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Frequency of Seedlings from Natural Self-Fertilization in Pacific Northwest Ponderosa Pine (Pinus ponderosa Dougl. ex Laws.)

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Summary

Phenotypic mutant markers were used to estimate natural selfing ($\hat{S}$) in 112 trees in 4 regions of the Pacific Northwest: 1) Siskiyou Mountains in southwest Oregon, 2) east side of the Cascade Range in Oregon, 3) Ochoco Mountains east of the Cascades in Oregon, and 4) east side of the Cascades near Wenatchee, Washington. In region 2, stands were classified by whether they were part of the main distribution, part of the forest-high desert ecotone, or disjunct populations. Estimated selfing was also related to filled seed percent in a sample of trees from regions 2 and 3 and to seed survival after several months of storage at room temperature in trees from region 1. Effects of crown position were examined in 6 trees. Mean $\hat{S}$ was 0.091 and 0.076 if trees were excluded that were in disjunct stands and in stands with ponderosa pine as a minor component. Median $\hat{S}$ was 0.056. Difference among regions was not significant; difference among stand types was. Heterogeneity among trees-in-regions was large and significant in all regions. $\hat{S}$ was significantly, but weakly and inversely, correlated with filled seed percent and with seed storability. Seeds from upper crown had lower estimates of selfing than seeds from mid and lower crown, but the difference was not significant.

Key words: Self-pollination, selfing rate, outcrossing rate, mating system, inbreeding, seed yield, seed storability, stand structure, geographic variation, crown level.

FDC: 165.3; 181.521; 174.7 *Pinus ponderosa*.

Introduction

Several reports of controlled and natural inbreeding of ponderosa pine have been published. Sorensen (1970) self- and cross-pollinated 19 trees in 2 stands in the Oregon Cascade Range. Mean percentages of round, normal-appearing seeds that were filled were 23.7 after self-pollination and 66.5 after cross-pollination giving a mean relative self-fertility of 0.367. Wang (1970) reports that germination of sound seeds from selfing was about 45 % that of

sound seed from wind-pollination. Using isozyme gene markers, Mitton et al. (1981) estimated the mean proportion of outcrossed offspring at the viable seed stage to be 0.96 (0.04 self-seed) but found no significant difference among 31 trees in a stand near Boulder, Colorado. Farris and Mitton (1984) reported an outcrossing rate of about 81 % (19 % self-seed) in a scattered stand at the forest-grassland ecotone. Sorensen and Miles (1974) estimate 11.3 % self seedlings in wind-pollination families of 17 ponderosa seed parents based on seedling mortality in self-, cross-, and wind-pollination families.

In the present study, phenotypic mutant markers were used to estimate natural selfing over a broad area in Oregon and Washington. Specific purposes were to 1) obtain a general estimate of natural selfing in Pacific Northwest ponderosa pine; 2) test for geographic, stand type, and individual tree variation in rates of selfing; 3) examine crown level effects on natural selfing; and 4) relate the magnitude of natural selfing to filled seed percent and to seed storability.

Materials and Methods

Distribution of marker-carrying trees

From controlled inbreeding (Sorensen, 1970) and 4 large common garden tests (unpublished), 112 seed parents were identified that carried readily detectable mutant markers (*Table 1*). Seed parent locations for the original common garden studies were distributed at a frequency of about 1 parent per half township (4700 h) to 1 parent per 2 townships (18 500 h) over the sampled area. In about 25% of the sample locations, cones were collected from 2 parents in the same stand; elsewhere from 1 tree per stand. In 2 cases, both trees in a stand carried a mutant marker but not the same one. Seed trees carrying mutant markers constituted about 8 % of the original tested population and were well distributed throughout the sample area.

Table 1. — Classification of mutant phenotypes and their frequencies[1].

Mutant phenotype	Number of families
Pale green cotyledons	24
Yellow cotyledons[2]	26
Albino	20
Cotyledonary lethal[3]	36
Fused cotyledons	3
Kinked cotyledons	1
Green cotyledons, white-tipped needles	1
Green cotyledons, yellow needles	1
Green cotyledons, white needles	1
Thick needles	1
Kinked hypocotyl	1
Budless at the end of first growing season	1

[1] Because some families segregated for more than 1 mutant, the total number of mutants is greater than the total for families.

[2] Includes all ranges of yellowness from slight yellow to yellow with no visually discernable green.

[3] Cotyledons initially green or pale green but turn gray green and wilt before or shortly after seed shed before elongation of primary needles.

Geographically, the trees came from 4 "regions": 1) Siskiyou Mountains of southwest Oregon (southwest Oregon), 31 trees; 2) east slopes of Oregon Cascade Range and extending east to the Warner Mountains in southern Oregon (east Cascades), 53 trees; 3) Ochoco Mountains of central Oregon and eastward to the Blue Mountains (Ochoco/Malheur), 14 trees; and 4) east slopes of the Cascade Range in central Washington (Wenatchee), 14 trees.

Mixed-conifer stands predominate in southwest Oregon. Ponderosa pine is rather widespread there, but its distribution is broken up; in many of the sample stands, it was a relatively minor component. In the other 3 regions, ponderosa pine was frequently a major component of the forest.

Identification of mutants and treatment of seeds

Six trees carrying mutants were identified during inbreeding studies (SORENSEN, 1970); the remainder in nursery plots. In the nursery plots, 114 seedlings per family were sown for southwest Oregon material, 144 for east Cascades and Ochoco/Malheur, and 152 for Wenatchee. Emergence generally exceeded 80 %.

Segregation ratios were counted in the nursery on families with mutant markers. Where possible, an additional 900 to 1100 seeds were germinated and mutant frequencies counted in growth chambers. This many seeds were available for 68 families. If less than ca. 900 seeds were available, all remaining seeds were germinated. Minimum family size was 61 seedlings; 8 additional families had less than 150 seedlings (i. e., had no extra seeds for growth chamber germination). Much larger numbers of seeds (4,000 to 8,000) were germinated from the 6 trees in the inbreeding study. One mutant phenotype, budless (*Table 1*), could be observed on seedlings only at the end of the growing season; additional seedlings from this family were tallied in the nursery bed. Some pale green phenotypes identified in the nursery could not be identified in the growth chamber. Such families were not included. Four trees carried 2 mutants. Values were calculated for each mutant and the mean used to represent the family.

For observation in the growth chamber, seeds were soaked ca. 24 hours in distilled, aerated water, placed in 11 cm x 11 cm x 3 cm plastic sandwich boxes 2/3 filled with wet vermiculite, covered with plastic lids, stratified 10 weeks to 14 weeks at 2 °C to 3 °C in the boxes, and then placed in a growth chamber at 25 °C day/20 °C night temperatures with 12-hour photo and thermoperiod. Light in the chamber was from mixed incandescent and warm white and cool white fluorescent bulbs at about 10% full sunlight (ca. 1000-foot candles). Lids were removed from sandwich boxes when emerging seedlings started to lift them. Seeds were moistened daily thereafter. Seedlings were tallied and removed when the mutant phenotype could be identified. Counts usually continued 2 weeks to 4 weeks after 1st emergence and until several days passed without new emergence in the box.

Crown level collections

Cone collections, stratified by crown level, were made in the 6 trees from the inbreeding study. These trees were 12 m to 20 m tall at the time of sampling and were in 2 stands in the east Cascade region. Green crown length averaged about 80 % of tree height. Collections were made in the upper, middle, and lower thirds of the cone-bearing crown, which was usually the entire green crown. Collections were made in 1 year, 2 years, or 3 years, usually 2 or 3, but depended on cone production. Fifty to 5,000 (usually >500) germinant seedlings were observed from each crown level for each year of collection.

Estimation of natural selfing

Except for the crown level collections, the conversion factor for determining the number of self-seedlings from the number of mutant seedlings was based on mean segregation ratios from 6 self-pollination families (*Table 2*). Mean segregation ratio of 3.926 normal seedlings: 1 mutant seedling was very similar to that reported for self-pollination families of loblolly pine (*Pinus taeda* L.) [3.8:1] (FRANKLIN, 1969), Douglas-fir (*Pseudotsuga menziesii* [MIRB.] FRANCO) [4.1:1] (SORENSEN, 1973), and lodgepole pine (*Pinus contorta* DOUGL. ex LOUD.) [3.9:1] (SORENSEN and ADAMS, 1993). It seemed reasonable to use this value as the basis for the conversion factor from mutant seedling fre-

Table 2. — Segregation ratios after self-pollination for 6 ponderosa pine trees in central Oregon.

| Tree number | Mutant phenotype | Number of seedlings | | Ratio |
		Normal	Mutants	Normal:Mutant
KS-4	Budless	372	106	3.509:1
KS-6	Yellow	334	101	3.307:1
KS-8	Pale green	1146	195	5.877:1
KS-30	White	152	36	4.222:1
LB-4	Cotyledonary lethal	428	159	2.692:1
LB-8	White	545	138	3.949:1
	Unweighted mean			3.926:1

quency. For the 6 trees with self-pollination families, conversion factors were based on segregation ratios of the individual families. Only seeds from the upper third of the crown were used to compute natural selfing when these trees were included in the 112-tree sample.

Because natural selfing can be affected by several factors, assumptions with regard to its estimate are listed below. Known evidence concerning the assumptions is noted.

1. All the mutants were deleterious, mostly early lethal. It is assumed that individually they are rare in the population and that there will not be unrelated carriers exchanging pollen (NAMKONG and BISHIR, 1987).

2. Regeneration is not in family clusters; i. e., related carriers are only rarely near neighbors. There is evidence for genetic patchiness associated with family clusters in plants and in Rocky Mountain ponderosa pine specifically (LINHART, 1989). How widespread it is and how much it would contribute to estimates of selfing is not known.

3. Filled self- and cross-pollination seeds have equal potential for germination. In 1 comparison, filled self-pollination seeds had slightly lower germination percent than cross-pollination seeds from the same trees (SORENSEN and MILES, 1974).

4. The conversion factor, mutant seedlings: self-seedlings, is appropriate to the population as a whole.

5. Segregation ratios are unaffected by treatment; e. g., year of sowing, growth chamber vs. nursery.

6. Seed storage did not differentially affect embryo survival of selfed and crossed seeds. Some seed lots had been stored several years before use, and the southwest Oregon group inadvertently had been stored at room temperature for several months after sowing of the nursery test. Freezer storage probably maintains viability for many years; but if there is a decrease in viability, it probably occurs first in self-pollination seeds (see Results).

7. Families with low natural selfing were detected in the common garden. Because mutant-carrying trees were identified from wind-pollination progenies of 100 seedlings to 150 seedlings, it is probable that some trees with very low frequency of natural selfing were missed.

8. Mutant phenotypes were due to single gene, recessive alleles.

Some of these assumptions, if violated, would tend to compensate for one another. For example, loss of self-embryo viability in storage (assumption 6) would reduce the estimate of the frequency of natural selfing. On the other hand, lack of detection of families with very low selfing (assumption 7) would increase the mean estimate.

Analyses

Assuming no nearby pollen sources carry the rare marker, the expected frequency of a marker (m) in a wind-pollination progeny is Sd, where S is the probability that a wind-pollination seedling results from self-fertilization, and d is the proportion of these seedlings that are homozygous for the mutant allele. Given that the observed number of marker seedlings is binomially distributed, the maximum likelihood estimate of S is,

$$\hat{S} = m/d, \text{ and}$$
$$\text{Var } \hat{S} = \hat{S}(1 - d\hat{S})/dN,$$

where N = total number of seedlings observed (SORENSEN and ADAMS, 1993).

1. Heterogeneity among trees within stands was tested using chi-square analysis, where

$$\chi^2 = \Sigma \frac{1}{\text{Var}\hat{S}_i} (\hat{S}_i - \bar{S})^2 .$$

2. Difference among "regions" was evaluated in 2 ways. First, variance among regions was tested against pooled variance among trees-in-regions in a nested analysis of variance. Second, field visits to the regions indicated that the distribution of ponderosa pine in southwest Oregon, compared to the other regions, was more broken up and included a higher proportion of populations in which ponderosa was a relatively minor component of the stand. This suggested there might be more stands and trees with high selfing estimates in southwest Oregon than elsewhere. This was tested by comparing regions for the proportion of trees with $\hat{S}$ > 0.15, using chi-square test of independence. The dividing value of 0.15 was arbitrary; 26 trees of the 112 trees had $\hat{S}$ > 0.15.

3. Sites of the 53 trees in the east Cascade region were classified by stand type at the time of cone collection. The 3 classes were main distribution of the species (46 trees), high desert fringe of the main distribution (3 trees), and disjunct stands (4 trees). High desert fringe in this case was part of the main distribution of the species in the east Cascades but represented a narrow transition from pine to juniper or desert shrub. Stand density on the desert side may grade down to a few trees per hectare; but usually within a few 100 meters or less in the direction of the main distribution, near-normal density is approached. Disjunct stands were stringers along streams in the high desert or steppe or were small stands of 25 to several 100 mature individuals on north-facing slopes of hills or of canyons in the steppe. Disjunct stands were

Table 3. — Analysis of variance for difference among regions[1] in estimated percent natural selfing. Percents transformed to arc sin √percent prior to analysis.

Sources of variation	Deg. of fr.	Sums of squares	Mean square	F-value	Probability
Total	111	8984.23			
Regions	3	66.93	22.31	0.27	0.8468
Southwest Oregon vs. others	1	53.90	53.90	0.65	0.4209
Among others	2	13.03	8.52	0.10	0.9021
Trees within regions	108	8917.30	82.57		

[1] Regions are southwest Oregon (Oregon Siskiyou Mountains), e ast slopes of Cascade Range in Oregon and extending east to the Warner Mountains in southern Oregon, Ochoco Mountains in c entral Oregon and extending east to the Blue Mountains, and east slopes of the Cascade Range in central Washington.

Table 4. — Number of families (P), mean number of seedlings classified per family (N), mean estimated proportions of self seedlings (Ŝ), and median values of Ŝ for four regions[1] of ponderosa pine in Oregon and Washington (standard errors[2]) in parentheses).

	Region				
Trait	Southwest Oregon	Oregon Cascades	Ochoco/ Malheur	Wenatchee, Washington	Mean
P	31	53	14	14	28
N Range	595 109-1051	1060 61-8228	798 217-1142	890 706-1037	877
Ŝ[3],[4] Range	0.109 (0.033) 0.005-0.497	0.085 (0.032) 0.006-0.432	0.081 (0.024) 0.004-0.318	0.094 (0.020) 0.005-0.349	0.091(0.029)
Median Ŝ	0.057	0.055	0.061	0.059	0.057

[1] Regions are southwest Oregon (Oregon Siskiyou Mountains), east slopes of Cascade Range in Oregon and extending east to the Warner Mountains in southern Oregon, Ochoco Mountains in central Oregon and extending east to the Blue Mountains, and east slopes of the Cascade Range in central Washington.
[2] Standard error, as square root of variance, was computed for individual families by using the formula in the text.
[3] All means are unweighted.
[4] Differences among trees within stand were highly significant ($p < 0.005$) for all stands; differences among regions were not significant (*Table 3*).

separated from the main distribution by 10 km to 30 km. Nested ANOVA was used to test for significance of difference among stand types.

4. Cone collections for 27 trees in the east Cascades and 10 trees in the Ochoco/Malheur regions were processed in our laboratory. Seeds were extracted by hand and number of round seeds counted. Most hollow seeds were then removed with a laboratory seed blower (SILEN, 1964). Number of filled seeds in the heavy seed proportion was determined from x-ray plates, and proportion of round seeds that were filled was calculated. Proportion of filled seeds differed greatly among trees. Because of large inbreeding depression in seed set (SORENSEN, 1970) and the possibility that seed set might be related to natural selfing, correlations between filled seed proportions and S were computed for both regions. The 2 correlation coefficients, after converting each to zs, were then tested to determine if they were estimates of the same population p and the common correlation computed by using weighted zs.

5. As noted above, seeds from southwest Oregon were stored at room temperature for several months. Seeds were x-rayed and percent filled was determined before

seeds were placed in the sandwich boxes for germination and emergence. S was correlated with percent emergence to determine if poorer emergence was associated with higher estimates of natural selfing.

6. For the 6 trees and 3 crown levels per tree, 15 crown levels within tree samples were made in more than 1
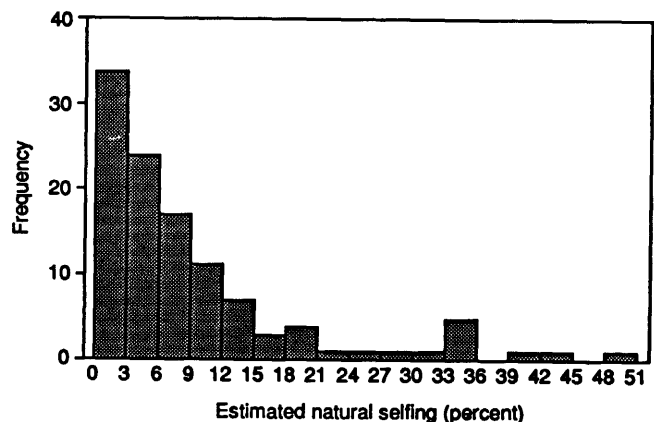

Figure 1. — Distribution of estimated natural selfing percents among 112 ponderosa pine families. Values are given in 3-% classes.

year. In 7 cases, the chi-square test for heterogeneity in Ŝ among years was significant. For analysis of effect of crown level, all years of collection were pooled and data analyzed as a cross-classification with crown levels as treatment and years as replication. No cones were collected from one crown level in 1 tree. This value was estimated for the analysis of variance table and degrees of freedom for error reduced by 1. Because heterogeneity among years was sometimes significant, sometimes not, the test was run twice. Weighted means were used in one analysis, unweighted means in the other. Number of seedlings per crown level in a tree ranged from 588 to 8,228 (mean 4,264).

All analyses followed SNEDECOR and COCHRAN (1980). All proportions were changed to percentages and all percentages transformed to arc sin $\sqrt{percent}$ before analysis. All means reported are raw means.

Results and Discussion

Difference among and within regions

Regions did not differ in Ŝ (F = 0.27, p = 0.8468, d. f. = 3, 108, *Table 3*), and the contrast between southwest Oregon and the other regions pooled was not significant (*Table 3*). Chi-square test comparing regions for proportion of trees with Ŝ > 0.15 was not significant (X^2 = 1.27, p > 0.50, d.f. = 3). Variation in Ŝ among trees within regions was highly significant for all regions (p > 0.005, *Table 4*).

All regions were considered parts of the same population with regard to natural selfing, with estimated mean value of Ŝ = 0.091, median 0.056. These values are higher than that reported for ponderosa pine in the Rocky Mountains where LINHART (1988), in summary, notes an outcrossing rate of 0.95 or more (equivalent to Ŝ = 0.05 or less) in stands where tree density is at average levels. Because of the skewness of the distribution and the long tail to the right (*Figure 1*), mean Ŝ is strongly influenced by several trees with high estimates of natural selfing. If known disjunct stands and stands where ponderosa is rare (8 trees total) are deleted, mean Ŝ for northwest ponderosa is 0.076. Perhaps the median Ŝ of 0.056 would be more representative of most stand values. Also, as mentioned earlier, I have assumed that all inbreeding is selfing. However, some of it is undoubtedly due to matings between relatives in family clusters (LINHART et al., 1981; LINHART, 1989). What is referred to as selfing is not necessarily all real selfing (see BROWN et al., 1985).

Variation in Ŝ among trees in regions was large for all regions (*Table 4*). SORENSEN and ADAMS (1983) report a similar result for trees in stands for lodgepole pine

(Pinus contorta DOUGL. ex LOUD.). A survey of conifer literature indicates that heterogeneity among trees in outcrossing (or selfing) rate is common, although MITTON et al. (1981) found no significant difference in outcrossing rate among 31 trees in a ponderosa stand in Colorado.

Proportion of self-pollination required to produce 9.1 % self-seedlings in the wind-pollination progeny was estimated by using mean Ŝ from this test, fertility from SORENSEN (1970), and equation (13) in SORENSEN and ADAMS (1993) assuming 1 embryo per ovule,

$$\alpha = [(\hat{S})(f_w)]/v_s = [(0.091)(0.752)]/(0.237) = 0.289,$$

where α = estimated proportion of self-pollination (self-fertilization);

Ŝ = proportion of viable self-offspring after wind-pollination = 0.091 (this paper);

f_w = frequency of filled seeds after wind-pollination = 0.752 (SORENSEN, 1970);

v_s = proportion of viable seeds after controlled self-pollination = 0.237 (SORENSEN, 1970).

The estimate of natural self-pollination of 0.289 indicates that for the tree with mean Ŝ, about 25% to 30% of natural pollinations were self-pollinations. Value of α for the median tree (Ŝ = 0.056) was 0.178.

Five families within the main distribution of ponderosa pine had high estimates for natural selfing. Several factors could contribute to this. Some ponderosa pines are highly self-fertile (see SORENSEN, 1970; *Table 3*, for examples). High self-fertility, combined with above average self-pollination due to early or late phenology, to high synchrony of timing of male and female flowering (ERICKSON and ADAMS, 1990), or to high male conelet production (SHEA, 1987; SMITH et al., 1988) could result in high selfing. Also, neighboring siblings carrying the allele for the same marker could result in the progeny of the carriers having a high frequency of the marker, even though it would not indicate selfing. Cone collections were made from naturally regenerated stands; but natural regeneration may occur from low frequency seed trees, from timber edges, or from the range of intermediate conditions (ISAAC and MEAGHER, 1936). This variation in regeneration may lead to considerable family structure in some areas and lack of family structure in others (RUDIN et al., 1977; KNOWLES et al., 1992). If family structure is present, light to moderate flowering might be concentrated in related (genetically similar) individuals; heavy flowering might dilute the family effect. Annual variation in reproductive output is very large in ponderosa pine (DAHMS and BARRETT, 1975). On the other hand, the relatively low frequency of high-Ŝ trees indicates that family clusters and sib mating are not common.

Table 5. — Analysis of variance of difference among stand types[1] within the east Cascade region in estimated percent of natural selfing. Percents transformed to arc sin $\sqrt{percent}$ before analysis.

Sources of variation	Deg. of fr.	Sums of squares	Mean square	F-value	Probability
Total	52	3378.72			
Among stand types	2	545.36	272.68	4.80	0.0124
(Main + fringe) vs. disjunct	1	472.42	472.42	8.34	0.0057
Main vs. fringe	1	72.94	72.94	1.29	0.2620
Trees within stands	50	2833.36	56.67		

[1] Stand types are the main distribution of ponderosa pine, the high desert fringe of the main distribution, and small disjunct stands separated from the main distribution by 10 km to 30 km. Further description is given in the text.

Sources of variation	Deg. of fr.	Sums of squares	Mean squares	F-values	Probabilities
Total	16[1]	408.31			
Replications	5	162.86	32.57	2.13	0.1535
Crown levels	2	104.63	52.31	3.34	0.0821
Error	9	140.83	15.65		

[1] Degrees of freedom for total and error were reduced by 1 because of missing value; 1 crown level in 1 tree did not produce any cones.

Finally, a comment on mixed mating and its relation to $\hat{S}$. Assuming 1 embryo per ovule, I estimated natural self-pollination of 25 % to 30 % for mean $\hat{S}$ or 15 % to 20 % for median $\hat{S}$ for ponderosa pine in this study. Lodgepole pine gave lower estimates of selfing ($\hat{S}$ = 0.017 and 0.020 for 2 stands) but about equivalent estimates of natural self-pollination (15 % to 25 %) (SORENSEN and ADAMS, 1993; Table 5, stands B and C). Natural Douglas-fir stands have an estimated selfing of 0.07 to 0.10 (SORENSEN, 1973; SHAW and ALLARD, 1982). The 0.07 value is a little lower than that reported here for ponderosa pine and was obtained using the same methods. However, because of the low-self-fertility of Douglas-fir (SORENSEN, 1971), it requires an estimated 50 % self-pollination to achieve the 0.07 level of natural selfing (SORENSEN, 1982). Thus, for different species, different components of the mating system might be combined to reach roughly equivalent levels of self-embryo frequencies. It would be of interest to compare these 2 measures of inbreeding (self-pollination and self-embryo production) in a still more self-fertile species such as noble fir (Abies procera REHD.), which shows the usual inbreeding depression in vigour (SORENSEN et al., 1976).

Difference among stand types

When the 3 classes of stands (main distribution, desert fringe, and disjunct) within the east Cascades were contrasted, trees in the disjunct stands had significantly higher mean $\hat{S}$ (0.258) than did trees in the other 2 classes (0.071 and 0.070) (F = 8.34, p = 0.0057, d. f. = 1, 50, Table 5).

Twelve parent trees had $\hat{S}$ > 0.20; 11 of these were visited to classify stand characteristics. Five were in stands where ponderosa was the major or only component of the forest (see preceding section), 4 were in mixed stands with low frequencies (< 10 %) of ponderosa pine, and 2 were in disjunct stands.

In addition, 2 marker-carrying trees, whose progenies were initially in the tests but were not included in the above sample of 112, were in 25- to 30-year-old ponderosa plantations in southwest Oregon. These plantations were now filled in with natural regeneration of other species, and there were no ponderosa in the immediately surrounding old-growth stands. $\hat{S}$ for the 2 trees was 0.232 and 0.475.

Although there are exceptions (XIE et al., 1991), these results (lack of difference among geographic areas, significant difference among stand types) seem in general agreement with other published information on conifers (SHAW and ALLARD, 1982; FARRIS and MITTON, 1984; BOYLE and MORGENSTERN, 1986; NEALE and ADAMS, 1985a and b;

FURNIER and ADAMS, 1986; PERRY and DANCIK, 1986; SHEA, 1987; KNOWLES et al., 1987; SCHROEDER, 1989; MUONA et al., 1990; PERRY and KNOWLES, 1990; MORGANTE et al., 1991a and b; SORENSEN and ADAMS, 1993), with the qualification that it is not always clear whether or not contrasted populations actually differ in stand structure. In the present study, ponderosa pine stands in southwest Oregon, compared to the other regions, seemed more dispersed and to have larger components of other species. The estimated selfing was highest for southwest Oregon (0.109, vs. weighted mean of 0.086 for the other regions), but the difference was not significant (Table 3) (see also FURNIER and ADAMS, 1986).

Estimates of natural selfing were much larger in small, disjunct populations than in the main distribution of the species. The majority of trees with high estimates of selfing were in these stands or in stands where ponderosa pine was a very small component of a mixed forest. PERRY and KNOWLES (1990) and SORENSEN and ADAMS (1993) report similar results in eastern white cedar (Thuja occidentalis L.) and lodgepole pine, respectively. In general, it can probably be expected in these situations that the tree's own pollen will make up an increasingly large part of its pollen cloud (FARRIS and MITTON, 1984; SMITH et al., 1988; MITTON, 1992). If stand conditions that increase the frequency of self-pollination are historical, selection accompanying past inbreeding may have "purged" some deleterious recessive alleles (DOLE and RITLAND, 1993). Trees in these stands also may have an increased capicity
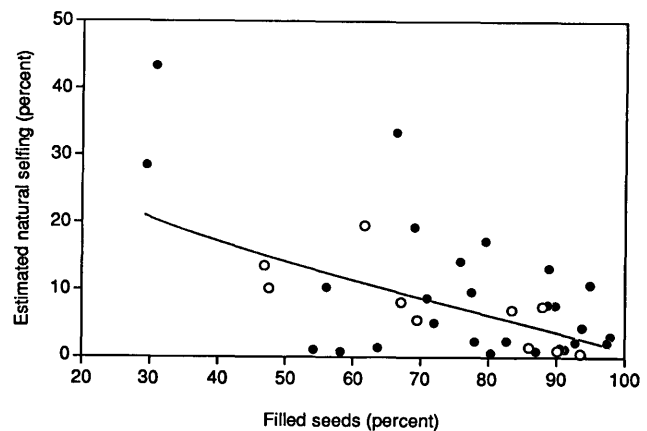

Figure 2. — Relation between round, normal-appearing seeds that were filled (filled seed percent) and estimated natural selfing. Hollow circles represent trees in the Ochoco and Malheur National Forests of central Oregon; solid circles represent trees along the east side of the Cascades. The plotted line is based on all points; values for the line were computed from the equation, Y = 40.8307 — 0.4157X, and back transformed to percents.

to set viable seeds after self-fertilization (PIESCH and STETTLER, 1971; SORENSEN and ADAMS, 1993) and give higher Ŝ for the equivalent self-pollination.

Natural selfing and seed set

Test of correlation between percent natural selfing and percent of round seeds that were filled was highly significant for both east Cascade families (r = —0.514, d.f. = 25, p < 0.01) and Ochoco/Malheur families (r = —0.798, d.f. = 8, p < 0.01). The r's did not differ (χ^2 = 1.49, p > 0.10). Best combined z_w gave an estimate of the population correlation coefficient = —0.596 (95 % confidence limits, —0.240 and —0.739). Families with large Ŝ had lower filled seed percents than did families with small Ŝ. The regression line is rather steep, but there is much scatter around it (*Figure 2*).

Natural selfing and seed storability

Seeds of the 31 southwest Oregon families inadvertently stored at room temperature had emergence percents in the growth chamber ranging from 23.1 to 100. The seed lots had all germinated well in a previous nursery test. Much of the emergence fall-off probably was associated with nongenetic aspects of seed quality (seed maturity at cone harvest, cone handling, etc.). Nevertheless, there was a significant correlation between emergence percent and Ŝ (r = —0.410, d.f. = 29, p < 0.05), indicating a tendency for seed lots with high frequencies of self-seeds to have more seeds become nonviable in storage than seed lots with low frequencies of self-seeds.

Comparable results have been reported for tree species that retain their seeds on the tree. Fruits of alpine ash (*Eucalyptus delegatensis* R. T. BAK.) were harvested at one time from 3 consecutive crops. Multilocus estimates of outcrossing rate increased from most recent to oldest crop, 0.66, 0.78, and 0.85, respectively (MORAN and BROWN, 1980). Similarly, CHELIAK et al. (1985) report a decrease in selfing rate in jack pine (*Pinus banksiana* LAMB.) and PERRY and DANCIK (1986) a nonsignificant decrease in selfing rate in lodgepole pine in seeds from younger to older serotinous cones. This indicates that self-embryos lose viability more rapidly than cross-embryos when seed "storage" is on the tree.

Many years ago, JONES and MANGELSDORF (1925) suggested that harsh storage conditions might be used to eliminate defective germ plasm from segregating lines. Later authors reported that certain mutant phenotypes lost viability quickly in storage. I tested this with progeny of a Douglas-fir cross carrying a common recessive allele for albinism (SORENSEN, 1975). No change in segregation ratio was observed over 6 years of good storage conditions. The viability may be more dependent on inbreeding than on mutant phenotype. In any case, the results suggest that seed storability is another trait that shows inbreeding depression.

Natural selfing and crown level

Results of the crown level analysis are shown in *table 6* for unweighted means. Ŝ was highest in the middle crown if year means for crown levels in trees were unweighted, highest in the lower crown if year means were weighted by the number of seedlings observed; but in neither case was the effect of crown level significant (F = 3.34, p = 0.0821, d.f. = 2, 9 for unweighted data, *Table 6*; F = 1.41, p = 0.3071, d.f. = 2,9 for data weighted by the number of seedlings in the sample).

Other studies have given mixed results. Significant, and sometimes large, crown level effects were observed in open-grown jack pine (*Pinus banksiana* L.) (FOWLER, 1965), in scots pine (*Pinus sylvestris* L.) HADDERS, 1972), in loblolly pine (*Pinus taeda* L.) (FRANKLIN, 1971), in natural Douglas-fir growing on road sides or on the edges of natural breaks (SHAW and ALLARD, 1982), in a 20-year-old grafted Douglas-fir orchard (OMI and ADAMS, 1986), and in intermediate- to low-density lodgepole pine stands (SORENSEN and ADAMS, 1983). Conversely, differences were slight or not observed in a young Douglas-fir grafted orchard (SHAW and ALLARD, 1982), in a low-density jack pine stand of variable tree height (CHELIAK et al., 1985), in a 14- to 17-year-old clonal/seedling Douglas-fir orchard phenologically isolated by sprinkler cooling (EL-KASSABY et al., 1986), and in even-aged, natural lodgepole pine stands (PERRY and DANCIK, 1986). Natural selfing was higher in the upper crown than in lower crown in one Scots pine orchard (RUDIN and EKBERG, 1982).

Several years of personal observations involving 2 species with contrasting results (ponderosa pine, this paper; and lodgepole pine, SORENSEN and ADAMS, 1993) have suggested that twig and branch distribution and production of pollen conelets may be important factors. Lodgepole pine had a crown-level difference in natural selfing. The lodgepole trees were moderately open grown with dense branching and heavy catkin production in the lower crown. Crown-level difference in selfing was nonsignificant in ponderosa pine. Ponderosa trees were mostly growing in stands, crowns were more open, and catkin production correspondingly less. Although actual pollen production is not reported in these studies, it appears that crown-level differences in Ŝ tended to occur in situations where crown structure may have offered the potential for heavy pollen production (FOWLER, 1965; SHAW and ALLARD, 1982; OMI and ADAMS, 1986; SORENSEN and ADAMS, 1993). Other factors such as self fertility (SORENSEN and ADAMS, 1993), synchrony of male/female flowering phenology within the tree (ERICKSON and ADAMS, 1990), and pollen dispersal characteristics, of course, could be determinative in individual cases.

Practical considerations

In artificial regeneration, deleterious effects associated with natural inbreeding can be reduced by avoiding seed lots that potentially have a high level of inbreeding. Situations to be avoided in ponderosa pine are cone collections in disjunct stands, small populations, isolated plantations, or in stands where the frequency of ponderosa in the reproducing individuals is less than about 20 %. If any of these situations cannot be avoided (for example, if a goal were to artificially perpetuate a small disjunct population with local stock), many of the depressed inbreds could be culled in the nursery (SORENSEN and MILES, 1974) although not in greenhouse culture (ERIKSSON and LINDGREN, 1975), or seedlings could be planted at high density to let nature remove the inbreds over time. Some inbreeding might be avoided by not collecting cones from trees with low filled-seed percents. Unfortunately, many factors affected seed set, and the relation between seed set and natural selfing shows much scatter (*Figure 2*). Based on my sample, a recommendation might be to not retain seed lots in which the filled-seed proportion is less than 50 % in good seed years.

Crown position, on the average, seems not so important in ponderosa pine. Exceptions might be collections from

open-grown trees in years of heavy pollen production or collections in a seed orchard in which large pollen crops have been artificially induced, particularly if the proportion of reproductive individuals is small. Until other information is available, it should be anticipated that natural inbreeding will be less in upper- than in mid- and lower-crown collections, but the difference will be small on the average.

Finally, it is worth repeating that ponderosa pine has moderate self-fertility. Any situation or procedure that increases the probability of self-pollination will have a greater affect on detectable selfing in ponderosa than in species with lower self-fertility such as lodgepole pine and Douglas-fir.

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Estimation of Genetic and Non-Genetic Parameters for Rooting Traits in Hybrid Larch

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Summary

Two experiments were established in 1992 and repeated in 1993 to study genetic and non-genetic effects on root-ability of hybrid larch cuttings. Cuttings from 80 clones of 8 full-sib families were rooted in the first experiment. In the second one, 3 primary ramets from each of 24 clones were used as the source of cuttings. Rooting percentage, stem increment length and in part of the experiments, some more detailed rooting traits were assessed. Both strong clonal and less significant family effects were found on the rootability of cuttings. Importance of ge-netic control was proved by a high broad-sense heritability based on clone means. A non-genetic effect or 'C-effect' could be an important source of bias in genetic parameter estimation. Low genetic correlations were found between rooting percentage and shoot increment. However stem in-crement was well correlated with some detailed root system traits.

Key words: Hybrid larch, *Larix*, vegetative propagation, cutting, genetic parameter, non-genetic effect.

FDC: 165.441; 165.72; 165.7; 181.51; 174.7 *Larix.*

Introduction

Rooting of cuttings, *i.e.* development of adventitious roots and subsequent development of the aboveground shoot, is a process which can influence subsequent growth of propagules in the nursery and in the forest. Rootability in a broader sense is the ability to develop a new root system and restitute complete and functional new plants. Besides growth traits, rootability is very often an im-portant selection criteria in creation of clonal varieties. Many different factors play an important role in the rooting process (RADOSTA, 1989). These factors can be di-vided into 2 broad groups: genetically inherited and non-genetic ones.

Among the genetic factors, clonal variation in rooting has been reported by a number of authors (e.g. KLEIN-SCHMIT, 1974; MORGENSTERN *et al.*, 1984; SPETHMANN, 1986; BENTZER, 1988). Less information has been published about the effect of family. For *Picea abies,* SKRØPPA and DIET-RICHSON (1986) and for *Pinus taeda,* FOSTER (1990) reported significant variation in rooting percentage due to a family effect. The second author cited papers giving different findings.

Non-genetic factors influencing rooting of cuttings are represented most frequently by the so-called 'C-effects'

(LIBBY and JUND, 1962). According to BURDON and SHEL-BOURNE (1974), 'C-effects' can be divided into maternal effects specific to the individual cutting due to its posi-tion (*e.g.* type, size), and maternal effects caused by the different environmental preconditioning and age of the respective ortet. 'C-effects' are considered a source of possible bias in clonal estimation (LIBBY and JUND, 1962) so that identification of the non-genetic variation in genetic estimation for rooting of cuttings has been investigated by several researchers.

WILCOX and FARMER (1968) first found for rooting traits in eastern cottonwood significant 'C-effects' estimated from primary ramet effects. FOSTER *et al.* (1984) estimated in an experiment with western hemlock that variance in rooting ability due to 'C-effects' represented approxima-tively one third of the total clonal variance. In another experiment using primary ramets as stock plants for a secondary propagation cycle, they found that nongenetic effects although still significant, were reduced to 2 % up to 6 % of total variation. FARMER *et al.* (1988, 1989, 1992) also reported low or non-significant 'C-effects' for rooting traits, when cuttings were taken from primary ramets grown in the same environmental conditions.

Within a programme of clonal testing of hybrid larch (*Larix x eurolepis*) in France, 2 experiments were set up in spring 1992 and 1993 to investigate genetic parameters of that clonal population when vegetatively propagated by stem cuttings.

Experiment 1 was designed to estimate genotypic para-meters of rooting traits while experiment 2 was set up with the aim to detect possible non-genetic effects which might bias the previous results. Our intention was to examine any common environmental effects of clones con-nected with the use of individual primary ramets as stock plants.

Materials and Methods

For experiment 1, 8 full-sib families of hybrid larch (*Larix decidua x L. kaempferi*) were used in 1992. They were represented by 10 clones each, randomly chosen without any consideration of their rootability. In 1993, only 54 clones out of the 80 were propagated.

In experiment 2, a subset of 24 clones was chosen from the 80 clones of experiment 1. Their choice depended upon the availability of 3 equally developed primary ramets per

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