, as a result, the amount of elongation was low and 2-yr height was small. These characteristics, coupled with the relatively high proportion of trees with blue-green succulent shoots, were more typical of a provenance from the high elevations near Truckee, California than of any of the other provenances tested. Trees from Truckee, however, exhibited a growth potential that was considerably less than the land race (Table 1, Figure 1), suggesting perhaps that the progenitors of the land race originated from climates in California that were milder than at 1900 m near Truckee.

For Douglas-fir, none of the 19 native provenances showed a statistically satisfying similarity with the Argentine land race. Still, shoot elongation in the land race was extended across a relatively long period and occurred at a rapid rate; total elongation, therefore, was relatively high. This pattern aligned the land race with provenances in maritime climates at moderately low elevations. However, like ponderosa pine, the progenitors of the Douglas-fir land race may also have been from mild climates in California rather than the coastal Washington and British Columbia provenances against which it was

compared. For both species, therefore, it is unfortunate that our comparisons neglected populations from low elevations in California.

Recommendations from these results for the Argentine introduction programs are particularly relevant to ponderosa pine, largely because the growth potential of the Argentine land race is far inferior to that of many existing provenances. The results suggest, therefore, that optimizing the growth potential of ponderosa pine in Patagonia should be based on the outcome of trials that consider genotypes from low elevations in northern Idaho, northeastern Washington, and northern California. For Douglas-fir, however, the growth potential of the land race was relatively high. It is debatable, therefore, whether attempts to increase the growth potential of the land race should concentrate on selections within the race itself or whether the genetic base should be augmented with fast growing Washington populations such as those from Rockport, Granite Falls, or Raymond. To this end, it would be desirable first to have measures of genetic diversity of the land races. Regardless, future introductions of both species most definitely should include improved races from coastal breeding programs in the United States and Canada.

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