

## RELATIONSHIP BETWEEN SELF-FERTILITY, ALLOCATION OF GROWTH, AND INBREEDING DEPRESSION IN THREE CONIFEROUS SPECIES

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**Abstract.**—Mortality and growth of self and outcross families of three wind-pollinated, mixed-mating, long-lived conifers, Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and noble fir (*Abies procera*) were followed from outplanting to age 26 (25 for noble fir) in spaced plantings at a common test site. Response to inbreeding differed greatly among species over time and in all regards. Only Douglas-fir and noble fir will be contrasted here, because ponderosa pine usually was intermediate to the other two in its response to inbreeding. In earlier reports, compared to noble fir Douglas-fir had a higher rate of primary selfing and larger inbreeding depression in seed set. Douglas-fir continued to have higher inbreeding depression in nursery and early field survival. The species differed in time courses of inbreeding depression in height and in allocation of growth due to crowding. Between ages 6 and 12, the relative elongation rate ( $\text{dm} \cdot \text{dm}^{-1} \cdot \text{yr}^{-1}$ ) of Douglas-fir was significantly greater in the selfs than in the outcrosses. The response was not observed in noble fir. At final measurement, inbreeding depression in diameter relative to inbreeding depression in height was greater in Douglas-fir than in noble fir. At final measurement inbreeding depression in height was inversely related to inbreeding depression in survival. Cumulative inbreeding depressions from time of fertilization to final measurement were 0.98, 0.94, and 0.83 for Douglas-fir, ponderosa pine, and noble fir, respectively, which indicates that selfs will not contribute to the mature, reproductive populations.

**Key words.**—*Abies procera*, Douglas-fir, inbreeding depression, noble fir, photomorphogenic effects, *Pinus ponderosa*, ponderosa pine, *Pseudotsuga menziesii*.

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Inbreeding depression (ID) is the reduction in fitness associated with increased homozygosity. Its magnitude in natural populations differs greatly among species and sometimes among populations within species. This variation, both in severity of depression and in its ontogenetic timing, has been related to differences in the mating system, particularly the degree of selfing (Charlesworth and Charlesworth 1987; Lande et al. 1994; Latta and Ritland 1994; Parker et al. 1995; Husband and Schemske 1996). The review by Husband and Schemske (1996) is recent and thorough, and the reader is referred to it for details.

The theoretical expectation is that high rates of primary selfing (selfing at the fertilization stage) will purge highly deleterious alleles (Lande and Schemske 1985; Charlesworth and Charlesworth 1987). Within- and among-species comparisons do indeed indicate that ID in embryo and neonatal survival and growth traits are negatively related with rate of primary selfing (Latta and Ritland 1994; Husband and Schemske 1996). However, the relationship also shows large variation around the regression line. This indicates that factors such as degree of dominance or complex modes of inheritance, magnitude of effect, genomic mutation rates, and particularly for growth traits, genotype  $\times$  environment or genotype  $\times$  age interactions may strongly influence the correlation (Barrett and Harder 1996; Helenurm and Schaal 1996). Also, little purging may occur if none of the selfed individuals reach reproductive age (Lande et al. 1994).

In general, conifers are mixed mating and selfing rates at the fertilization stage (primary rates) are intermediate (Sorensen and Adams 1993; Sorensen 1994). During embryogenesis, regeneration, and stand development, selection removes self progeny, and mature reproductive populations usually consist of outcrossed individuals (Shaw and Allard

1982b; Muona et al. 1988; Bush and Smouse 1992). In this paper, I describe the contrasting ontogenies of ID in survival and vigor to ages 25 or 26 of three coniferous species with greatly differing rates of primary selfing.

Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and noble fir (*Abies procera* Rehd.) are long-lived, wind-pollinated, monoecious gymnosperms. Douglas-fir and ponderosa pine have extensive geographic distributions and occupy wide ranges of latitude, longitude, and elevation in western temperate North America. Douglas-fir occurs in moister and milder environments, ponderosa pine in drier and climatically more continental environments. Noble fir is generally restricted to upper slopes in the Washington and Oregon Cascade Range. All are classified as intolerant or relatively intolerant to shade, with ponderosa pine the most shade intolerant (Daniel et al. 1979, pp. 292–298; Minore 1979).

Because of relatively low shade tolerance, successful natural regeneration for all three species is primarily in openings, broken stands, or light shade. All are prolific seeders (Isaac 1943; Dahms and Barrett 1975; Carkin et al. 1978; Reukema 1982), but where natural disturbance is extensive and repeated, restocking is sparse (Isaac and Meagher 1936) and distributed over many years.

Studies with Douglas-fir (Orr-Ewing 1957) and *Pinus peuce* Griseb. (Hagman and Mikkola 1963) indicate no incompatibility mechanism in conifers. Douglas-fir, ponderosa pine, and noble fir differ greatly in rates of primary selfing, but estimates of measured selfing rates (selfing rates determined at the viable seed or germinant seedling stage) are all low, 10% or below (Table 1). Thus, the low measured rates are generated via different paths: high primary selfing and high ID for seed set in Douglas-fir, low primary selfing and

TABLE 1. Mean primary and measured selfing rates and inbreeding depression (ID) in seed set for Douglas-fir, ponderosa pine, and noble fir.<sup>1</sup>

Species	ID <sub>seed set</sub>	Selfing rates	
		Primary <sup>2</sup>	Measured <sup>3</sup>
Douglas-fir	0.90 <sup>4</sup>	≈0.50 <sup>5</sup>	≤0.10 <sup>6</sup>
Ponderosa pine	0.64 <sup>7</sup>	≈0.20 <sup>8</sup>	0.09 <sup>8</sup>
Noble fir	0.29 <sup>9</sup>	≤0.13 <sup>10</sup>	≤0.10 <sup>10</sup>

<sup>1</sup> Conifers are polyembryonic. Values in the table are based on one embryo per ovule, but use of assumption of more than one embryo would not change values greatly and would not change the contrast (Sorensen 1982).

<sup>2</sup> Selfing rate at time of fertilization.

<sup>3</sup> Selfing rate as measured at viable seed or germinant seedling stage.

<sup>4</sup> Combined from Sorensen (1971) and Piesch and Stettler (1971).

<sup>5</sup> Sorensen (1982).

<sup>6</sup> Sorensen (1973); El-Kassaby et al. (1981); Shaw and Allard (1982a); Neale and Adams (1985).

<sup>7</sup> Sorensen (1970).

<sup>8</sup> Sorensen (1994).

<sup>9</sup> Sorensen et al. (1976).

<sup>10</sup> Siegismund et al. (1996); Siegismund and Kjær (1997). Estimates obtained in seed orchards and planted stands far outside the natural range of the species. Only one estimate of measured selfing was significantly different than zero.

low ID for seed set in noble fir, and intermediate for both in ponderosa pine.

The three species apparently differ in their growth response to light quantity and quality. Compared to Douglas-fir, ponderosa pine shows little plasticity in elongation rate (Emmingham and Waring 1973; Chen 1997) and in shoot-root balance (Drew and Ferrell 1977) in response to light. No direct evidence is available on response of noble fir to decreasing light, but its near relative, *Abies magnifica* var. *shastensis* Lemm., shows more height growth depression at low light than does Douglas-fir (Emmingham and Waring 1973). For Douglas-fir (Ritchie 1997; Scott et al. 1998), but not ponderosa pine (Seidel 1985), there is evidence that low-fluence side light high in far-red wavelengths increases shoot elongation and diameter increment. This photomorphogenic response in Douglas-fir occurs prior to competitive shading.

These growth comparisons are based on young plants, and none of them include noble fir, but they do show interspecific differences in allocation of growth in response to shade and plant density. Because the crowns of self plants are in the lower canopy, response to side light and to decreasing light will affect development of size inequality and expression of ID as the stand closes.

The material in this study has been cultured similarly from time of controlled self- and cross-fertilization through the nursery phase to age 25 or 26 in the field plantations. It offers a unique opportunity to compare the ontogeny of inbreeding depression, both from the genetic and the plant-developmental standpoints, among three species with quite similar life histories and reproductive potentials, but with greatly different rates of primary selfing (Table 1) and possibly different growth responses to stand development and light regime. The comparison poses the following questions. Do the interspecific differences in inbreeding depression in embryo survival (Table 1) continue through nursery and field establishment? What is the impact on inbreeding depression in height of the transition from open growth to crown closure? Are selfs as competitive for their size as outcrosses? Does

light-mediated allocation of biomass (Ballaré et al. 1987; Ritchie 1997) affect the expression of inbreeding depression? How does inbreeding depression accumulate across these stages for species that differ in rate of primary selfing? Do the species differ in cumulative inbreeding depression after 25 years?

## MATERIALS AND METHODS

Thirty-five Douglas-firs, 20 ponderosa pines, and 10 noble firs, all growing in natural stands, were self and cross-pollinated. Douglas-fir seed trees were located in six stands along latitude 44°30'N ± 15' extending from the Oregon Coast Range to the east slopes of the Cascade Range. Elevations of the stands ranged from 50 m to 1350 m. All stands, except one with one seed parent, were pure or predominantly Douglas-fir and were treated as a common population for the purposes of mating system measures and inbreeding effects. Ponderosa pine parents were in two stands at 1250 m and 1600 m at about 44°N, 121°30'W, on the eastern slopes of the Cascade Range. Both stands were predominantly ponderosa pine and were treated as a single population (Sorensen 1994). The noble firs were growing in a single, extensive, noble fir stand on the crest of the western Cascade Range (44°23'N, 122°09'W, 1450 m).

The pollination procedure included removal of male cone buds from branch ends bearing female cone buds and isolation of female buds in pollination bags prior to opening of bud scales. Branches bearing male catkins were collected at time of first natural pollen shed, sealed in kraft paper bags, and returned to our laboratory for extraction of pollen and packaging in vials. Because buds on trees and trees in stands vary in floral phenology, stands were visited twice weekly during the receptive period, and flowers in individual bags were pollinated on two, or sometimes three, successive visits. Additional details are given in Sorensen (1970, 1971) and Sorensen et al. (1976). Outcross pollen was applied as a four-to eight-tree mix. Only current year's pollen was used. Most outcross pollen trees were separated from seed trees by 0.5–3 km; minimum separation was 200 m. In all cases, pollen trees were growing in the same site conditions as the seed trees.

Three to about 50 selfed and outcrossed cones were collected from each tree. Ten healthy cones of each pollination type, if available, were chosen at random and dissected by hand. Round-full and round-empty seed numbers were determined from X-rays, and self-fertility calculated as filled seeds per round seed after selfing divided by filled seeds per round seed after controlled outcrossing (Sorensen 1970). Inbreeding depression in seed set (1 – self-fertility) is given in Table 2, and is based on all trees that were pollinated.

Seeds for each seed tree-pollination type combination were bulked prior to sowing. Initial progeny size depended on seed availability and ranged from 10 to 100+ seeds for Douglas-fir, 15 to 100+ for ponderosa pine, and 13 to 100+ for noble fir. At the end of the nursery phase, 19 Douglas-fir, 14 ponderosa pine, and seven noble fir family pairs produced sufficient seedlings for outplanting. Low self-fertility, female cone abortion, and technical errors accounted for the differ-

TABLE 2. Mean inbreeding depression in height at age 26 (25 for noble fir) and in survival for three growth phases, seed set, nursery period, and field test for Douglas-fir,<sup>1</sup> ponderosa pine, and noble fir.

Species	Height	Survival		
		Seed set	Nursery	Field
Douglas-fir	0.25	0.89	0.16 <sup>2</sup>	0.23 <sup>1</sup>
Ponderosa pine	0.33	0.64	0.05 <sup>2</sup>	0.16
Noble fir	0.40	0.29	0.03 <sup>3</sup>	0.09

<sup>1</sup> Inbreeding depression in field survival for Douglas-fir is given for age 18, for the other species at the final observation. This was done to exclude suppression mortality (see text).

<sup>2</sup> Sorensen and Miles (1974).

<sup>3</sup> Sorensen et al. (1976).

ence between numbers of seed trees pollinated and numbers of family pairs available for outplanting.

Seedlings were raised for two (Douglas-fir) or three years in a research nursery at Corvallis, Oregon, (44°35'N, 123°20'W, 75 m) and outplanted as bare-root seedlings. Nursery tests were at wide spacing (Douglas-fir, 7.6 × 7.6 cm; ponderosa pine and noble fir, 10 × 10 cm) to minimize suppression mortality. Small seedlings were not culled at the time of transplanting. Noble fir was sown one year later than the other species.

The field tests were established on abandoned agricultural land in the Douglas-fir zone in the eastern foothills of the Coast Range about 6 km southwest of Monmouth, Oregon (44°48'N, 123°18'W). Douglas-fir and ponderosa pine plantings were at about 110 ± 10 m elevation and adjoined each other; the noble fir planting was 1 km south and about 20 m lower in elevation. All plantations were on a genetics experimental area with a common environment, both with regard to climate and land-use history prior to planting. Spacing was 3.0 × 3.0 m for noble fir, 3.7 × 3.7 m for the other species. Ponderosa pine families also were planted at two other sites. Environmental effects on inbreeding depression will be reported elsewhere.

Numbers of plants per family differed due to seed availability. For each seed tree (with one exception) the same number of seedlings were planted in both self and outcross families and ranged from eight to 34 per pollination type and seed tree (mean, 23) for Douglas-fir, 12 to 27 (mean, 22) for noble fir, and five to 10 (mean, 9) for ponderosa pine. In time, family numbers also came to differ because of variation in plant survival. In analysis of pollination-type differences and in estimating mean inbreeding depression, families were weighted equally (Husband and Schemske 1995).

Heights were measured annually from planting to age 8, every two years between eight and 20 years, and every three years between 20 to 26 years (noble fir was measured annually to age 9, and was one year younger than the other species in subsequent measurements). Ponderosa pine showed symptoms of an unidentified needle rust at age 10. Symptoms were so severe by age 12 that measurement was stopped. However, the trees recovered, there was no mortality due to rust, and the plantation was again measured at age 26. Diameters at 1.4 m aboveground were measured on Douglas-fir starting at age 12 and on the other two, slower growing, species at the last measurement only.

Self and cross families from one seed tree were in rows adjacent to one another in the plantations; that is, the seed tree was the unit of replication. This was dictated primarily by the variation among seed trees in self-fertility and the desire to keep progeny of seed trees with low self fertility in the test population.

The model used for testing significance of differences between self and outcross families was  $X_{ij} = \mu + F_i + M_j + \epsilon_{ij}$ ; with  $i = 1 \dots f$ ,  $j = 1, 2$ ;  $\epsilon_{ij} = N(0, \sigma)$ , where  $X_{ij}$  is the value of individual family,  $\mu$  is the test mean,  $F_i$  is the random female parent,  $M_j$  is the fixed self- or cross-pollination type, and  $\epsilon_{ij}$  is the female × pollination type interaction.

The treatment of interest,  $M$  (pollination type) was large and highly significant ( $P < 0.001$ ) for all traits. Female × pollination type, which is large in most inbreeding studies, could not be tested because of the design. Because the species were in separate locations within the outplanting site, no statistical comparison of species is possible. Interest here will be in the ontogenetic pattern of ID in survival and height increment and its contrast among species.

Inbreeding depression at each measurement age was calculated as  $ID = (1 - [W_s/W_x])100$ , where  $W$  is the performance of the self ( $W_s$ ) and polymix outcross ( $W_x$ ) populations regardless of family origin (Lynch 1988; Johnston and Schoen 1994). Differences between family and population estimates of ID were small; for example, population ID for Douglas-fir 26-year height was 0.252 and mean family ID was 0.255. The difference would not affect ontogenetic comparisons. Family IDs were used to calculate the 0.95% two-tailed confidence interval of the population ID (Johnston and Schoen 1994, eq. 8). All estimates of ID were based on cumulative survival and size at each measurement age. Inbreeding depression was determined for the following traits, survival percentage (S), height (H), stem diameter at 1.4 m (D), individual tree volume (V), and living volume in row (RV). Individual stem volume was calculated for Douglas-fir using equations in Bruce and DeMars (1974). Because no volume equations for small trees of the other species were available, stem volume was calculated as the sum of a column below 1.4 m and a cone above 1.4 m. ID in living row volume was calculated as the multiplicative effect of ID in S and ID in V,  $ID_{\text{living row volume}} = 1 - ([1 - ID_{\text{survival}}] \times [1 - ID_{\text{tree volume}}])$ . This value is analogous to surviving plot volume, but is independent of number of trees initially planted in the pair of rows. No confidence interval was calculated for this trait.

Finally, to compare species for total ID from time of fertilization, primary and measured selfing rates are distinguished. Measured rate ( $R_m$ ) is that recorded at the filled-seed or germinant-seedling stage and was determined for these three species using isozymes or morphological markers (references given in footnotes 6, 8, and 10 in Table 1). Primary rates ( $R$ ) were calculated from measured rates,  $R_m$ , and ID in seed set (Maki 1993),  $R = R_m / (1 - ID_{\text{seed set}} + [R_m \cdot ID_{\text{seed set}}])$ . Rates are given in Table 1. For Douglas-fir and noble fir, they are combined estimates based on several values of  $R_m$  and  $ID_{\text{seed set}}$  published in the literature, and on the assumption given in footnote 1 (Table 1).

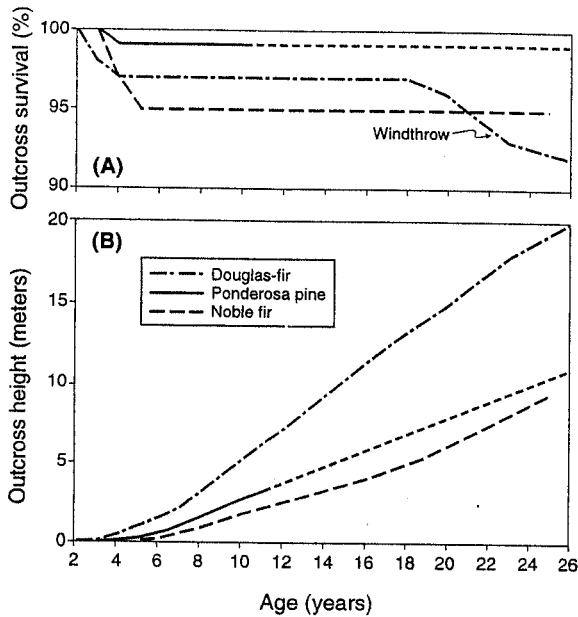


FIG. 1. Mean survival (A) and height (B) of outcross families of three species at the Monmouth outplanting site. Dashed line for ponderosa pine means that no observations were made between ages 10 and 26 years. Observations made annually to age 8 (age 9 for noble fir), biennially to age 20 (age 19 for noble fir), and triennially to age 26 (age 25 for noble fir).

## RESULTS

### *Performance of Outcross Plants*

Plant growth and ID in the nursery were reported in Sorensen and Miles (1974) and Sorensen et al. (1976). In the field tests, there was slight mortality of outcross plants immediately after outplanting and little mortality thereafter (Fig. 1A), which is indicative of a nonstress planting site. (The mortality in Douglas-fir after age 20 was from blow-down during a winter storm. The other species were not affected, because of less dense crowns or deeper rooting.) During the first four to six years after outplanting, the seedlings were in a phase of accelerating height increment (Fig. 1B) typical of outplanted seedlings (Overton and Ching 1978). Subsequent height increment was nearly linear.

### *Inbreeding Depression in Survival*

Self compared to outcross progenies of all three species had greater mortality during the two-year stress period after outplanting (Fig. 2), but only in Douglas-fir was ID in survival significant after two years in the field ( $0.171 \pm 0.057$ , vs.  $0.045 \pm 0.072$  and  $0.040 \pm 0.077$  for ponderosa pine and noble fir). After plants became established (ages 5 or 6), ID in survival increased only moderately for several years. Mortality during this period was mostly due to unknown causes. Sometimes it was because slower-growing self seedlings remained longer in a stage susceptible to some biotic agent, for example, pocket gopher (*Thomomys* spp.) damage to Douglas-fir between ages 14 and 16. The second main stage of ID in survival came with the onset of suppression mortality after stand closure in the faster growing Douglas-fir. In this

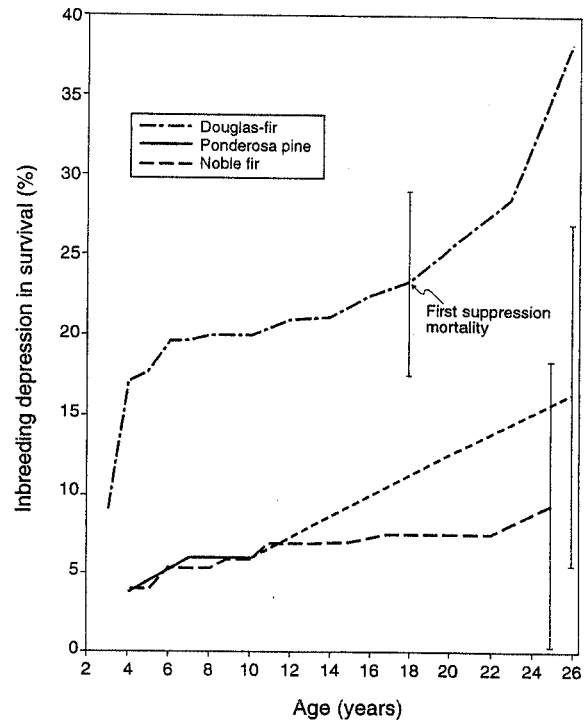


FIG. 2. Mean inbreeding depressions in survival for three conifer species at Monmouth site from outplanting to age 25 or 26 years. Dashed line for ponderosa pine means that no observations were made between ages 10 and 26. Vertical lines at final observation indicate 95% confidence intervals. Age 18 is used for Douglas-fir because that was the last age that survival was not influenced by suppression mortality. Observations made annually to age 8 (age 9 for noble fir), biennially to age 20 (age 19 for noble fir), and triennially to age 26 (age 25 for noble fir).

species, the slope of the ID line increased rapidly over the last three observation periods (Fig. 2).

Interspecific differences in ID in survival across the three life stages of seed (or embryo), nursery, and field to age 18 (i.e., before suppression mortality became a factor in any species) were consistent, with Douglas-fir having the greatest depression and noble fir the least (Table 2).

### *Inbreeding Depression in Height*

Time courses of ID in height, particularly in the 10 years after outplanting, were strikingly different for the three species (Fig. 3). Up to age 6, ID in total height increased rapidly. The increase was largest in Douglas-fir, from 0.26 to 0.41. The increase was not due to mortality of smallest selfs (with heights of trees dead at age 12 deleted from younger datasets, the increase in ID in Douglas-fir was 0.25 to 0.41), but to interspecific differences in elongation rates of self plants compared to outcross plants. Expressed as relative elongation rate ( $\text{dm} \cdot \text{dm}^{-1} \cdot \text{year}^{-1}$ ) from age 2 to 6, ID for Douglas-fir was  $0.116 \pm 0.041$ .

After age 6, ID in total height decreased in Douglas-fir and ponderosa pine. The decrease was strong and continued to age 12 in Douglas-fir (Fig. 3). Although absolute growth of outcross progeny was still greater than self progeny, the downward slope of the line (Fig. 3) meant that the elongation

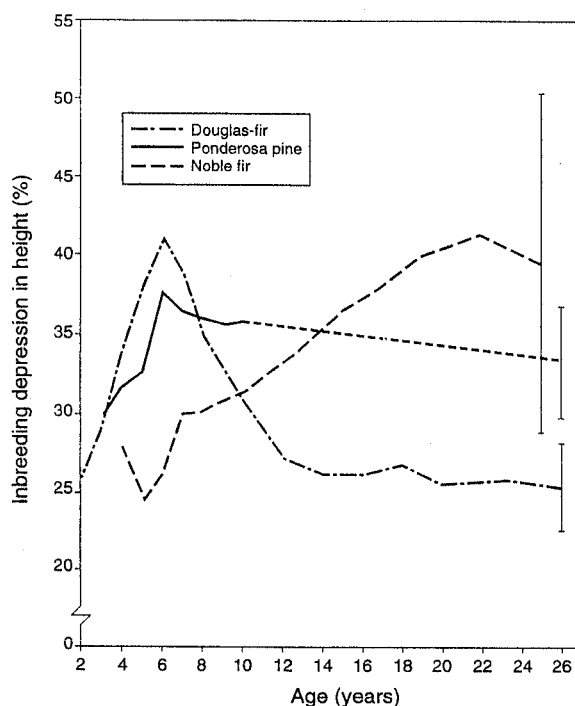


FIG. 3. Mean inbreeding depressions in height for three conifer species at Monmouth site from outplanting to age 25 or 26 years. Dashed line for ponderosa pine means that no observations were made between ages 10 and 26. Vertical lines at final measurement indicate 95% confidence intervals. Observations made annually to age 8 (age 9 for noble fir), biennially to age 20 (age 19 for noble fir), and triennially to age 26 (age 25 for noble fir).

rate of the selfs was greater than that of the outcrosses. Inbreeding depression in relative elongation rate of Douglas-fir for ages 6–12 was significantly negative,  $-0.140 \pm 0.033$ . Greater elongation rate of Douglas-fir inbreds also was observed the second year in the nursery (Sorensen 1997), but to a much lesser degree. During the same ages, the age line for noble fir was completely different (Fig. 3). After a small initial drop, ID in height increased to about age 20.

For all species, an age or size was reached after which selfs and outcrosses elongated at about the same rate. This was about age 7 for ponderosa pine, age 12 for Douglas-fir, and age 20 for noble fir. Suppression mortality of the shortest selfs contributed to keeping the age line flat after the stand closed (age 18) in Douglas-fir, but mortality in the other species was not due to suppression and was not restricted to the shortest selfs. In comparison among species, there was an inverse relationship between the IDs in height and in survival (Table 2).

#### *Inbreeding Depression and Stem Form*

At final measurement, IDs in total height for Douglas-fir, ponderosa pine, and noble fir were  $0.251 \pm 0.028$ ,  $0.333 \pm 0.036$ , and  $0.395 \pm 0.108$ , respectively (Fig. 3), and in diameter were  $0.439 \pm 0.033$ ,  $0.490 \pm 0.040$ , and  $0.474 \pm 0.159$ , respectively. The larger difference in ID for height compared to diameter for Douglas-fir (0.144) and ponderosa pine (0.157) than for noble fir (0.035) suggested that the species might differ in biomass allocation in response to in-

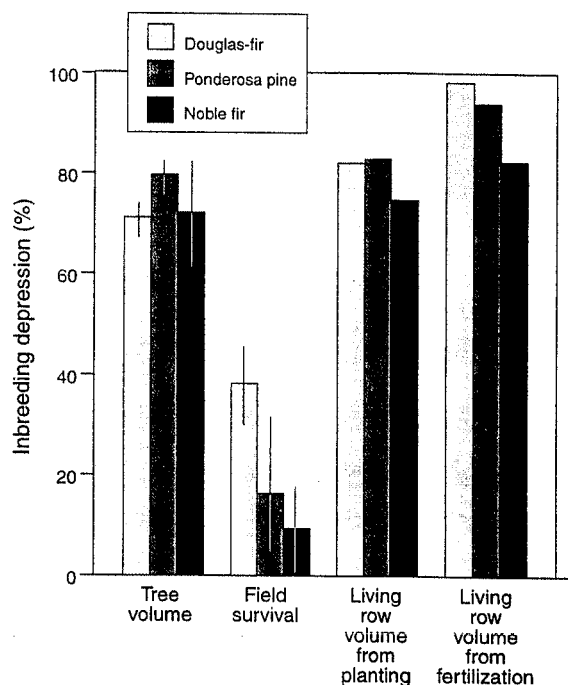


FIG. 4. Inbreeding depressions in individual tree volume at final measurement, survival from outplanting to final measurement, surviving row volume from time of outplanting, and surviving row volume from time of fertilization. Vertical lines give 95% confidence intervals for mean individual tree volume and field survival.

breeding or to competitive stress. To further evaluate this, the ID in height:diameter ratio was determined and was greater for Douglas-fir ( $-0.297 \pm 0.069$ ) and ponderosa pine ( $-0.308 \pm 0.068$ ) than for noble fir ( $-0.153 \pm 0.114$ ). In all cases, the suppressed inbreds, compared to outcrosses, put more biomass into height growth. The difference between noble fir and the other species indicated that in this test suppressed noble fir inbreds, compared to Douglas-fir and ponderosa pine, were less able to allocate biomass to height increment.

#### *Total Inbreeding Depression*

Inbreeding depression in three productivity traits, individual tree volume, surviving row volume from time of planting, and total inbreeding depression from time of fertilization, were calculated for the final measurement age. Inbreeding from time of fertilization assumes one fertilization per ovule and is a product of ID in seed set (embryo survival), ID in nursery survival, and ID in living row volume (which includes plantation survival and stem biomass). Inbreeding depression in these traits is very large (0.83 to 0.98 from time of fertilization to age 25 or 26, Fig. 4), which indicates no or very few selfs will remain in the mature stands, even if the mature stand is a spaced plantation in a mild setting.

## DISCUSSION

### *Survival*

Douglas-fir had the highest ID in field survival (Fig. 2) despite a high level of primary selfing (Table 1). This suggests

that purging of lethal and severely detrimental alleles has not been effective. This is in contrast with other reports (Piesch and Stettler 1971; Sorensen and Adams 1993; Sorensen 1994; Kärkkäinen et al. 1996) that indicate reduced embryonic genetic loads in stands of low density or in mixed stands where the study species is a minor component. Lande et al. (1994) noted that if no self progeny contribute to the next generation, no purging can occur, even when selfing rates are intermediate. That appears to be the status of the normal Douglas-fir stand. The exception in low-density stands may be that inbred plants survive to maturity.

Presumed suppression mortality first occurred in Douglas-fir at age 18. Based on visual impression, the stand was still open at that age and mortality was surprising. Curtis's index of stand density (Curtis 1982) indicated relative density to be low at age 18, compared with the "normal" stand. This agrees with the visual observation that competitive thinning of self Douglas-fir plants started when density was low, and agrees with other observations of ID in "competitive ability" (Schmitt and Ehrhardt 1990; Latter and Mulley 1995).

Although the Douglas-fir selfs die when stand density is still relatively low, the term competitive ability may be a partial misnomer. The self plants have a very low crown position. Results from the analysis of form indicate that Douglas-fir, at least compared to noble fir, may have unusual plasticity in allocating biomass to height growth in response to crowding. This appears to be positive competitive ability, but may result in a root/shoot imbalance in self progeny striving to maintain crown position both during and after crown closure. Suppression mortality of self trees was almost always observed as complete browning of the needle complement in late summer or early autumn (i.e., between height measurement in late August or early September and diameter measurement in late October). This suggests that moisture stress rather than shade may have been the cause of death (Daniel et al. 1979; Davies 1985).

### *Height Increment*

There were large differences among the three species in the ontogenetic path of ID in height (Fig. 3). Inbreeding results have been reported twice previously on this material, at the end of the nursery phase and at age 10. These were the ages that IDs in height were smallest (Fig. 3), and lack of interspecific difference was emphasized in earlier reports (e.g., Sorensen and Miles 1982). That was a mistaken conclusion, and Figure 3 points out the importance of long and detailed records for comparison of long-lived perennials.

Both Douglas-fir and ponderosa pine, but particularly Douglas-fir, showed an increase in ID for several years after outplanting (Fig. 3). Presumably this was partly an inbreeding response to the stress of transplanting from the nursery to the field environment. Height growth of noble fir selfs did not show an immediate increase in ID after transplanting. It is assumed that the aftereffect of transplanting did not persist beyond the first two to three years in the field.

The most interesting portion of Figure 3 is the Douglas-fir curve between ages 6 and 12, during which time the self progeny were elongating at a faster rate than the outcross progeny (ID in relative elongation rate,  $\text{dm} \cdot \text{dm}^{-1} \cdot \text{year}^{-1}$ ,

$= -0.140 \pm 0.033$ ). Three explanations for the negative ID in age 6–12 relative elongation rate are suggested.

First, mortality of the shortest individuals might artificially inflate the mean heights of the self progeny more than the outcross progeny. The curves in Figure 3 were plotted using means based on all living trees at each age. For comparison a second set of age curves was plotted using only trees alive at age 12. The two datasets were almost identical, because few self plants died and mortality was only weakly size dependent. Thus, differential mortality of selfs and outcrosses was not a factor.

Second, smaller plants often have greater growth rates than larger plants because of differences in self-shading, differences in proportion of support tissue, and other factors (van den Driessche 1992). The effect of plant size would be to position selfs at an earlier point on the accelerating part of the elongation curve (Overton and Ching 1978). In this situation, selfs would still be in the accelerating phase of elongation when outcrosses were in the early linear phase. This explanation was proposed by Sorensen and Miles (1982) based on comparison of Gompertz growth curves fitted to annual height measurements to age 10. Based on the plots in Figure 3, this explanation seems reasonable for the shape of the ponderosa pine curve, but not for the prolonged decreasing trend in Douglas-fir.

Finally, height growth in some species shows a plastic response to photomorphogenic signaling from low-fluence side light (Ballaré et al. 1987). Proximity signaling can occur before actual shading from neighboring plants (Ballaré et al. 1990), and has the effect of delaying development of size inequality between neighbors (Ballaré et al. 1994). Ritchie (1997) provides strong experimental evidence for photomorphogenic signaling in growth of Douglas-fir seedlings, and results of Scott et al. (1998) are indicative of the same response in young field-grown plants. In both of these studies, the plants showed increased height and diameter increment prior to mutual shading.

If photomorphogenic signaling is contributing to reduction in size inequality between ages 6 and 12 in Douglas-fir, why is there no comparable response in ponderosa pine and noble fir? (With height measurements missing for ages 12–23 in ponderosa pine, it is unknown if the ponderosa pine height curve [Fig. 3] continued down past age 10. Clearly, the noble fir curve did not.) Elongation response is usually more plastic in early than in late successional species (Morgan and Smith 1979). The conifers in this comparison all tend to be early successional. They differ mainly in that Douglas-fir is more vigorous and is more frequently found in mild, productive habitats that favor competitive ability, whereas noble fir is usually found in climatically more stressful environments. Importance of competitive ability for Douglas-fir may have favored selection of photomorphogenically more responsive individuals (Schmitt 1997; Sierra-de-Grado et al. 1997).

Although speculative, I suggest that interspecific differences in inbreeding depression in height to age 12 are mainly due to both differences in growth rates and responses to photomorphogenic signaling, with the latter most important for Douglas-fir. As possible confirmation, I mention a younger Douglas-fir test of lower level of inbreeding (full-sib inbreeding) and planted at closer spacing (2.7 m). In this test,

TABLE 3. Inbreeding depression in seed set, height, and diameter for several conifer species. Heights and diameters were measured in field tests, and plants were more than 10 years of age at time of measurement. Age refers to plant age when last measurements were made. Species are arrayed according to inbreeding depression in seed set.

Species	Age (yrs)	Inbreeding depression			Reference
		Seed set	Height	Diameter	
<i>Picea sitchensis</i>	15	—	0.32	0.39	Samuel (1991)
<i>Pinus pinaster</i>	11	0.21	0.15	0.25	Durel et al. (1996)
<i>Abies procera</i>	25	0.29	0.40	0.47	Sorensen et al. (1976); this paper
<i>Picea mariana</i>	14	0.55	0.39	—	Park and Fowler (1984); Boyle (1987)
<i>Pinus ponderosa</i>	26	0.64	0.33	0.49	Sorensen (1970); this paper
<i>Picea abies</i> <sup>1</sup>	10	0.65	0.32	0.39	Skrøppa and Tho (1990); Skrøppa (1996)
<i>Pinus elliotii</i>	26	0.79 <sup>2</sup>	0.22 <sup>3</sup>	0.29 <sup>3</sup>	Squillace and Kraus (1962); Snyder and Squillace (1966); Matheson et al. (1995)
<i>Pinus taeda</i>	19	0.81	0.19	0.32	Franklin (1968); Bush and Smouse (1991)
<i>Picea glauca</i>	17	0.85 <sup>4</sup>	0.44	0.64	Coles and Fowler (1976); Fowler and Park (1983)
<i>Pseudotsuga menziesii</i>	26	0.89 <sup>4</sup>	0.25	0.42	Piesch and Stettler (1971); Sorensen (1971); this paper

<sup>1</sup> Values are means of 23 pairs of families reported at age 10 (Skrøppa 1996).

<sup>2</sup> Seed set is mean of two datasets.

<sup>3</sup> Height and diameter are mean of four datasets. Numbers used were unadjusted for breeding values and were converted to  $F = 0.5$  assuming a linear relationship between  $F$  and inbreeding depression in height and diameter over the range of  $F$  from 0.1 to 0.5.

<sup>4</sup> Seed set is mean of four datasets.

inbreeding depression in height increased from ages 2 to 5 and decreased from ages 5 to 7, the last year of measurement (unpubl. data).

#### Other Vigor Traits

Inbreeding depression in diameter is always greater than inbreeding depression in height. This is true for the three species in this comparison as well as for all conifers reported in the literature (Table 3). Plants anticipating competition or responding to it favor height increment at the expense of diameter and root growth (Mohler et al. 1978). Consequently, slow growing inbreds show more depression in diameter and much more depression in volume than they do in height. The three species compared in this test differed in the relative inbreeding depression of height and diameter (i.e., in response of height:diameter ratio to inbreeding). The present test does not show whether the species differ in purely genetic control of growth (see next section) or in growth plasticity in response to photomorphogenic signaling and suppression.

#### Survival versus Vigor

The decline in heterozygosity accompanying inbreeding is often less than mating system expectations (Hayman and Mather 1953; Mina et al. 1991). In the present comparison, there was a strong inverse relationship between inbreeding depression in survival (embryo + plant) and in height at final measurement (Table 2). This suggests that selection against deleterious embryonic alleles and chromosome segments linked to them may increase heterozygosity in the surviving self plants (Sorensen 1967; Matthews and Craig 1989; Brouwer and Osborn 1997).

To check this further, I correlated survival and vigor in 10 conifer tests that were 10 years of age or older (Table 3). Among the larger sample of species, there was no relationship between ID in seed set and ID in height ( $r = 0.039$ ,  $df = 7$ ,  $P > 0.05$ ). Although an inverse relation between the two is plausible, it may not be valid across species because of factors such as interspecific differences in growth plasticity. Alternatively, it may be that species comparisons need to be made

TABLE 4. Comparative inbreeding depression in Douglas-fir (DF), ponderosa pine (PP), and noble fir (NF) for several survival and size traits.

Trait	Comparative depression		
	DF	PP	NF
Rate of primary selfing	High	Mid	Low
Inbreeding depression in seed set	High	Mid	Low
Inbreeding depression in nursery survival	High	Mid	Low
Inbreeding depression in early field survival	High	Mid	Low
Inbreeding depression in height, age 25 or 26	Low	Mid	High
Total inbreeding depression at age 25 or 26	High	Mid	Low
Inbreeding effect on height : diameter ratio	High	High	Low

in a common environment and, for long-lived perennials, be evaluated at a common age, as both environment and age influence expression of inbreeding depression.

#### CONCLUSION

The ontogenetic pattern of inbreeding depression differed among the three species (Table 4). Results presented above suggest that interspecific differences both in self-fertility and in plasticity in allocation of biomass may be important. In any case, the ultimate genetic outcome appears to be the same for all. Over time, either early or late but before reproductive maturity, essentially all of the selfs will be lost because of ID. Published assessments indicate that usually inbreeding is negligible or there is an excess of heterozygotes at the adult stage (Shaw and Allard 1982b; Yazdani et al. 1985; Muona et al. 1987; Bush and Smouse 1992). The results of this test indicate the same outcome when the material is carefully cultured in spaced nursery and field trials in a mild location. Only where population density is low enough that crown position is not a factor in survival, is it likely that self plants will persist in the population.

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#### LITERATURE CITED

- BALLARÉ, C. L., R. A. SÁNCHEZ, A. L. SCOPEL, J. J. CASAL, AND C. M. GHERSA. 1987. Early detection of neighbour plants by phytochrome perception of spectral changes in reflected sunlight. *Plant Cell Environ.* 10:551-557.
- BALLARÉ, C. L., A. L. SCOPEL, AND R. A. SÁNCHEZ. 1990. Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science* 247:329-332.
- BALLARÉ, C. L., A. L. SCOPEL, E. T. JORDAN, AND R. D. VIERSTRA. 1994. Signaling among neighboring plants and the development of size inequalities in plant populations. *Proc. Natl Acad. Sci. USA* 91:10094-10098.
- BARRETT, S. C. H., AND L. D. HARDER. 1996. Ecology and evolution of plant mating. *Trends Ecol. Evol.* 11:73-79.
- BOYLE, T. J. B. 1987. A diallel cross in black spruce. *Genome* 29:180-186.
- BROUWER, D. J., AND T. C. OSBORN. 1997. Molecular marker analysis of the approach to homozygosity by selfing in diploid alfalfa. *Crop Sci.* 37:1326-1330.
- BRUCE, D., AND D. J. DEMARS. 1974. Volume equations for second-growth Douglas-fir. U. S. For. Serv. Res. Note PNW-239.
- BUSH, R. M., AND P. E. SMOUSE. 1991. The impact of electrophoretic genotype on life history traits in *Pinus taeda*. *Evolution* 45:481-498.
- . 1992. Evidence for the adaptive significance of allozymes in forest trees. *New Forests* 6:179-196.
- CARKIN, R. E., J. F. FRANKLIN, J. BOOTH, AND C. E. SMITH. 1978. Seedling habits of upper-slope species. IV. Seed flight of noble fir and Pacific silver fir. U. S. For. Serv. Res. Note PNW-312.
- CHARLESWORTH, D., AND B. CHARLESWORTH. 1987. Inbreeding depression and its evolutionary consequences. *Annu. Rev. Ecol. Syst.* 18:237-268.
- CHEN, H. Y. H. 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. *Can. J. For. Res.* 27:1383-1393.
- COLES, J. F., AND D. P. FOWLER. 1976. Inbreeding in neighboring trees in two white spruce populations. *Silvae Genet.* 25:29-34.
- CURTIS, R. O. 1982. A simple index of stand density for Douglas-fir. *For. Sci.* 28:92-94.
- DAHMS, W. G., AND J. W. BARRETT. 1975. Seed production of central Oregon ponderosa and lodgepole pines. U. S. For. Serv. Res. Pap. PNW-191.
- DANIEL, T. W., J. A. HELMS, AND F. S. BAKER. 1979. Principles of silviculture. 2d ed. McGraw-Hill, New York.
- DAVIES, R. J. 1985. The importance of weed control and the use of tree shelters for establishing broadleaved trees on grass-dominated sites in England. *Forestry* 58:167-180.
- DREW, A. P., AND W. K. FERRELL. 1977. Morphological acclimation to light intensity in Douglas-fir seedlings. *Can. J. Bot.* 56:2033-2042.
- DUREL, C. E., P. BERTIN, AND A. KREMER. 1996. Relationship between inbreeding depression and inbreeding coefficient in maritime pine (*Pinus pinaster*). *Theor. Appl. Genet.* 92:347-356.
- EL-KASSABY, Y. A., F. C. YEH, AND O. SZIKLAI. 1981. Estimation of the outcrossing rate of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) using allozyme polymorphisms. *Silvae Genet.* 30:182-184.
- EMMINGHAM, W. H., AND R. H. WARING. 1973. Conifer growth under different light environments in the Siskiyou Mountains of southwestern Oregon. *Northwest Sci.* 47:88-99.
- FOWLER, D. P., AND Y. S. PARK. 1983. Population studies of white spruce. I. Effects of self-pollination. *Can. J. For. Res.* 13:1133-1138.
- FRANKLIN, E. C. 1968. Artificial self-pollination and natural inbreeding in *Pinus taeda* L. Ph.D. diss., North Carolina State University, Raleigh, NC.
- HAGMAN, M., AND L. MIKKOLA. 1963. Observations on cross-, self-, and interspecific pollination in *Pinus peuce* Griseb. *Silvae Genet.* 12:73-79.
- HAYMAN, G. I., AND K. MATHER. 1953. The progress of inbreeding when homozygotes are at a disadvantage. *J. Agric. Res.* 60:453-472.
- HELENURM, K., AND B. A. SCHAAL. 1996. Genetic and maternal effects on offspring fitness in *Lupinus texensis* (Fabaceae). *Am. J. Bot.* 83:1596-1608.
- HUSBAND, B. C., AND D. W. SCHEMSKE. 1995. Magnitude and timing of inbreeding depression in a diploid population of *Epilobium angustifolium* (Onagraceae). *Heredity* 75:206-215.
- . 1996. Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution* 50:54-70.
- ISAAC, L. A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Pack Forest Foundation, Washington, DC.
- ISAAC, L. A., AND G. S. MEAGHER. 1936. Natural reproduction on the Tillamook burn two years after the fire. Pac. Northwest For. Exp. Stn. R-NW, M-1, Portland, OR.
- JOHNSTON, M. O., AND D. J. SCHOEN. 1994. On the measurement of inbreeding depression. *Evolution* 48:1735-1741.
- KÄRKKÄINEN, K., V. KOSKI, AND O. SAVOLAINEN. 1996. Geographic variation in the inbreeding depression in Scots pine. *Evolution* 59:111-119.
- LANDE, R., AND D. W. SCHEMSKE. 1985. The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. *Evolution* 39:24-40.
- LANDE, R., D. W. SCHEMSKE, AND S. T. SCHULZE. 1994. High inbreeding depression, selective interference among loci, and the threshold selfing rate for purging recessive lethal mutations. *Evolution* 48:965-978.
- LATTA, R., AND K. RITLAND. 1994. The relationship between inbreeding depression and prior inbreeding among populations of four *Mimulus* taxa. *Evolution* 48:806-817.
- LATTER, B. D. H., AND J. C. MULLEY. 1995. Genetic adaptation to captivity and inbreeding depression in small laboratory populations of *Drosophila melanogaster*. *Genetics* 139:255-266.



- LYNCH, M. 1988. Design and analysis of experiments on random drift and inbreeding depression. *Genetics* 120:791-807.
- MAKI, M. 1993. Outcrossing and fecundity advantage of females in gynodioecious *Chionographis japonica* var. *kirohimensis* (Liliaceae). *Am. J. Bot.* 80:629-634.
- MATHESON, A. C., T. L. WHITE, AND G. R. POWELL. 1995. Effects of inbreeding on growth, stem form and rust resistance in *Pinus elliottii*. *Silvae Genet.* 44:37-46.
- MATTHEWS, T. C., AND G. B. CRAIG, JR. 1989. Isozyme polymorphisms maintained by lethal loci in inbred strains of *Aedes triseriatus*. *J. Hered.* 80:53-57.
- MINA, N. S., B. H. SHELDON, B. H. YOO, AND R. FRANKHAM. 1991. Heterozygosity at protein loci in inbred and outbred lines of chicken. *Poul. Sci.* 70:1864-1872.
- MINORE, D. 1979. Comparative autecological characteristics of northwestern tree species—a literature review. U. S. For. Serv. Gen. Tech. Rep. PNW-87.
- MOHLER, C. L., P. L. MARKS, AND D. G. SPRUGEL. 1978. Stand structure and allometry of trees during self-thinning of pure stands. *J. Ecol.* 66:599-614.
- MORGAN, D. C., AND H. SMITH. 1979. A systematic relationship between phytochrome-controlled development and species habitat for plants grown in simulated natural radiation. *Planta* 145:253-258.
- MUONA, O., R. YAZDANI, AND D. RUDIN. 1987. Genetic change between life stages in *Pinus sylvestris*: allozyme variation in seeds and planted seedlings. *Silvae Genet.* 36:39-42.
- MUONA, O., A. HARJU, AND K. KÄRKÄINEN. 1988. Genetic comparison of natural and nursery grown seedlings of *Pinus sylvestris* using allozymes. *Scand. J. For. Res.* 3:37-46.
- NEALE, D. B., AND W. T. ADAMS. 1985. The mating system in natural and shelterwood stands of Douglas-fir. *Theor. Appl. Genet.* 71:201-207.
- ORR-EWING, A. L. 1957. A cytological study of the effects of self-pollination on *Pseudotsuga menziesii* (Mirb.) Franco. *Silvae Genet.* 6:179-185.
- OVERTON, W. S., AND K. K. CHING. 1978. Analysis of differences in height growth among populations in a nursery selection study. *For. Sci.* 24:497-509.
- PARK, Y. S., AND D. P. FOWLER. 1984. Inbreeding in black spruce (*Picea mariana* [Mill.] B.S.P.): self-fertility, genetic load, and performance. *Can. J. For. Res.* 14:17-21.
- PARKER, I. M., R. R. NAKAMURA, AND D. W. SCHEMSKE. 1995. Reproductive allocation and the fitness consequences of selfing in two sympatric species of *Epiobium* (Onagraceae) with contrasting mating systems. *Am. J. Bot.* 82:1007-1016.
- PIESCH, R. F., AND R. F. STETTLER. 1971. The detection of good selfers for haploid induction in Douglas-fir. *Silvae Genet.* 20:144-148.
- REUKEMA, D. L. 1982. Seedfall in a young-growth Douglas-fir stand: 1950-1978. *Can. J. For. Res.* 12:249-254.
- RITCHIE, G. A. 1997. Evidence for red:far red signaling and photomorphogenic growth response in Douglas-fir (*Pseudotsuga menziesii*) seedlings. *Tree Physiol.* 17:161-168.
- SAMUEL, C. J. A. 1991. The estimation of genetic parameters for growth and stem-form over 15 years in a diallel cross of Sitka spruce. *Silvae Genet.* 40:67-72.
- SCHMITT, J. 1997. Is photomorphogenic shade avoidance adaptive? Perspectives from population biology. *Plant Cell Environ.* 20:826-830.
- SCHMITT, J., AND D. W. EHRHARDT. 1990. Enhancement of inbreeding depression by dominance and suppression in *Impatiens capensis*. *Evolution* 44:269-278.
- SCOTT, W., R. MEADE, R. LEON, D. HYINK, AND R. MILLER. 1998. Plant density and tree-size relations in coast Douglas-fir. *Can. J. For. Res.* 28:74-78.
- SEIDEL, K. W. 1985. A ponderosa pine-grand fir spacing study in central Oregon: results after 10 years. U. S. For. Serv. Res. Note PNW-429.
- SHAW, D. V., AND R. W. ALLARD. 1982a. Estimation of outcrossing rate in Douglas-fir using isozyme markers. *Theor. Appl. Genet.* 62:113-120.
- . 1982b. Isozyme heterozygosity in adult and open-pollinated embryo samples of Douglas-fir. *Silva Fenn.* 16:115-121.
- SIEGISMUND, H. R., AND E. D. KJÆR. 1997. Outcrossing rates in two stands of noble fir (*Abies procera* Rehd.) in Denmark. *Silvae Genet.* 46:144-146.
- SIEGISMUND, H. R., E. D. KJÆR, AND U. B. NIELSEN. 1996. Mating system estimates and effective population numbers for an isolated noble fir (*Abies procera*) clonal seed orchard in Denmark. *Can. J. For. Res.* 26:1135-1141.
- SIERRA-DE-GRADO, R., B. MOULIA, M. FOURNIER, R. ALÍA, AND R. DíEZ-BARRA. 1997. Genetic control of stem form in *Pinus pinaster* Ait. seedlings exposed to lateral light. *Trees Struct. Funct.* 11:455-461.
- SKRØPPA, T. 1996. Diallel crosses in *Picea abies*. II. Performance and inbreeding depression of selfed families. *For. Genet.* 3:69-79.
- SKRØPPA, T., AND T. THO. 1990. Diallel crosses in *Picea abies*. I. Variation in seed yield and seed weight. *Scand. J. For. Genet.* 5:355-367.
- SNYDER, E. B., AND A. E. SQUILLACE. 1966. Cone and seed yields from controlled breeding of southern pines. U. S. For. Serv. Res. Pap. SO-22.
- SØRENSEN, F. C. 1967. Linkage between marker genes and embryonic lethal factors may cause disturbed segregation ratios. *Silvae Genet.* 16:132-134.
- . 1970. Self-fertility of a central Oregon source of ponderosa pine. U. S. For. Serv. Res. Pap. PNW-109.
- . 1971. Estimate of self-fertility in coastal Douglas-fir from inbreeding studies. *Silvae Genet.* 20:115-120.
- . 1973. Frequency of seedlings from natural self-fertilization in coastal Douglas-fir. *Silvae Genet.* 22:20-24.
- . 1982. The roles of polyembryony and embryo viability in the genetic system of conifers. *Evolution* 36:725-733.
- . 1994. Frequency of seedling from natural self-fertilization in Pacific Northwest ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). *Silvae Genet.* 43:100-108.
- . 1997. Effects of sib mating and wind pollination on nursery seedling size, growth components, and phenology of Douglas-fir seed-orchard progenies. *Can. J. For. Res.* 27:557-566.
- SØRENSEN, F. C., AND W. T. ADAMS. 1993. Self fertility and natural selfing in three Oregon Cascade populations of lodgepole pine. Pp. 358-374 in D. Lindgren, ed. *Pinus contorta*—from untamed forest to domesticated crop. Meeting of IUFRO WP 2.02.06 and Frans Kempe symposium. August 24-28; Umeå, Sweden. Department of Forest Genetics and Plant Physiology, Swed. Univ. Agric. Sci., For. Genet. Plant Physiol. Rep. 11.
- SØRENSEN, F. C., AND R. S. MILES. 1974. Self-pollination effects on Douglas-fir and ponderosa pine seeds and seedlings. *Silvae Genet.* 23:135-138.
- . 1982. Inbreeding depression in height, height growth, and survival of Douglas-fir, ponderosa pine, and noble fir to 10 years of age. *For. Sci.* 28:283-292.
- SØRENSEN, F. C., J. F. FRANKLIN, AND R. WOOLLARD. 1976. Self-pollination effects on seed and seedling traits in noble fir. *For. Sci.* 22:155-159.
- SQUILLACE, A. E., AND J. F. KRAUS. 1962. Effects of inbreeding on seed yield, germination, rate of germination, and seedling growth in slash pine. Pp. 59-63 in Forest genetics workshop proceedings. Southern Forest Tree Improvement Committee Publication 22.
- VAN DEN DRIESSCHE, R. 1992. Absolute and relative growth of Douglas-fir seedlings of different sizes. *Tree Physiol.* 10:141-152.
- YAZDANI, R., O. MUONA, D. RUDIN, AND A. E. SZMIDT. 1985. Genetic structure of a *Pinus sylvestris* L. seed-tree stand and naturally regenerated understorey. *For. Sci.* 31:430-436.