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Allocation of varietal testing efforts for implementing conifer multi-varietal forestry using white spruce as a model species

Yuhui Weng · Yill-Sung Park · Marek J. Krasowski ·
T. J. Mullin

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Abstract

• **Introduction** Multi-varietal forestry (MVF) is the deployment of tested tree varieties in plantation forestry. Computer simulation using POPSIM Simulator identified optimal combination of numbers of families, varieties per family and ramets per variety (n_f , n_c and n_r , respectively) yielding the largest genetic gain for a specific status number (NS) in a varietal test (VT) intended for MVF of conifers.

• **Results and discussion** Testing 40 to 80 full-sib families and 20 to 30 varieties per family would be optimal for a VT. This n_f interval was insensitive to the number of candidate varieties planted, ratio of genetic variances and selection restriction. It was influenced somewhat by individual narrow-sense heritability (h^2), required NS and mating design. Lower h^2 , lower NS and designs with fewer

matings per parent tree favoured the lower range of the n_f interval. The optimal n_r was 6. It was not markedly affected by the required NS, family size or selection restriction but was strongly influenced by h^2 and the ratio of genetic variances. Larger h^2 or an introduction of non-additive genetic variance allowed planting fewer ramets per variety.

Keywords POPSIM Simulator · Genetic gain · Status number · Optimization

1 Introduction

In this paper, we define multi-varietal forestry (MVF) as the use of tested tree varieties in plantation forestry. We use the term ‘tree variety’ in a similar manner as it is used in horticulture where a ‘horticultural variety’ is an individual selected for desirable characteristics (Columbia Electronic Encyclopaedia 2003). Owing to recent refinement in somatic embryogenesis (SE) and cryopreservation techniques for conifers, the same varieties (i.e. genotypes or clones) are propagated consistently over time and commercially deployed to plantations. The main advantage of MVF is its ability to increase productivity through utilization of all available genetic variance (Park 2002). This benefit can be fully realized only through accurate varietal selection based on varietal tests (VT). Thus, VT is critical to MVF success. The term ‘VT’ is purposely used in this paper to discern it from a clonally replicated genetic test. VT focuses on varietal selection for deployment, while clonally replicated genetic tests are used primarily for genetic parameter estimation and breeding population selection.

Before establishing a genetic test, tree breeders must decide how many families and progenies per family need to be planted. Earlier relevant studies focused on maximizing

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Y. Weng (✉)

New Brunswick Department of Natural Resources,
Kingsclear Forest Nursery,
E3E 1G3, Island View, NB, Canada
e-mail: Yuhui.Weng@gnb.ca

Y.-S. Park

Natural Resources Canada,
Canadian Forest Service-Canadian Wood Fibre Centre,
P.O. Box 4000, E3B 5P7, Fredericton, NB, Canada

M. J. Krasowski

Faculty of Forestry and Environmental Management,
University of New Brunswick,
28 Dineen Drive, P.O. Box 4400, E3B 5A3, Fredericton, NB,
Canada

T. J. Mullin

BioSylve Forest Science NZ Limited,
45 Korokoro Road,
Lower Hutt 5012, New Zealand

gain through accurate evaluation of family means (Cotterill and James 1984; Cotterill 1990) or through balancing between the choice (the more families are tested, the greater the choice) and accuracy of each family evaluation (Robertson 1957). Optimal numbers of progenies per family have been reported for a fixed number of families in genetic tests (Lambeth et al. 1983; Cotterill and James 1984). Likewise, optimal family numbers for forming breeding populations have been calculated (Lindgren et al. 1997; Danusevicius and Lindgren 2005). These studies provided bases for allocating testing efforts in genetic tests with seedlings aimed at an advancement of breeding populations.

Genetic testing for varietal selection results in another level of tradeoffs, i.e. how many ramets per variety must be raised. Efforts made toward this end concentrated on maximizing gain in varietal selection for deployment (Russell and Libby 1986; Russell and Loo-Dinkins 1993; Isik et al. 2005). These efforts identified two to six ramets per variety as being optimal, the actual number depending on broad-sense heritability, selection intensity and family size.

The studies cited above aimed mainly at maximizing gain. A selection and deployment strategy which maximizes gain without considering its effects on genetic diversity is not acceptable at present. The current goal for MVF is to guarantee that the genetic diversity of a varietal mixture remains above a threshold of acceptability, and under this constraint, the gain is maximized (Libby 1982; Lindgren 1993). In search of an optimal allocation of testing efforts for a VT, genetic diversity must be kept above that threshold, while numbers of families, varieties per family and ramets per variety are allowed to vary.

Comparisons of testing efforts regarding optimizing gain at a given genetic diversity are complex, but simulation techniques make such comparisons relatively straightforward (King and Johnson 1993; Mullin and Park 1995; McKeand and Bridgewater 1998). Simulation models may be classified into ‘deterministic’ and ‘stochastic’. One of the latter, the POPSIM, is especially suitable for simulating genetic systems (Mullin and Park 1995). Using the POPSIM simulator, the objectives of this study were to (1) determine optimal distribution of testing efforts in a VT and (2) evaluate the sensitivity of involved factors to changes in allocation of testing efforts.

2 Methods

2.1 Simulation model

Simulation was done using the stochastic quantitative genetic infinitesimal breeding simulator POPSIM. Theoretical basis and assumptions for POPSIM were described in

detail elsewhere (Mullin and Park 1995; Rosvall et al. 1998). In summary, the additive breeding value (A) for a parent tree was sampled from a normal distribution $N(\mu, V_A)$, where μ is the population mean and V_A is the variance due to additive effects. The dominance effects (D) for full sibs were sampled from a normal family distribution with variance equal to $N(0, 0.75V_D)$; the within-family portion of dominance variance) and with a family mean dominance effect sampled from $N(0, 0.25V_D)$, where V_D is the variance due to dominance effects. The epistatic effects (I) and environmental effects (E) were sampled from $N(0, V_I)$ and $N(0, V_E)$, respectively, where V_I and V_E are epistatic and environmental variances, respectively. The phenotypic value of an individual was simulated as a sum of its A , D , I and E .

2.2 The reference MVF plan and alternatives

The following symbols are used: n_f , number of families; n_c , number of varieties per family; n_r , number of ramets per variety; N_C , total number of tested candidate varieties ($n_f \times n_c$); N_F , family size, total trees per family planted ($n_c \times n_r$); N_V , census number of varieties so that its diversity reaches a specified level; and N , total number of trees planted.

A complete MVF plan involves mating, testing and selection (Table 1). In the reference plan, 40 unrelated trees were selected as parent trees and subjected to a double-pair mating (DPM) scheme (each individual parent tree being mated twice), producing 40 full-sib families. Parent pairs were formed randomly, and selfing was excluded. For each family, 30 individuals were designed as candidate varieties, and for each variety, five ramets were vegetatively propagated to establish a VT. Selection was applied to a polygenic trait or an index of several traits and was based on the varietal genetic value, which was calculated on the basis of a combined index, where the performance of an individual and its relatives was weighted by their respective heritabilities (Mullin and Park 1995). Selection was made under a constraint of diversity level expressed as status number (N_S), which is defined as half of the inverse of group co-ancestry (Lindgren et al. 1996). Incidentally, the status number used here is identical to the founder genome equivalents (Lacy 1995) in conservation biology. A $N_S=15$ was designed as the diversity threshold. No restriction on the full-sib family contributions (each full-sib family could provide unlimited number of varieties) to the varietal mixture was applied in the selections.

Alternative options were set to test their influence on testing effort distribution, which is the combination of n_f , of n_c and of n_r . The alternatives included various (1) parent tree numbers, (2) N_S thresholds, (3) mating designs (single-pair mating (SPM) and quadric-pair mating (QPM), representing each individual parent tree being mated once

Table 1 The reference and alternative parameters for the simulation of breeding, testing and selection for implementing multi-varietal forestry (MVF)

Parameters	Reference	Alternative options
Breeding		
No. of parent trees	40	20, 60, 80, 120, 200, 240
Allocation of mates	Random	
Mating frequency per parent tree	Double-pair	Single-pair, quadric-pair
Testing		
Number of families (n_f)	40	20, 60, 80, 120, 200
Number of varieties per family (n_c)	30	6, 10, 15, 20, 60
Number of ramets per variety (n_r)	5	2, 4, 6, 8, 10, 12, 20
Number of varieties tested (N_C)	1,200	300, 600, 1,800, 2,400
Number of trees per family (N_F)	150	60, 120, 180, 240
Total no. of tested trees (N)	6,000	3,600–13,200
Selection		
Status number (N_S) threshold	15	10, 20
Max no. of varieties per full-sib family	Unlimited	2, 4
Other restrictions on relatedness	None	

and four times, respectively), (4) selection restrictions on family contributions to varietal mixtures and (5) N_C or N_F . It was assumed that there was no biological limit to creating families and producing candidate varieties or ramets.

2.3 Parameter input values

Table 2 lists the input values of the population parameters. In all simulations, the population mean (100), V_A (80) and standard rate of inbreeding depression (0) were kept constant, while V_D , V_I and V_E were varied to represent an assortment of narrow-sense individual heritabilities (h^2) and ratios among V_A , V_D and V_I . The h^2 (ranging from 0.05 to 0.5) was varied by changing the V_E while keeping the genetic variances constant. The $V_A:V_D:V_I$ ratio was varied by changing V_D or V_I while keeping h^2 constant through changes to its associated V_E . The V_D or V_I was assumed to be in the range between zero and V_A . The genetic parameters, $V_A:V_D:V_I=80:2:18$ and $h^2=0.2$, which were observed in a clonally replicated test series of white spruce (*Picea glauca* (Moench) Voss.; Weng 2009), were used as the baseline parameter scenario.

2.4 Optimization

In simulations, tradeoffs in gain at a specified N_S between n_f and n_c or between n_c and n_r were investigated under the same total testing effort, expressed as the same N . Under a model of fixed N , N_C is also fixed in the optimization between n_f and n_c , or N_F is fixed if the objective is to optimize n_c and n_r . In the optimization between n_f and n_c , we varied n_f and n_c at a given n_r , whereas in the optimization between n_c and n_r , we varied n_c and n_r at a given n_f . Such methods of optimizing the distribution of testing efforts under a fixed N were used by other investigators (Shaw and Hood 1985; Russell and Libby 1986; Rosvall et al. 1998). The optimal n_c was also investigated by varying n_c while keeping n_f and n_r constant. This model represented different total testing efforts and was used in other studies (Cotterill and James 1984; Russell and Libby 1986).

Simulations were made by modifying one factor in the baseline parameter scenario or the reference plan at a time and, as much as possible, to keep the level of an effort constant. In each case, the interpretation was based on

Table 2 Input parameter values for the baseline and alternative scenarios

Parameter	Fixed/varied	Baseline	Alternative values
Population mean value of trait	Fixed	100	
Rate of inbreeding depression	Fixed	0	
Additive variance (V_A)	Fixed	80	
Dominance variance (V_D)	Varied	2	0, 40, 80
Epistatic variance (V_I)	Varied	18	0, 40, 80
Environmental variance (V_E)	Varied	300	60, 1,500
Narrow-sense heritability (h^2)	Varied	0.20	0.05, 0.50

average result of 100 runs. The simulations were done in two consecutive steps. The first step was to find a N_V for a varietal mixture so that a specified N_S could be achieved for a combination of testing efforts. This was done using a linear approximation (Li and Lindgren 2006). The N_V found in step 1 was then used as the input for that specific combination so that gains obtained from various effort combinations could be compared at the same N_S level. The optimal allocation of testing efforts for a set of conditions is defined as that combination among n_f , n_c and n_r which yields the largest gain at a specified N_S or, failing that, as the combination after which further numerical increases in n_f , n_c and n_r increase gain at a specified N_S negligibly.

3 Results

3.1 Tradeoffs between numbers of families (n_f) and of varieties per family (n_c)

Under the baseline parameter scenario and the reference plan but re-distributing n_c and n_f , gain from selecting 20 top varieties increased quickly with $n_c \times n_f$ combinations of 60×20 to 30×40 , but after that, it stabilized. On the other hand, there were substantial differences among the combinations with respect to N_S ; larger n_f paired with smaller n_c made N_S larger. The functional differences in gain and N_S among the combinations reflected relative efficiency of gain at a specified N_S (Fig. 1a). Overall, testing more families with fewer varieties per family resulted in higher gain at a specified N_S . However, the increase in gain was not linear; it increased quickly with $n_f=20$ to 40; the increase slowed down when $n_f=40$ to 80 and gain stabilized thereafter. For example, over 95% of gain at $N_S=15$ obtained from the 6×200 combination could be realized by the 15×80 combination. Changing the N_S threshold did not change the optimal n_f interval but did change the relative efficiency in gain between the combinations (Fig. 1a). For example, the 30×40 combination captured 90% of the gain obtained in the 6×200 combination when $N_S=10$ but reduced it to 74% when $N_S=20$. Thus, testing 40 to 80 families with corresponding n_c ranging from 15 to 30 could be an optimal interval for a VT of 1,200 candidate varieties. The lower bound of the optimal n_f interval was preferred when lower N_S was required.

Operationally, a given n_f can be created by various mating designs when required parent trees are available. For a given n_f , gain at a specified N_S was higher when the n_f was created by designs in which parent trees mated fewer times, although this effect gradually vanished for combinations of larger n_f paired with smaller n_c (Fig. 1b). In the $n_c \times n_f$ combination of 30×40 , gain at $N_S=15$ was 18.2% when the 40 families were created by SPM, compared to 16.5%

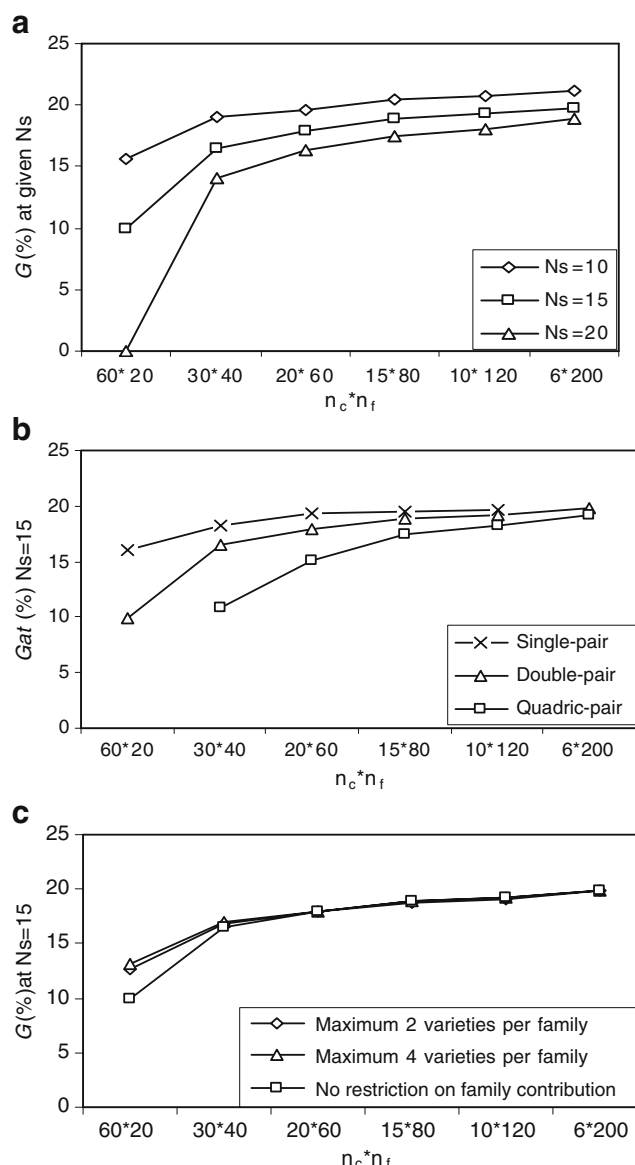


Fig. 1 Tradeoffs in gain at a specific status number (N_S) between numbers of varieties per family (n_c) and of families (n_f) under various (a) N_S levels (the 60×20 combination selected all varieties to reach a $N_S=20$, thus resulting in zero G), (b) mating designs (the N_S failed to reach 15 in the 60×20 combination by quadric-pair mating) and (c) restrictions on family contributions

and 10.9% when they were created by DPM and QPM, respectively. The optimal n_f (40 to 80) was similar among the three mating designs, although the designs with more matings per parent tree favoured the upper bound of n_f interval. Imposing restriction on selection differently affected gain and N_S ; a selection allowing fewer varieties per family resulted in lower gain but higher N_S (data not shown). As shown in Fig. 1c, restriction on family contributions, however, did not change the optimal n_f interval. Gains at $N_S=15$ were similar among the three restriction levels for all $n_c \times n_f$ combinations except that of

60×20, where the unrestricted selection had a lower gain than the other options. It can be seen that imposing family restrictions was effective when n_f was small (i.e. 20).

Increasing N_C ($n_f \times n_c$) in a VT will increase gain and N_S , thus increasing gain at a specified N_S . When N_C was increased from 300 to 2,400, the optimal n_f interval was fairly stable, but the corresponding n_c increased considerably (Fig. 2a). Although gain at a specified N_S increased with N_C , the additional gain from planting more than 1,200 candidate varieties at a given n_f would have been small. These results suggested that planting more than 30 varieties per family in a VT under the baseline parameter scenario was not worth the effort. This optimal n_c was further confirmed by a model with an increasing n_c at a given n_f (Fig. 2b). The additional gain at a specified N_S from testing more than 30 varieties per family was small. For example, at $n_f=40$ or 80, over 92% of gain obtained at $N_S=15$ from testing 60 varieties per family would be captured by testing only 30 varieties per family, and this would decrease the total testing effort by 50%.

As expected, gain at a specified N_S increased with larger h^2 or with the introduction of non-additive genetic variance

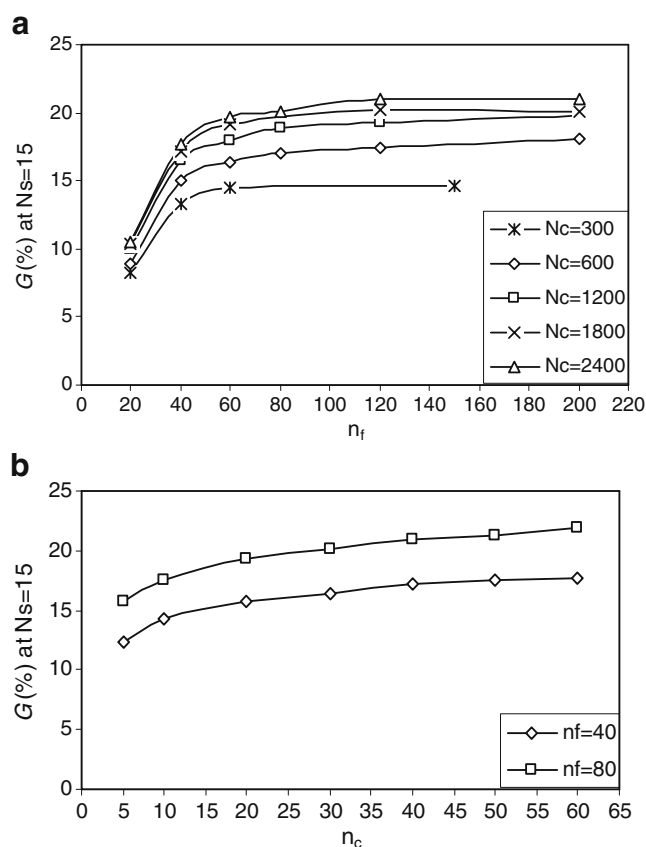


Fig. 2 Tradeoffs in gain at a status number (N_S) of 15 between numbers of varieties per family (n_c) and of families (n_f) under various candidate varietal numbers ($N_C=n_c \times n_f$) by (a) varying n_f and n_c combinations and (b) increasing n_c at fixed n_f

(Fig. 3). The optimal $n_c \times n_f$ combination was somewhat influenced by h^2 ; the smaller h^2 preferred the lower optimal n_f bound (Fig. 3a). For example, the 30×40 combination could capture 88% of gain at $N_S=15$ obtained in the 6×200 combination when $h^2=0.05$, but it would decline to 77% when $h^2=0.5$. Unlike with h^2 , the introduction of V_D or V_I did not significantly change the optimal combination of n_c with n_f (Fig. 3b). An introduction of V_I resulted in a slightly higher gain at $N_S=15$ than when an equal amount of V_D was introduced, although this advantage gradually diminished with increasing n_f (Fig. 3b).

3.2 Tradeoffs between varietal numbers per family (n_c) and ramet numbers per clone (n_r)

While adhering to the baseline parameter scenario and the reference plan but redistributing n_r and n_c for a VT of $N_F=120$, gain from selecting 20 varieties maximized at $n_r=6$, while N_S values were fairly stable, around 11 (data not shown). Consequently, the optimal n_r for maximizing gain

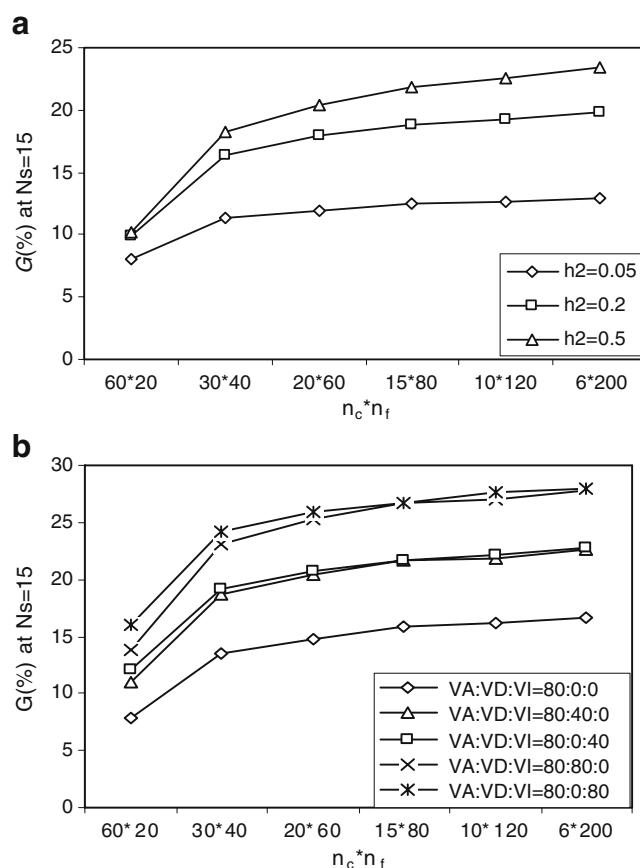


Fig. 3 Tradeoffs in gain at a status number (N_S) of 15 between numbers of varieties per family (n_c) and of families (n_f) under various genetic parameters: (a) individual heritability (h^2) and (b) ratio of genetic variances. Note that in b, the h^2 was kept constant at 0.2; thus, the respective broad-sense heritabilities were 0.20 (80:0:0), 0.30 (80:40:0 and 80:0:40) and 0.4 (80:80:0 and 80:0:80)

at a given N_S was around 6, and the corresponding n_c was 20. The optimal n_r and n_c were not changed by the assigned N_S , although there was a tendency to require planting of more ramets with a smaller required N_S (Fig. 4a). Imposing selection restriction on family contributions changed gain and N_S but did not markedly change the optimal allocation between n_r and n_c (Fig. 4b).

Tradeoffs between n_r and n_c were also examined for different N_F (Fig. 5a). Under the baseline parameter scenario, the optimal n_r was 4 when $N_F=60$ and increased to 6 when $N_F=120$ –180 and to around 8 when $N_F=240$, with the corresponding n_c increasing from 15 to 30. For a given n_r , increasing N_F (through increasing n_c) increased gain at a specified N_S . However, the additional gain at a specified N_S increased at a diminishing rate as N_F increased. This was demonstrated by the curves in Fig. 5a getting progressively closer together as N_F was rising. It can be seen that the interval of N_F between 120 and 180 would be a reasonable choice. Taking all factors into consideration, testing 120 to 180 trees per family with six ramets per variety seemed to be appropriate and corresponds to an

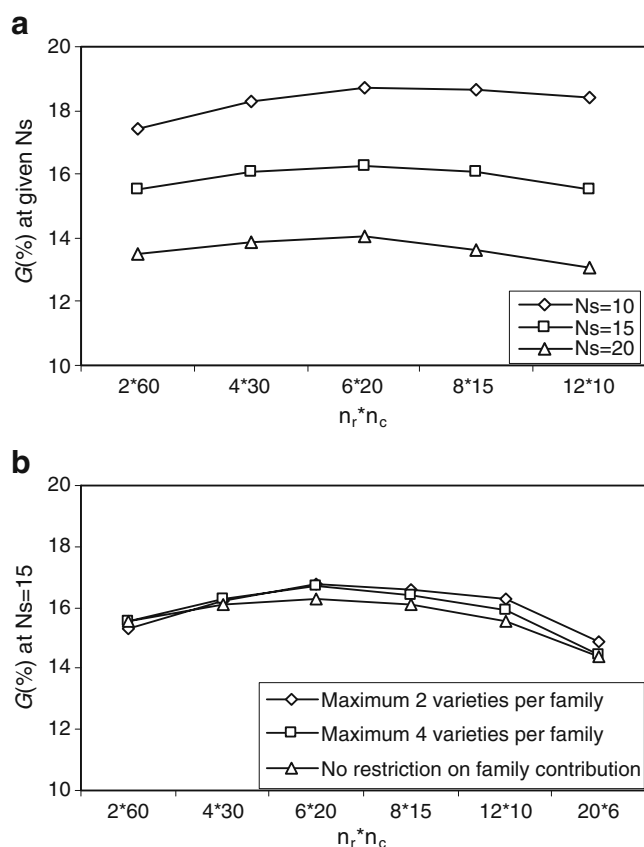


Fig. 4 Effects of redistribution between numbers of varieties per family (n_c) and of ramets per variety (n_r) on genetic gain (G) at a specific status number (N_S) level under various (a) N_S levels and (b) selection restrictions on family contributions

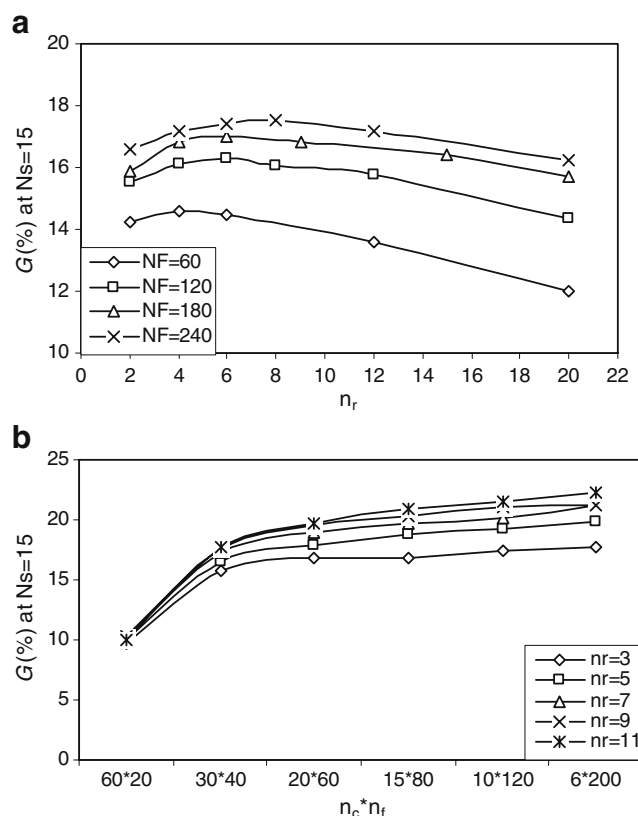


Fig. 5 Effects of numbers of ramets per variety (n_r) on genetic gain (G) at a status number (N_S) of 15 under various tree numbers per family (N_F) by varying (a) numbers of varieties per family (n_c) and n_r and (b) numbers of families (n_f), n_c and n_r . Note that $N_F=n_c \times n_r$

optimal interval of n_c between 20 and 30. The optimal n_r interval was further investigated under various $n_c \times n_f$ combinations (Fig. 5b). For each $n_c \times n_f$, gain at $N_S=15$ increased with increasing n_r , but this increase was much reduced with larger n_r . In general, combinations of larger n_c with fewer n_f required planting of fewer n_r . In the combination of 60×20, the additional gain at $N_S=15$ from testing more than three ramets per variety was negligible. The corresponding n_r increased to 5 for the combinations of 30×40 and to 7 thereafter. Overall, these results suggest that it is unnecessary to plant more than seven ramets per variety.

As expected, h^2 had significant effects on optimal distribution of n_c versus n_r ; the larger h^2 favoured combinations of larger n_c with smaller n_r (Fig. 6a). Gain at $N_S=15$ maximized at the $n_r \times n_c$ combination of 2×60 when $h^2=0.5$ but of 20×6 when $h^2=0.05$. Introduction of non-additive genetic variances also affected the optimal distribution between n_c and n_r . Overall, small ratios of additive to non-additive variance favoured planting fewer ramets per variety and yielded more gain at a specified N_S than cases where the ratio was large, in particular when the V_I was the main source of non-additive variance (Fig. 6b).

For example, gain at $N_S=15$ was maximized at the $n_r \times n_c$ combination of 2×60 when $V_A:V_D:V_I=80:80:0$ or $80:0:80$.

4 Discussion

4.1 Optimum testing effort allocation

Simulations were done not so much to estimate genetic gains at specific diversity levels but to compare efficiency among various effort allocations. The baseline parameter scenario was specific for white spruce, but alternative options (Table 2) were deliberately selected to cover other conifers. Extensive studies on conifers have demonstrated that additive effects are the main contributor to genetic variance, whereas non-additive genetic variance is unlikely to contribute more than half of the total genetic variance (see Weng (2009) and references therein). A partitioning pattern of $V_A:V_D:V_I=80:20:0$ has been usually assumed for coniferous species and used in other simulations (Russell

and Loo-Dinkins 1993; Rosvall et al. 1998). The optimal allocation of VT efforts under the '80:20:0' scenario (data not shown) was virtually the same to the recommendation found in this study.

The minimum varietal number for a MVF plantation is debatable, but theoretical studies generally suggest that planting more than ten unrelated varieties in a plantation should suffice for protection against unpredicted biotic and environmental stresses (Lindgren 1993; Park et al. 1998). Biologically, N_S can be interpreted as the size of a non-inbred population in which all selections are unrelated (White et al. 2007). Thus, a N_S ranging from 10 to 20 for a varietal mixture corresponds well to the above theoretical recommendation. Further increases in N_S may be preferred for evolutionary purposes but may contribute little to productivity (Lindgren 1993).

Thus, results of this study provide insights into optimum effort allocation for establishing a VT at reasonable diversity levels for conifers. If families can be created at low cost, it will be wise to include more families. For most conifers, producing fewer crosses is always attractive operationally because it increases the likelihood that mating work can be completed within a reasonable time. Our study suggests that a VT should include 40 to 80 families, 20 to 30 varieties per family and about six ramets per variety in field environments. Tests made under more uniform environments (e.g. in a greenhouse) may need fewer ramets per variety than tests made under more variable conditions. The recommended n_f interval is a prudent compromise between gain and feasibility and should be treated as an optimal approximation.

Other than maximizing gain at a specific N_S , an optimization should consider the operational feasibility of cloning genotypes. SE is one of the key techniques which make the implementation of MVF possible. Operationally, raising trees from fewer varieties is always desirable, and this should be another criterion in optimizing effort allocation. To obtain a specific N_S , combinations of fewer n_f paired with more n_c required including more varieties in the mixture (larger N_V). Under the baseline parameter scenario, a varietal mixture of $N_S=15$ needed to include as many as 250 varieties (N_V) under the $n_c \times n_f$ combination of 60×20 . The corresponding N_V would decrease to about 50 under the 30×40 combination and to 30 or less when 60 or more families were involved (Fig. 7). In this regard, a n_f of 40 or larger seems indispensable, which is consistent with the optimum n_f required for maximizing gain at a specific N_S . Although the number of varieties actually required for a specific combination of n_f and n_c may vary with heritability (Fig. 7), mating design and selection restriction (data not shown), the conclusion found here seems to hold.

Field testing is often constrained by limitations in resources and logistics. The optimal distribution effort

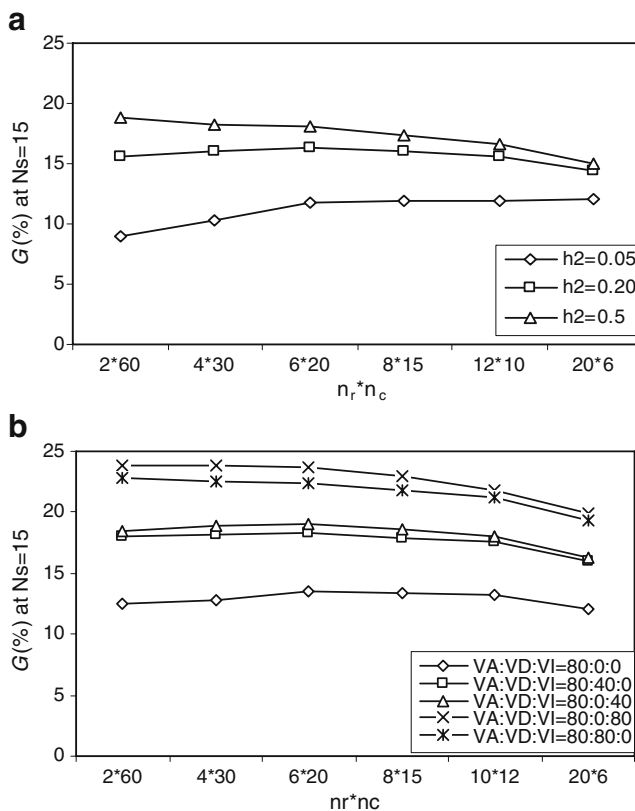


Fig. 6 Effects of redistribution between numbers of varieties per family (n_c) and of ramets per variety (n_r) on genetic gain (G) at a status number (N_S) of 15 under various genetic parameters: **(a)** individual heritability (h^2) and **(b)** ratios of genetic variances. Note that in **b**, the h^2 was kept constant at 0.2; thus, the respective broad-sense heritabilities were 0.20 (80:0:0), 0.30 (80:40:0 and 80:0:40) and 0.4 (80:80:0 and 80:0:80)

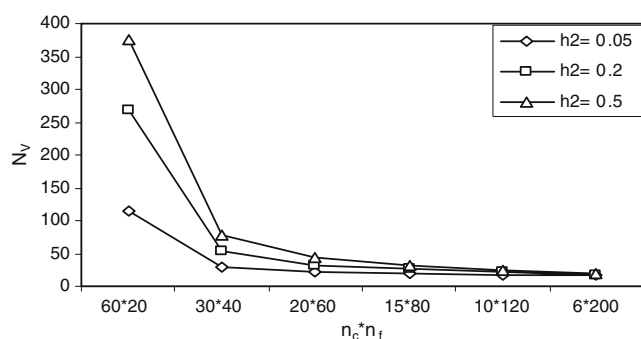


Fig. 7 Effects of redistribution between numbers of families (n_f) and of varieties per family (n_c) on the required number of varieties (N_v) in mixtures so that their status numbers (N_s) reach 15 under various individual heritability (h^2)

(40–80 families and 20–30 varieties per family with six ramets) results in a testing size of 4,800 to 14,400 trees, which is much larger than the typical genetic testing size of 2,500 trees (i.e. 1 ha planted at 2×2 m spacing). One solution to this situation is to establish testing series over time, planting about 20 families (2,400 to 3,600 trees) each year. In such a way, each series can stand alone, and reasonable gain can still be obtained by selection from it (Table 3). Whenever data are available for all testing series, they should be analyzed together and selections be made across the series for maximizing gain at a given N_s .

4.2 Effects of other factors on the effort distribution

Other factors investigated in this study represent those that are under breeder's control or those that can be determined in advance from earlier studies. Generally, the optimal n_f interval (40 to 80) is insensitive to the tested N_C , introduction of non-additive variance and selection restriction on family contributions. Consideration of the following factors may require the lower bound of the optimal n_f when (1) a lower N_s threshold is required, (2) h^2 is lower or (3) a mating design is used in which each parent tree is mated fewer times. In these cases, effects of relatedness among the varieties (or constraint of N_s) on gain were smaller, resulting in an optimal n_f closer to that (40) with no

constraint on N_s . At lower h^2 , more varieties per family are needed so that the precision of family evaluation can be improved (Lindgren et al. 1997).

Overall comparison among the three mating designs suggests that SPM would be preferred due to its simplicity, smaller optimal n_f and higher gain at a given N_s (Fig. 1b), although it requires more available parent trees. The parent trees should be selected from the ongoing long-term tree improvement programs. More complicated mating designs, such as complete diallel, were not evaluated in this study because they are not likely to be used in future MVF programs.

Under fixed N_F , the tradeoff between n_c and n_r reflects the balance of selection accuracy and intensity. Increasing n_r may increase the precision of varietal selection but may limit N_C that can be tested, thus decreasing selection intensity. The balance between n_c and n_r is not likely to be greatly changed by the required N_s level, N_F and selection restriction, at least not under the ranges tested, but it may vary markedly with h^2 and an introduction of non-additive variance. Lower h^2 means that larger n_r is required from a smaller n_c (Fig. 6a; White et al. 2007). The introduction of non-additive variances forced a lower V_E under a constant h^2 , resulting in a higher broad-sense heritability (Fig. 6b). Varietal genetic values can be accurately predicted even if few ramets per variety are planted in a VT with high broad-sense heritability (Fig. 6b; Shaw and Hood 1985; Russell and Libby 1986).

Since the optimal n_f and n_r intervals are fairly insensitive to the factors investigated in this study (except effects of h^2 and ratio of genetic variances on n_r), the optimal n_c is virtually a function of N_C or N_F . Given there is no limit on available funds and land, testing larger N_C or N_F by increasing n_c would be appropriate and recommended. The additional gain resulting from testing more than 1,200 candidate varieties or 180 trees per family, however, was small (Figs. 2a and 5a), not encouraging such an effort economically. The optimal n_c can be much larger than those when h^2 is higher or when more non-additive genetic variance is introduced (Fig. 6).

4.3 Comparison to other studies

In MVF, we face two critical issues that must be considered simultaneously: (a) developing varietal lines that maximize genetic gain through best utilization of the available number of genetic entries (families and varieties within them) and (b) maintaining the acceptable level of genetic diversity in MVF plantations. Our study addresses these two issues by focussing on optimization of testing efforts in VT that maximize gain under a constraint on N_s . The importance of sufficient N_s in MVF has been emphasized in the literature (Roberds and Bishir 1997), and some

Table 3 Genetic gain (percent) and status number (N_s) of variety mixtures consisting of 20–40 selected varieties (N_v) from a varietal test of 20 families (n_f) paired with 20–30 varieties per family (n_c) and six ramets per variety according to the baseline parameter scenario

$n_c \times n_f$	$N_v=20$		$N_v=30$		$N_v=40$	
	Gain	N_s	Gain	N_s	Gain	N_s
20×20	16.8	10.0	15.4	12.7	14.7	14.4
30×20	17.5	9.5	16.3	11.8	15.3	13.4

jurisdictions defined the minimum for that number (e.g. Alberta Sustainable Resource Development 2003; British Columbia Ministry of Forests and Range 2004).

Several investigators have studied numbers of families and progeny per family required in genetic tests. Robertson (1957) recommended testing as few as five individuals per family so greater efforts could be directed to testing more families. Robertson's solution is a tradeoff between the availability of families for selection and accuracy of comparing family means. Cotterill (1990) recommended planting five to ten families per provenance and 20 to 40 trees per family if the objective was to evaluate accurately provenance means. In a family test, planting 10–20 progeny per family would suffice if the objective were to accurately calculate the family mean (Cotterill and James 1984). However, unlike our study, these studies did not consider genetic diversity and focused more on the accuracy of estimating means than on optimizing genetic gain.

For establishment of breeding populations, optimum number of families was investigated considering the genetic gain, diversity and cost efficiency (Lindgren et al. 1997; Danusevicius and Lindgren 2005). In their models, however, the genetic diversity was treated as a penalty factor reducing gain. The objectives of these studies were relevant to managing breeding populations; therefore, they were different from our objectives aiming at maximizing genetic gain at a defined level of diversity in MVF plantations.

Most early VTs were established following breeder's intuition, i.e. planting many clones from few elite families (White et al. 2007) or creating families by complicated mating designs, to maximize genetic gain. Varietal selection from such tests might result in a high gain but increase genetic relatedness among selections (NBTIC 1999). As demonstrated in our study, such high gains may not be attainable due to loss of diversity when a N_S is imposed. Our study also shows that single-pair mating is better than the structured mating designs, for example, diallel mating, to reduce relatedness among families and varieties.

The optimal n_r for a test with clonal replicates has been well investigated both for breeding population (Shaw and Hood 1985; Russell and Loo-Dinkins 1993; Rosvall et al. 1998) and production population (Russell and Loo-Dinkins 1993; Isik et al. 2005), using a model of maximizing genetic gain but without considering genetic diversity. Russell and Libby (1986) presented a model based on selecting and deploying a fixed number of clones without considering relatedness among clones. Our model, which includes a constraint of N_S and genetic relationships, would be more flexible and closer to reality. The result of our study that planting around six ramets per variety was comparable to numbers recommended by all of the studies cited above, but some differences should be noted. Unlike

in Shaw and Hood's study (1985), our results showed that the restriction on family contribution did not affect the optimal n_r . Under similar model parameters, the optimal n_r was slightly larger than that reported by Russell and Libby (1986). They found that the optimal n_r was 2 or 3 when 10 or 20 unrelated clones were selected from a clonal test with its broad-sense heritability of 0.24.

There are other aspects of VT which are not addressed here. Optimizing effort allocation of a VT should consider $G \times E$ interaction. Russell and Loo-Dinkins (1993) found that the extra gains from planting more than two sites were small when the $G \times E$ interaction was less than 25% of the genetic variance. It should also be noted that the optimal effort allocation reported here targeted to candidacy testing, with many varieties and few ramets per variety. These selected varieties should be further tested across more landscape environments and by different experimental designs (i.e. large block of monoclonal or mixed clonal plots) to get more detailed productivity information on these varieties. The number of varieties at this level would be modest, and the number of ramets per variety would be large.

Another important but unaddressed aspect is the cost of optimization. In forest operations, the same N_C created by varying n_f and n_c , or the same N_F created by varying n_c and n_r may involve different expenses. As suggested by Lindgren (1985), a cost–benefit analysis is needed to fully determine optimal distribution among n_f , n_c and n_r for a genetic test with clonal replicates. The optimal n_r for a VT does not seem to be affected by including a cost analysis (Isik et al. 2004).

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