Similarly, if rooted cuttings are used in extensive refor-estation, and clones of different or undesirable maturation states are employed, then undesirable or unnecessarily variable growth rates or other characteristics may result.

Forest-tree breeders may be able to affect the utility of a clone by manipulation of the cutting donor's maturation state. For example, cuttings from more mature radiata pines typically produce trees with less volume, but they develop better stem form, have fewer and smaller knots, and take less time to prune, compared to juvenile cuttings or seedlings. If the objective is high-quality lumber pro-duction, then management may be willing to sacrifice some per-tree volume growth for these better bole characteristics, perhaps reducing initial spacing to recover some unit-area volume production. If the objective is high per-tree stem volume, or biomass for energy production, then a juvenile maturation state seems most desirable. Experiments are now in progress to determine whether different maturation states can effectively be set and maintained, depending on the height of the hedge. These same experiments are investigating whether low and frequent hedging maintains a very juvenile maturation state, similar to that of young seedlings.

The study reported in this paper, in concurrence with several others, indicates that hedging at least slows and perhaps arrests the maturation rate of cutting donors. Furthermore, the effects of hedging on growth and form of rooted cuttings are detectable (in fact, are increasingly detectable) during the first 7 growing seasons after planting cuttings from hedge and tree-form donors of the same clone.

Acknowledgements

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Differentation of Larix occidentalis Populations from the Northern Rocky Mountains

By G. E. Rehfeldt[1]

Summary

Differentiation of populations of Larix occidentalis was studied in 2-year-old seedlings representing 82 populations from the Northern Rocky Mountains. Nursery studies of growth and phenology in three contrasting environments and laboratory tests of cold hardiness were used to assess differentiation. In accord with exogenous control of shoot growth, effects of nursery environments on growth and phenology were strong. Analyses of variance detected population differentiation for growth potential, phenology, and hardiness of buds when tissues were near maximum hardiness.

Multiple regression analyses related population differen-tiation to geographic, ecologic, and physiographic variables.

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Elevation of the seed source most strongly influenced re-gression analyses which accounted for 21, 39, 47, and 53 percent of the variance among populations in hardiness of buds,, bud burst, bud set, and height, respectively. Re-gression models suggested that seed transfer can be rela-tively broad geographically, but limited to ± 225 m alti-tudinally.

Key words: population differentiation, seed transfer, Larix occi-dentalis.

Zusammenfassung

Unterschiede zwischen Populationen von Larix occiden-talis wurden anhand zweijähriger Sämlinge von 82 Her-künften der nördlichen Rocky Mountains untersucht. Baum-schuluntersuchungen für Höhe und Phänologie an drei kontrastierenden Standorten und Labortests der Frost-härte wurden verwendet, um die Unterschiede zu schätzen. Der Baumschulstandort hatte auf Triebwachstum und Phä-nologie einen signifikanten Einfluß. Varianzanalysen erga-

ben Populationsunterschiede für Wuchspotential, Phänologie und Frosthärte der Knospen. Multiple Regressionsanalysen brachten die Populationsunterschiede mit geographischen, ökologischen und physiographischen Variabeln in Beziehung. Die Höhenlage der Saatgutherkunft beeinflußte die Regressionsanalysen am stärksten und machte 21, 39, 47 und 53% der Varianz zwischen Populationen in Knospenhärte, Austrieb, Vegetationsabschluß bzw. Höhe aus. Regressionsmodelle machen deutlich, daß ein Samentransfer über große Entfernungen möglich ist, wenn der Höhenunterschied ± 225 m nicht übersteigt.

Introduction

The ecological genetics, genetic structure of populations, and quantitative genetics of western larch *(Larix occidentalis),* the fastest growing conifer in the Northern Rocky Mountains (SCHMIDT *et al.* 1976), are virtually unknown. Because interest in tree improvement of larch has recently developed, a supportive program in genetics research has been initiated. The present study of adaptive differentiation relates patterns of variation in phenology, growth potential, and cold hardiness to seed transfer rules and breeding zones within which tree improvement will be concentrated.

As discussed by SCHMIDT *et al.* (1976), most of the botanical and commercial range of western larch lies within the Northern Rocky Mountains *(Figure 1).* In this region, western larch has achieved adaptation to environments of extreme heterogeneity. A climate with a decided maritime component on the west and northwest gradually becomes continental as westerly air masses cross a series of rugged mountain ranges; superimposed on climatic trends are the strong effects of topography in mountainous terrain (DAU-

BENMIRE and DAUBENMIRE 1968). And everywhere, western larch, an early successional species, displays a broad ecological amplitude. At elevations as low as 600 m, larch may occur on habitat types as dry as the *Pseudotsuga menziesii/Physocarpus malvaceous,* or as moist as the *Tsuga heterophylla/Clintonia uniflora;* and, at elevations near 2000 m, larch is a component of the cold subalpine forests dominated by *Abies lasiocarpa* (PFISTER *et al.* 1977).

Materials and Methods

Seedlings derived from wind pollinations in 82 populations *(Figure 1)* were grown for 1 year in plastic containers (65 cm³) arranged in unreplicated plots in a shadehouse at Moscow, Idaho. Populations were represented by a mixture of seeds from 10 trees that had been selected for the Inland Empire Cooperative Tree Improvement Program. Consequently, the growth and form of selected trees were above the phenotypic mean of each population. Although this nonrandom sample may upwardly bias estimates of growth potential, assessment of ecological adaptations should not be affected. The populations represented altitudes from 600 to 1700 m and reflected the ecological amplitude of the species within the region of study.

First-year seedlings were transplanted in early autumn into three contrasting environments. At Moscow, Idaho (latitude 46.5⁰, elevation 800 m, growing season 130 days), seedlings were transplanted into beds containing a mixture of peat and vermiculite (1:1) to a depth of 30 cm. A nursery at the Priest River Experimental Forest, 190 km north of Moscow, represented a cool environment (90-day growing season) at low elevation (700 m) with a residual forest
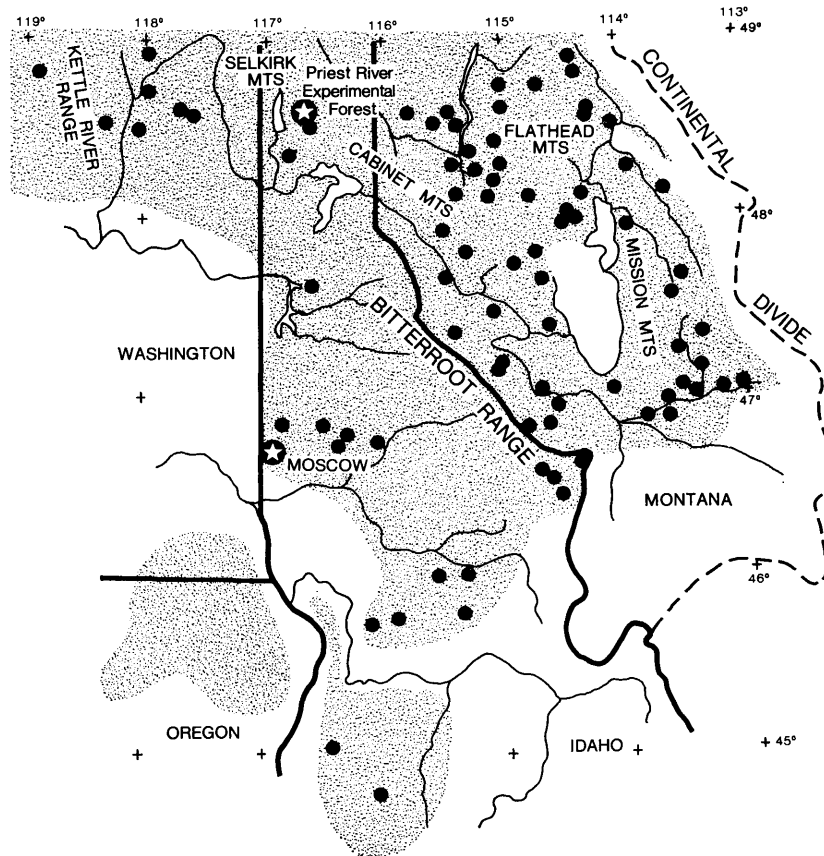

Figure 1. — Drainage map of the northern Rocky Mountains showing the general distribution of larch (shading) and location of populations in relation to individual mountain ranges.

soil. And finally, nursery beds at Tarlac provided a cold environment at 1500 m elevation on the Priest River forest. Here, seedlings were planted in the residual soil from which rocks, roots, and competing vegetation had been removed before tilling.

A randomized complete block design was used at all locations. Two blocks were established at Moscow and Tarlac, but only one block was planted at the Priest River nursery. Populations were represented in each block by two 7-tree row plots. Plots were randomly distributed. Fifteen cm separated rows and seedlings within rows.

The following data were obtained from each plot in all blocks:

1. The day after March 1 by which 50 percent of the seedlings had burst bud during the second growing season.
2. The week (transformed to $\sqrt{X + 1/2}$) after July 21 by which 50 percent of the seedlings had set buds during the second growing season.
3. Mean 2-year height (cm).

Following completion of nursery studies, freezing tests (LEVITT 1972) were conducted to assess cold hardiness of populations. During November, at least 1 month after frosts had occurred in all nurseries, the terminal shoot from the current growing season was cut from each seedling, moistened, packaged in plastic bags, and stored at 2°C. Soon after, 8 sets of 10 twigs (8 to 10 cm long) containing a terminal bud were cut for each population in order to assess differentiation of populations in hardiness of buds. Likewise, 8 sets of 10 twigs were packaged for each population to assess hardiness of wood. Each set contained one twig from each of 10 seedlings.

In accord with the procedures of SAKAI and WEISER (1973), maximal levels of hardiness were induced by storing plant materials for 2 weeks at −3° C, for 1 week at −5° C, and for 3 days at −10° C. Thereafter, temperatures were decreased at the rate of 5° C per day in a freezing chamber equipped with two fans for providing circulation. Hardiness of buds was tested at −35° C, −40° C, −45° C, and −50° C; that of wood samples was tested at −50° C, −56° C, −62° C, −68° C, and −75° C. Appropriate test temperatures were inferred from data presented by SAKAI and WEISER (1973). Two sets of 10 twigs from each population were frozen to each test temperature. Twigs were removed from the freezer according to remote sensing of internal air temperatures, were stored for 24 hours at −17° C, thawed for 24 hours at 2° C, and placed in a greenhouse with cut ends immersed in water within plastic cups. After 1 week, damage was scored according to discoloration of tissue. The proportion of twigs or buds damaged was recorded for both sets from each population at all test temperatures.

Statistical analyses of population differentiation in nursery environments involved an analysis of variance of growth potential and phenology according to a model of random effects:

$$X_{ijkl} = \mu + n_i + r_{ij} + p_k + g_{ik} + e_{ijk} + \delta_{ijkl}$$

where X = the growth or phenology of seedlings in plot l of population k in replicate j of environment i; μ = overall mean; n = effects of environment i; r = effects of replicate j in environment i; p_k = effects of population k; g_{ik} = interaction of nursery i with population k; e_{ijk} = interaction of population k with replicate j in environment i; and δ_{ijkl} = the effects of plot l within population k of replicate j in environment i.

Analyses of variance for freezing injury were made according to the model of random effects:

$$X_{ijk} = \mu + t_i + r_{ij} + p_k + g_{ik} + e$$

where X_{ijk} = injury (arcsin $\sqrt{\%}$ in radians) to population k of replicate j in temperature i, μ = overall mean; t_i = effect of temperature i; r_{ij} = effect of replicate j within temperature i; p_k = contribution of population k; g_{ik} = interaction of population k in temperature i and e = residual.

Regression techniques were used to relate variation among populations to geographic, physiognomic, and ecologic criteria of the seed sources. Twenty-eight independent variables, both quantitative and qualitative, were screened for association with growth potential, phenology, and cold hardiness: elevation, latitude, longitude, northwest departure, state (Montana or Idaho), latitude in each state, longitude in states, elevation in states, northwest departure in states, Idaho departure in states, the six major drainages along which populations were concentrated (Figure 1), and six major habitat types of PFISTER et al. (1977). Of the independent variables, the boundary between Idaho and Montana generally follows the crests of the Bitterroot and Cabinet Mountains. These mountains not only alter climatic and ecologic conditions (DAUBENMIRE and DAUBENMIRE 1968), but they also influence patterns of genetic variation in Pseudotsuga menziesii (WRIGHT et al. 1971, REHFELDT 1978) and in Pinus contorta (REHFELDT 1980a). Northwest departure is the distance along an imaginary grid that runs from northwest to southeast in general accord with the orientation of the Bitterroot Mountains (Figure 1). Idaho departure is the distance from the boundary between Idaho and Montana. All statistical analyses involving qualitative variables were made by fitting constants, values of zero or one (DRAPER and SMITH 1966).

Univariate associations of the mean growth, phenology, or cold hardiness of populations with variables describing population origin revealed that the elevation of the seed source was generally the most closely associated with population differentiation. Moreover, the relationships between elevation and performance were essentially the same for populations from Montana as for those from Idaho. Consequently, to simplify assessment of geographic variation, population performance was first related to elevation according to the model:

$$Y_i = b_0 + b_1 X_i$$

where Y_i is the mean performance (growth, phenology, or cold hardiness) of population i; b's are regression coefficients; and X_i is the elevation of population i. Residuals from these regressions, calculated as the difference between observed and predicted values, were randomly distributed with respect to elevation.

Residuals were related to geographic variables according to a linear stepwise regression program for maximizing R^2, the goodness of fit. This procedure (BARR et al. 1979) is begun by the selection of a model with one independent variable that explains the most variance in the dependent variable. Next, the variable that contributes the greatest increase in R^2 is added to the model. Then, all independent variables in the model are compared to those not in the model to determine if R^2 can be increased by substitution of variables. After the "best" two-variable model is selected, similar evaluations are begun for selecting the "best" three-

variable model. The process ends when no improvement is possible for R^2.

Results

Environments exerted a tremendous effect on phenology and growth *(Table 1)*. These effects are readily apparent in mean values: as compared to seedlings growing at Tarlac, seedlings growing at Moscow burst bud nearly 2 months earlier, set buds about 1.5 weeks earlier, and were 25 cm taller *(Table 2)*. The tallest trees at Moscow were nearly 80 cm while those at Tarlac were only 34 cm. As evidenced in the range of mean values for populations *(Table 1)*, variances, however, differed greatly at the three sites. In fact, tests of homogeneity of variances (STEELE and TORRIE 1960) were decidedly significant (P < .001) for all variables. Therefore, analyses of variance were made on standardized normal deviates (STEELE and TORRIE 1960) that provided homogeneity:

$$Z = \frac{X_i - \overline{X}_i}{\sigma_i}$$

where Z is a standard normal deviate; X_i and $\overline{X}_i$ are values of an observation and its mean at site i, and σ_i is the standard deviation at site i.

Analyses of variance of phenology and growth potential *(Table 2)* were dominated by the main effects of populations. On the average, populations differed by as much as 7.3 days in bud burst, 2.7 weeks in bud set, and 18 cm in height. Moreover, differences among populations were essentially the same in all environments.

Results of freezing tests corresponded to those of SAKAI and WEISER (1973). Near maximum hardiness, 5 percent of the larch buds were damaged at -35^0 C, 15 percent were damaged at -40^0 C, 50 percent were damaged at -45^0 C, and 98 percent were damaged at -50^0 C. No damage was observed, however, to wood samples at -75^0 C, the coldest temperature tested! While hardiness of woody tissues of all populations was equally and extremely high, populations differed in the proportion of buds injured *(Table 3)*. Even though test temperatures spanned only 15^0 C, mean injury to populations varied from 38 to 61 percent. But, differences among populations were detected at a relatively

Table 1. — Environmental means and range of population means for growth and phenology according to nursery.

	Moscow	Priest River	Tarlac
Bud burst (days)			
Mean	21.8	46.7	71.2
Range	12.0	3.5	7.2
Bud set (weeks)			
Mean	6.9	7.0	8.3
Range	3.4	4.4	1.2
Height (cm)			
Mean	48.6	38.1	23.2
Range	31.1	23.8	10.5

Table 2. — Mean squares of standardized normal deviates from analyses of variance of growth potential and phenology.

Source of variance	Degrees of freedom	Bud burst	Bud set	Height
Environments	2	0.0004	0	0
Blocks/environments	2	1.2692	2.2563	49.3508**
Populations	81	2.6117**	2.2758**	3.0065**
Environments x populations	162	1.0092	.8594	.8896*
Block interactions	162	.6928	.9414	.5276
Among plots	410	.7978	.8203	.5982

* Statistical significance at the .05 level of probability.
** Statistical significance at the .01 level of probability.

low probability (0.05). On the one hand, the low probability could reflect relatively large sampling errors. On the other hand, the residual variance, which represents a sampling error *(Table 3)*, is only slightly larger than the theoretical variance (0.025) of an observation from a binomial distribution based on samples of 10 (STEELE and TORRIE 1960). This correspondence between the residual and theoretical variance implies relatively high statistical precision. Moreover, previous freezing tests could not differentiate larch populations according to hardiness in September (REHFELDT 1980b). Thus, populations may differ in maximum hardiness of buds, but differences seem small.

Regression of mean values for growth, phenology, and hardiness of buds on elevation of the seed source *(Table 4)* showed that elevation alone accounted for significant proportions of variance in all dependent variables except hardiness. Not only were the effects of elevation similar for populations from Montana as for populations farther west, but also, effects of elevation were relatively independent of other geographic variables. Populations from relatively low and high elevations were represented in all

Table 3. — Results of the analysis of variance of freezing injury to buds.

Source of variance	Degrees of freedom	Mean square
Temperatures	3	57.6353**
Replication in temperatures	4	.1270
Populations	81	.0580*
Temperatures x populations	243	.0424
Residual	324	.0308

* Statistical significance at the .05 level of probability.
** Statistical significance at the .01 level of probability.

major river drainages; and simple correlations of elevation with latitude ($r = -.31$) and longitude ($r = -.38$) were significant (1 percent level), but accounted for relatively little covariance. Thus, regardless of geographic origin, populations separated by 1,000 m differed by an average of 1.4 days in bud burst, 1.1 weeks bud set, 7.8 cm (21 percent) height, but only 4 percent in hardiness of buds.

Stepwise multiple regression models account for variance residual to that determined by elevation alone. Thus, results of stepwise analyses illustrate geographic patterns of variation relatively independent of elevation. For bud burst, the model that accounted for the most residual variance included 9 independent variables and produced an R^2 of 0.34; that for bud set included 7 variables with $R^2 = 0.24$; that for height included 7 variables with $R^2 = 0.40$; and that for injury to buds included 5 variables with $R^2 = 0.18$. Consequently, the elevational and geographic models together accounted for 39 percent of the variance among populations in bud burst, 47 percent for bud set, 53 percent for height, and 21 percent for hardiness.

Patterns of geographic variation depicted by multiple regression models are presented as contours of equal performance (Figures 2 to 5). Relatively consistent patterns of variation are illustrated for most variables. First, the in-

Table 4. — Results of regressions of growth potential and phenology on elevation (m) of the seed source.

Statistic	Bud burst	Bud set	Height	Freezing injury
b_0	44.738	3.0682	46.213	0.680
b_1	0.00145	-0.00019	-0.0776	6.947×10^{-5}
R^2	.08**	.30**	.22**	.03
$s_{y \cdot x}$	1.15	.0675	3.28	.082

** Statistical significance at the .01 level of probability.

Figure 2. — Results of the multiple regression model describing geographic variation in bud burst. Contour interval scaled to a value = 1/2 [lsd(.2)] = 0.6 days.

Figure 3. — Results of the multiple regression model describing geographic variation in bud set. Contour interval scaled to a value = 1/2 [lsd (.2)] = 0.25 weeks.

Figure 4. — Results of the multiple regression model describing geographic variation in 2-year height. Contour interval = 1/2 [lsd (.2] = 18 cm.

fluence of the rugged Bitterroot Range and Mission Mountains is obvious on patterns of differentiation for all variables. Secondly, a clinal pattern of variation for all variables, except hardiness, is generally associated with latitude in northern Idaho. All traits seem to vary clinally across eastern Washington and extreme northern Idaho in general correlation with longitude. Finally, growth potential, bud set, and cold injury of populations increase with distance from a region of low values in Montana. This pattern is the reverse of that for Larix decidua: growth potential decreases with distance from a central region of high growth potential (GIERTYCH 1979).

The contour intervals chosen to illustrate geographic differentiation are scaled to a value equalling one-half of the least significant difference among populations at the

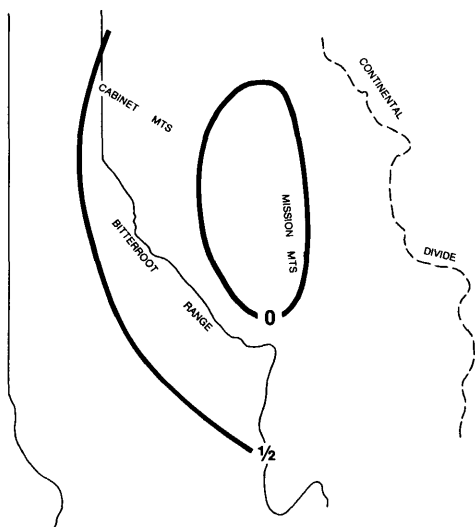80 percent level of probability *(lsd* (.2)). This value of *lsd,* calculated from results of the analysis of variance, but expressed in units of the original measurements, is based on a relatively low level of probability in order to reduce the possibilities of Type II errors, accepting no differences when differences actually exist (STEELE and TORRIE 1960). Thus, the figures not only illustrate patterns of geographic variation, but also express an approximate geographic interval associated with differences among populations at a probability of about 80 percent.

Discussion

Results reflect the exogenous nature of shoot growth in *Larix.* Since long shoot buds are composed primarily of early leaf primordia, relatively little shoot elongation is predetermined (CLAUSEN and KOZLOWSKI 1970). Because shoot elongation is essentially free growth, both the amount and the periodicity of elongation are controlled by the environment during the current growing season. Thus, nursery environments exerted tremendous influence on growth and phenology. In addition, exogenous shoot elongation in contrasting nursery environments produced extremely heterogeneous variances that needed correction before population differentiation could be assessed.

Populations differed in phenology, growth potential and cold hardiness of buds. The differences, however, were not dependent on the environment. While populations from high elevations should express greatest adaptation and growth at the Tarlac site, those particular environmental effects eliciting expression of associated adaptations did not occur in the short duration of the study. Consequently, differential adaptation must be inferred from the main effects of populations and their patterns of variation.

A portion of the variation among populations was related to elevation. For elevation to influence differentiation is not surprising. It is well known that the length of the growing season is negatively related to altitude. Thus, with increasing elevation of the seed source, bud burst was delayed, bud set occurred earlier, and growth potential declined. Only maximum hardiness of buds inexplicably was not related to elevation of the seed source.

Geographic patterns of variation conform to the physiography, ecology, and climate of the region. As reflected in the distribution of plant communities in the northern Rockies, the maritime influence in westerly air masses declines with the crossing of each mountain range (DAUBENMIRE and DAUBENMIRE 1968, PFISTER et al. 1977). Thus, the Bitterroot and Cabinet Mountains sufficiently alter air masses such that environments are more continental, and thus, more severe in Montana than in northern Idaho. Like current results, patterns of adaptive variation in *Pseudotsuga menziesii* (WRIGHT et al. 1971, REHFELDT 1978) and in *Pinus contorta* (REHFELDT 1980a) also appear discontinuous between Idaho and Montana. Secondly, the region east of the Mission Mountains is nestled between two rugged mountain ranges that reach over 3000 m altitude. As a result, this region is rather moist. In association, patterns of geographic variation relate to the position of the Mission Mountains. Finally, the region in western Montana where populations tend to be of lowest growth potential and greatest hardiness *(Figures 2 to 5)* corresponds to a dry, nonforested area *(Figure 1).* One can assume, therefore, that populations adjacent to this prairie occupy severe environments that approach the limit of ecological tolerance of the species.

From patterns of adaptive differentiation, guidelines can be developed for limiting the transfer of seed in reforestation, and, thereby, minimizing maladaptation in planted trees. Such guidelines are also used in tree improvement to delimit breeding zones within which genetic gains may accrue without inadvertent degeneration of adaptive traits. One approach to zoning incorporates results of analyses of variance with those of multiple regression to depict appropriate geographic and ecologic limits to seed transfer (REHFELDT 1979a). Accordingly, the expression lsd (.2)/b [where lsd (.2) = least significant difference at the 80 percent level of probability, and b is the regression coefficient] represents, for the present data, an elevational interval across which differences among populations can be detected with a probability of about 80 percent. These intervals involve 895 m for bud burst, 447 m for bud set, 464 m for height and 1900 m for freezing injury. Therefore, as a general guideline, seed zones should be about 450 m broad and transfers of seed reforestation should be limited to ± 225 m from a given seed source.

Since the contours used to illustrate regression models *(Figures 2 to 5)* are based on values of lsd, geographic limits for seed transfer can be inferred directly from the figures. In general, seed for reforestation should not be transferred more than ± 1 contour [± 1/2 lsd (.2)] from a given source, and breeding zones should be limited to about two contours. Consequently, three geographic zones seem suitable for the region as a whole: (1) Idaho south of 48° latitude, (2) eastern Washington and Idaho north of 48°; and (3) western Montana.

In addition, the present results add to those accumulating on the adaptation of forest trees to the heterogeneous environments of the Northern Rocky Mountains. At one extreme is *Pseudotsuga menziesii*, a species for which population differentiation is closely related to elevation, geography and physiography in both inland (REHFELDT 1979a) and coastal (CAMPBELL 1979) environments. At the other extreme is *Pinus monticola*, a species for which essentially all the genetic variability is within populations (STEINHOFF 1979, REHFELDT 1979b). *Pinus ponderosa* (REHFELDT 1980c) and now western larch seem intermediate.

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Regardless, regression models accounted for about half of the variance among populations. Although the unexplained variance could be random, it could also reflect adaptation of populations to environmental variables not considered in regression models. Because the present data constitute the genetics literature for western larch and because the data involve trees that were only 2 years old, there is little doubt that additional tests are needed to fully assess ecological adaptation within the species. Nevertheless, the observed patterns of variation are not only statistically detectable, but they are also clearly related to the environment. Therefore, until refined by additional tests, the present results are suitable for establishing breeding zones in tree improvement and for limiting seed transfer in artificial reforestation.

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Self Incompatibility in Gmelina arborea L. (Verbenaceae)

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Summary

G. arborea, a medium-sized to large tree native to the tropical forests of South and East Asia, is widely cultivated in tropical regions. Investigations of the pollination biology and the breeding system, conducted on trees cultivated in Costa Rica, reveal that the species is self-incompatible and pollinated by medium-sized to large bees. The abundant fruit set on Costa Rican trees suggest that the native bees are effective as pollination vectors for this species.

Key words: floral biology, pollination biology, apomixis, Costa Rica, pollen tube growth.

Zusammenfassung

Gmelina arborea L., ein mittelgroßer bis großer Baum, der in den tropischen Wäldern Süd- und Ostasiens natürlich vorkommt, wird in tropischen Regionen häufig kultiviert. Untersuchungen der Befruchtungsbiologie in Verbindung mit einem Züchtungsprogramm, die an Bäumen in Costa Rica durchgeführt wurden, zeigen, daß die Art selbstinkompatibel ist und von mittelgroßen bis großen Bienen bestäubt wird. Der reichliche Fruchtansatz der Bäume in Costa Rica macht deutlich, daß die einheimischen Bienen als Pollenüberträger für diese Art effektiv sind.

Introduction

Gmelina arborea L. (Verbenaceae) is a medium-sized to large tree native to the deciduous and semi-deciduous forests of tropical South-east Asia (Troup, 1921; Lamb, 1968; Webb et al., 1980). The species yields excellent timber that is used for a wide variety of purposes, including general light construction, fuel and charcoal, and building poles (Pearson and Brown, 1932; Lamb, 1968; Webb et al., 1980). It is a fast growing plantation forestry species, and in recent years has emerged as a potentially important source of wood pulp (Doat, 1976). As a result, G. arborea plantations are being established throughout the old and new world tropics, and interest has developed to the point that the FAO Panel of Forest Gene Resources considers this species as one of top priority whose gene resources need exploration, utilization, and conservation (Greaves, 1977; Nas, 1980). Despite the considerable commercial potential of this species, not much is known about its reproductive biology, especially factors regulating the quality and quantity of seeds produced. Since most plant breeding involves the regulation of variation through control of the reproductive system, success in breeding programs is contingent upon knowledge concerning the reproductive biology of the spe-

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