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Comparison of selection methods for optimizing genetic gain and gene diversity in a red pine (*Pinus resinosa* Ait.) seedling seed orchard

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Abstract Four selection methods, individual selection (IS), family selection (FS), family plus within-family selection (FWFS) and combined selection (CS), were used to estimate genetic gain [$E(g)$] for stem volume and gene diversity (GD) for ten theoretical selection intensities in a 108-family, 12-year-old red pine seedling seed orchard. Estimated genetic gain for stem volume ranged from 4.6% to 11.8% across all selection methods and intensities with CS consistently having the highest gains and FS the lowest for any given selection intensity. Genetic diversity ranged from 0.9797 to 0.9954 across all selection methods and intensities. Individual selection was the best selection method for retaining GD , especially at the higher selection intensities, while FWFS was more efficient at the lowest selection intensity. An optimization point, which maximized $E(g)$ and GD relative to each other, was calculated for each selection method. In all cases the optimization point indicated that both $E(g)$ and GD would be favorably high when optimized relative to each other. The implications for volume gain, genetic diversity and potential inbreeding in red pine, a species with inherently low levels of genetic variation, are discussed.

Keywords Red pine · Selection · Genetic gain · Genetic diversity · Seedling seed orchard

Introduction

Red pine is a major reforestation species in the Upper Great Lakes region and is used for sawtimber, bolts, posts, pilings, cabin logs and pulpwood (Burns and Honkala 1990). Red pine is also known as a genetically depauperate species (Fowler and Morris 1977) with levels of genetic heterozygosity, allelic richness and percent polymorphic loci all lower than expected for a long-lived, monoecious, wind-pollinated species (Hamrick and Godt 1989).

Despite this low level of genetic variability there is continued interest in genetic improvement of red pine because even small increases in stem volume on a per tree basis result in large increases in total productivity due to the number of seedlings that are planted annually. The establishment of seedling seed orchards (Zobel and Talbert 1984) is a relatively easy, cost-effective approach for increasing both the genetic gain and the supply of genetically improved seed. Genetic gain from the seedling seed orchard is manipulated by the selection method and intensity of selection that is used to rogue the orchard shortly after crown closure. However, roguing also decreases the gene diversity (GD) and, by extension, the genetic variation found in the retained trees. This reduction in GD results in a decrease in genetic diversity in the seed produced by the seed orchard, and in the seedlings used for reforestation efforts. Therefore, the selection method and intensity level used should be chosen after careful consideration of the impacts on both the genetic diversity and genetic gain of seed produced from the orchard.

Seed orchard managers typically rely on one of four selection methods to remove undesirable trees in a seedling seed orchard. Family selection (FS) ranks families based on family means and retains all the individuals in the selected families regardless of their individual performance (Carter et al. 1990; Adams and Morgenstern 1991; Morris et al. 1992). Individual selection (IS), or mass selection, ranks each individual tree and rogues those below a minimum threshold level. Family

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plus within-family selection (FWFS) retains a specific number of individuals in the best families (Wilson 1974; Canavera 1975). Combined selection (CS) creates an index value for each tree based on individual and family performance weighted according to individual and family heritabilities, respectively. Any individual tree whose index value ranks below a minimum threshold value is then rogued (Magnussen and Yeatman 1990). Each of these selection methods will increase the expected genetic gain of a particular trait in the seedling seed orchard. However, due to differences in family representation after roguing, these selection methods will have varying effects on the genetic diversity.

The goals of the study reported here were to utilize the St. Louis County red pine seedling seed orchard as a case study to: (1) calculate the variance components and heritabilities, (2) calculate the estimated genetic gain and gene diversity for the four selection methods and ten selection intensities and (3) calculate for each selection method the optimal selection intensity which maximizes both genetic gain and gene diversity.

Materials and methods

Site, seedlings and data collection

The red pine seedling seed orchard is located in St. Louis County near Central Lakes, Minnesota at approximately 47°18' north latitude 92°29' west longitude. The site has a 0–5% slope, sandy loam soil and was formerly occupied by a mixture of quaking aspen (*Populus tremuloides*), balsam fir (*Abies balsamifera*) and paper birch (*Betula papyrifera*). The seedling seed orchard consists of 108 open-pollinated families from single tree selections in Minnesota, Wisconsin and the northern peninsula of Michigan arrayed in single-tree plots in 24 replications for a total of 2,382 planted seedlings (not all families were fully replicated). Seedlings were planted in May 1988 as 1-0 containerized stock at 3 × 3-m spacing and were 12 growing seasons from planting at the time of measurement.

Individual tree heights were measured to the nearest 0.1 m, and diameters were measured at 1.37 m above ground to the nearest 0.5 cm. Stem volume (dm^3) was calculated using a formula for total cubic foot stem volume (Ek 1985) modified to calculate volume in cubic decimeters:

$$dm^3 = \left((0.42 + 0.01969(9.144 - ht)) \cdot \left((3.1416) \left(\frac{dbh}{2} \right)^2 (0.0001) \right) (ht) \right) (10^3)$$

where dbh is diameter and ht is total height. Eight families with low representation in the orchard (number of individuals per family fewer than five) were removed from analysis leaving 100 families.

Calculation of variance components and heritabilities

Variance components were estimated using PROC VARCOMP (SAS Institute 1999) and the following model:

$$Y_{ijkl} = \mu + R_j + F_k + \varepsilon_l$$

where Y is the total tree volume, μ is the overall mean, R_j and F_k are the effects of replication ($j = 1 \dots 24$) and family ($k = 1 \dots 100$), respectively and ε_l is the experimental error. Family and individual

tree heritabilities were calculated using the variance components and the following formulas for family heritability

$$h_f^2 = \frac{\sigma_F^2}{\sigma_F^2 + \frac{\sigma_e^2}{R}}$$

and individual tree heritability

$$h_i^2 = \frac{(4)\sigma_F^2}{\sigma_F^2 + \sigma_e^2}$$

where σ_F^2 is the variation due to family and σ_e^2 is the remainder of the genetic variation plus variation due to experimental error and R is the number of replications.

Simulation of selection methods

Ten selection intensities (7%, 10%, 12%, 15%, 17%, 20%, 23%, 25%, 27% and 30%) that represent the likely range of selection intensities for a seedling seed orchard of this size were used to calculate $E(g)$ for stem volume for each selection method following formulas from Falconer (1989):

individual selection

$$E(g) = i_1 \sigma_P h_i^2$$

family selection

$$E(g) = i_1 \sigma_P h_i^2 \left[\frac{(1 + (n-1)r)}{(\sqrt{n(1 + (n-1)t)})} \right]$$

family + within-family selection

$$E(g) = i_2 \sigma_P h_i^2 \left[\frac{(1 + (n-1)r)}{\sqrt{n(1 + (n-1)t)}} \right] + i_3 \sigma_P h_i^2 \left[(1-r) \sqrt{(n-1)/(1-t)n} \right]$$

combined selection

$$E(g) = i_1 \sigma_P h_i^2 \sqrt{1 + \frac{(r-t)^2}{(1-t)} \times \frac{(n-1)}{(1 + (n-1)t)}}$$

where i_1 , i_2 , and i_3 are the standardized selection intensities (Becker 1984) for individual, family and within-family, respectively, h_i^2 is the individual tree heritability, σ_P is the phenotypic standard deviation, n is the harmonic mean number of individuals in the selected families, r is the genetic correlation among half-sibs ($r = 0.25$) and t is the intraclass phenotypic correlation, which is the between group variance as a proportion of the total variance, and is calculated for half-sibs as (Falconer 1989)

$$t = \frac{\sigma_F^2}{\sigma_P^2} = 0.25(h_i^2)$$

Family size for FWFS was arbitrarily set at seven individuals because this was the smallest family size that still allowed the selection method to span the full range of selection intensities. Individual tree volumes were adjusted for differences in replication effects using the deviation from replication mean (Cotterill 1987; Cotterill and Dean 1990). Adjusted individual volumes were then used to rank individuals, determine family means and calculate the index value (*index*) for combined selection:

$$index = (vol_i - vol_f)(h_w^2) + vol_f(h_f^2)$$

where vol_i is the volume of the individual, adjusted for replication effects, vol_f is the mean volume of the family adjusted for replication effects, h_i^2 and h_f^2 are the individual and family heritabilities, respectively, and h_w^2 is the within-family heritability calculated as:

$$h_w^2 = \frac{1-r}{1-t} (h_i^2)$$

where r , t and h_i^2 are the genetic correlation among half-sibs, the intraclass phenotypic correlation for half-sibs and individual heritability, respectively.

Gene diversity is a measure of the probability that genes are not identical by descent in the gene pool and is calculated as:

$$GD = 1 - T$$

where T is the group coancestry of the population, which describes the probability that two genes are identical by descent

$$T = \sum \left(\frac{n_i}{n} \right) \left(\frac{0.5 + 0.5 r(n_j - 1)}{n} \right)$$

and r , n_j and n are the intraclass correlation (0.25), the number of individuals in family j , and the total number of trees retained, respectively (Wei et al. 1997; Kang et al. 2001).

To determine the selection intensity that maximizes both $E(g)$ and GD relative to each other, we plotted values for $E(g)$ and GD using a 0.0–1.0 relative scale, and quadratic equations were used to estimate regression lines from the data points using SIGMAPLOT (SPSS 2001). An iterative process using these quadratic equations was used to determine the point where both lines intersected, which was considered the optimal number of trees to retain in the seed orchard for a particular selection method. This optimal number of retained trees was used to determine the optimal selection intensity and then used in the quadratic equations to estimate $E(g)$ and GD at the point of optimization.

Results

Plantation survival was high at 93.3%, the average tree height was 5.6 m, average tree diameter was 10.4 cm and the plantation average for stem volume was 27.1 dm³. Type-I estimates of variance components for individual tree stem volume were made, and individual (h_i^2) and family (h_f^2) heritabilities were calculated as 0.189 and 0.523, respectively (Table 1).

To compare among the four selection methods, selection intensities were held constant for all selection simulations at 7%, 10%, 12%, 15%, 17%, 20%, 23%, 25%, 27% and 30% or, in the case of FS and FWFS, as close to these percentages as possible given the constraints of family size. Although three of the four selection methods (FS, FWFS and CS) have a family component in their calculation, there was a marked difference in family representation between them. Indi-

Table 1 Estimated mean squares, variance components and calculated heritabilities for the St. Louis County red pine seedling seed orchard

Source	df	Expected mean square
Rep	23	Var (Error) + 0.0945 Var (family) + 92.067 Var (rep)
Family	99	Var (Error) + 22.077 Var (family)
Error	2,087	Var (Error)
<i>Type-I estimates</i>		<i>Heritabilities</i>
Var (Rep) = 2.7819		$h_i^2 = 0.523$
Var (Family) = 2.5257		$h_f^2 = 0.189$
Var (Error) = 50.8761		

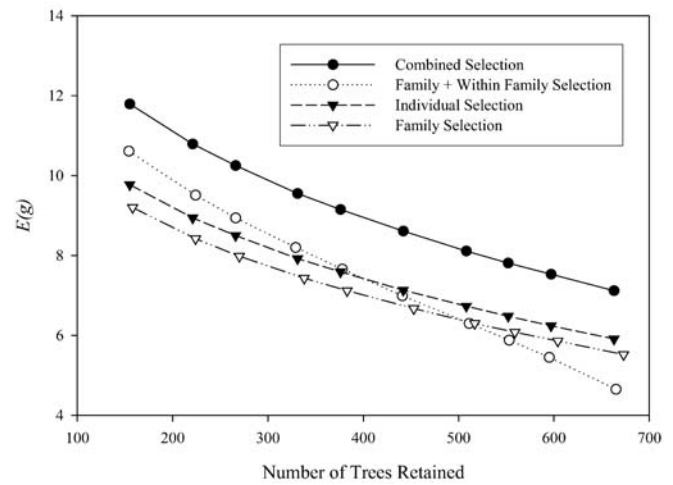


Fig. 1 Percent estimated genetic gain, $E(g)$, for the St. Louis County red pine seedling seed orchard when rogued with four different selection methods across ten different selection intensities ranging from 7% to 30%

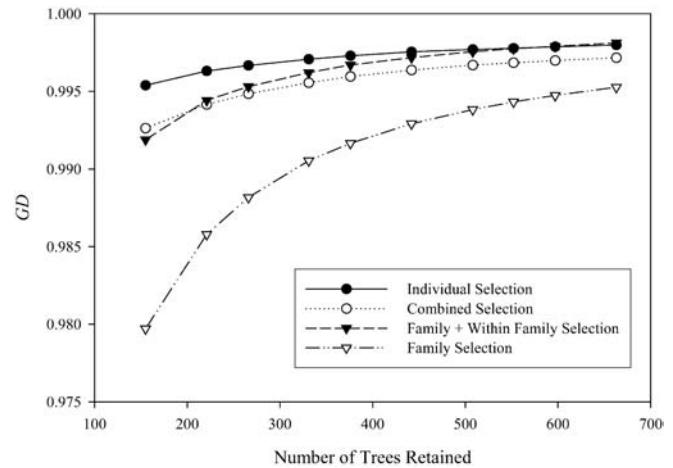


Fig. 2 Gene diversity, GD , for the St. Louis County red pine seedling seed orchard when rogued with four different selection methods across ten different selection intensities ranging from 7% to 30%

vidual selection retained the highest number of families at each selection intensity and, except for FWFS, it had the lowest maximum number of individuals per family of any selection method (Table 2). Combined selection had fewer families and a higher maximum number of individuals per family than IS at any given selection intensity. With the number of individuals per family preset at seven FWFS was the most balanced selection method, with the range between minimum and maximum number of individuals per family being zero. Family plus within family selection also retained far fewer families than IS or CS but for any given selection intensity it had roughly three times the number of families found in FS. Family selection had the lowest number of families retained across all selection intensities as well as the

Table 2 Calculated parameters for the four selection methods and ten selection intensities

Individual selection										
Selection intensity	7.0%	10.0%	12.0%	15.0%	17.0%	20.0%	23.0%	25.0%	27.0%	30.0%
Number of trees retained	155	221	266	331	376	442	508	552	597	663
Number of families	74	84	88	94	96	97	98	99	100	100
Max. no. per family	5	8	8	10	10	10	11	12	13	13
Min. no. per family	1	1	1	1	1	1	1	1	1	1
$E(g)$	9.8%	8.9%	8.5%	7.9%	7.6%	7.1%	6.7%	6.5%	6.2%	5.9%
GD	0.9954	0.9963	0.9967	0.9971	0.9973	0.9975	0.9977	0.9978	0.9979	0.9980
Family selection										
Selection intensity	7.1%	10.1%	12.2%	15.3%	17.3%	20.5%	23.4%	25.3%	27.3%	30.5%
Number of trees retained	158	224	270	338	383	453	517	559	604	673
Number of families	7	10	12	15	17	20	23	25	27	30
Max. no. per family	24	24	24	24	24	24	24	24	24	26
Min. no. per family	20	20	20	20	20	20	20	20	20	20
$E(g)$	9.2%	8.4%	8.0%	7.4%	7.1%	6.7%	6.3%	6.1%	5.9%	5.5%
GD	0.9797	0.9858	0.9882	0.9905	0.9917	0.9929	0.9938	0.9943	0.9947	0.9953
Family + within-family-selection										
Selection intensity	7.0%	10.1%	12.0%	14.9%	17.1%	20.0%	23.1%	25.0%	26.9%	30.1%
Number of trees retained	154	224	266	329	378	441	511	553	595	665
Number of families	22	32	38	47	54	63	73	79	85	95
Max. no. per family	7	7	7	7	7	7	7	7	7	7
Min. no. per family	7	7	7	7	7	7	7	7	7	7
$E(g)$	10.6%	9.5%	8.9%	8.2%	7.7%	7.0%	6.3%	5.9%	5.4%	4.6%
GD	0.9919	0.9944	0.9953	0.9962	0.9967	0.9972	0.9976	0.9977	0.9979	0.9981
Combined selection										
Selection intensity	7.0%	10.0%	12.0%	15.0%	17.0%	20.0%	23.0%	25.0%	27.0%	30.0%
Number of trees retained	155	221	266	331	376	442	508	552	597	663
Number of families	48	55	59	64	68	72	74	76	78	80
Max. no. per family	12	15	17	18	19	20	21	21	21	21
Min. no. per family	1	1	1	1	1	1	1	1	1	1
$E(g)$	11.8%	10.8%	10.2%	9.6%	9.2%	8.6%	8.1%	7.8%	7.5%	7.1%
GD	0.9926	0.9942	0.9948	0.9956	0.9960	0.9964	0.9967	0.9968	0.9970	0.9972

Table 3 Selection intensity, number of retained trees, estimated genetic gain ($E(g)$) and genetic diversity (GD) at the optimization point of $E(g)$ and GD for each selection method

Selection method	Selection intensity	Number of trees retained	$E(g)$	GD
Individual selection	6.83%	151	9.77%	0.9955
Family selection	7.15%	158 ^a	9.13%	0.9810
Family + within-family selection	6.65%	147 ^b	10.58%	0.9922
Combined selection	6.83%	151	11.76%	0.9937

^a Number of trees retained was rounded down to the closest full family from the actual optimization point of 163 trees

^b Number of trees retained was rounded down to the closest seven member family from the actual optimization point of 150 trees

highest maximum and minimum number of individuals per family.

Estimated genetic gain for stem volume ranged from 11.8% (CS at 7% selection intensity) to 4.6% (FWFS at 30.1% selection intensity). The combined index method always generated the largest $E(g)$ followed by either FWFS or IS. Family selection typically provided the lowest $E(g)$ except at the very lowest selection levels where FWFS was lowest (Fig. 1).

GD ranged from 0.9981 (FWFS, 30.1% selection intensity) to 0.9797 (FS, 7.1% selection intensity). IS had the highest GD value across most selection intensities, while FWFS had the highest GD value for the two lowest selection intensities. Family selection consistently had the lowest GD value (Fig. 2).

Determination of the optimal selection intensity that maximizes both $E(g)$ and GD was calculated for each of the selection methods (Fig. 3a–d). The number of retained trees as indicated by the optimal selection intensity was then used to calculate $E(g)$ for stem volume and GD at the optimization point for each selection method. After changing the optimization points for FS and FWFS to accommodate full families and full seven member families, respectively, the four selection methods optimized GD and $E(g)$ at selection intensities of 6.65% (FWFS) to 7.15% (FS). At the optimization points $E(g)$ varied from 11.76% (CS) to 9.13% (FS) and GD ranged from 0.9955 (IS) to 0.9810 (FS). Family selection had the lowest optimized $E(g)$ and GD values (Table 3).

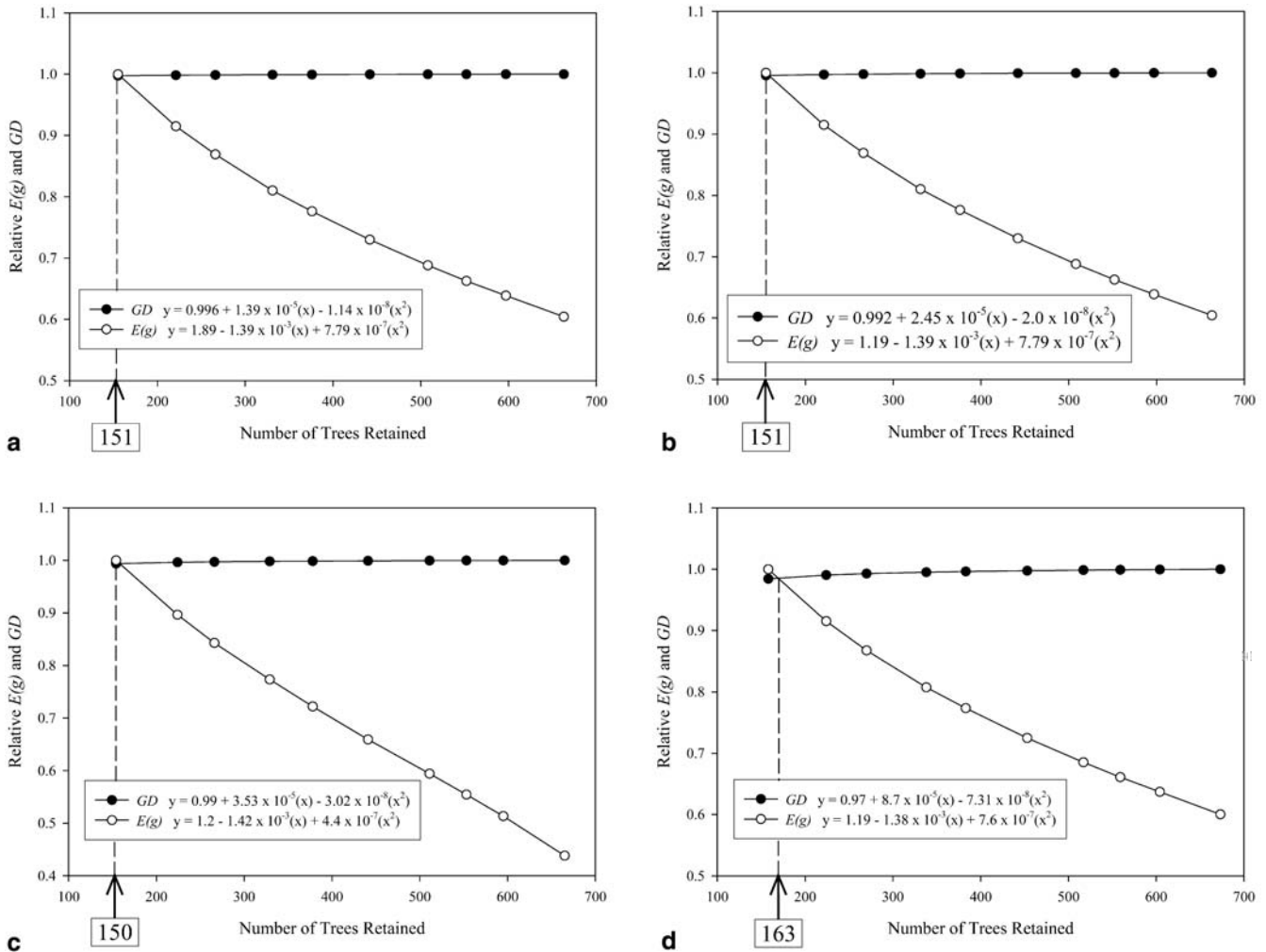


Fig. 3 **a** Optimization point for $E(g)$ and GD for individual selection. **b** Optimization point for $E(g)$ and GD for combined selection. **c** Optimization point for $E(g)$ and GD for family +

within-family selection. **d** Optimization point for $E(g)$ and GD for family selection

Discussion

The high survival rate across all families resulted in well-balanced representation with a range of family sizes from 17 to 26 and an average of 22.1 individuals per family. Narrow-sense heritability for individual stem volume, $h_i^2 = 0.189$, compared favorably with that of other pine species such as *P. tecunumanii* (0.15), *P. oocarpa* (0.29), *P. elliottii* (0.12), *P. palustris* (0.31) and *P. caribaea* (0.11) (Hodge and Dvorak 1999; Moura et al. 1998; Dieters et al. 1995; Adams et al. 1994; Ledig and Whitmore 1981, respectively) indicating that stem volume is a trait under low to moderate genetic control in this population of red pine.

All four selection methods increased $E(g)$ for stem volume, indicating that improvements in volume for red pine are possible despite an inherently low level of natural genetic variation. Across the ten selection intensities the four selection methods provided estimated genetic gains that varied by no more than 2.6%. Combined selection

resulted in the highest estimated stem volume gains across all selection intensities and an 11.8% increase in stem volume when applied at the 7% selection intensity. This is higher than the 9.0% increase in stem volume reported for a 290-family, 10-year-old red pine seedling seed orchard in Wisconsin (Guries and Ager 1980). Individual selection was slightly better than FS across all selection intensities and FWFS, which provided the lowest stem volume at the 30% selection intensity, transitioned to become the second best method by the 17% selection intensity. The relative order of the four selection methods for $E(g)$ (CS > FWFS > IS > FS) is not unexpected given the level of h_i^2 and structure of the population (Falconer 1989), however the relative amount of $E(g)$ is notable for a species with perceived low levels of genetic variation.

Gene diversity is a measure of the probability that genes are not identical by descent. Implicit in this estimate is the assumption that the genetic diversity of seed produced in the seedling seed orchard is reflective of the level of gene diversity in the orchard after roguing.

This assumes that all seed produced is half-sib, i.e. pollination in the seed orchard is completely random. However, due to differences in flowering phenology among individuals, the amount of male and/or female flowers produced among individuals and the amount of foreign pollen entering the seed orchard, the actual level of sib mating is unknown. Therefore, comparisons between selection methods based on GD are used only in a relative manner.

Gene diversity varied across the range of selection intensities due to the manner in which families are represented in each selection method. Individual selection had the highest GD value for all but the lowest two selection intensities because it retained a few individuals from a large number of families. It was the only selection method that retained all 100 families at any selection intensity (27.0% and 30.0%), and even at the highest intensity of selection (7.0%) IS retained 74 different families, which was 26 more families than CS, the next closest selection method. The large number of included families in IS was influenced by the low level of family differentiation (data not shown). Family + within-family selection retained a large number of families in each selection intensity, and at seven individuals per family all families were equally represented. However, because it retained fewer families it ranked behind IS GD for all selection intensities except 27.0% and 30.0%. Combined selection retained more families than FWFS but fewer than IS, resulting in a higher range of individuals per family than IS. Consequently, CS ranked third for GD at all selection intensities except 7.0%, where it was second. Family selection had the lowest GD values of any selection method because the retention of all individuals in a family meant that only a small number of families could be retained, which maximized genetic similarity (Table 2).

Optimization points for the four selection methods ranged in selection intensity from 6.65% (147 trees) to 7.15% (158 trees). This level of selection intensity results in fairly high values for both $E(g)$ and GD , indicating that the two are not mutually exclusive. The actual optimization points for FS and FWFS could not be used because selection intensities had to be adjusted to accommodate complete families in both selection methods. The overall impact of changing the selection intensities for these two selection methods is negligible as the change in number of retained trees was three for FWFS and five for FS (Table 3). The little differentiation in optimization points between the four selection methods is a function of the low level of family differentiation (data not shown). If family differentiation had been stronger, GD for CS and IS would have been lower due to increased selection in the better families, resulting in a lower optimization point for these two selection methods.

When optimized, CS provided 1.2% more volume than FWFS and was second only to IS in GD despite retaining a similar number of trees (Table 3). At its optimization point FWFS had a higher $E(g)$ than IS and was marginally worse than CS for GD . Family selection was clearly the

worst selection method for rogueing the seedling seed orchard. At its optimization point it resulted in the lowest $E(g)$ value, the lowest GD value and the highest number of trees to manage.

The results presented here demonstrate that both $E(g)$ and GD can be favorably high when optimized relative to each other and that even in a species with relatively little genetic differentiation selection methods and intensities have a considerable impact on $E(g)$ and GD . Earlier attempts to balance gain and diversity in clonal seed orchards focused on using algorithms to maximize gain at a given diversity (Lindgren and Matheson 1986; Lindgren et al. 1989). These algorithms increased the proportion of better clones to maximize gain and then included small numbers of clones from below the selection criteria to enhance diversity. Others (Klieve et al. 1994; Quinton and Smith 1995) have used gain versus inbreeding coefficient (F) in an attempt to balance genetic gain and genetic diversity, but recently it was pointed out that F has limitations and that status number, N_s , is preferred (Lindgren and Mullin 1997). Status number is derived from the average coancestry, including selfs, and is defined as the size of the population that undergoes the same amount of inbreeding expected from a population of unrelated non-inbred individuals (Lindgren et al. 1996). Wei et al. (1997) demonstrated that genetic gain and N_s were inversely related in a breeding program but made no attempts to balance them. Lately, the concept of population or group merit selection (GMS) has been introduced. In GMS the merit of a population is the combination of its average breeding value and average coancestry weighted by a factor, c , (Lindgren and Mullin 1997). Rosvall and Andersson (1999) have shown that GMS is superior to conventional restricted selection and that it is particularly beneficial for traits with low heritabilities although assigning the correct weighting for c can be problematic.

The method employed here uses the relative gain in $E(g)$ and relative loss in GD to plot a point where the two intersect. We have chosen to use GD , which like N_s , is derived from the average coancestry (Kang et al. 2001) because it provides a more direct measurement of gene diversity, while still describing the ancestral status of the particular population.

Because $E(g)$ and GD vary according to the selection method and intensity chosen, it is necessary to have a clear understanding of the objectives and limitations of the orchard owner prior to rogueing. For example, if genetic gain is the priority, then CS is the selection method of choice. If genetic diversity is the major priority, then IS or FWFS would be the best selection method, depending on the selection intensity desired. If both $E(g)$ and GD are equal priorities, then an optimization strategy such as outlined here is an effective way to determine an appropriate selection intensity. Additionally, specific information about the estimated seed needs for reforestation, a species' ability to tolerate inbreeding (high for sib-mating in red pine, see Fowler 1965) or the availability of personnel to manage trees and harvest

cones will impact the selection method and intensity that is chosen. Clearly, multiple factors play a role in determining which selection method and intensity to select when roguing a seedling seed orchard.

It should be noted that the measurements and selection simulations are based on 13-year-old trees that have not reached rotation age. Growth patterns of individuals and/or families may assert themselves later in the rotation, or they may become less distinct, changing the individuals or families that would be retained. Height and stem volume calculations made on red pine seedling seed orchards in Wisconsin indicated that families and stands were a significant source of variation at age 6 but that by age 10 stands had become a nonsignificant source of variation (Lester 1976; Guries and Ager 1980). Regardless, after 12 growing seasons, selection in this seedling seed orchard was necessary to retain full crowns for maximizing seed production. Earlier measurements, if they had been made, may have detected a trend regarding family differentiation and indicated whether family differences could be expected to increase or decrease in this population of red pine.

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