

Evaluation of Selfing Effects on Western Redcedar Growth and Yield in Operational Plantations Using the Tree and Stand Simulator (TASS)

Tongli Wang and John H. Russell

Abstract: Seed lots of western redcedar (*Thuja plicata*) from both wild stands and seed orchards contain a relatively large proportion of self-pollinated seeds compared to other tree species. Selfed seeds do not exhibit early inbreeding depression, and thus have the same probability of producing acceptable seedlings for field planting as outcrossed ones. However, selfed trees show, on average, about 10% reduction in 9-year height after outplanting. To evaluate the potential negative effects of selfing on productivity at harvest, growth and yield of stands comprising selfs were simulated using TASS (tree and stand simulator) with various planting sites and initial planting densities in this study. Height distributions of selfed and outcrossed individuals were also compared and modeled, which provided a solid basis for accurate TASS simulations and some inside view of selfing in this species. Our results indicate that effects of selfing are smaller on stand final productivity (8% on average) than on 9-year-young trees due to natural selection (competition) against slower-growing trees after crown closure, resulting in more selfs being purged than outcrossed trees. Using better planting sites with higher initial planting densities can substantially intensify the selection and reduce the negative effects of selfing on final productivity. FOR. SCI. 52(3):281–289.

Key Words: Inbreeding depression, height distribution, competition, TASS.

NEGATIVE EFFECTS OF INBREEDING due to related matings have been widely observed on fitness and growth in forest trees (Griffin and Lindgren 1985, Snieszko and Zobel 1988, Woods and Heaman 1989, Sorensen and Cress 1994, Durel et al. 1996, Williams and Savolainen 1996, Sorensen 1997, 1999, Wang et al. 1999, Woods et al. 2002). As a result, reducing the probability of inbreeding in seed orchards through orchard design and management (Vanclay 1991, Chakravarty and Bagchi 1993), and sublining breeding populations (Lowe and van Buijtenen 1986, McKeand and Bridgwater 1998) has become a priority. Low to moderate levels of inbreeding such as half- and full-sib are of particular concern since these can result in viable seed and acceptable seedlings for operational plantations, and thus affect productivity of mature stands (Woods et al. 2002, Wang et al. 2004). In contrast, selfing is not usually as much of a concern in seed orchards since viability of selfed seeds is generally low ($\leq 10\%$) for most conifers due to self-incompatibility mechanisms (Shaw and Allard 1982, Woods and Heaman 1989, Prat and Caquelard 1995, Stoehr et al. 1998, Sorensen 1999). In addition, a significant proportion of selfed seedlings is usually purged at the nursery stage because of the expression of lethal and sublethal genes affecting seedling quality (Woods et al. 2002). Therefore, the number of selfed seedlings being included in operational plantations is usually negligible.

Western redcedar (*Thuja plicata* D. Don) is one of a few

exceptions among conifers. Selfing rates are relatively high in western redcedar compared to other coniferous species in both natural populations (30%) (O'Connell et al. 2001) and seed orchards (60%) (El-Kassaby et al. 1994, Glaubitz et al. 2000). The resultant seed exhibits no detectable inbreeding depression at the nursery stage (Cherry 1995, Russell et al. 2003). Thus, selfed seeds have the same probability of producing acceptable seedlings for field planting as outcrossed seeds. After outplanting, however, selfed trees show, on average, about 10% reduction in height compared to outcrossed trees at age 9 with no inbreeding depression in mortality (Russell et al. 2003). Although these levels of inbreeding depression are small in comparison with most other conifers at the same inbreeding level (Durel et al. 1996, Williams and Savolainen 1996, Sorensen 1999, Wang et al. 2004), the late-expressed inbreeding depression in height could significantly affect growth and yield of operational plantations. Examples of other conifers having relatively high rates of selfing include *Thuja orientalis* L. (Xie et al. 1991), *Abies alba* (Kormutak and Lindgren 1996), *Pinus radiata* (Griffin and Lindgren 1985), and *P. resinosa* (Fowler 1965).

Seed orchard managers and collectors are currently developing techniques to minimize selfing in future seed lots. Any additional management that reduces selfing could potentially improve final stand productivity. The quantification of this improvement would assist in evaluating the

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economic impact and feasibility associated with increased management efforts in reducing selfing. However, inbreeding depression results obtained from field trials (Russell et al. 2003) are not appropriate for directly calculating final stand productivity levels since the data were observed on juvenile trees and the trial was not designed for stand-level realized gain assessment. An objective of this study was to simulate the long-term effects of selfing on final stand yields using the growth-and-yield model TASS (tree and stand simulator), developed by the Research Branch, British Columbia Ministry of Forests (Mitchell 1975).

If management techniques are not effective in reducing the proportion of selfs in seed lots, or are too expensive relative to final yield increases, then alternative measures for minimizing inbreeding depression in mature stands should be explored, including silvicultural practices. A previous study has indicated that the negative effects of inbreeding on final stand yield can be reduced through increasing competition by establishing plantations on better planting sites with higher initial planting densities (Wang et al. 2004). Thus, another objective in this study was to explore the effects of site index and initial planting density on inbreeding depression and final stand yield.

Inbreeding depression for juvenile height growth is relatively smaller in western redcedar than that reported in other conifers (Durel et al. 1996, Williams and Savolainen 1996, Sorensen 1999). Analysis and modeling of the height distributions of selfed and outcrossed trees is an essential step for providing a solid basis for accurate TASS simulations. In addition, this information, along with findings from neutral makers (El-Kassaby et al. 1994, O'Connell et al. 2001) may provide additional insight with respect to the genetics of selfing in western redcedar.

Materials and Methods

Plant Materials

A field trial designed to measure inbreeding depression in western redcedar was established at Jordan River (latitude 48°25'N, longitude 124°02'W, elevation 100 m) in coastal British Columbia in 1991. It was composed of 16 selfed and 16 outcrossed families derived from common parents. A randomized complete block design was used with six blocks. Each family was represented by a four-tree row plot in each block. The trial was planted at 2 m × 2 m spacing with 1-year-old seedlings. The founders of the two cross types were selected from wild populations within the Maritime Seed Planning Zone (Meidinger and Pojar 1991) on Vancouver Island, British Columbia. A detailed description of the founders and mating design used for producing selfs and outcross controls is documented in a previous study (Russell et al. 2003). Mortality was very low (<3%) with no significant differences between the two mating types. Observed heights of the two cross types at age 9 were used in TASS simulations. At this age, the average height of selfed trees (4.30 m) was 11.5% smaller than outcrossed trees (4.86 m).

TASS and its Input Parameters

The tree and stand simulator (TASS) is a three-dimensional growth simulator that generates growth and yield information for even-aged stands of pure coniferous species of commercial importance in coastal and interior forests of British Columbia. The model is maintained by the British Columbia Ministry of Forests and can be obtained via the worldwide web (<http://www.for.gov.bc.ca/hre/gymodels/TASS>).

The development of TASS started in the 1960s with white spruce (Mitchell 1969) and coastal Douglas-fir (Mitchell 1975). The latest version (2.07.12), released in Apr. 1999, has been calibrated for four coastal and four interior commercially important species including western redcedar (Goudie 1998). It incorporates a number of sub-models, such as (1) ROTSIM, a laminated root-rot model (Mitchell and Bloomberg 1986); (2) SWAT, a spruce weevil attack model (Alfaro et al. 1996); and (3) TRAYCI, a light interception model (Brunner 1998). TASS is calibrated to conform with data from research trials and re-measured plots located in managed and unmanaged stands (Goudie 1998).

The computer model grows trees and simulates crown competition in a three-dimensional growing space. The crowns of individual trees add a shell of foliage each year and either expand or contract asymmetrically in response to (1) internal growth processes (e.g., height growth); (2) physical restrictions imposed by the crowns of competitors; (3) environmental factors (e.g., site quality, defoliation, pest damage); (4) cultural practices (e.g., thinning, pruning, fertilization); and (5) genetic variation among trees. The volume increment produced by the foliage is distributed over the bole annually, and is accumulated to provide tree and stand statistics.

For this study, TASS was used to simulate the growth of western redcedar plantations comprising different proportions of selfed and outcrossed trees to rotation. It required the following input parameters: (1) initial number of trees per hectare; (2) site index; and (3) spatial distribution of individual trees with assigned initial relative height growth vigor from 0 to 1.1 (i.e., TASS input data set). The initial relative growth vigor for crossing types (i.e., self and out-cross) was based on the results of the 9-year-old inbreeding field trial.

Statistical Analysis of the Field Trial Data

To minimize experimental noise and better capture the effects of two crossing types on growth performance in the simulation, the effects of block, family, and the interaction of these two effects were removed based on the linear model,

$$Y_{ijk} = \mu + b_i + f_j + bf_{ij} + \varepsilon_{ijk}, \quad (1)$$

where Y_{ijk} is the observed height of each individual tree, μ is the overall mean, b_i is the effect of the i th block, f_j is the effect of the j th family, bf_{ij} is the interaction between the i th

block and j th family, and ε_{ijk} is the residual comprising the effects of treatment and random error.

The sum of μ and ε_{ijk} was used as adjusted height, which comprised only the effects of treatment (i.e., outcross versus selfing), random error, and the general mean. Tree height was then converted into relative height with the range from 0 to 1.1 to meet the requirements of the TASS input data set.

To assign a value of growth vigor for each tree in the TASS input data set, the relative height frequency distribution tables were needed for each cross-type. The more classes used to calculate height frequency distributions, the higher the resolution of the simulation. However, the smaller the interval of the classes, the fewer trees in each class, and thus the poorer the representation of that class. This resulted in large random errors due to a limited number of individuals per cross-type in the field trial. This problem was solved by initially using larger intervals, i.e., 22 classes, to generate a smooth frequency distribution and to model the distribution for each cross-type. The modeled distributions were then used to generate the frequency-distribution tables with a finer interval, i.e., 44 classes, for input into TASS.

The best-fitting models for the relative height distributions chosen with SigmaPlot (version 5.0) were a five-parameter pseudo-Voigt function (Equation 2) for outcrossed trees and a five-parameter Weibull function (Equation 3) for selfed trees, as follows:

$$y = y_0 + a \left(c \left(\frac{1}{1 + [(x - x_0)/b]^2} \right) + (1 - c) \exp \left[-0.5 \left(\frac{x - x_0}{b} \right)^2 \right] \right), \quad (2)$$

$$y = y_0 + a \left(\frac{c - 1}{c} \right)^{(1-c)/c} \left[\frac{x - x_0}{b} + \left(\frac{c - 1}{c} \right)^{1/c} \right]^{c-1} \cdot \exp \left\{ - \left[\frac{x - x_0}{b} + \left(\frac{c - 1}{c} \right)^{1/c} \right]^c \right\} + \frac{c - 1}{c}, \quad (3)$$

where y is the probability density of x (height class), and a , b , c , x_0 , and y_0 are the five parameters to be estimated for each of the two functions. The parameters were estimated with SigmaPlot (version 5.0).

Simulation Design

Twelve scenarios were developed to cover the full range of outcrossed and selfed tree mixes (Table 1). The scenarios

were skewed toward greater outcrossed proportions, as these are more likely to occur in reality.

A factorial design was used with the following treatments: (1) 12 crossing type proportion scenarios; (2) three site indices (average top height of dominant trees at 50 years): 18, 25 (predominantly observed in plantations) and 32 meters; and (3) three planting densities: 800, 1,200 (most frequently applied in reforestation) and 1,600 stems per hectare. In total, there were 108 combinations. To account for different competition environments for the individual trees, TASS simulations were repeated 20 times with the individual trees in the stand randomly reassigned for each simulation.

Statistical Analysis of TASS Output

Analysis of variance (ANOVA) was applied to examine the effects of site index, planting density, scenario, and their interactions on final stand merchantable volume (MV, m³/ha) at the putative harvesting age of 60 years. The analysis was conducted using the GLM procedure in SAS (SAS Institute Inc. 1989). The linear model was as follows:

$$y_{ijkl} = \mu + s_i + d_j + sd_{ij} + c_k + sc_{ik} + dc_{jk} + sdc_{ijk} + e_{ijkl}, \quad (4)$$

where y_{ijkl} is the MV of the l th model run for the k th scenario at the i th site index and the j th planting density; μ is the general mean; s_i is the fixed effect of the i th site index; d_j is the fixed effect of the j th planting density; sd_{ij} is the interaction between the i th site index and the j th planting density; c_k is the fixed effect of the k th scenario; sc_{ik} is the interaction between the i th site index and the k th scenario; dc_{jk} is the interaction between the j th planting density and the k th scenario; sdc_{ijk} is the three-way interaction among the i th site index, the j th planting density, and the k th scenario; and e_{ijkl} is the error term.

Regression using the REG procedure in SAS (SAS Institute Inc. 1989) was applied to examine the effect of selfed trees on MV for each combination of site index and planting density, using the linear model,

$$MV = bP_s + a, \quad (5)$$

where b is the regression coefficient, P_s is the proportion of selfs, and a is the intercept. If all trees are outcrossed ($P_s = 0$), MV equals a . Thus, a selfing index representing the effect of selfs on MV at the harvesting age was defined as the ratio (or percentage) of the absolute value of b to a . Assuming selfing affects MV negatively, a greater selfing index indicates a larger negative effect of selfing on MV.

Table 1 Scenarios comprising various percentages of outcrossed and selfed trees deployed in initial plantations for TASS simulations

	Scenario #											
	1	2	3	4	5	6	7	8	9	10	11	12
Outcross (%)	100	95	90	85	80	75	70	60	50	35	15	0
Selfing (%)	0	5	10	15	20	25	30	40	50	65	85	100

A selfing index representing the average effect of selfed trees on MV across different site indices and planting densities was estimated using the same procedure above after the effects of site, density, and site*density on MV were removed, leaving the sum of the mean and the residual from the linear model,

$$Y_{ijk} = \mu + s_i + d_j + sd_{ij} + \varepsilon_{ijk}, \quad (6)$$

where Y_{ijk} is the average MV at the i th site index and j th planting density, μ is the general mean, s_i is the effect of the i th site index, d_j is the effect of the j th planting density, sd_{ij} is the interaction between the i th site index and j th planting density, and ε_{ijk} is the residual comprising the effects of scenario and random error.

The effects of interactions between scenario and the other two main factors were omitted from the model since they only accounted for a small proportion of the variation in MV. Multiple regressions were used to develop a model for predicting selfing indices for the combinations of site index and planting density that were not included in this study. The MAXR method from the REG procedure in SAS (SAS Institute Inc. 1989) was applied to perform this analysis using the second-order polynomial function,

$$Y = b_0 + b_1S + b_2D + b_3S^2 + b_4D^2 + b_5S*D \quad (7)$$

where Y is the selfing index; b_0 , b_1 , b_2 , b_3 , b_4 , and b_5 are intercept and regression coefficients to be estimated; and S , D , and $S*D$ are site index, planting density, and the product of site index and planting density, respectively.

Results

Height Distributions

The observed distributions of 9-year height were plotted with 22 classes for selfed and outcrossed trees in Figure 1. These distributions were well modeled with a five-param-

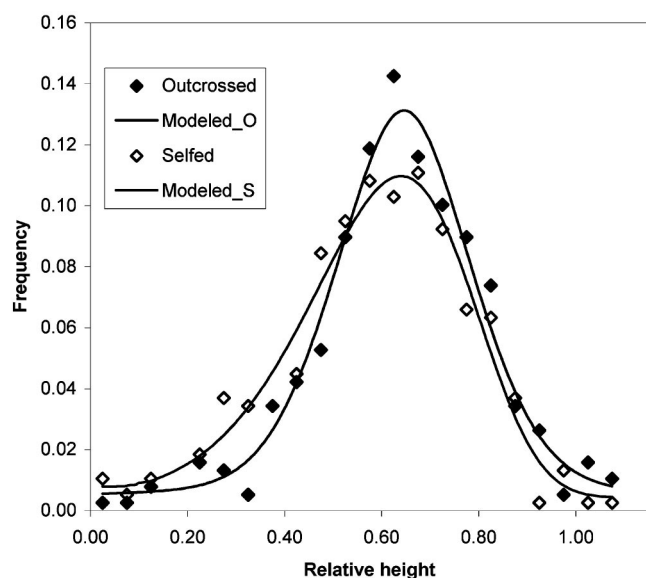


Figure 1. The distributions of relative height and their modeled curves for outcrossed and selfed families.

ter pseudo-Voigt function (Equation 2) for outcrossed trees ($r^2 = 0.97$, $P < 0.0001$) and a five-parameter Weibull function (Equation 3) for selfed trees ($r^2 = 0.96$, $P < 0.0001$), respectively. Therefore, the assignment of growth vigor to each tree in the TASS input data set based on modeled height distributions are reliable, while the resolution of the TASS simulation was enhanced through reduced class intervals of the height distribution tables.

Analysis of TASS Output

Results of ANOVA showed that site index, planting density, crossing type scenario, and their interactions all had significant effects on TASS predictions of merchantable volume (MV) at age 60 years (Table 2). The effects of site index, planting density, and their interaction accounted for the majority of the total variation in MV. The effects of scenario, reflecting different proportions of selfed seed in a seed lot, accounted for a much greater amount of the total variation than its interactions with site and density. Although statistically significant ($P < 0.0001$), the two interactions together accounted for less than 10% of the scenario effect.

Effects of Selves on Merchantable Volume

The effect of inbreeding depression on MV at each combination of site index and planting density was determined by regression of MV on percentages of selfed trees in initial plantations using the model (Equation 5). The regressions were highly significant, with r^2 greater than 0.94 for all cases (Table 3). The regression of average MV, with the effects of site index and planting density removed, on the percentage of selfs in initial plantation is shown in Figure 2. The percentage of selfed trees in initial plantations accounted for 98.7% of the total variation among scenarios in final stand MV.

Selfing indices estimated based on regression coefficients and intercepts varied between 0.065 and 0.129 for different combinations of site indices and planting densities, with an average of 0.081 (Table 3). The reduction in MV due to planting selfed seedlings can be estimated by multiplying the selfing index by the proportion of selfs in the initial plantation, for different combinations of site indices and planting densities. For example, with 50% selfs in an initial plantation with a site index of 18 m and planting density of 800 stems per hectare, the reduction in MV relative to 100% outcrosses will be

$$0.5 \times 0.129 \times 100 = 6.4\%.$$

On average, with 50% selfs, the reduction in MV relative to 100% outcross will be

$$0.5 \times 0.081 \times 100 = 4.1\%.$$

Similarly, the improvement in MV due to a reduction of selfing can be estimated by multiplying the selfing index by the proportion of selfs reduced in initial plantations. For

Table 2 Effects of site index, planting density, scenarios, and their interactions on merchantable volume (MV) at age 60 yr from TASS simulations

Effect	DF	Sum of square	F value*
Site index (<i>S</i>)	2	83,479,746	1.65E+07
Planting density (<i>D</i>)	2	2,076,361	409,962
<i>S</i> * <i>D</i>	4	232,871	22,989
Scenario (<i>C</i>)	11	192,536	6,911
<i>S</i> * <i>C</i>	22	34,049	611
<i>D</i> * <i>C</i>	22	3,423	61
<i>S</i> * <i>D</i> * <i>C</i>	44	1,660	15

* $P < 0.0001$ for all terms.

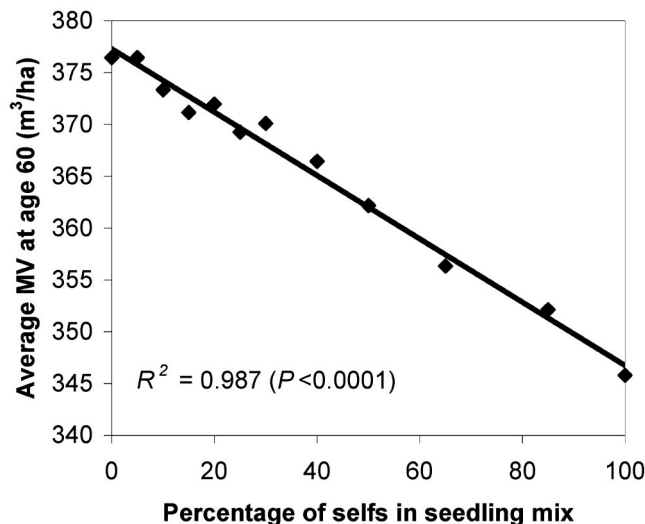
Table 3 Results of regression of merchantable volume per hectare (MV) at 60 yr on proportion of selfs (P_s) in initial plantations for different combinations of site indices (tree height in meter at age 50) and planting densities (stem/ha) from TASS simulations using the model (Equation 5)

Site index (m)	Density (stem/ha)	Intercept (m ³ /ha)	Regression coefficient	R^2 *	Selfing index
18	800	121.79	-15.71	0.980	0.129
18	1,200	153.71	-16.06	0.988	0.104
18	1,600	164.46	-14.80	0.983	0.090
25	800	305.34	-31.06	0.980	0.102
25	1,200	361.86	-29.21	0.983	0.081
25	1,600	376.97	-27.84	0.963	0.074
32	800	578.42	-51.83	0.972	0.090
32	1,200	657.45	-44.24	0.972	0.067
32	1,600	675.68	-44.09	0.945	0.065
Average**		377.29	-30.54	0.987	0.081

Intercept is defined as the MV with 100% outcross. Selfing index is the proportional reduction in MV for the seedling population, with 100% selfs.

* $P < 0.0001$ for all combinations of site indices and planting densities.

**The average effect of selfs was estimated using the model (Equation 5) after the effects of site and density and their interactions were removed using the model (Equation 6).

**Figure 2.** The relationship between average MV after the removal of effects of site index and planting density at harvest (age 60) and the percentage of selfs in initial plantations from TASS simulations.

example, 20% reduction in selfing will, on average, improve the final yield by 1.62%.

The selfing indices were well modeled based on planting density and site index ($r^2 = 0.996$ and $P = 0.0004$) using the second-order polynomial function (Equation 7; Table 4 and Figure 3). Selfing indices can be estimated for additional levels and combinations of site indices and planting densities not included in this study, from the polynomial function with the parameters listed in Table 4.

Results of multiple regressions (Table 4) and the response surface shown in Figure 3 suggest that site index and initial planting density significantly affect the level of inbreeding depression on mature stand final yield. The selfing index decreased with either an increase in site index or an increase in planting density. The decline in selfing index is particularly sharp with increases in both site index and planting density. This was also indicated by the significant contribution of the product of site index and planting density (S * D) to the model and the positive value for the S * D regression coefficient (Table 4).

Discussion

Differences in Height Distributions

Observed and modeled height distributions (Figure 1) provided an insight into the differences between the two crossing types beyond simple statistics, such as means and variances. Height growth of the two crossing types followed different patterns of distribution. The outcrossed trees showed a nearly symmetrical distribution, whereas the selfed trees displayed a considerably skewed distribution pattern toward the left side of the curve (smaller trees). Contrary to what was expected, the two crossing types had overlapping peaks. This pattern of distributions is different from what was found in coastal Douglas-fir in a previous study (Wang et al. 2004), in which the distribution of selfs skewed toward the left side of the curve (smaller trees) while the distribution of outcrossed trees skewed toward the

Table 4. Results of multiple regression of selfing index at the rotation age 60 on site index (m) and planting density (stem/ha) from TASS simulations using the second-order polynomial function (Equation 7)

Independent variable	Parameter estimate	Standard error	F value	Pr > F
Intercept	1.362E-1	2.534E-2	204.54	0.0007
S	-9.590E-3	1.620E-3	35.28	0.0095
S ²	1.124E-4	3.088E-5	13.24	0.0358
D	-1.817E-4	2.472E-5	54.02	0.0052
D ²	4.629E-8	9.456E-9	23.97	0.0163
S*D	1.300E-6	3.821E-7	11.64	0.0421
Model		R ² = 0.996	144.97	0.0004

S = site index, D = planting density, and S*D = product of S and D.

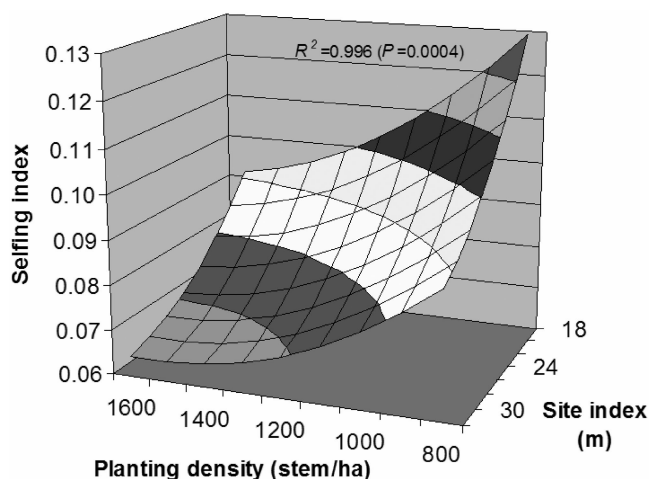


Figure 3. Changes in selfing index with site index and planting density modeled based on the selfing indices in Table 3.

right side of the curve, with their peaks far apart (i.e., the peak of outcrossed trees is 35% larger than that of selfs). In addition, lower levels of inbreeding in coastal Douglas-fir, including matings between full-sibs and between half-sibs, also had shifted peaks toward the left side of the curve, away from the outcross control.

The two crossing types had only small differences in height distribution at the right side of the curve (relative height >0.70) in this study (Figure 1), suggesting that selfing in western redcedar can result in nearly the same proportion of fast-growing trees as outcrossing. Inbreeding depression due to selfing on height growth appears mainly expressed as a smaller proportion of medium-size trees and a greater proportion of smaller-size trees than outcrossing. In contrast, selfing only produces a small fraction of fast-growing individuals relative to outcrosses in coastal Douglas-fir (Wang et al. 2004). This difference can partially be attributed to the large difference in inbreeding depression due to selfing between the two species. However, there are still substantial height growth distribution differences between selfing in western redcedar and half-sib matings in coastal Douglas-fir, despite the two mating types having a similar level of inbreeding depression for tree height at the same age (i.e., 10.4%, data not published). The latter produced a much smaller proportion of fast-growing trees than the former. The relatively larger proportion of fast-growing trees produced by selfing in western redcedar might be

related to high rates of selfing observed in this species (El-Kassaby et al. 1994, O'Connell et al. 2001, Russell et al. 2003). It has been indicated by paleobotanical records that this species experienced a severe population bottleneck during the most recent ice age (Hebda and Mathewes 1984), which most likely caused measurable genetic drift and inbreeding to occur, resulting in a partial switch from outcrossing to selfing (Kirkpatrick and Jarne 2000, Lande and Schemske 1985). Purging of deleterious alleles through the combination of selfing and selection reduces the level of inbreeding depression (Barrett and Charlesworth 1991, Sorensen 2001). Selfing can also result in a large number of alleles being fixed (Doolittle 1987, Falconer 1989). Loci with fixed alleles do not contribute to inbreeding depression if inbreeding occurs. Excessive proportions of fixed alleles were found in previous studies using neutral genetic markers (El-Kassaby et al. 1994, Glaubitz et al. 2000, O'Connell et al. 2001). In addition, fixed loci associated with higher growth vigor might have a better chance to be preserved through natural selection over generations. This could explain the overlapping peak of the two crossing types shown in Figure 1.

However, a greater frequency of selfed trees at the smaller-size end in Figure 1 indicates that a larger proportion of selfed trees are more likely to be purged in mature stands than outcrossed trees, as competition among individuals normally eliminate the poorest individuals first. However, the process of competition also depends on planting density, site conditions, neighborhood, and other factors that are considered in the TASS simulations (Mitchell 1975).

Negative Effects of Selfing on Final Stand Yield

The negative effect of selfing on merchantable volume (MV) at age 60 is, on average, 8.1%. This value is much smaller than the inbreeding depression observed from the field trial at age 9 (11.5%) for height, which would equate to approximately 23% for total juvenile volume (Xie and Yanchuk 2003). The decline in the negative effect of inbreeding on growth from the individual tree level at an early stage to the effect of inbreeding on MV of a simulated mature stand is primarily the result of competition, which eliminates slower-growing individuals in a stand. As shown in Figure 1, selfing produces more slow-growing trees than outcrossing, thus more selfed trees are likely to be purged

from the stand. This can be illustrated in the simulations by following the changes in number of trees per cross-type as the stand matures. For example, with a site index of 25 meters and a planting density of 1,200 stems per hectare, there is a sharp decline in survival of selfed trees starting at about age 35 that would appear to continue even after age 60 (Figure 4). Thus, a longer rotation could result in a further decline in the effects of inbreeding depression on mature stand final yield.

The negative effect of selfing on MV is less in this study than the 13% on average found for half-sib matings in coastal Douglas-fir (Wang et al. 2004), despite having similar juvenile height growth inbreeding depression of individual trees as mentioned earlier. This discrepancy can be partially explained by the difference in the two species' inbred height distributions relative to their respective outcross controls. Overlapping height distributions with outcross trees at the slower-growing end for half-sib matings in coastal Douglas-fir results in less competition-induced mortality of inbred individuals, which has an increased negative effect on mature stand final yield compared to western redcedar. These comparisons suggest that differences in height distribution are more critical than differences in general means or even in variances among mating types in determining the effect of inbreeding on final stand yield, as these simpler statistics may not specifically reflect the differences at the slower-growing end of the height distribution among mating types.

Results of this study suggest that site index and initial planting density significantly affect the level of inbreeding depression on final yield of mature stands. Selfing index varied considerably (0.065–0.129) among the combinations of site index and planting density included in this study (Table 3). The negative effect of selfing on final yield will be substantially smaller if a plantation is established at a better site and/or with a higher initial planting density. The combination of a better site and higher planting density will be more effective in reducing inbreeding depression on productivity than either increasing site index or planting

density alone, as the cross product between these two variables linearly contributes to the selfing index. Effects of site index and planting density can be explained by the timing of canopy closure and the intensity of competition among individuals in a stand. Earlier canopy closure on better sites with a higher planting density results in earlier simulated competition among trees, and more competition-induced mortality of slower-growing trees. As it is usually not easy to improve site index, planting density should be particularly considered in reforestation for this species. Based on the nonlinear relationship shown in Figure 3, the increase in selfing index becomes sharp with the decrease in planting density below ~1,200 stems per hectare, which is the most common planting prescription for pure western redcedar plantations in coastal British Columbia. Thus, we recommend initial planting densities not to be below this number, especially at poor sites.

Implications for Seed Management and Breeding Programs

A large percentage of selfs is expected in seed lots collected either from natural stands (30%) (O'Connell et al. 2001) or seed orchards (60%) (El-Kassaby et al. 1994, Glaubitz et al. 2000). How much effort should be made to reduce the percentage of selfed seed in seed lots depends on the level of the improvement in final yield of a stand at harvest. Based on the results of this study, a total elimination of the 60% selfed seed from a seed orchard seed lot, for example, will increase the production of merchantable stem volume at harvest by 4.9% on average, ranging from 4.0 to 7.8% depending on site quality and planting density. With this result and the market value of the final product, appropriate investment in reducing selfed seed in seed lots can be quantified.

Some techniques being explored both for feasibility and cost-effectiveness, to reduce selfing in seed orchards and natural stands, include (1) developing seed-producing trees with a greater female-to-male cone production ratio through crown manipulation and hormone induction, to be pollinated by trees with more male cones for pollen production only; (2) partial or complete female isolation during pollination in conjunction with supplemental mass pollination; and (3) stratifying seed collection by crown position.

However, as selfing is a natural phenomenon for this species, it will not be easy to avoid selfing in either natural stands or seed orchards. Particularly in seed orchards, problems in synchronization of flowering phenology among clones resulted in a higher selfing rate (El-Kassaby et al. 1994) than in natural populations (O'Connell et al. 2001). Similarly, it will also be difficult to separate selfed seed from outcrossed seed in wild stand seed lots. Therefore, a more practical approach may be taking advantage of selection against the slower-growing selfs through competition by increasing stocking in plantations as an additional measure to reduce inbreeding depression on final productivity.

Another possible approach is to select parents with either low selfing rate or low level of inbreeding depression. Since

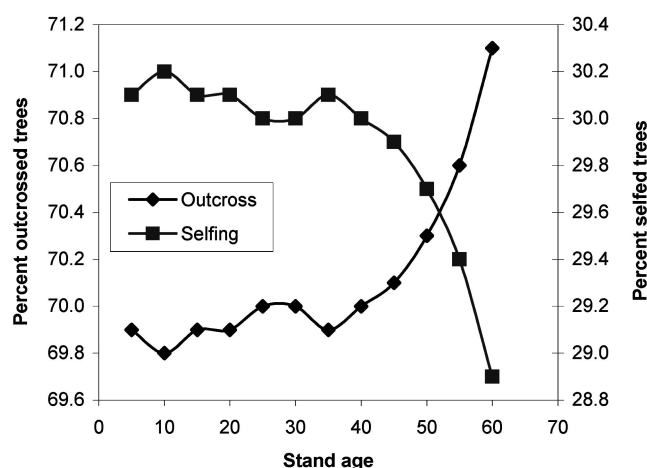


Figure 4. Changes in percent selfed and outcrossed trees with age in a simulated stand using TASS at a site index of 25 meters and planting density of 1,200 stems per hectare.

there is no evidence of any recessive lethals or sublethals in any traits observed from reproduction to survival (Owens et al. 1990, Russell et al. 2003), it does not seem promising to select parents with low selfing rate in this species. However, significant variations in inbreeding depression are found in height growth at an early age in field trials (Russell et al. 2003) and the data used for this study. In this study, six (38%) selfed families showed no or less than 4% inbreeding depression on 9-year height. However, three (19%) selfed families expressed an inbreeding depression greater than 20%, suggesting a potential opportunity to select breeding materials with low inbreeding depression. At least it may be possible to exclude individuals that show substantial inbreeding depression in breeding populations. In addition, at these low inbreeding depression levels, it may be possible to select out of any potential inbreeding depression through recurrent selection for GCA/additive effects (Mullin et al. 1978, Shaw 1995).

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