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## Balancing Genetic Gain and Relatedness in Seed Orchards

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### Summary

The traditional way to avoid related mating and subsequent inbreeding depression in seed orchards is to use only unrelated clones for orchard establishment. As tree-breeding programs move to advanced generations, relatedness (coancestry) among candidates for seed orchard selections becomes more common, especially for high breeding value candidates. The traditional way of selecting the ones with the highest breeding value, provided they are unrelated, is referred to Restricted Selection (RS). In order to consider breeding value as well as relatedness, an alternative selection method, based on a value criterion for the whole group of selected clones, is presented in this paper. The method, here called Group Merit Selection (GMS), is based on a suggestion by LINDGREN and MULLIN (1997), but modified for seed orchard selection by neglecting selfing and self-coancestry. The method can be regarded as the selection of a group of clones that maximizes expected genetic value (predicted genetic gain minus inbreeding depression).

A case study was conducted in which twenty clones for a seed orchard were selected among second-generation loblolly pine (*Pinus taeda* L.) selections from the NCSU-Industry cooperative breeding program. Assuming an observed inbreeding depression of 40% for one unit coefficient of inbreeding, penalty constants based on estimated breeding values at age 8 was corresponding with inbreeding depression. That gave 12% more genetic value for GMS than Restricted Selection. Predictions of the penalty constant considering additional relevant factors (such as pollen contamination, breeding values based on immature trials, and unrepresentative experimental sites) resulted in selection of the same clones. Changes among the selected clones did not occur until relatedness reached twice the penalty constant, suggesting that GMS solutions are rather robust.

*Key words:* seed orchard, group merit selection, restricted selection, inbreeding, relatedness, status number, genetic gain, loblolly pine.

### Introduction

The objective of a seed orchard is to produce seeds with high genetic quality. The implication may be that a seed orchard should give seeds with high breeding value and low inbreeding. To avoid inbreeding depression only unrelated clones are traditionally used for seed orchard establishment. When a tree-breeding program moves to advanced generations, the number of unrelated families is reduced. Breeders are thus faced with a dilemma. Would the acceptance of related selections in a seed orchard result in substantial genetic gain or would it result in an intolerable inbreeding depression? LINDGREN and MULLIN (1997) suggested a selection algorithm to select a group of genotypes, where both breeding value and relatedness are considered in an optimal way. It seems possible to develop this algorithm as a means for seed orchard composition, where related clones can be considered.

The loblolly pine (*Pinus taeda* L.) breeding program at the N.C. State University has completed two cycles of breeding with 45 years of genetic improvement operations. Substantial genetic gains have been achieved in forest tree species by establishment of seed orchards with phenotypically and genetically selected parents (ZOBEL and TALBERT, 1984). The second-generation breeding program began in the 1970's and 2<sup>nd</sup> generation seed orchards are now producing more than 50% of the total seed harvest in the program with an average gain of 10% in rotation volume compared to the 1<sup>st</sup> generation seed orchards (LI *et al.*, 1999). If only the best 30% of the parents were to be used to establish new seed orchards, i.e. 2.5 generation seed orchards (ZOBEL and TALBERT, 1984), an additional 13.5% gain increase compared to unrogued 2<sup>nd</sup> generation seed orchards could be expected (LI *et al.*, 1999). This prediction assumes that no inbreeding depression would occur. However, in reality, there is a high relatedness among the top-ranked clones (based on progeny tests) in an advanced tree-breeding program.

It is generally well known that mating of related individuals can result in inbreeding depression of growth and adaptation

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for most out-crossing species. The relationship between inbreeding depression and inbreeding coefficient varies between species and families (DUREL *et al.*, 1996). Loblolly pine is reported to show a height reduction of 4% to 5% per 0.1 inbreeding coefficient increase (Annual Report, 1998). At age nine, half-sib mating resulted in a height reduction of 4.7%, full-sib mating in 11.6%, and selfing in 16.7% height reduction respectively. For half-sib mating the family mean height growth reduction in percent declined slightly from age three to age six and to age nine, 5.8%, 5.2% and 4.7%, respectively.

The objective of this study is to develop and evaluate a method to select a number of clones among related candidates in order to obtain a maximized genetic value of the seed orchard crop considering the breeding value as well as the relatedness of the selections.

## Material and Method

### Selection

#### Assumptions

Coancestry for candidate clones is 0 if they are unrelated, 0.125 if they share one parent and 0.25 if they share both parents. The candidate clones are not inbred. Unknown parents (wind-pollen) are considered unrelated since they were selected from various natural stands. Selfing was neglected for the model although it occurred at a very low frequency. All selected clones are assumed to be able to contribute equally to the seed orchard offspring. The breeding values of the clones are assumed known or estimated precisely from progeny tests. Possible relaxations or violations of these assumptions are discussed below.

#### Group merit selection (GMS)

Relatedness is a characteristic of a group of clones, not of individual clones. To consider relatedness in selection, it is thus necessary to describe the characteristics of a group, not just individual characteristics of its members. A genetic value of a group of genotypes can be described by group merit. Group Merit is a way of evaluating the genetic value of the whole group of individuals based on their breeding values and the relatedness among members of the group. Group Merit can be considered to be a weighted sum of two terms: mean breeding value of the group and the average of all coancestries among the group members. In the current application Group Merit can be seen as a description of the predicted genetic value of the foreseen seed orchard crop. It can be regarded as the predicted breeding value penalized for the average coancestry. It may also be seen as the genetic gain with subtraction of the predicted inbreeding depression. The idea of Group Merit Selection (cf. LINDGREN and MULLIN, 1997, who called it "population merit selection") is to select, from available candidates, the group that maximizes group merit. Group Merit Selection, in that sense, uses the average of all coancestry values among the group members, including the self-coancestries and reciprocals. This average is called "group-coancestry".

There is an alternative way to define average coancestry by excluding the self-coancestry, which corresponds to average group cross-coancestry. This is used in the present study and is called Cross-Coancestry. The capitalization of Group Merit, Cross-Coancestry and Group Merit Selection emphasizes that they are characteristics of a group. Cross-Coancestry can be regarded as the expected offspring coefficient of inbreeding after random mating with no selfing, and it thus seems suitable for seed orchard application.

The algorithm for Group Merit Selection was modified and applied in this study to a group of clones constituting a seed

orchard. The genetic value of the expected seed orchard crop is defined as Group Merit (GM) and written as

$$GM = a\overline{BV} - bc'\overline{f} \quad (1)$$

where  $\overline{BV}$  is the mean Breeding Value of the seed orchard clones,  $c'$  is the genetic loss (in the same scale as Breeding Value) caused by relatedness,  $\overline{f}$  is the mean Cross-Coancestry for seed orchard clones (it is often useful to interpret it as expected inbreeding coefficient for the seed orchard crop),  $a$  is a factor for adjusting Breeding Value, and  $b$  is a factor for adjusting Cross-Coancestry and genetic loss caused by relatedness.

As scaling (units of measurement) does not matter for the mathematical optimization, the constants can be simplified as a quotient,  $c = b c'/a$ , where  $c$  is called "penalty constant". Penalty constant can be conceived of as the genetic loss, in the same scale as Breeding Value, for every unit change of  $\overline{f}$ . The formula of Group Merit can thus be rewritten as

$$GM = \overline{BV} - c\overline{f} \quad (2)$$

The Breeding Value for a group of size  $n$  is calculated as:

$$\overline{BV} = \frac{1}{n} \sum_{i=1}^n BV_i \quad (3)$$

where  $BV_i$  is the breeding value of group member  $i$ .

The Cross-Coancestry of the group is:

$$\overline{f} = \frac{1}{n^2 - n} \left( \sum_{i=1}^n \sum_{j=1}^n \theta_{ij} - \sum_{i=1}^n \theta_{ii} \right) \quad (4)$$

where  $\theta_{ij}$  is the coancestry between individual  $i$  and individual  $j$ , and  $\theta_{ii}$  is the self-coancestry of individual  $i$ .

The maximum Group Merit can in theory be determined by an exhaustive search of all possible sets of  $n$  individuals from  $N$ . With  $N$  candidates, there will be  $N! / ((N-n)!n!)$  possible combinations. A full search must investigate a huge number of combinations when  $N$  is reasonably high. There are no practical possibilities for such a search. A computer program (OLSSON and LIDSTRÖM, 1999; OLSSON *et al.*, 2000) was developed to perform an iterative search for sets of  $n$  selections with maximum GM. The search was performed through an add-and-remove procedure in the same way as done by LINDGREN and MULLIN (1997), although the current algorithm had less depth for the search to run faster.

#### Restricted selection (RS)

The Restricted Selection was to select only unrelated clones with the highest breeding values. Breeding values ranked the candidate clones. A clone was selected if it had the highest rank and did not share a parent with a previously selected clone. The process stopped when  $n$  clones had been selected.

#### Gene diversity and status number

In the present study the gene diversity ( $GD$ ) of a group was expressed with the status number ( $N_s$ ), which describes the effective number of clones in the seed orchard as the corresponding number of unrelated and non-inbred individuals (LINDGREN *et al.*, 1997).

Status number is calculated from group-coancestry:

$$N_s = \frac{0.5}{\Theta} \quad (5)$$

where group-coancestry is the average coancestry of all individuals (including self-coancestry),

$$\Theta = \frac{1}{n^2} \sum_{i=1}^n \sum_{j=1}^n \theta_{ij} \quad (6)$$

Gene diversity can be expressed as

$$GD = 1 - \frac{1}{N_s} = 1 - 0.5/N_s \quad (7)$$

#### A case study with loblolly pine

Data from 24 open-pollinated 8-year old progeny tests of 2<sup>nd</sup>-cycle selections, established by the Tree Improvement Program coordinated by North Carolina State University for the Atlantic Coastal Region was used. The number of families in each test ranged from 19 to 44 including several unimproved check-lots. Each test series generally included four tests, established over a two-year period, at two locations. The experimental design was typically randomized complete blocks with six blocks and 6-tree row plots. A total of 1023 individuals were evaluated for breeding values of height. Best linear unbiased predictions (BLUP) were used to estimate parental breeding values for tree height. The breeding values (BV) for tree height were given as the percentage superiority over unimproved check-lots, where the BV is 0. More details of the data analysis and genetic gain estimates of the progeny tests were reported by Li *et al.* (1997).

As a simple main alternative we consider a seed orchard where all pollination comes from the selected trees and that the estimates of individual BV in young experiments are valid for the mature forests arising from the seed orchard crops. From studies mentioned above we assume a height reduction of 40% per unit increase of the coefficient of inbreeding, thus a penalty constant of 40.

#### Results

Figure 1 demonstrates how Breeding Value varies with status number when the number of clones selected changed. GMS resulted in higher Breeding Value than Restricted Selection at the same status number. The difference was larger when rather low gene diversity (low status number) was tolerated. It was thus more favorable to accept alternatives with related clones when the required census number of clones was low. At status number 10, GMS gave 8.7% higher Breeding Value than Restricted Selection.

Table 1 shows the group merit obtained by GMS at three penalty levels in comparison with Breeding Value obtained by restricted selection for different number of selected clones. Group merit was equivalent to mean Breeding Value when the penalty constant was 0. For restricted selection, Group Merit was the same as Breeding Value because selected clones were not related. The GMS gave a higher Group Merit (and breeding value, data not shown) than RS at all numbers of selections. When clone number varied from 6 to 20, GMS with the penalty

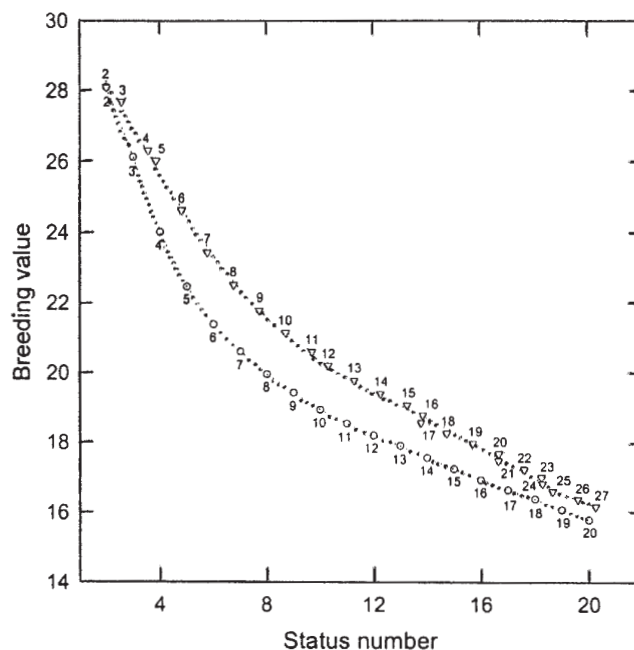


Figure 1. – Breeding Value versus Status Number for Group Merit Selection ( $\nabla$ ) with penalty constant 40 and Restricted Selection ( $\circ$ ) at different numbers of selected clones. The numbers on the lines correspond to different numbers of selected clones. Note that for Restricted Selection, when all clones are unrelated, the clone number and the status number are identical.

constant 40 gave 9% to 11% higher Group Merit than Restricted Selection. As the penalty constant increased from 0 to 40, and to 80, Group Merit obtained by GMS decreased. The reason was not mainly that different clones were selected, but that the subtraction for cross-coancestry was proportional to the penalty constant. GMS with the penalty constant 80 was at least 7.9% superior to Restricted Selection when selections were higher than 10.

In table 2, the 28 candidates with the highest breeding values are listed together with their pedigree. Among these candidates, 20 clones were selected for a seed orchard, using different algorithms. Restricted Selection did not select all the high-rank candidates, but went down to the 28<sup>th</sup> rank on the list because of the relatedness considerations. GMS selected the same candidates as the selection based only on breeding value, when the penalty constant was below 37. When penalty constants were between 38 and 83, GMS selected the 17 candi-

Table 1. – A Group Merit obtained with different number of selections. Restricted Selection (RS) and Group Merit Selection (GMS) with penalties for relatedness  $c=0, 40, 80$  are compared. Group Merit equals Breeding Value when the penalty for relatedness is zero ( $c=0$ ). In restricted selection related clones are never selected, and thus Group Merit equals the breeding value (as there is no cross-coancestry). Note that for the tabulated cases GMS selects the clones top-ranked for breeding value only when  $c=0$ . The last columns show the superiority of GMS expressed in percent of group merit progress (which is actually the progress in Genetic Value with inbreeding considered).

Selections	RS	GMS			100*(GMS-RS)/RS		
	BV(=GM)	$c = 0$	$c = 40$	$c = 80$	$c = 0$	$c = 40$	$c = 80$
2	28,10	28,65	28,10	28,10	2,0	0	0
4	24,01	26,99	25,48	24,65	12,4	6,1	2,6
6	21,39	24,64	23,64	22,64	15,2	10,5	5,8
8	19,96	22,51	21,97	21,44	12,8	10,1	7,4
10	18,94	21,20	20,81	20,48	11,9	9,9	8,1
12	18,21	20,22	19,91	19,65	11,0	9,4	7,9
14	17,57	19,45	19,18	18,97	10,7	9,2	8,0
16	16,93	18,84	18,58	18,37	11,2	9,7	8,5
18	16,39	18,30	18,01	17,81	11,6	9,9	8,7
20	15,80	17,76	17,48	17,27	12,4	10,6	9,3

Table 2. – Top candidate clones with their parents, ranked for breeding value (BV) and four alternatives to select 20 clones for a seed orchard among the candidates. The seed orchard selections obtained by Restricted Selection (RS), and GMS with penalty constants 0 to 37, 38 to 83, and 84 respectively, are indicated by crosses.

Clone ID	Parent 1 ID	Parent 2 ID	BV	RS	GMS 0-37	GMS 38-83	GMS 84
1	A	B	30,44	x	x	x	x
2	C	B	26,86		x	x	x
3	D	E	25,76	x	x	x	x
4	G	B	24,90		x	x	x
5	H	I	22,19	x	x	x	x
6	J	K	17,67	x	x	x	x
7	unknown	unknown	16,25	x	x	x	x
8	L	unknown	16,01	x	x	x	x
9	M	N	15,96	x	x	x	x
10	O	K	15,92		x	x	x
11	unknown	unknown	15,42	x	x	x	x
12	P	B	15,22		x	x	
13	Q	R	15,18	x	x	x	x
14	unknown	unknown	14,56	x	x	x	x
15	S	T	14,54	x	x	x	x
16	unknown	unknown	14,51	x	x	x	x
17	C	U	14,43	x	x	x	x
18	C	N	13,55		x		
19	unknown	unknown	13,10	x	x	x	x
20	unknown	unknown	12,80	x	x	x	x
21	C	V	12,60				
22	Y	unknown	12,14	x		x	x
23	unknown	unknown	12,10	x			x
24	O	unknown	12,01	x			
25	Z	O	11,33				
26	J	a	10,86				
27	unknown	unknown	10,53	x			
28	unknown	unknown	10,43	x			

dates with the highest breeding values (Table 2). A new candidate was chosen in order to reduce average relatedness when the penalty constant increased (GSM84 in Table 2). When the penalty constant rose from 83 to 84, the clone ranked 12 for breeding value was ignored because it had three half sibs with parent B in common among the clones with higher breeding values. Restricted Selection selected candidates with rather low breeding value, the lowest ranking included had the breeding value 10.43, while the lowest breeding value candidate selected by GMS with penalty constants 38-83 was 12.14 and by GMS with penalty constant 84 it was 12.10. The average breeding values of the selections by GMS was 12% higher than those for Restricted Selection.

Gene diversity is reduced when related or inbred clones are put together in a seed orchard. The candidates considered in the study belonged to the second breeding generation. There was no inbreeding and no relatedness except that some candidates had parents in common, and therefore the status numbers were equal to the census numbers following Restricted Selection. Status numbers obtained by GMS were lower at the same census number. If a higher penalty constant was used the gene diversity obtained was higher (up to the maximum status number 20).

## Discussion

Our results showed a costly compromise to completely avoid relatives in the seed orchard, the magnitude of the loss of genetic gain in this case study was 10%. The complete avoidance of relatives in advanced generation seed orchards may imply losing considerable genetic improvement benefits. Moreover, strict prevention of relatedness in advanced seed orchards is not realistic in practice since most of the highly ranked clones may be related. The GMS may be a good alternative to deal with this problem and maximize the genetic gain.

If only breeding value (no penalty) was used as a selection criterion, the level of Cross-Coancestry in seed orchard was only 0.007 in this case study (Table 2). The corresponding levels of inbreeding cannot cause a large reduction of forest production and are probably common in nature. Maybe a rule of thumb can be formulated: "If there is some relatedness among candidates we may try to select only by breeding value and accept the result if Cross-Coancestry is less than X". The value of X could be 1%, 0.5%, or 0.3% depending on the degree of sophistication of the breeding program. We believe that GMS (or some other non-trivial consideration of inbreeding) is preferable if  $X > 0.006$ , while for lower values the decision may be dependent on availability of competence.

In the "optimally" composed seed orchard (GMS40, Table 2) Cross-Coancestry was as low as 0.005. Tolerating the low level of cross-coancestry obtained by GMS means that 3 to 4 selected clones were different from the Restricted Selection, and no less than four clones had the same parent in common (parent B probably has an outstanding breeding value). Thus GMS means a rather considerable alteration of selections compared to Restricted Selection. GMS seems much more similar to simply selecting by breeding value. The difference in Breeding Value between GMS40 and GMS0 (which is selecting by breeding value only) was very small.

For the same number of selected clones, GMS reduced the gene diversity of the seed orchard crop compared to Restricted Selection. The "effective clone number" may still be regarded as reasonable and acceptable for a seed orchard of loblolly pine (ZOBEL and TALBERT, 1984). It is possible to select a few more clones with GMS and in that way it increases the status number to the same as RS of a lower number of clones. That would reduce the Breeding Value, and thus the superiority of GMS. However, if Breeding Value is plotted versus status number for the different alternatives (Figure 1), the superiority of GMS

seems considerable, even when compared with RS at the same status number. Group Merit considers gene diversity, thus the values of *table 1* consider the ensuing lower gene diversity from GMS.

There may be reasons to be a little cautious when recommending the use of related clones in a seed orchard. Inbreeding depression is a well-known phenomenon, and inbreeding can cause certain gain reduction. The predicted gain can be less accurate because of the following factors: breeding goals may change over time, the prediction of breeding values are based on observations in young and perhaps unrepresentative trials, fertility variations may cause large deviations from predictions. The “cost” of using such a “safety device” seems, according to this study, to be marginal. The same clones are selected when the penalty constant varies with a factor larger than two (*Table 2*).

Selfing was neglected, but this will not matter if the loss of genetic value by inbreeding depression due to selfing is the same for all clones and as long as the clone number is considered. In a real seed orchard the clones differ in inbreeding coefficient, selfing, fertility and phenology, but such unconsidered differences should not be systematically different for different chosen clones. To reduce selfing, the ramets of the same clone are planted apart from each other. Selfing usually gives a high frequency of empty seeds, thus the yield of viable inbred seeds is likely to be less compared to that of crossbred seeds (GRIFFIN and LINDGREN, 1985; WILLIAMS and SAVOLAINEN, 1996). There are many studies indicating that selfing has very limited effect on forest production.

The algorithm in this study is based on the assumption that every clone has the same expected fertility. But fertilities are likely to vary between clones (BILA, 2000) and that has considerable effects on the status numbers of the seed orchard crops (LINDGREN and MULLIN, 1998). However, we do not think that such random unknown variations in fertility will affect the superiority of GMS. It may be favorable to use a higher number of ramets of the clones with high breeding value (LINDGREN and MATHESON, 1986). This option can be roughly estimated with the current algorithm by considering selecting the same clone several times among the fixed number selected.

Estimates of  $a$ ,  $b$  and  $c'$  could be inserted in formula 1 to estimate GM, but it is more convenient to insert  $c$  in formula 2 to simplify computing. Some further considerations for the adjusted factors  $a$  and  $b$  are discussed below.

Firstly, the factors influencing estimated breeding values on productivity of seed orchard seeds:

- All genes in the seed orchard crops are not improved. There is pollen contamination in most seed orchards. Loblolly pine seed orchards are often located within natural range of Loblolly pine natural stands. About 40% pollen contamination from unimproved trees outside the orchard may be a reasonable value (LINDGREN, 1992). Considering this, the breeding value of the seed orchard crop is reduced by a factor 0.8 (mean value of 100% improved mothers and 60% improved fathers).

- The breeding value is often evaluated at young ages, but the breeding values and genetic gain at mature age are the relevant target for practical forestry. Selection of genotypes with the best breeding values was based on juvenile tests. These selected genotypes may not always remain the top-ranked ones at mature age. The accompanied reduction of gain can be expressed by a juvenile-mature correlation factor. LAMBETH (1980) suggested a formula for the development of juvenile-mature correlation over time. That formula is  $r_{jm} = 1.02 + 0.308 * \text{Log}(Q)$ , where  $r_{jm}$  is the juvenile-mature correlation and  $\text{Log}(Q)$  is the natural logarithm of the quotient

between the juvenile age and the mature age (rotation age). The progeny trials were typically evaluated at the age of 8 years and the rotation time is typically 25 years, thus  $Q = 8/25$ , which gives  $r_{jm} = 0.67$ . The BV at mature age can be adjusted by a factor 0.67.

- The breeding values are usually based on results from a limited number of test sites representing just a few specific sites which may not be typical for the seed orchard crop sites. The silvicultural methods used during the test (site selection, site preparation, plant production, fencing, planting techniques, spacing, weed control, damage control etc.) are different from the methods that will be applied in operational forestry. Considering unknown future forestry methods and the fact that a seed orchard crop may not be used exactly where it was targeted, it is not even possible to predict the exact seed use. But we do not believe the influence of these factors will be large, and we therefore suggest adjusting with a factor 0.9.

- “Maternal effects” or “after effects” may occur, e.g. depending on seed quality or conditions during seed formation (LINDGREN and WEI, 1994). The seeds may be differently affected in different years, and the seed orchard “after effects” may interact with those of the test seeds. The breeding values may be confounded with “maternal” and “after effects” in such a way that the estimated BVs are not exactly relevant for the seed orchard conditions. The general importance of these phenomena is little known but it certainly depends much on the specific circumstances. We assume it is small and suggest correction by multiplying with 0.95.

The adjusted factor  $a$ , with these considerations, will be  $0.8*0.67*0.9*0.95 = 0.458$ .

Secondly, the factors contributing to Cross-Coancestry and genetic loss of the seed orchard crop caused by relative mating:

- Seed orchards are subject to pollen contamination. We assume that pollen contamination in the seed orchard is 40%, and that the outside pollen is related neither with the selected clones, nor among each other. Thus a seed, resulting from pollen contamination, will not suffer from inbreeding. The pollen contamination causes reduction of the mating among relatives and less inbreeding in the orchard seeds, thus  $\bar{f}$  is reduced by a factor 0.6.

- As stated above, the genetic loss in term of inbreeding depression for height growth in experiments is 40% per unit of inbreeding coefficient ( $\bar{f}$ ).

- Actually, inbreeding depression is calculated referring to “100%” for trees not suffering from inbreeding depression. In the seed orchard crop in this study the genetic gain will be of a 15% magnitude (average breeding value obtained as shown in the results section, *Table 1*). Inbreeding depression might thus be 1.15 time larger in this case study.

- Inbred trees grow slower than non-inbred trees because the latter can use the available resources more efficiently. In operational forestry inbred and out-bred trees will be mixed and the inbred trees are likely to be more suppressed than measured in an experiment since out-bred trees will occupy much of the ecological space made available by the reduced growth of inbred trees. Thus the average gain will not be as reduced as the growth of the inbred trees. We consider this by multiplying with a factor 0.7.

Taking these factors into consideration, the adjusted factor  $b$  for the cross-coancestry and the genetic loss caused by cross-coancestry is  $0.6*0.4*1.15*0.7 = 0.193$ .

The “penalty constant” ( $c$ ), which defined as  $bc/a$ , will be  $0.193 / 0.458 = 0.42$ . After all assumptions and estimations were made, the penalty constant was close to the inbreeding

depression. The results (Table 2) show that the selection is not very sensitive to penalty constant variation. Therefore it may be sufficient to use inbreeding depression as the penalty constant when GMS is applied for seed orchard selection. In a more complex case the identification of an adjusted penalty constant is similar to the simplified case; the corrections are mainly cancelled out. Thus, a penalty constant corresponding to inbreeding depression seems to be the most relevant value when GMS is applied for establishing a seed orchard.

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## Clonal Differences and Relations Between Diameter Growth, Stem Cracks and Fungi in a 36-year-old Clonal Seed Orchard of Norway Spruce (*Picea abies* (L.) KARST.)

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### Summary

A study was carried out during 1987 to 1999 in seed orchard of *Picea abies* (L.) KARST. located in central Lithuania to estimate differences in diameter growth, occurrence of stem cracks, bark beetle (*Dendroctonus micans* KUG.) attacks, tree dieback and fungal infections among 20 different clones. Those were represented by 1333 clonal grafts that, at the time of the study, were 36-year-old. The results had shown: 1) significant differences in diameter growth among the different clones; 2) significant differences in the occurrence of stem cracks among the different clones; 3) significant positive relationship between average diameter at breast height (d.b.h.) of the clone and amount of trees with the stem cracks within the clone ( $r = 0.511$ ;  $p < 0.05$ ); 4) that within the clone, trees of larger d.b.h. are more likely to have cracked stems. Analysis of the data by chi-squared tests revealed four significant ( $p < 0.000001$ ) relationships: 1) in trees that possessed stem cracks occurrence of the dieback (66 dead out of 197, or 33.5%)

was much higher than in trees without cracks (44 dead out of 1136, or 3.9%); 2) in trees that possessed stem cracks frequency of *D. micans* attack was much higher (52 attacked out of 197, or 26.4%) than in trees without cracks (10 attacked out of 1136, or 0.9%); 3) the survival rate of trees with the stem cracks that were attacked by *D. micans* was much lower (2 survived out of 52, or 3.8%) than survival rate of trees with the stem cracks that were not attacked by *D. micans* (129 survived out of 145, or 89.0%); 4) the trees that suffered both from stem cracks and *D. micans* attack were less likely to survive (2 survived out of 52, or 3.8%) than sound-looking ones which were attacked by the bark beetle (9 survived out of 10, or 90%). Among the fungal species, *Sarea resiniae* KUNTZE and *Sarea dif-*

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