

Deployment of clones to seed orchards when candidates are related

Dag Lindgren ¹⁾ and Darius Danusevičius ²⁾

¹⁾Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden. E-mail: dag.lindgren@genfys.slu.se

²⁾Lithuanian Forest Research Institute, Liepu 1, Girionys, LT-53101, Kaunas district, Lithuania. E-mail: darius.danusevicius@takas.lt

Abstract

This paper deals with deployment of clones to seed orchards in situations when the candidates are relatives. Possible strategies comprise finding the best solution by an advanced computer algorithm, restricting against relatives and neglecting relatedness. Linear deployment versus truncation was considered. The value of application of a strategy has to be quantitatively defined to make comparisons among strategies; here it was defined as “Net gain”, considering predictions of breeding values, inbreeding depression, gene diversity (status number) and effective number. The efficiency of the strategies was studied in a (ideal) population of candidates composed of half-sib families. Results showed that, if the number of families available is considerable higher than the number of desired selections a close to optimal and simple strategy is to restrict against any relatedness and deploy the single best individual from the best families by linear deployment. Otherwise a more sophisticated algorithm is suggested. Here it is suggested that the simpler procedure can be used when the status number of the candidate population is 8 times higher than the status number of the clone deployment suggested. It is suggested that the effect by relatedness on gene diversity is more constraining on the extent of relatives in seed orchards than the inbreeding depression following mating of relatives.

Introduction

When tree breeding has passed its infancy, the option arises to select related clones to seed orchards. One way out of this dilemma is to structure the breeding population in unrelated compartments and select one clone from each (Lindgren and Gregorius 1976). However, this strategy has disadvantages. It is a restriction on selection and the best related selection is likely to have a much larger breeding value than the best unrelated. Inbreeding is a problem in the breeding population, it is an additional cause of variation and it reduces the variance available for selection. The consequences of restricting against relatives in seed orchards become more severe and annoying as breeding continues over generations. A limited number

of relatives in a seed orchard has only a small and may be neglectable negative effect (Olsson 2001).

This study deals with how the deployed proportion of each candidate clone can be decided at the establishment of a seed orchard when the breeding values are available for each candidate in a population of half-sib families. Conventional seed orchard deployment strategies relied on simple truncation selection: selecting the candidates with breeding values above a certain threshold and deploying the candidates in equal proportions. Lindgren (1974) showed that deployment of candidates proportionally to their breeding value is a more efficient approach. If the candidates are unrelated, the deployment of clones in proportions linearly related to their breeding value is the most efficient strategy to maximise genetic gain (Lindgren and Matheson, 1986). In advanced breeding cycles, however, the candidates tend to be related and the linear deployment strategy does not guarantee an optimum solution. The emphasis on breeding value of related candidates may increase relatedness, hence inbreeding in the orchard to harmful levels (Olsson, 2001; Wang Tongli *et al.* 2003). One simple approach to cope with the negative effects of relatedness is to introduce constraints on relatedness, such as restricting candidates to say, the one top-ranking individual per family and then use linear deployment for the ramet number. Is there a better deployment solution?

The aim of the present study is to develop and investigate procedures to deploy tested, related genotypes to clonal seed orchards with variable numbers of ramets across a range of scenarios with simple relatedness patterns. Simulation procedures are used based on artificial data generated for half-sib families that provide the candidates pool for seed orchards. Results may help to guide forest tree breeders about the potential and application of the method over a range of circumstances.

Material and methods

The following deployment strategies were compared: (a) truncation selection by selecting the clones with the breeding values exceeding certain threshold and deploying equal number of ramets (*Truncation* strategy); (b) truncation selection by selecting only one best individual within each family (*Truncation unrelated*); (c) maximizing gain at a given effective clone number (*Linear deployment*); (d) linear deployment by selecting one best individual within each family (*Linear deployment unrelated*) and (e) maximizing net gain at a given gene diversity (*Optimal proportions*).

Net gain was the target parameter to be maximized and was calculated as the average breeding value of seeds produced from the orchard with a deduction for the expected inbreeding due to matings between related clones:

$$BVI = (1 - ID * \Theta_p) \sum p_i g_i, [4]$$

where:

BVI is the predicted average breeding value of the ramets adjusted for the expected inbreeding (ignoring selfing).

$(1 - ID * \Theta_p)$ is a factor reducing the breeding values for inbreeding;

ID is the inbreeding depression "coefficient", which converts pair-coancestry to adjust for the expected inbreeding depression to the same scale as the breeding values. In this study, we assume no difference in inbreeding depression between orchard ramets and so set $ID = 1$, which is a reasonable value for forest tree applications and can be interpreted that production will be zero if there is complete homozygosity (if $ID = 1$ and pair-coancestry = 1, then the term $(1 - ID * \text{pair coancestry}) = 0$ and $BVI = 0$).

Although in principle it is desirable to use the optimal procedure for all cases, in practice it may be difficult to implement because specific software and expertise are needed.

The study focus on "linear deployment unrelated" and described its advantages and characteristics for a number of possible typical cases. The genetic gain adjusted for predicted inbreeding depression (*Net gain*), gene diversity and effective clone number were considered as the main ranking criteria. The data used in this study were simulated breeding values for unrelated half-sib families, which are considered as candidates for deploying in a seed orchard.

Order statistics were used to generate the "true" family and within family breeding values, expressed as standard deviations from the total mean set to 0 (Lindgren and Nilsson, 1985). The breeding values were expressed as "units of coefficient of additive genetic variation (CV_A)". The optimization was carried out according to the main and alternative scenarios of the key-parameter values (*Table 1*). When testing an alternative value of a parameter the values of the other parameters were kept at the main scenario values. Status number (N_{sd}), the number of unrelated and not inbred individuals desired in the seed orchard was used as the diversity measure. Group coancestry can be interpreted as the loss of the gene diversity in the wild forest by the implementation of tree breeding (Lindgren and Kang, 1997; Lindgren and Mullin, 1998 and Rosvall 1999). The first term expresses the self-coancestry, which depends on the number of ramets of a clone. The second term depends on the relatedness among

different clones (pair-coancestry) and their occurrence in the orchard. *Net gain* was considered as the parameter to be maximised. In our study, net gain refers to the difference between the average breeding value of the ramets in the orchard adjusted for expected inbreeding depression and the average breeding value of the test, which is set to 100 to allow interpretation of the numbers as percentages. The *Net gain* is calculated as the average breeding value of seeds produced from the orchard with a deduction for the expected inbreeding due to matings between related clones. The number of half-sib families, the number of individuals from each family as well as number of ramets of each individual (expressed as proportion) to be included in the seed orchard were optimized to achieve maximum net at a desired status number in the seed orchard. For the calculations MS EXCEL 2003 was used.

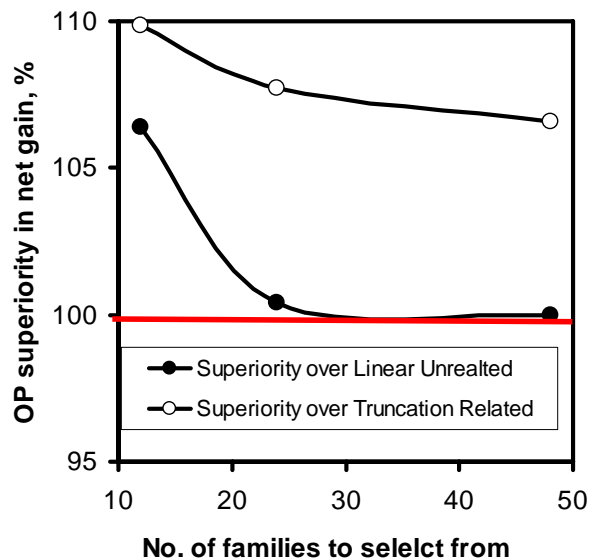


Figure 1. Superiority of Optimal strategy over the second ranking Linear Deployment unrelated (filled circles) and the worst Truncation related strategy.

Results and discussion

The *Optimal proportion deployment* strategy returned the highest *Net gain* at all scenarios considered here (Figure 1). The *Optimal proportion* strategy produced 5% greater *Net gain* than simple truncation selection for all scenarios except when there was no inbreeding depression and many candidates from many families were available (Figure 1). Thus, there are better strategies than simple truncation selection for breeding value as supported by Lindgren and Matheson (1986). The *Optimal proportion deployment* strategy was most efficient at the scenarios. *Linear deployment unrelated* was the second best approach in most cases (Figure 1). The efficiency of the *Linear deployment unrelated* strategy was especially low when the number of families dropped to 12 at the desired N_s of 12.

In certain situations, the efficiency of the *Optimal proportion deployment* strategy was not markedly different from that of the *Linear Deployment unrelated* strategy (Figure 1). A technical disadvantage of the *Optimal proportion* strategy is that it requires a more complex software than practical breeders usually operate and the optimization procedure is more difficult to understand if compared with the *Linear deployment* strategy. Thus, it seems worthwhile to closer examine the cases where the *Linear Deployment unrelated* may replace the *Optimal proportions* deployment. The basic difference between these two strategies is that *Linear deployment* considers the breeding value only, whereas, *Optimal proportion* is searching for the combination of genetic gain and relatedness to maximize the *Net gain* and in this way it takes account the relatedness of the candidates. Therefore, in cases when there were more families to select from, there was no marked difference between *Optimal proportions* and *Linear deployment unrelated* strategies, because both tended to select one top ranking individual in each family (Figure 1). However, fewer available families (low genetic diversity available for deployment) forced the selection of relatives and the *Optimal proportion* strategy was more efficient to optimize the numbers of the related half-sibs.

Inbreeding had generally rather small effect on net gain, even in the most drastic cases analyzed (selection of a status number 12 seed orchard from 6 half sib families by truncation selection of the best) inbreeding depression reduces net gain only about 2 percent, and if there was much diversity in the candidate population inbreeding had almost no importance and it turned out favorable to select unrelated clones anyway. Comparing 6 and 12 families of size 40, the presence of inbreeding depression reduced the superiority of selecting from 12 from 5.0 to 3.9, indicating that diversity considerations was a more severe constraint for gain than inbreeding considerations. Thus the demand for a certain status number among seed orchard ramets forces to go further down in the list to clones with a lower breeding value rather than to avoid inbreeding.

Another point where optimization of deployment may be made is family number and family size under constant test size in the tests from which the selections to the orchards are made. Figure 2 illustrates that if demand for diversity is high, it is an advantage to test more families of small size versus few but large families. However, if there is high diversity to choose from (the number of half sibs available is larger than the desired status number), the number of families and their size ratio is of little importance.

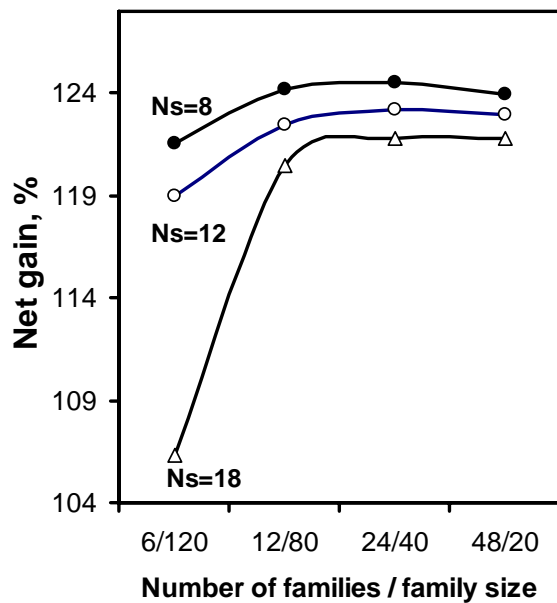


Figure 2. Effect of variable combinations of family number and family size at a fixed test size on net gain from Optimal proportions strategy for the three diversity levels desired in the seed orchard (expressed by status number (N_s)).

The total number of clones deployed was never higher than 40. The largest number of clones was obtained in the scenarios where high diversity requirement forced selection more families (scenario with 48 families for N_s of 24). For a more realistic scenario with the desired N_s of 12, the optimum number of clones varied at about 20. At constant N_s of 12, doubling the family number from 24 to 48 did not affect the optimum number of the deployed clones. Thus, if N_s of 12 can be accepted as sufficient diversity level in the new seed orchards, then not more than 20 clones are needed. Lindgren and Prescher (2005) optimized number of tested clones in the seed orchards and suggested a similar figure of 20 clones for the first cycle of orchards comprising tested clones given similar conditions as in our study.

In conclusion this study shows that if there is a large number of half-sib families available for deployment to seed orchards (e.g. status number available among candidates is at least 8 times greater than the status number desired in the seed orchard), the best advice is to use linear deployment unrelated strategy: take the single best candidate from the best families and deploy the ramets linearly according to the individual breeding values. The number of families to select from can be selected to satisfy the desired status number. If such large reduction of diversity is not tolerable or the candidates tend to be related, optimization with the *Optimal proportions* strategy is recommendable.

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