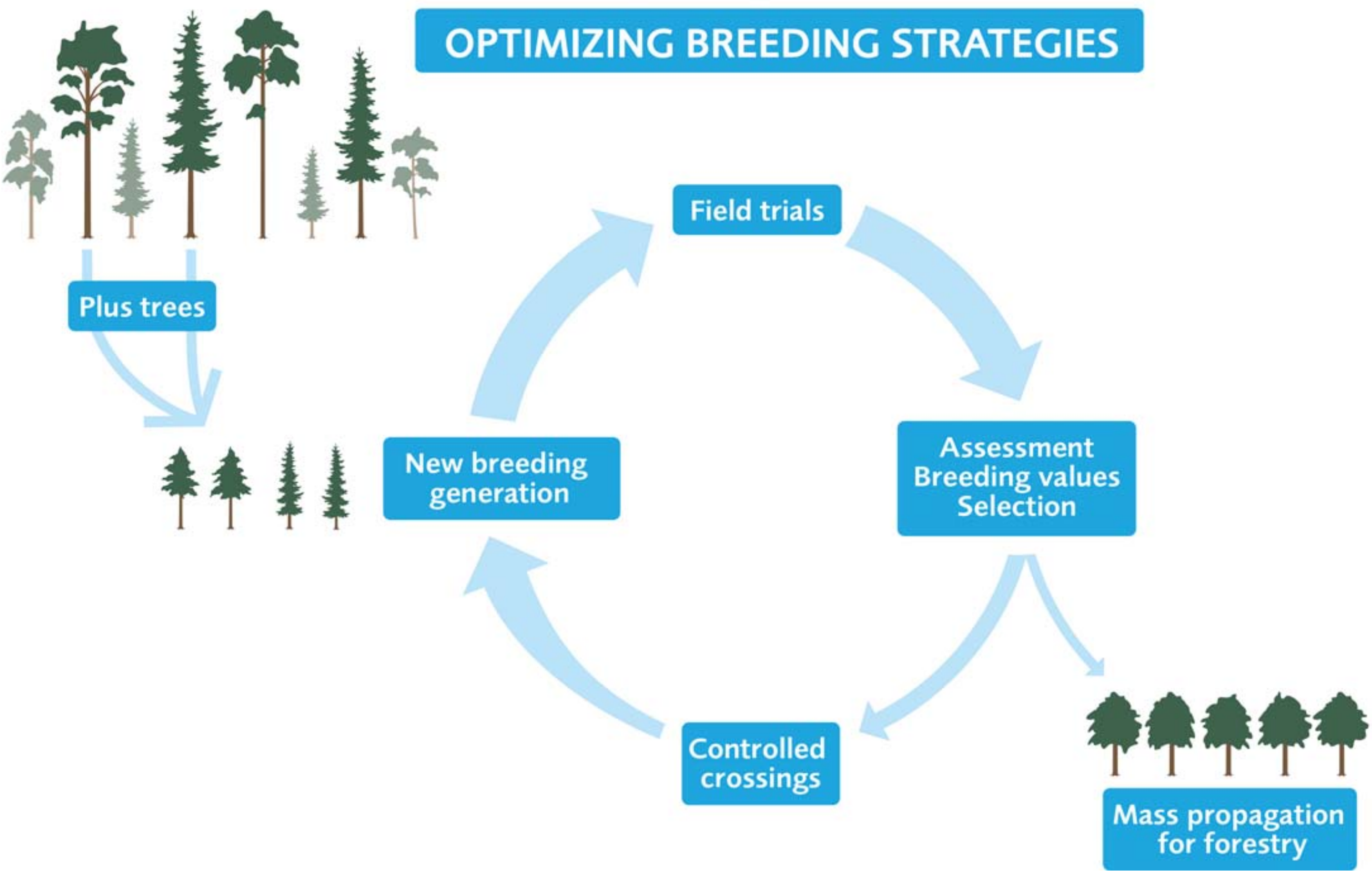

Arbetsrapport

Från Skogforsk nr. 882–2015

Optimizing breeding strategies at different effective population sizes

Optimering av förädlingsstrategier vid olika effektiv populationsstorlek

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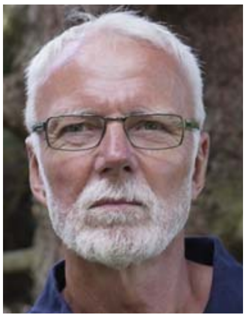

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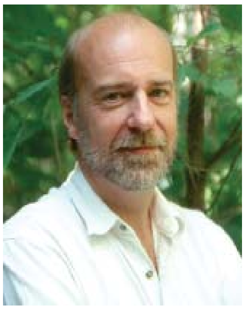

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Abstract

Earlier analyses have demonstrated that the current Swedish breeding strategy for Scots pine based on progeny testing and backward selection gives less gain per year than forward selection of individual trees in field tests. The study reported here compares four strategies based on forward selection in field tests with full-sib progeny from crosses of the breeding population: 1) forward selection of individual trees; 2) forward selection based on clonally replicated testing; 3) expansion of the breeding population by initially selecting more trees per family for crossing; and 4) expansion in combination with clonally replicated testing.

We carried out multi-generation simulations with POPSIM, where the new selection tool OPSEL can optimize selection at a predetermined increase in relatedness per cycle. To evaluate the strategies, we explored the response to two levels of each of the following factors: heritability, expansion of the breeding population, resources in terms of total number of progeny in field tests, allocation of clones and ramets within the total resource, and effective population size. The results confirm that clonally replicated testing and expansion are two ways to increase selection accuracy with similar improvements in genetic gain, although there is little incentive to combine the two techniques.

Contents

Summary

Earlier analyses have demonstrated that the current Swedish breeding strategy for Scots pine based on progeny testing and backward selection gives less gain than forward selection of individual trees in field tests if both time and annual input of resources are taken into account. The study reported here compares four strategies based on forward selection in field tests with full-sib progeny from crosses of the breeding population: 1) forward selection of individual trees; 2) forward selection based on clonally replicated testing; 3) expansion of the breeding population by initially selecting more trees per family for crossing to enhance options for forward selection both among and within families; and 4) expansion in combination with clonally replicated testing. The size of the non-expanded breeding population was 50 trees, and these were mated to generate 50 full-sib families. Under expansion this was doubled.

We created scenarios in the simulation program POPSIM where the new selection tool OPSEL can optimize selection at a predetermined increase in relatedness per cycle. Much work was spent on learning, testing and improving the selection tool, some of which is reported in the appendixes. To evaluate the strategies, we planned to explore the influence of three to four levels of each of the following factors: heritability, expansion of the breeding population, resources in terms of total size of progeny in field tests, allocation of clones and ramets within the total resource, and effective population size. From these 576 scenarios, 32 were carried out using two levels of each factor. By using OPSEL, the increase in relatedness was adjusted to those of population effective sizes Ne_V 100 and 50. Ne_V 100 corresponds to strict within-family selection, conserving maximum genetic diversity (i.e. current breeding strategy), and 50 is the stipulated long-term minimum level for the Swedish program.

While not all scenarios were carried out, the results are of interest to Swedish breeders and are presented as a basis for discussion and possible further analysis.

If the strategies are compared in terms of genetic gain in a seed orchard selected from the breeding population, with the gain reduced for inbreeding depresssion following increased relatedness and corrected for extending the breeding cycle as required when tests are clonally replicated, all strategies give about the same genetic net gain. Under balanced selection (Ne_V *100*) simple forward selection gives less net gain, but if a small degree of family selection is allowed (Ne_V 50), simple forward selection is about as good as strategies with expansion or clonally replicated testing. The good effect by simple forward selection assume that it is possible to produce very large families and apply high selection intensity. If those sizes can't be reached cloning is superior. The larger increase of breeding-population additive effects by expansion and less restricted selection was accompanied by a reduction in breeding population additive variance. The reduced variance almost halved the additional additive gain when selecting the top-ranking trees for an orchard.

The results confirm that clonally replicated testing and expansion are two different ways to increase selection accuracy with similar improvement of genetic gain. Clonal replication in general gives slightly higher gain, but the difference is small if the longer time required for propagation of cloned material is accounted for. Considering the additional work load, there is little incentive to combine expansion and clone testing. In general there was a small effect of increasing test resources at the levels studied.

Depending on how the effects of increase in relatedness and cycle time are valued, one can highlight greater or smaller differences among strategies. We have focused on analyzing gain and relatedness for a few of the top-ranking trees of the breeding population, which are both greater in magnitude than in the population as a whole. We have shown the possibility to reduce relatedness among these trees by restricted selection to a seed orchard and by letting the proposed seed orchard come from three unrelated populations and by reducing for inbreeding depression. Based on this, our preliminary conclusion concerning the breeding population is that the effective population size should be closer to Ne_V 100 than 50. We suggest a comprehensive discussion about the suitable level of effective size. Finally, we suggest what more analyses should be done and how breeders should respond to these results.

Sammanfattning

Tidigare analyser har visat att nuvarande strategi för svensk tallförädling med urval bakåt baserat på avkommeprövning, ger lägre vinst än urval framåt av enskilda träd i fältförsöken om man mäter vinst per tidsenhet och årlig resursinsats. Den här rapporten jämför fyra förädlingsstrategier för urval framåt i fältförsök med helsyskonavkommor till de träd som valts och korsats i förädlingspopulationen:1) urval framåt av enskilda avkommor/träd, 2) urval framåt baserat på klontestning 3) expansion av förädlingspopulationen genom att initialt selektera fler träd per helsyskonfamilj som korsas så att det blir möjligt med urval framåt både mellan och inom familjer, 4) expansion i kombination med klontestning. Den icke expanderade förädlingspopulationen bestod av 50 träd som korsades för att ge 50 helsyskonfamiljer. Vid expansion fördubblades detta.

Vi skapade scenarier i simuleringsprogrammet POPSIM där det nya selektionsverktyget OPSEL kan optimera urvalet vid en bestämd släktskapsökning i varje cykel. Mycket arbete lades ner på att lära oss, testa och utveckla selektionsverktyget, varav en del redovisas i rapportens appendix. För att utvärdera strategierna planerade vi att undersöka inflytandet av tre eller fyra nivåer på följande faktorer: heritabilitet, expansion av förädlingspopulationen, resursnivå mätt som antal avkommor i fältförsök, fördelning av kloner och rameter inom resursnivån samt effektiv populationsstorlek. Av dessa 576 scenarier genomfördes 32 med 2 nivåer för varje faktor: Med OPSEL reglerades t.ex. släktskapsökningen att motsvara populationsstorlekarna Ne_V 100 och 50. Ne_V 100 motsvarar strikt urval inom familj med maximalt bevarad genetisk diversitet (d.v.s. nuvarande förädlingsstrategi) och 50 är den stipulerade långsiktigt lägsta nivån i det svenska programmet.

Trots att alla scenarier inte är genomförda är resultaten av intresse för förädlarna och presenteras för att kunna diskuteras och för att vara underlag för eventuellt fortsatta analyser.

Om man jämfört strategierna i termer av genetisk vinst i en fröplantage med reduktion för inavelsdepression till följd av ökat släktskap och med korrektion för att klontestningen förlänger cykeltiden ger alla strategier ungefär samma genetiska vinst. Vid balanserat urval (Ne_V =100) ger enkelt urval framåt något lägre vinst men tillåts ett visst familjeurval (Ne_V =50) är enkelt urval framåt ungefär lika bra som strategierna med expansion eller kloning. Den goda effekten av enkelt urval framåt förutsätter att det går att framställa riktigt stora avkommor och tillämpa hög selektionsintensitet. Om dessa storlekar inte kan uppnås är klontestning överlägset. Den större ökningen av förädlingspopulationens additiva genetiska nivå till följd av, expansion eller mindre restriktivt urval åtföljdes av minskad additiv varians i förädlingspopulationen. Den minskade variansen nästan halverade den ytterligare vinsten av att välja de högst rankade träden till en fröplantage.

Resultaten verifierar att klontestning eller expansion är två sätt att öka urvalssäkerheten som ger ungefär samma förbättring av vinsten. Klontestning ger genomgående något högre vinst men skillnaden är liten om man tar hänsyn till den längre tid kloningen medför. Med tanke på merarbetet är det inte mycket som motiverar att kombinera expansion och kloning. Det var generellt en liten effekt av att öka testresurserna i det undersökta intervallet.

Beroende på hur man värderar effekter av släktskapsökning och tidsskillnader mellan strategier kan man lyfta fram större eller mindre skillnader mellan strategierna. Vi har fokuserat på att analysera vinst och släktskap bland de bästa träden i förädlingspopulationen som båda är högre än i populationen som helhet. Vi har visat på möjligheten att reducera släktskapet mellan toppträden genom restriktivt urval till en fröplantage och genom att låta en tänkt fröplantage komma från tre obesläktade populationer samt genom att reducera för inavelsdepression. Med det underlaget är vår preliminära slutsats angående förädlingspopulationen att den effektiva populationsstorleken skall ligga närmare Ne_V 100 än 50. Vi föreslår en fördjupad diskussion om vad som är en lämplig effektiv populationsstorlek. Avslutningsvis föreslår vi även vilka ytterligare analyser som skulle behövas samt hur förädlarna skall förhålla sig till de här resultaten

Introduction

The aim of our breeding strategy investigations undertaken in the spring of 2014 was to study, in more detail, some of the strategies described in the earlier Skogforsk breeding investigation (Rosvall et al. 2011) and further considered as part of the NovelTree "best practices" document (Rosvall and Mullin 2013). The comprehensive analyses presented here became possible with the availability of a new selection tool called OPSEL (Mullin 2014). OPSEL uses "branch-and-bound" optimization algorithms (Mullin and Belotti 2015) to maximize gain in a breeding population (BP) with a given census size, while constraining on effective population size (Status Number, group coancestry, etc.).

Alternative strategies can be evaluated and compared by computer simulation. One of the software tools used by Skogforsk breeders for such evaluations is POPSIM (Mullin et al. 2010; Mullin and Park 1995). POPSIM is a stochastic model mimicking the sampling process of alleles that takes place over multiple generations in a closed population. It is based on the proven genetic theory of the infinitesimal model and is equipped to analyze operational breeding activities. With OPSEL built into POPSIM as an optimal selection tool, it is now possible to constrain exactly the increase in group coancestry per cycle (GC) to that which maintains a constant variance effective population size (Ne_V), and thus compare strategies at a common level of gene diversity.

The focus of our new simulation studies was on variants of forward selection, with and without expanding the breeding population in cycle 1 (the first F_1 generation), and with and without the use of clonal replication of field tests:

1. *Field forward:* applying forward selection in the F_{n+1} full-sib field tests to directly identify a final breeding population of 50 trees, using BLUP BV estimates. The selected trees are mated by double-pair mating (DPM) with positive assortment (PAM) to produce a new F_{n+2} recruitment population to be planted as seedlings in new field experiments.

2. *Field forward clonal replicates:* identical to the preceding, but the recruitment population is established in field tests with cloned replicates, rather than with seedlings. Copies of each clone (ramets) are kept in a parallel breeding archive for making crosses, after selection.

3. *Field forward with expanded BP:* similar to "field forward", in that forward selection is practiced in field tests, but differs in the number of families produced and the number of breeding parents selected. By selecting more than one parent within-family, we "expand" the breeding population, selecting multiple individuals and crossing these under DPM and PAM to produce additional families.

4. *Field forward with expanded BP and clonal replicates:* identical to the preceding, but establishing the recruitment population in field tests with cloned replicates, rather than with seedlings.

Previous simulation studies have demonstrated that comparisons are highly sensitive to factors that affect the resulting effective population size. By applying the optimizing capability now embedded into POPSIM, our objective in this investigation was to develop a clearer understanding of how these various strategies of interest behave, when constrained to a common level of genetic diversity.

Methods

BASELINE FOR STRATEGY COMPARISONS

Of interest in this study were comparisons among levels of:

1. Narrow-sense heritability (h^2)
2. Expansion of the breeding population after selection of the initial 50 tested founders
3. Field testing of seedlings versus varying numbers of clonal replicates
4. Resources available, expressed as numbers of individuals tested in recruitment populations
5. Rate of accumulation of GC (loss of gene diversity and corresponding Ne_V)

Levels of interest for each factor are given in Table 1. To test every combination would have required 576 simulation scenarios – a rather heavy task even with several computers running for many months. We prioritized the comparisons by identifying two levels of each factor, requiring $2^5 = 32$ simulation scenarios – a much more manageable task.

Table 1.
Conditions used in the analysis of breeding strategies.

	Levels of interest[1]			
Factor	**1**	**2**	**3**	**4**
h^2 (corresponding rTI)[2]	**0.05 (0.22)**	**0.2 (0.45)**	0.4 (0.63)	
Expansion factor after cycle 1 (BP size)	**1 (BP50)**	**2 (BP100)**	3 (BP150)	4 (BP 200)
Number of ramets (1 is testing with seedlings rather than clones)	**1**	5	**10**	15
Resource level – size of recruitment population[3]	6 500	**13 000**	**26 000**	
ΔGC, per cycle increase in group coancestry (corresponding Ne_v)[4]	**0.005 (Ne_v = 100)**	0.0075 (Ne_v= 75)	**0.01 (Ne_v = 50)**	0.015 (Ne_v = 25)

[1] Levels used for the comparisons discussed in this report are indicated in **underlined bold** type.

[2] The correlation between the "true" and predicted breeding value, the square root of h^2, and directly proportional to accuracy.

[3] Current Swedish resource levels for Scots pine and Norway spruce are 20 000 PX progeny and 28 000 rooted cuttings for an estimated generation of 33 and 23 years respectively, corresponding to 606 and 1217 trees per year.

[4] Balanced selection is fulfilled with GC-increase 0.005 and no expansion of the BP.

The first BP (50 trees in cycle 0) was selected from the 300 tested founders, and regenerated by DPM and PAM. When arranging crosses, parent combinations involving full or half sibs were minimized by means of a relative avoidance algorithm available within POPSIM. This algorithm scans down the list of crosses proposed under PAM, swapping out related parents as necessary with lower-ranked parents. Individual breeding values are estimated by BLUP for all trees in the recruitment population using information from relatives. The per-cycle increase in group coancestry to maintain a predetermined effective population size was achieved by setting the maximum accumulated group coancestry that should be allowed in each cycle as a constraint on selection by OPSEL.

Comparisons were made after three cycles of breeding to avoid excessive execution time. From experience, we know that the BP development is approximately linear for many generations if a reasonable restriction is used on relatedness (if not, additive variance is probably reduced in a way causing a non-linear development). While three cycles are sufficient to establish most trends, these are probably too few to follow the development of additive variance (V_A) over cycles due to PAM.

A fair comparison should be at the same expenditure of resources and loss of GC per unit time. The strategies studied are all variants of forward selection, having about the same cycle time. To simplify, we used equivalent resources per cycle rather than per year, expressed by the size of the recruitment population for each cycle. Therefore, in the final evaluation it should be remembered that rooting cuttings for clonal testing will add about two years to the 20-year breeding cycle for simple forward selection. To adjust the comparison on basis of annual results, gain should be reduced by a factor 20/22 = 0.91 and diversity increased. It should also be remembered that there are other operational differences to be considered when comparing strategies, such as costs of rooting cuttings, crossing efforts, archive management, etc.

We also believe that a fair comparison should be in terms of gain from a selected seed orchard sub-population, rather than the level of genetic change in the BP itself. In that case, we calculated the net gain by subtracting the expected inbreeding depression in the orchard progeny.

PRELIMINARY STUDIES

We did a series of simulations to find suitable conditions for the main study, to understand the influence of our conditions and the behavior of the new selection tool OPSEL. Detailed results from these studies are documented in Appendices 1 through 6. Here we summarize the results and in the section Future studies we suggest further investigations to be done.

Net gain (details in Appendix 1)

We selected two alternative seed orchards during our simulation. The first was a seed-orchard production population (SeedPP) selected without restrictions, reporting the additive effect (Aeff), GC and pair-wise coancestry (pwC) for the very top 6 trees of the BP. A second alternative utilized POPSIM's clone mixture options (ClonePP) to select 6 genotypes, applying the hardest restrictions possible, i.e., allowing a maximum of one progeny genotype per parent. If gain is about the same for these 6 trees selected in different ways, there must be little relatedness among the top trees in the ranking list. If gain is reduced, there is more relatedness in the top and the less-related trees are found further down the ranking list. For their use in production orchards, we assumed that the 6 selections would be part of an 18-parent orchard, together with selections from 2 additional breeding populations, 3 BPs in total.

While recurrent selection will accumulate gain, it will also accumulate relatedness among orchard selections that could lead to a reduction in gain due to inbreeding depression. To calculate Net Gain (NG) from orchards, we assume that selfing will not produce viable seed, so we apply a reduction in the Aeff for the rate of inbreeding depression (b) only on the average pairwise coancestry (pwC) of the orchard parents; thus, NG = Aeff – b(pwC). From the literature, we expect that selfing (where $F = 0.5$) in Scots pine will produce progeny with about 50% less production than outcrosses (Lundkvist et al. 1987), so for a trait with mean 100 (as in our simulations here), we might find the progeny from selfing produce only 50, so the rate of depression per unit F is 50/0.5 = 100, and the reduction due to inbreeding depression is –100 × pwC.

Applying this correction to the selected 6 trees and to the 18-tree orchard assembled from 3 BPs, we have:

NG_6 (6 seed orchard trees of one BP) = $Aeff_6 - 100 \times pwC_6$.

NG_{18} (18 seed orchard trees from 3 BP) = $Aeff_6 - 100 \times pwC_6/3$.

OPSEL settings and candidate list truncation (details in Appendices 2 and 3)

These studies focused on establishing effective settings for the optimal search engine, and the impact of population expansion. The optimal selection of the best set of breeding parents is a computer-intensive procedure and can run into several hours. Several strategies were employed to avoid excessive execution time to complete the optimization algorithm:

1. *Truncation of candidate list:* With many progeny field-tested per cross, only the best are likely to be included in an optimal set of selected individuals. A candidate short-list can be produced using a simple truncation, with a fixed number of best progeny per family. Our tests demonstrated that a truncation of the candidate short list to the best 5 progeny for each full-sib family was effective for all conditions and level of population expansion for our high-priority comparisons.
2. *Limiting optimization time:* Normally, OPSEL will find a "good" solution within a very short time. Additional execution time is required to prove that a solution is the "true" optimum, and meanwhile the solution may improve little, if at all. Setting the search engine time limit to 600 seconds was effective in finding an optimum or close-to-optimum solution, while sacrificing little if any gain.
3. *Limiting number of nodes in the search:* Similarly, OPSEL offers the user the ability to limit the number of "nodes" considered during the branching part of the optimization algorithm. Setting the nodes switch to 60 000, OPSEL would always run a full 600 seconds without terminating by hitting the node limit.
4. *Limiting the "gap":* OPSEL can also consider the gap between its current solution and that of the theoretical optimum. The gap will decrease until the solution is found to be truly the best. There was essentially no difference in the final solution if we accepted a gap tolerance limit of 0.5%.

Expansion of the breeding population (details in Appendix 4)

Earlier studies have demonstrated that it is optimal to expand the BP by a factor 2, i.e., doubling the size (Rosvall and Mullin, 2013). Expansion initially involves making additional selections within crosses between founder, and in subsequent cycles a combination of among-family and within-family selection from the expanded number of crosses. Verifying these findings under the conditions used here and with the precise control of relatedness possible with OPSEL confirmed that expanding the BP size from 50 to 100 is optimal. However, by expanding the original BP of 50 to 100, 150 and 200 by using expansion factors 2, 3 and 4, we also became aware of some consequences of the expansion when allowing for a constant increase in group coancestry.

The repeated sampling of sibs within families to expand the BP will increase the chance to select more of the alleles from the parents and decrease GC and increase Ne_v and Ns, as shown in Figure 1 (left) for expansion of the BP from size 50 to 100 and using balanced selection (Expansion balanced 100). In this way, the expansion creates extra "space" for selection up to the GC of a BP with constant size 50 (50 balanced in Figure 1). Therefore, at the time of expansion in cycle 1 (generation 0 is when the BP of 50 trees are selected from 300 for the first breeding) there is a greater extra "space" of GC than is generated in later generations. In later generations, the extra space just comes from the larger population size being 100 instead of 50. When expanding the BP from 50 to 100 trees and using balanced selection of 2 instead of 1 tree per family, selection intensity is decreased resulting in a lower Aeff (Figure 1 right). However, when allowing unbalanced selection and the same restriction for GC-increase as for the original BP size 50 under balanced selection the Aeff is much increased (Figure 1 right).

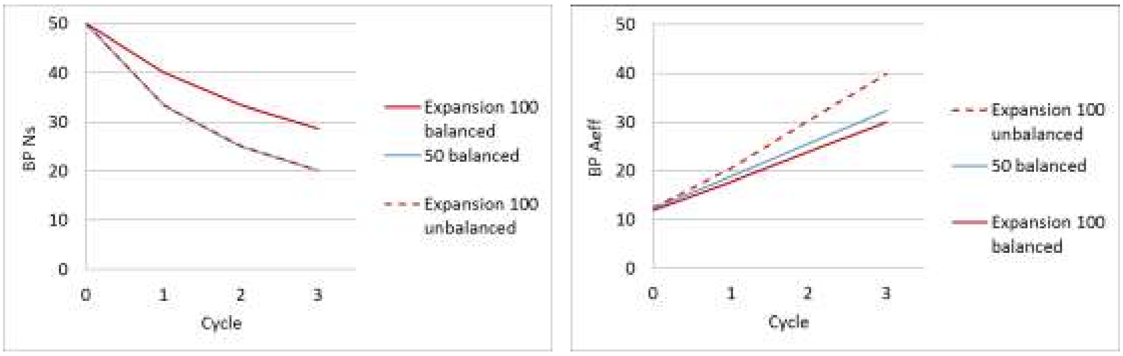

Figure 1.
Effect of selection balance on BP *Ns* (left) and BP Aeff (right) showing the extra space in *Ns* to be explored after expansion from BP size 50 to 100.

To our understanding, it is the extra space of GC to be exploited by OPSEL in the expansion generation (i.e., cycle 1) that defines the level for truncation required to give the shortest short-list giving the largest optimum when selecting with OPSEL. If too few sibs per family are taken to the shortlist OPSEL is unable to increase GC to the predetermined level.

Our results indicate that for expansion factor 2 (BP size 100) 5 trees per family are needed although 4 gives almost identical results, giving room for imbalance in the selection while satisfying the constraint on GC. For expansion factor 4 (BP 200), at GC-increase 0.005 and 0.010, 7 and 10 trees per family, respectively, are needed in the short-list, making a total of 350 and 500 candidates. To expand from 50 to 100 and 200, 2 and 4 trees per family, respectively, are used just for the expansion and the additional trees to create room for unbalanced selection.

Ramet numbers (details in Appendix 5)

This study was to find the optimal distribution of ramets and clones within a family of given size, depending on resource level and BP expansion (both affecting family size), heritability, and GC increase. We concluded that using 10 ramets is a good compromise for all conditions keeping in mind that h^2 is not fully known in advance and that some additional gain can be achieved for some of the conditions used. Appendix E will also help breeders when they plan their experiments or find themselves short of ramets for testing, by increasing their understanding of the combined effect of ramet number, selection intensity and gain under a given total resource.

3:2:1 mating design (details in Appendix 6)

The standard mating design used in our simulations, both for expanded and non-expanded breeding populations, was DPM under PAM, giving exactly the same number of crosses and progeny for each parent in the BP. The purpose of our sub-investigation using 3:2:1 mating in combination with OPSEL was to vary selection intensity among the top and bottom ranking part of the recruitment population without changing diversity. More progeny are generated from the high-ranking trees by doing 3 crosses (the same number of progeny per cross), while making just 1 cross with each of the low-ranking parents. With OPSEL, selection could be done at the same rate of increase in coancestry as the alternative of using exactly 2 crosses per parent. As expected, the increase in additive effect in the top-ranking part of the BP was counteracted by an equivalent decrease in the bottom part, leaving the BP mean unchanged. Also as expected, the Aeff of the 6-tree SeedPP was increased, although the effect was small under these conditions.

Using 3:2:1 mating to generate some imbalance in combination with balanced selection of one tree per family has been used earlier to relax selection restriction (Lstibůrek et al. 2004; Rosvall et al. 2003). These studies showed that sacrificing just a few crosses from bottom to do more high-ranking crosses generated good response and a favorable structure of relatedness. The exploration of this has still to be completed.

Results – Comparisons among the 32 high-priority scenarios

The detailed results of the 32 high-priority scenarios after 3 cycles of breeding are found in Tables 2 and 3. The development over cycles of BP Aeff and BP V_A for these scenarios is illustrated in Figure 2 (left and right graphs, respectively), with the series of results for moderate resources (recruitment size of 13 000 per cycle) and high resources (26 000 per cycle) shown in Figures 2a and 2b, respectively. These graphs show differences in rate of progress among scenarios. In the following presentation we concentrate on the cycle 3 results, keeping in mind that the most often presented results would have been for five cycles and therefore showing greater differences among scenarios.

GAIN FROM EXPANDING THE BP VERSUS CLONAL TESTING

When GC increases at a rate of 0.005 per cycle (corresponding to Ne_V of 100 and balanced selection of a BP of size 50), Field forward with the expanded BP to 100 combined with clone testing has the highest Aeff for both the BP and SeedPP (6 top trees), at both levels of h^2 and resources (Figure 3). This is also true for the net gain of the more restrictive selection of the ClonePP at the lower level of $h^2 = 0.05$, but not when $h^2 = 0.2$, where the best result is without expansion but with clone testing (Figure 4 top). In this study, the ClonePP was used to select a seed orchard (6 trees) with the highest restrictions on relatedness possible (i.e., maximum one per parent), while the SeedPP was selected as the 6 top trees without restrictions. Net gain is the Aeff corrected for inbreeding depression in a seed orchard of 18 trees coming from 3 unrelated groups of 6 trees.

When GC increases more rapidly, at a rate of 0.01 per cycle (corresponding to Ne_V of 50), Field forward with clone testing (without expansion), keeping the BP at size 50, has the highest Aeff in both the BP and SeedPP (Figure 3), and greatest net gain in the ClonePP (Figure 4).

Using clonal testing is always better than not using it. In general, the effect is larger for BP of size 50 than for an expanded BP of size 100 (Figures 3 and 4). Since clonal replication lengthens the breeding cycle by about 2 years, selection effects should be reduced to 20/22, or 91%. Even after this reduction and considering net gain, clone testing is still beneficial for BP of size 50 at both rates of increase in GC, and for a BP expanded to size 100 when GC increases at 0.005 per cycle, but not at 0.01 per cycle (Figure 4).

Expanding the BP and clonally replicated field testing are both efficient ways to increase the Aeff. There is a small effect of combining the two under fully balanced selection, i.e., GC-increase of 0.005 per cycle. When restrictions are relaxed to a GC-increase of 0.01 per cycle, expansion does not give much extra but cloning does, and the effect of both done together is negative.

The resource level of 26 000 tested trees per 22 year cycle is close to the 28 000 of the current Swedish spruce program, while the pine program tests 20 000 seedlings over 33 years, which is much fewer per year. Our results suggest a rather small decrease in gain by reducing the test resource from 26 000 to 13 000 tested trees per cycle, the tendency being that the simple Field forward strategy is the least resource demanding.

Table 2.

Additive effect (Aeff) and variance (V_A) after 3 cycles for the 32 scenarios based on variants of the field forward strategy, with and without “expansion” (exp), with both seedling and clonally replicated field testing, grouped by combination of heritability (0.05 and 0.2),resource level (13 000 and 26 000) and per cycle increase in group coancestry (ΔGC).

						BP		SeedPP		ClonePP							
Strategy	**h^2**	**Resource level**	**Number of ramets**	**ΔGC /cycle**	**Number of families**	**Aeff**	**sd**	**V_A**	**sd**	**Aeff**	**sd**	**V_A**	**sd**	**Aeff**	**sd**	**V_A**	**sd**
Seedling	0.05	13 000	1	0.005	50	18.36	1.9	134.7	34.5	32.3	3.6	71.8	41.1	37.40	4.51	66.7	30.0
Seedling-exp	0.05	13 000	1	0.005	100	+8.66	1.6	102.7	21.1	+5.18	4.3	57.8	37.9	+5.87	4.34	66.4	36.5
Clonal	0.05	13 000	10	0.005	50	+8.87	2.3	121.8	23.1	+8.54	3.5	56.7	32.0	+11.3	3.42	55.2	49.1
Clonal-exp	0.05	13 000	10	0.005	100	+14.14	1.9	82.9	15.4	+10.12	3.7	36.0	24.3	+14.4	4.43	47.3	28.7
Seedling	0.05	13 000	1	0.01	50	29.05	2.1	97.4	24.5	37.4	4.2	59.1	42.6	42.68	5.30	47.3	28.2
Seedling-exp	0.05	13 000	1	0.01	100	+2.83	2.0	72.5	13.1	+2.05	4.8	45.8	37.8	+2.46	4.56	56.4	33.7
Clonal	0.05	13 000	10	0.01	50	+8.57	1.6	86.0	22.3	+8.55	4.6	44.3	23.3	+13.0	4.01	50.1	32.5
Clonal-exp	0.05	13 000	10	0.01	100	+6.58	1.9	64.2	14.1	+5.28	3.3	39.6	15.8	+9.73	3.52	55.6	37.5
Seedling	0.05	26 000	1	0.005	50	19.49	2.3	125.9	35.8	32.7	5.0	50.4	26.0	38.30	5.61	63.6	26.1
Seedling-exp	0.05	26 000	1	0.005	100	+8.9	2.2	108.7	16.2	+8.14	4.5	46.8	30.9	+8	4.19	65.2	31.9
Clonal	0.05	26 000	10	0.005	50	+10.4	2.0	117.9	29.3	+11.48	3.1	52.5	34.3	+13.4	4.14	59.2	38.2
Clonal-exp	0.05	26 000	10	0.005	100	+16.83	2.2	87.4	22.3	+14.31	5.5	39.0	18.4	+17.7	5.69	50.2	26.5
Seedling	0.05	26 000	1	0.01	50	31.16	2.3	112.1	31.0	41.2	5.0	44.5	29.2	46.91	4.31	57.3	43.5
Seedling-exp	0.05	26 000	1	0.01	100	+2.21	2.2	77.5	9.6	+-0.66	4.4	44.7	35.8	+0.28	4.36	54.7	27.9
Clonal	0.05	26 000	10	0.01	50	+9.25	2.9	82.8	26.5	+7.77	5.7	44.4	24.3	+10.2	5.32	49.6	30.1
Clonal-exp	0.05	26 000	10	0.01	100	+9.05	2.5	70.3	13.0	+6.74	4.1	44.0	36.8	+10.9	4.52	51.3	33.0
Seedling	0.2	13 000	1	0.005	50	32.32	1.4	117.0	24.1	45.2	4.1	55.8	37.1	53.97	3.52	56.5	30.6
Seedling-exp	0.2	13 000	1	0.005	100	+7.5	1.8	87.7	18.6	+6.2	3.9	47.7	21.0	+5.21	3.77	51.4	36.1
Clonal	0.2	13 000	10	0.005	50	+9.15	1.4	102.8	24.7	+10.28	3.3	28.2	18.0	+11.1	3.22	41.7	21.7
Clonal-exp	0.2	13 000	10	0.005	100	+11.3	1.9	68.6	15.0	+9.02	3.9	29.3	15.0	+11.2	3.57	36.0	20.3
Seedling	0.2	13 000	1	0.01	50	43.02	2.0	94.4	27.4	52.8	4.4	54.7	30.3	62.93	4.76	52.4	26.6
Seedling-exp	0.2	13 000	1	0.01	100	+0.79	1.8	70.5	12.4	+-1.96	4.0	35.1	20.9	+-	3.51	59.9	32.2
Clonal	0.2	13 000	10	0.01	50	+7.41	1.4	60.5	20.3	+5.96	4.2	30.4	21.7	+7.07	2.63	44.2	21.6
Clonal-exp	0.2	13 000	10	0.01	100	+3.47	2.0	56.3	15.0	+3.09	3.9	40.1	24.3	+3.98	3.66	38.4	23.0
Seedling	0.2	26 000	1	0.005	50	34.71	2.1	116.3	25.6	48.0	3.6	60.7	56.2	56.89	5.26	67.0	40.6
Seedling-exp	0.2	26 000	1	0.005	100	+7.74	1.9	92.9	18.0	+5.74	4.8	49.8	34.6	+6.09	5.51	46.3	36.5
Clonal	0.2	26 000	10	0.005	50	+10.81	1.5	93.6	19.3	+10.06	3.1	36.4	24.2	+13.8	3.18	38.1	27.7
Clonal-exp	0.2	26 000	10	0.005	100	+13.6	1.6	60.7	9.7	+10.92	3.9	31.8	20.4	+14.6	3.23	36.9	25.7
Seedling	0.2	26 000	1	0.01	50	44.77	2.5	92.4	25.1	53.7	5.0	52.6	35.3	63.93	4.91	57.7	46.5
Seedling-exp	0.2	26 000	1	0.01	100	+2.41	1.9	75.8	16.0	+0.66	4.6	44.9	23.9	+2.13	4.57	51.2	29.1
Clonal	0.2	26 000	10	0.01	50	+9.21	2.0	60.3	20.6	+8.71	4.0	23.7	13.6	+11.1	3.68	27.5	18.0
Clonal-exp	0.2	26 000	10	0.01	100	+6.07	1.6	48.3	10.9	+4.88	4.1	36.6	19.4	+8.11	3.84	37.3	22.1

Table 3.
Additive effect (Aeff), group coancestry (GC) with corresponding Status number (N_s), pair-wise coancestry (pwC) and net gain (NG) for the 32 scenarios after 3 cycles. NG_{18} is for 18 trees, 6 from each of 3 unrelated BPs. For clonal strategies, NG_{18} is also corrected for 2 additional years of clonal propagation (20/22=0.91).

						BP				**SeedPP**					**ClonePP (Cycle 2)**					
Strategy	h^2	Resource level	Numbers of families	Number of ramets	ΔGC/ cycle	Aeff	N_s	GC	pwC	Aeff	N_s	GC	pwC	NG_{18}	Aeff	N_s	GC	pwC	NG_{18}	$NG_{18\text{-}20/22}$
Seedling	0.05	13 000	50	1	0.005	18.36	20.0	0.025	0.015	32.31	3.97	0.127	0.043	30.89	32.31	3.97	0.127	0.043	30.89	
Seedling-exp	0.05	13 000	100	1	0.005	27.02	20.0	0.025	0.020	37.49	2.36	0.216	0.131	33.12	36.65	3.77	0.135	0.049	35.01	
Clonal	0.05	13 000	50	10	0.005	27.22	20.0	0.025	0.015	40.85	3.96	0.127	0.043	39.42	40.86	3.95	0.128	0.043	39.42	35.84
Clonal-exp	0.05	13 000	100	10	0.005	32.49	20.1	0.025	0.020	42.43	2.99	0.174	0.088	39.49	41.83	3.71	0.138	0.052	40.10	36.46
Seedling	0.05	13 000	50	1	0.01	29.05	12.5	0.040	0.030	37.36	2.30	0.224	0.139	32.74	36.04	3.48	0.149	0.063	33.94	
Seedling-exp	0.05	13 000	100	1	0.01	31.87	12.5	0.040	0.035	39.41	2.00	0.256	0.170	33.51	37.42	3.30	0.155	0.069	35.40	
Clonal	0.05	13 000	50	10	0.01	37.62	12.5	0.040	0.030	45.91	2.50	0.213	0.127	41.86	45.87	3.46	0.152	0.065	42.79	38.90
Clonal-exp	0.05	13 000	100	10	0.01	35.63	12.6	0.040	0.034	42.64	2.70	0.196	0.109	39.02	42.42	3.53	0.145	0.058	40.49	36.81
Seedling	0.05	26 000	50	1	0.005	19.49	20.0	0.025	0.015	32.68	4.19	0.120	0.036	31.49	32.68	4.19	0.120	0.036	31.49	
Seedling-exp	0.05	26 000	100	1	0.005	28.38	20.0	0.025	0.020	40.82	2.14	0.238	0.151	35.79	38.50	3.35	0.154	0.067	36.86	
Clonal	0.05	26 000	50	10	0.005	29.88	20.0	0.025	0.015	44.17	4.03	0.125	0.041	42.97	44.19	4.03	0.125	0.041	42.99	39.08
Clonal-exp	0.05	26 000	100	10	0.005	36.32	20.1	0.025	0.020	46.99	2.80	0.186	0.100	43.65	46.26	3.52	0.145	0.059	44.30	40.27
Seedling	0.05	26 000	50	1	0.01	31.16	12.5	0.040	0.030	41.20	2.16	0.236	0.150	36.19	39.00	3.30	0.156	0.070	36.68	
Seedling-exp	0.05	26 000	100	1	0.01	33.37	12.5	0.040	0.035	40.54	2.02	0.253	0.166	33.66	39.70	3.31	0.155	0.068	35.62	
Clonal	0.05	26 000	50	10	0.01	40.41	12.5	0.040	0.030	48.97	2.51	0.208	0.122	45.02	47.98	3.43	0.150	0.064	45.58	41.44
Clonal-exp	0.05	26 000	100	10	0.01	40.21	12.6	0.040	0.035	47.93	2.61	0.203	0.115	44.09	47.79	3.39	0.154	0.067	45.57	41.43
Seedling	0.2	13 000	50	1	0.005	32.32	20.0	0.025	0.015	45.22	4.08	0.123	0.039	43.92	45.17	4.07	0.124	0.040	43.85	
Seedling-exp	0.2	13 000	100	1	0.005	39.82	20.1	0.025	0.020	51.43	2.36	0.218	0.131	47.06	48.77	3.40	0.151	0.064	46.62	
Clonal	0.2	13 000	50	10	0.005	41.46	20.0	0.025	0.015	55.51	4.25	0.120	0.036	54.30	55.51	4.25	0.120	0.036	54.30	49.37
Clonal-exp	0.2	13 000	100	10	0.005	43.62	20.1	0.025	0.020	54.24	2.92	0.182	0.095	51.08	54.59	3.46	0.149	0.062	52.51	47.74
Seedling	0.2	13 000	50	1	0.01	43.02	12.5	0.040	0.030	52.84	2.07	0.246	0.159	47.53	51.75	3.26	0.159	0.072	49.33	
Seedling-exp	0.2	13 000	100	1	0.01	43.80	12.6	0.040	0.035	50.88	2.36	0.220	0.133	46.45	49.67	3.54	0.146	0.059	47.70	
Clonal	0.2	13 000	50	10	0.01	50.43	12.5	0.040	0.030	58.80	2.75	0.193	0.107	55.24	57.60	3.54	0.146	0.060	55.60	50.55
Clonal-exp	0.2	13 000	100	10	0.01	46.49	12.7	0.039	0.034	55.93	2.68	0.196	0.108	52.31	55.01	3.36	0.153	0.066	52.82	48.02
Seedling	0.2	26 000	50	1	0.005	34.71	20.0	0.025	0.015	47.97	4.09	0.123	0.039	46.66	47.97	4.09	0.123	0.039	46.66	
Seedling-exp	0.2	26 000	100	1	0.005	42.45	20.1	0.025	0.020	53.71	2.39	0.217	0.130	49.38	52.20	3.51	0.149	0.061	50.15	
Clonal	0.2	26 000	50	10	0.005	45.52	20.0	0.025	0.015	58.03	4.07	0.124	0.040	56.70	58.03	4.07	0.124	0.040	56.70	51.55
Clonal-exp	0.2	26 000	100	10	0.005	48.31	20.0	0.025	0.020	58.89	2.67	0.197	0.111	55.21	58.36	3.55	0.146	0.059	56.38	51.25
Seedling	0.2	26 000	50	1	0.01	44.77	12.5	0.040	0.030	53.73	2.25	0.229	0.143	48.97	51.83	3.36	0.154	0.068	49.55	
Seedling-exp	0.2	26 000	100	1	0.01	47.18	12.6	0.040	0.035	54.39	2.30	0.232	0.145	49.57	53.11	3.35	0.156	0.069	50.82	
Clonal	0.2	26 000	50	10	0.01	53.99	12.5	0.040	0.030	62.43	2.82	0.185	0.099	59.14	61.36	3.37	0.153	0.066	59.16	53.79
Clonal-exp	0.2	26 000	100	10	0.01	50.84	12.6	0.040	0.034	58.61	2.81	0.187	0.100	55.26	57.90	3.47	0.148	0.061	55.87	50.79

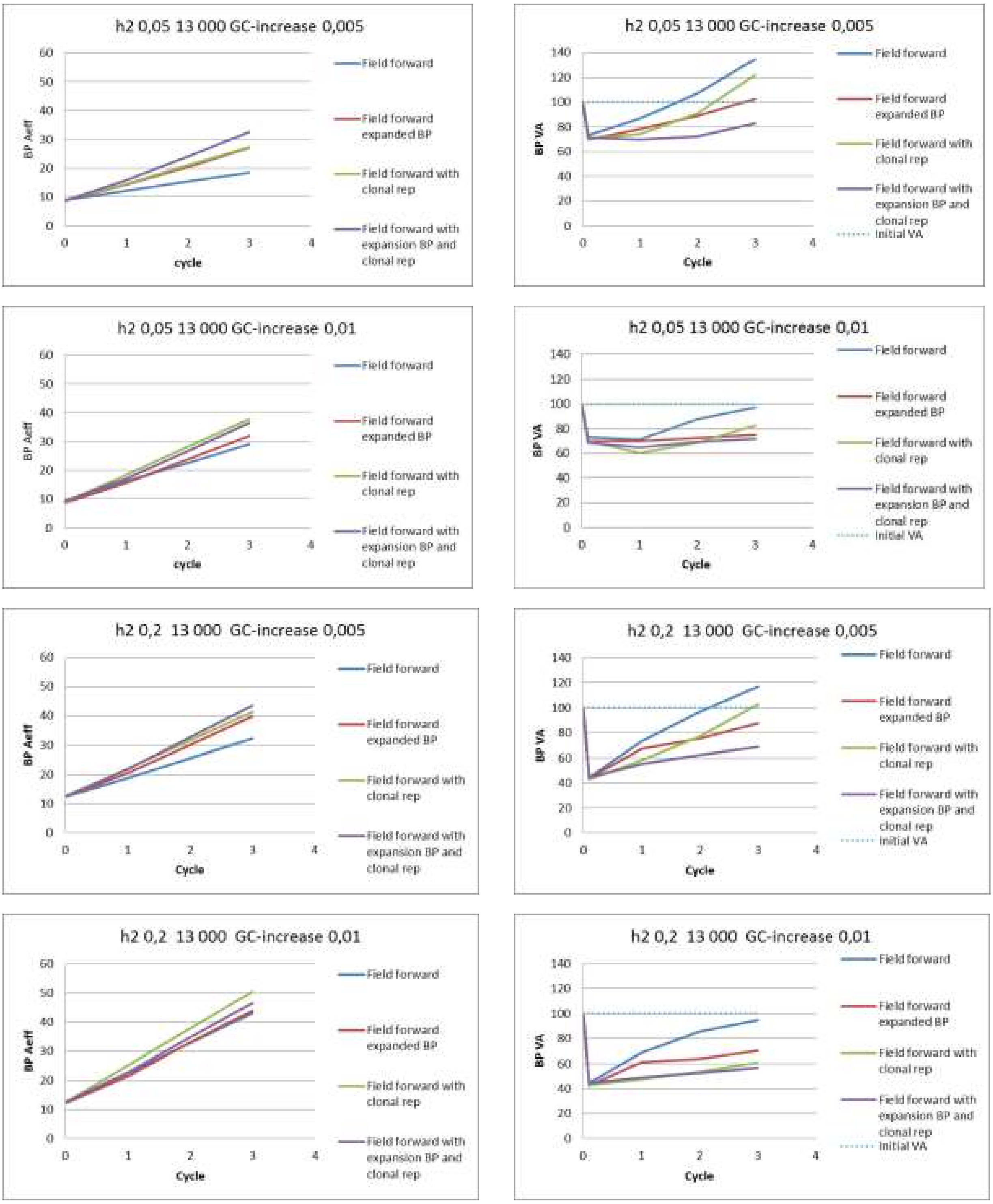

Figure 2a.
Development of BP Aeff and BP V_A over breeding cycles for the four baseline scenarios at resource level 13 000, h^2 = 0.05 and 0.2, and GC-increase 0.005 and 0.01.

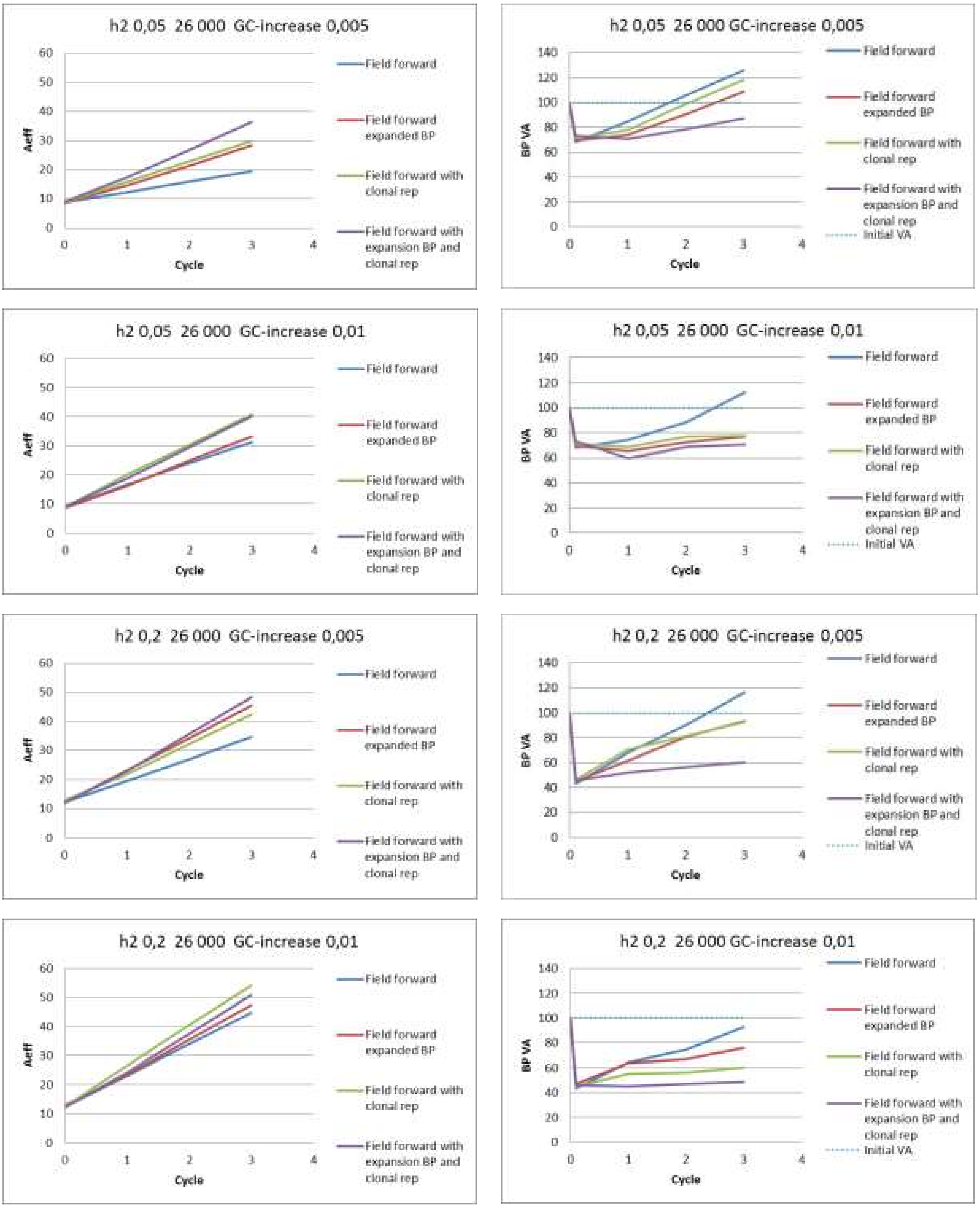

Figure 2b.
Development of BP Aeff and BP V_A over breeding cycles for the four baseline scenarios at resource level 26 000, h^2 = 0.05 and 0.2, and GC-increase 0.005 and 0.01.

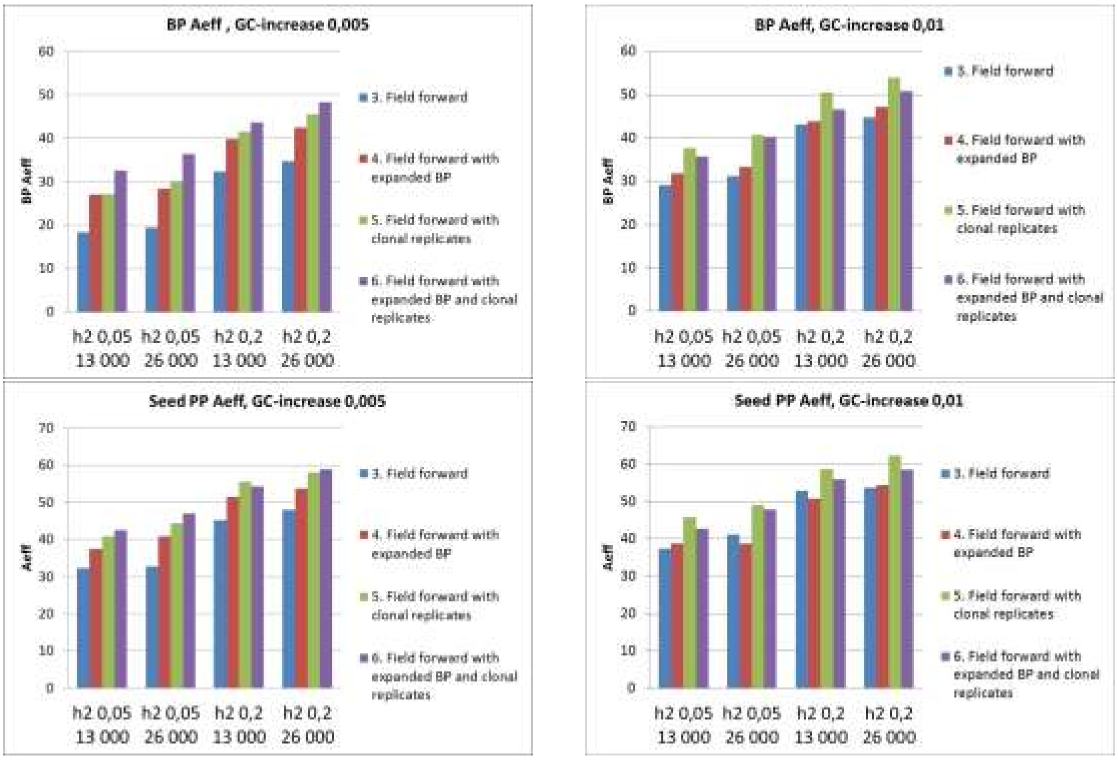

Figure 3.
BP and SeedPP Aeff (6 top trees) for the 4 baseline scenarios at different h^2, resource level and rate of increase in GC.

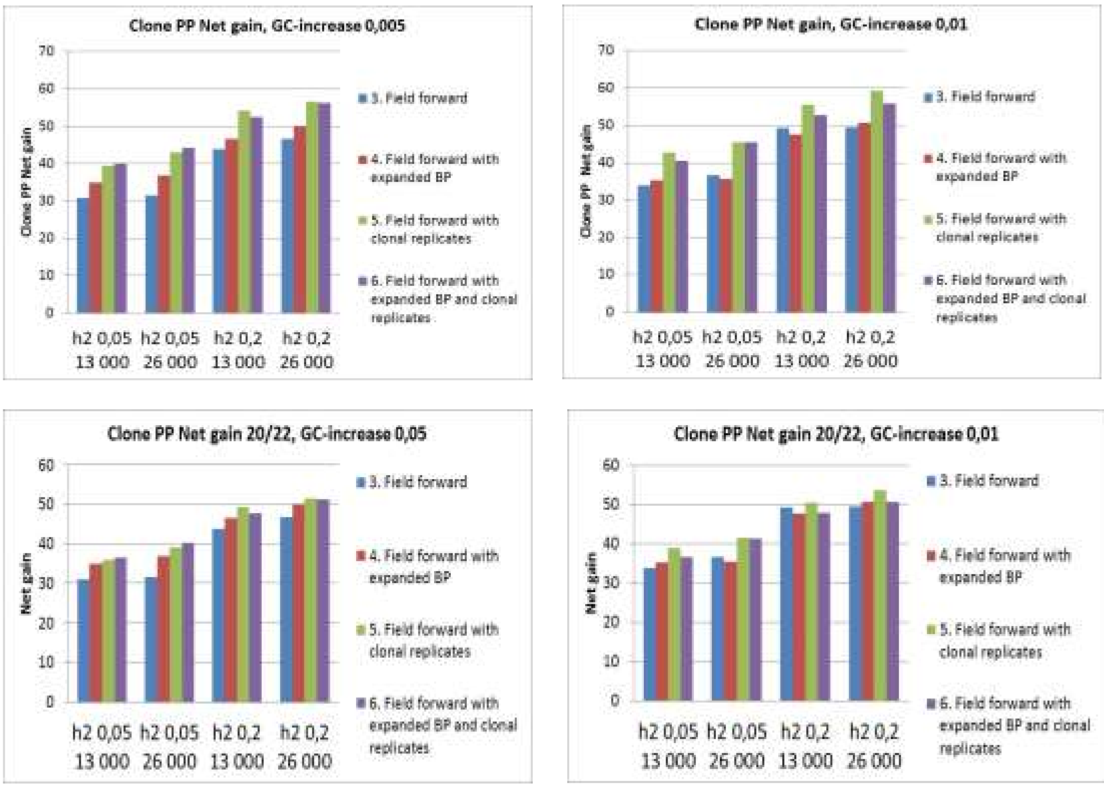

Figure 4.
ClonePP net gain (6 top trees) of the BP selected with restrictions of one per parent for the 4 baseline scenarios at different h^2, resource levels and per cycle increase in GC. The lower two figures are corrected for the 2-year longer cycle time due to clone testing.

BP ADDITIVE VARIANCE AND THE ADDITIONAL GAIN IN PPS

The level of additive variance in the BP (the right portions of Figures 2a and 2b) determines the additional gain possible when selecting a production population within the BP. The V_A of the BP is reduced temporarily by selection (the “Bulmer effect”) and permanently by inbreeding. The Bulmer effect is the result of the selected trees being alike. The effect is temporary as it is counteracted by the recombination of genes in new generations. The importance of inbreeding on variance is insignificant in these scenarios where the inbreeding is low. The Bulmer effect is strong and the initial V_A is already reduced from 100 to 40 in cycle 0, when for all scenarios 50 tested parents are selected from 300 initial founders using progeny testing. This decrease in variance is counteracted by increased among-family variance when crossing in rank order under PAM and by Mendelian sampling. The V_A is therefore partly reestablished both in the recruitment and in the breeding populations.

From the right portions of Figures 2a and b, it is evident that, compared to the effect of PAM under balanced selection (GC constrained to 0.005), the PAM effect is much reduced when restrictions are relaxed with GC increased from 0.005 to 0.01 and when selection is more accurate as for clonal replication. Under expansion, selection is unbalanced also for GC-increase 0.005 and BP V_A will not return to the initial levels of 100 for the 3 cycles of PAM investigated. In general, when relaxing selection restrictions and when expanding the population, the Aeff is increased in the BP, while BP V_A is decreased, giving less “space” for additional gain when selecting the PP subset.

The additional Aeff for the top 6 trees of the BP selected to the SeedPP without restrictions is therefore greatest when the BP is not expanded or when using balanced selection (higher for GC-increase 0.005 than for 0.01) (Figure 5).

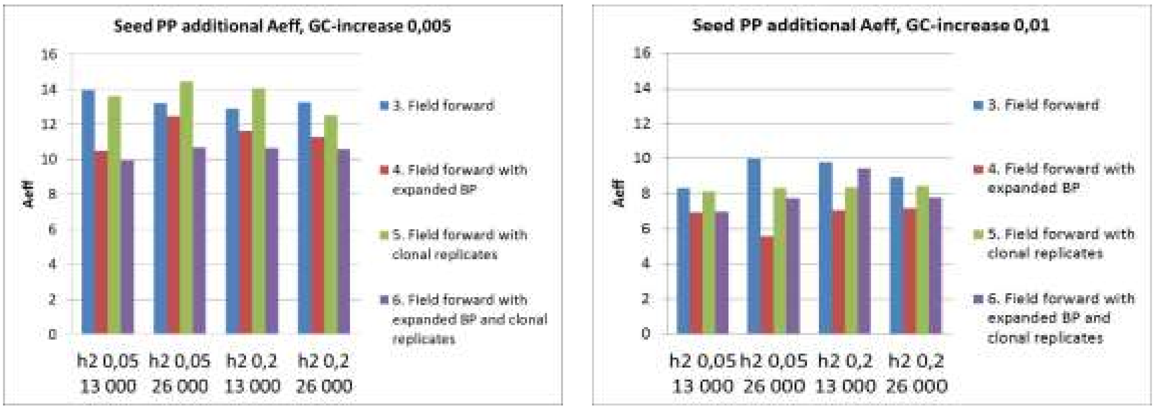

Figure 5.
Additional Aeff from selecting 6 top trees for the SeedPP without restrictions for the 4 baseline scenarios at different h^2, resource levels and N_e.

INCREASE IN PAIR-WISE COANCESTRY

Since group coancestry is controlled when advancing the BP, there is no difference between BP GC of the different strategies; however, GC and pwC differ among the PPs. Under balanced selection (GC-increase 0.005) and no expansion of the BP, the pwC of the 6 SeedPP trees was about 0.04, while for the expanded BP the pwC of the SeedPP was in the range 0.09-0.15 (Figure 6 top part).

When selection restrictions were relaxed (GC-increase 0.01), also the pwC of the SeedPP from the not expanded BP increased. All SeedPP pwC were in the range of 0.10-0.16 (Figure 6 top part). In this case, cloning reduces the increase of pwC. This may be an effect of more accurate estimation of individual breeding values, giving less weight to the family mean and information from other relatives when using BLUP.

Using restrictions when selecting the 6 top trees (ClonePP) reduces the pwC to about 0.06 under all expanded or relaxed conditions (Figure 6 lower part). This corresponds to a reduction of the Aeff from inbreeding depression of 6% which is reduced to 2% in a seed orchard recruited from 3 breeding populations.

In general, at least under the conditions studied to date, the higher Aeff of the top 6 trees if selected without restrictions (SeedPP) compensates for the inbreeding depression loss due to the higher pwC as compared to the more restricted selection giving less Aeff (ClonePP), but also less depression. Therefore, the net gains from both the SeedPP and ClonePP are about the same and the loss in gain due to inbreeding is small, about 0.5 – 2.5 units for an orchard of 18 trees from three populations (Table 3).

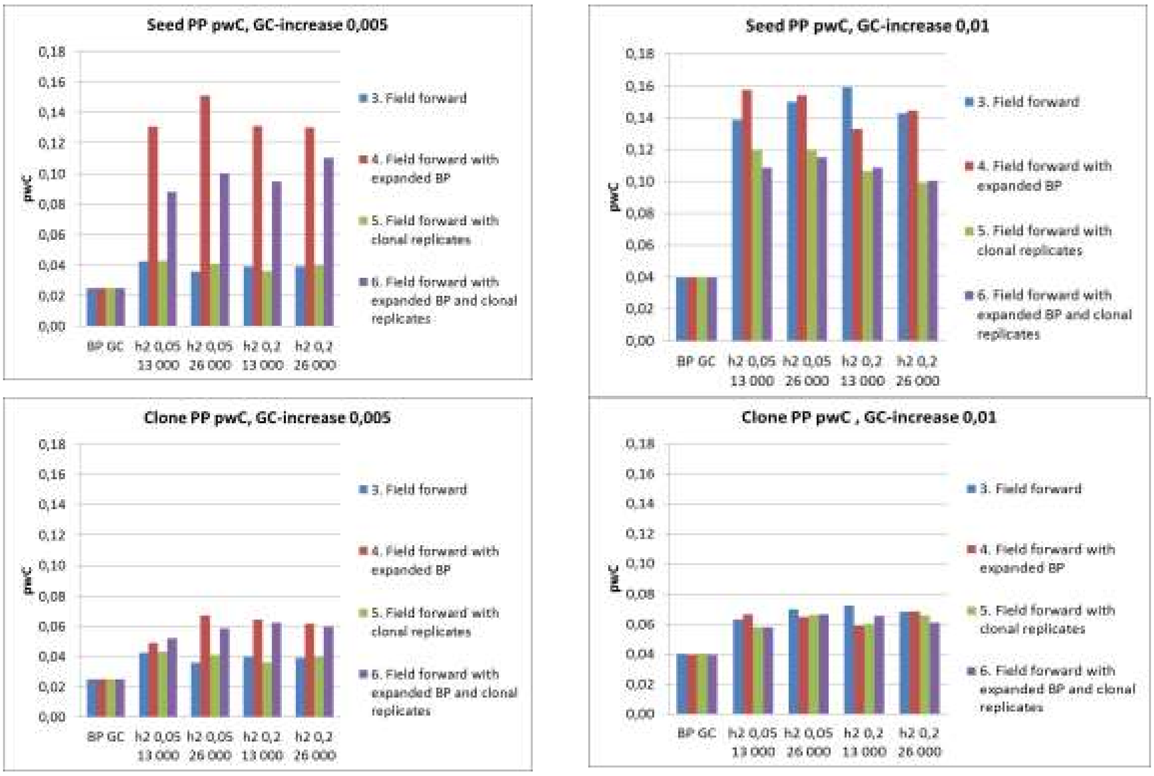

Figure 6.
Seed and ClonePP pwC (6 top trees of the BP selected without and with restrictions) for the 4 baseline scenarios at different h^2, resource levels and N_e.

Discussion

Making more crosses when expanding the BP under constant resource expenditure decreases family size. While this enables among-family selection, it also decreases within-family selection intensity. Using clonal replicates increases selection accuracy, but also decreases selection intensity. Both of these tradeoffs and their interaction when combined will differ in strength depending on conditions such as resource level, heritability and selection constraints on GC. Therefore, no strategy is truly best under all conditions. It would have been good to have even more extreme scenarios, to see where the trends start to deviate.

Expanding the BP to allow for among-family selection and clonally replicated field testing are different approaches to increase the accuracy of selection among sibs in a family. In the case of expansion, this results from the ability to select more than one sib per family, crossing them to form progeny-families, and selecting among these families with greater accuracy. Although there is a small effect of combining the two approaches under fully balanced selection, i.e., GC increase of 0.005 per cycle, for practical and economic reasons these methods should be seen as alternatives. When restrictions are relaxed to a GC increase of 0.01 per cycle, expansion does not give much extra but cloning does, while the effect of both done together is negative. Taking into account the additional two years for cloning and considering net gain, the simple forward selection strategy with no expansion is almost as good as using cloning when GC is relaxed. Of course, the good results obtained by simple forward selection assume that it is possible to produce very large families (say, 200 or more) and apply high selection intensity. If such family sizes can't be reached, then cloning is likely superior.

In summary, under highly restricted selection and low heritability there are substantial effects of expansion or cloning. Practical considerations for crossing and rooting of cuttings will determine the choice between the two strategies. If an increase in GC per cycle of 0.01 is accepted, then clonal testing is the only way to increase the Aeff; the realized gain per year is diminished, due to the 2-year longer cycle time favoring the simple forward selection strategy.

We emphasize that it is the development of an orchard or clone-mix that should determine the choice of breeding strategy. Although the higher Aeff seems to compensate for the increase in pwC from expanding the BP under relaxed constraints on GC, there may be other drawbacks from relatedness that motivate the choice of a strategy with slightly less gain, but also less relatedness. The doubling of GC from 0.02 to 0.04 in the BP and the high pwC among the 6 top trees already after three generations is a concern. It may be that calculating net gain from a seed orchard composed of trees from three different populations made us accept too much relatedness in a single population, which will generate inbreeding, but effects of inbreeding depression have not yet been analyzed in detail.

When deciding the absolute level of acceptable increase in coancestry for these production populations, and the corresponding requirements on the breeding population, there are alternative ways of thinking (see Appendix 1). One could argue that the same rate of loss of diversity would be acceptable in a production population as in the breeding population. One could also argue that there should be no loss of diversity at all over time. In that case the inevitable loss of diversity in a breeding population has to be compensated for by using more and more trees in the production populations.

Another concern is how best to use the lower relatedness that occurs when expanding the BP in cycle 1. Here we have exploited all in one selection step, but an alternative would be to economize the extra room for family selection, perhaps by a gradual relaxation of the constraint on GC over generations.

Finally, we are a bit surprised by the small difference between the two resource levels 13 000 and 26 000 trees and that this did not much effect the difference between strategies. The expectation was that the more demanding strategies of expansion and cloning would benefit more from greater resources than would simple forward selection. Carrying the simulations for additional cycles would likely make differences more apparent.

HOW SHOULD BREEDERS RESPOND?

What should breeders take away from these strategy comparisons, and how should they apply the results to management of actual breeding populations? To some extent, the discussion must be tempered by the desired rate of accumulation of relatedness, or loss of gene diversity.

The original Swedish breeding strategy was formulated around a BP of size 50, with completely balanced mating and selection, corresponding to Ne_V of 100 or an increase of GC with 0.005 per cycle. At this rate of loss of gene diversity, breeders can effectively utilize population expansion to achieve greater gain in seed orchards, at least for traits with h^2 up to 0.2. This suggests that it is advantageous to introduce some imbalance in the mating and selection by increasing the size of breeding populations somewhat over the original target of 50, even while the overall testing effort remains the same.

The above applies when increase of GC is constrained to 0.005, or Ne_V of 100, but the original breeding strategy in Sweden anticipated that this extremely conservative diversity objective could be safely relaxed to Ne_V of 50. Under this relaxed constraint, imbalance in mating and selection is achieved even while maintaining the overall BP at size 50. The imbalance is sufficient to maximize gain above that which would result from an expansion of the BP to size 100.

What we learn is that some imbalance is extremely effective to maximize gain. This can be achieved by applying some relaxation of the diversity constraint, or by some expansion of the BP, or perhaps a combination of the two. It is probably not necessary to relax the diversity constraint or expand the population to the full degree tested in our simulations. Additional simulations with intermediate parameter values will likely find a “sweet spot”.

The question of whether or not to use clonal replication of field testing depends, to some extent, on the h^2 of the target trait. Not surprisingly, cloning is most effective in increasing selection accuracy for traits with low narrow-sense heritability; its efficacy is less for traits having high heritability. This is true regardless of whether or not the breeding population is expanded, even if the effect is larger when testing is constrained to 50 parents and diversity maximized by constraining GC to 0.005 per cycle. If it is not possible to clone material efficiently for testing, the breeder should seriously consider a reduction in the maintained Ne_V, or introducing imbalance by way of expansion, or both. However; if the population is to be maintained for maximum diversity with a minimum number of breeding parents, then it is definitely worth the effort to clonally replicate field testing.

We see from these results that clonally replicated testing and expansion are two different ways to increase selection accuracy with similar improvement of genetic gain. Clonal replication in general gives slightly higher gain, but the difference is small if the longer time required for propagation of cloned material is accounted for. Considering the additional work load, there is little incentive to combine expansion and clone testing.

It should be noticed that the good results from simple forward selection assume that it is possible to produce very large families (say, more than 200 progeny) and apply high selection intensity. If that is a problem and there is just a limited amount of seeds, cloning is more effective. Making many crosses under expansion might add as much time as cloning does, lowering the benefit of expansion. On the other hand making many crosses might simplify reaching the progeny number target when working on selected trees with few flowers per tree.

In general, there was a small effect of increasing test resources at the levels studied. There is always the question of how much effort to invest in breeding and testing a given breeding population. Our simulations suggest that simple field testing and forward selection with seedlings on a modest budget (13 000 trees per cycle) can capture much of the possible gain. Of course investing additional resources can capture some additional gain, but one must be careful to ensure that time lines are not adversely affected in the attempt to complete elaborate crossing or cloning, as anything that lengthens the cycle length has a large negative impact on the gains per year.

On the question of mating, our simulations again suggest that PAM is an effecttive way to broaden additive genetic variance and leads to larger gains in orchards. When inbreeding depression is expected to be a problem in the recruitment population, the simulations suggest that avoiding close relatives during mating can still retain most of the positive impact of PAM. Our scenarios specified that each parent be crossed twice with equal family sizes and that they be assigned mates under something close to PAM, while avoiding close relatives. The algorithm used in POPSIM could be used by operational breeders to automate the planning of such designs, or they can be planned manually by the breeder and adjusted as operational constraints require.

To make recommendations based on the simulations currently available, we would recommend introducing imbalance by relaxing the target rate of accumulation of GC, but perhaps to a level somewhat less than that tested here, perhaps 0.0075 per cycle. Effective and timely cloning is largely a technical issue, but where it is possible and where heritabilities are known to be 0.01 or lower, cloning should be considered as a way to increase selection accuracy.

FUTURE STUDIES

It is still of interest to fulfill the initial plan of analyzing three levels of all conditions listed in in Table 1, some 576 scenarios, as well as running more than 25 iterations to improve precision of the mean results. It would also help to see the big picture if the simulations were to be continued for additional cycles. While three cycles is sufficient to establish most trends, these are too few to determine the difference in rate of genetic progress and to follow the increase in additive variance (V_A) over cycles due to PAM (Figure 2a and 2b). We suggest running at least five cycles and analyze the differences in rate among scenarios, not just for accumulation of gain in the BP, but also for net gain of an orchard.

Investigating the effect of single-pair mating (SPM), 3-pair mating, random assortment of mates (RAM) and the effect of inbreeding depression (ID) would give a better understanding of the results. We also suggest to incorporate OPSEL for selecting the 6 PP trees at a pre-set value of coancestry to generate results that are comparable; this latter suggestion requires a small modification to POPSIM's orchard selection routine, to incorporate OPSEL's optimization of seed-orchard contributions (Ahlinder et al., 2014).

In particular, it will be of value to broaden our simulations to the case where the rate of increase in GC is 0.0075 per cycle (Ne_V). It would also be of interest to compare Lindgren's truly balanced grand-parent model (Lindgren et al. 2008) with expanding the BP to 100 (compared to a non-expanded BP of size 50) and rate of increase in GC of 0.005; both can achieve the same Ne_V, but the expanded BP is not completely balanced. It is the structure of relatedness among the elite trees that is of special interest. For similar reasons, it is of interest to study the 3:2:1 mating design, which generates unbalanced mating combined with balanced selection and could be used as an alternative to using OPSEL. Earlier studies have shown its advantage when accounting for inbreeding depression (Rosvall et al., 2003).

To further study suitable strategies for handling diversity in the production populations, one suggestion is to investigate an increase in group coancestry and associated pwC at the level of genetic drift of the BP (balanced selection and GC-increase 0.005) or to allow for the same increase as is allowed when forwarding the BP. These suggestions are based on the idea that allelic diversity *per se* measured by GD or N_s is of little value, rather it is the net gain (Aeff-inbreeding depression) that counts.

Another suggestion is to investigate the consequences of keeping a constant level of diversity by compensating for the losses due to drift under the balanced selection cases, or drift and selection under unbalanced selection cases. If we start with Lindgren's suggestion of N_s = 16 for an orchard (Lindgren and Prescher, 2005), this level could be maintained in a BP of size 50 under balanced selection for about 4 breeding cycles (maximum N_s of the BP after 5 cycles of breeding is 14). At this point all trees used in the orchard can originate from one BP, but in the next cycle one has to add trees from another BP. It could be quite "politically correct" to show that the GD of seed orchards can be conserved without compromise forever; however, the consequences should be studied before making such a promise.

We started to investigate the effect of varying resources among selected BP trees in terms of progeny size depending on parent breeding value (Lstibůrek et al. 2005). The idea is to vary selection intensity to increase gain in the top-ranking part of the BP, without any effect on diversity. This can also be accomplished by using the 3:2:1 mating design to generate more crosses among the best trees and increase selection intensity, while maintaining the effective size by using OPSEL for restricted selection (Appendix 6). There are a several additional simulations to be done to do a complete analysis of this scheme.

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Appendix 1.

Net gains in production populations as evaluation criteria

INTRODUCTION

One of the basic concepts of the Swedish breeding strategy is to conserve both allelic diversity and additive variance in the breeding population, allowing for intense selection within the breeding population (BP) for seed orchards or other production populations. This is achieved by combining highly balanced selection and positive assortative mating (PAM). The top trees in the BP will have much more gain and will be just slightly more related than average. While balanced selection keeps relatedness at its lowest level, corresponding to the inevitable increase of group coancestry (GC) by genetic drift, we expect that some imbalance will be beneficial.

The constraint on relatedness is relaxed by allowing a larger increase of GC per cycle. In this way, more full-sibs (and half sibs) are selected in the highest-ranking families and fewer (or none) in the low-ranking ones. While the top-ranking trees of the BP can include a number of full and half-sibs, this relatedness should be considered when selecting a seed orchard.

One of the objectives of this investigation of breeding strategies is to examine the consequences of easing the restriction on relatedness in order to increase the mean additive effect (Aeff) of the BP. One consequence is that the additive variance (V_A) of the BP will be reduced, resulting in less additional Aeff when selecting the very best trees. These trees will also be more related, causing a possible reduction in gain by inbreeding depression in the seed crop of the orchard. On the other hand, avoiding close relatedness (inbreeding depression) by selecting lower-ranked tress will also reduce the Aeff. One has to find a way to understand these conflicting trends and to optimize the trade-off between gain and diversity.

We suggest that a breeding strategy should be evaluated in terms of how it can provide the best gain in production populations. By comparing the results of the alternative ways POPSIM selects PPs, we can learn much about the structure of the top members of the BP.

METHOD

We selected two alternative seed orchards during our simulation. The first was a seed-orchard production population (SeedPP) selected without restrictions, reporting the additive effect (Aeff), GC and pair-wise coancestry (pwC) for the very top 6 trees of the BP. A second alternative utilized POPSIM's clone mixture options (ClonePP) to select 6 genotypes, applying the hardest restrictions possible, i.e., allowing a maximum of one progeny genotype per parent. If gain is about the same for these 6 trees selected in different ways, there must be little relatedness among the top trees in the ranking list. If gain is reduced, there is more relatedness in the top and the less-related trees are found further down the ranking list. For their use in production orchards, we assumed that the 6 selections would be part of an 18-parent orchard, together with selections from 2 additional breeding populations, 3 BPs in total.

While recurrent selection will accumulate gain, it will also accumulate relatedness among orchard selections that could lead to a reduction is gain due to inbreeding depression. To calculate Net Gain (NG) from orchards, we assume that selfing will not produce viable seed, so we apply a reduction in the Aeff for the rate of inbreeding depression (b) only on the average pairwise coancestry (pwC) of the orchard parents; thus, NG = Aeff – b(pwC). From the literature, we expect that selfing (where F = 0.5) in Scots pine will produce progeny with about 50% less production than outcrosses (Lundkvist et al. 1987), so for a trait with mean 100 (as in our simulations here), we might find the progeny from selfing produce only 50, so the rate of depression per unit F is 50/0.5 = 100, and the reduction due to inbreeding depression is –100 × pwC.

Applying this correction to the selected 6 trees and to the 18-tree orchard assembled from 3 BPs, we have:

NG6 (6 seed orchard trees of one BP) = Aeff6 –100 × pwC6.

NG18 (18 seed orchard trees from 3 BP) = Aeff6 –100 × pwC6/3.

RESULTS

Net gains for 4 of the 32 scenarios at the high resource level (26 000) and h2 = 0.2 are given in (Table 1-1), including expansion of the BP from 50 to 100 at a rates of increase of GC per cycle of 0.005 and 0.01. When GC increases at a rate of 0.005, the pwC for the BP of size 50 and for the expanded BP of 100, are about 0.02 and 0.025, respectively. The top 6 trees in the SeedPP of the unexpanded and expanded BPs had pwC of 0.05 and 0.15, respectively, and pwC in the ClonePP as 0.05 and 0.08, respectively. When GC increases at the rate of 0.01, the pwC of the BP 50 and 100 both reached to about 0.04, as well as both SeedPPs and ClonePPs reaching 0.16 and 0.08, respectively, corresponding to levels of F of about 0.05 and 0.025, respectively, for 18 trees from 3 BPs.

The additional gain from selecting the top 6 trees of the BP is greatest for the case of balanced selection in the BP of 50, where GC increased at 0.05 per cycle. In general, expanding the BP and/or using the weaker constraint on GC at 0.01 per cycle results in greater Aeff, but the additional gain in the PP is less. The additional gain is further reduced when inbreeding depression is considered by calculating net gain.

In no case was there a shift in rank among strategies by comparing net gain rather than Aeff. Expanding the BP to 100 with GC increasing at 0.01 per cycle gives both the highest Aeff and the highest net gain, but in this case there is a shift between which PP to choose. In general, if inbreeding depression is not considered, the SeedPP Aeff is greater than that of the ClonePP, reflecting the more restrictive selection of the latter. When inbreeding depression is accounted for, the differences between the SeedPP of 18 trees and the ClonePP are very small. The decrease in Aeff by selecting more unrelated trees in the SeedPP compared to the ClonePP is roughly compensated for by less depression.

When considering mating only among the 6 trees from a single BP, depression becomes greater and the ClonePP generally produces more net gain than the SeedPP, the exception being the balanced case when BP is of size 50 and GC increasing at 0.05 per cycle, where they are equal.

Table 1-2 illustrates the increase in pwC over cycles for the PPs that vary from 0.006 to 0.021, while it is 0.005 or 0.01 in the BP. The large variation is due to the small sample size and would decrease with more iterations (currently 25). One can also observe the larger increase in pwC in cycle 1 for the BP, as a consequence of the greater increase in GC in this cycle due to expansion to keep the GC following the same development over time.

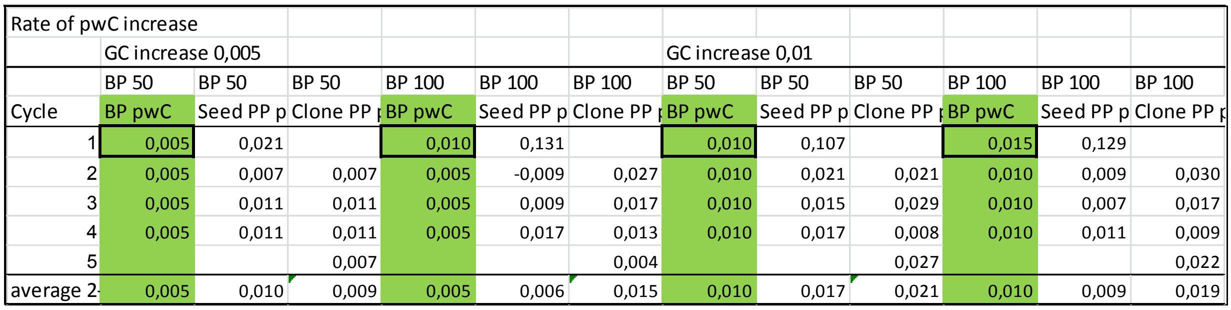
Figure 1-1 illustrates how quickly relationship accumulates among the top 6 trees (SeedPP) when the selection restrictions are relaxed, either by expanding the BP or by increasing the rate of increase in GC. There is, however, a moderate long-term increase after the big jump in in the first cycle. The long-term rate of increase for the pwC is not much faster than the rate of increase of the GC and pwC in the BP.

Table 1-1.
Net gain calculated by reducing Aeff due to inbreeding depression[1]. The pwC of the 6 trees is divided by 3, representing a final seed orchard of 18 trees from 3 unrelated BPs. In the green columns, the pwC of the 6 trees is used to calculate inbreeding depression and net gain for the case of using only these 6 trees in an orchard.

				BP					Seed orchard								Clone mix								Clone mix-Seed orch	
Resource	GC increas	BP size					Effect of expansion				Net gain		Additional gain		Effect of expansion				Net gain		Additional gain		Effect of expansion		Net gain	
			Cycle	Aeff	pwC	Net gain	Aeff	Net gain	Aeff	pwC	18 trees	6 trees	Aeff	Net gain 1	Aeff	Net gain 1	Aeff	pwC	18 trees	6 trees	Aeff	Net gain 1	Aeff	Net gain 18	18 trees	6 trees
26 000	0,005	BP 50	0	12,38	0,0000	12,38			20,15	0,0000	20,15	20,15	7,77	7,77												
			1	18,87	0,0050	18,37			28,28	0,0214	27,57	26,14	9,41	9,20			28,28	0,0214	27,57	26,14	9,41	9,20			0,00	0,00
			2	25,54	0,0100	24,55			37,07	0,0283	36,12	34,24	11,52	11,58			37,07	0,0283	36,12	34,24	11,52	11,58			0,00	0,00
			3	32,32	0,0149	30,82			45,22	0,0391	43,92	41,31	12,91	13,09			45,17	0,0396	43,85	41,21	12,85	13,02			-0,07	-0,11
			4	38,96	0,0198	36,98			53,97	0,0504	52,29	48,93	15,01	15,31			53,97	0,0504	52,29	48,93	15,01	15,31			0,00	0,00
																	63,30	0,0576	61,38	57,54						
		BP 100	0	12,40	0,0000	12,40			19,75	0,0000	19,75	19,75	7,34	7,34												
			1	20,52	0,0100	19,52			28,98	0,1308	24,61	15,89	8,45	5,09			26,48	0,0208	25,79	24,40	5,96	6,27			1,17	8,51
			2	30,23	0,0149	28,73			40,23	0,1217	36,18	28,07	10,01	7,45			38,38	0,0479	36,79	33,59	8,16	8,06			0,61	5,52
			3	39,82	0,0198	37,84			51,43	0,1311	47,06	38,32	11,61	9,22			48,77	0,0644	46,62	42,33	8,95	8,78			-0,43	4,01
			4	49,27	0,0247	46,80	10,31	9,82	61,73	0,1483	56,79	46,90	12,46	9,99	7,76	4,50	59,18	0,0774	56,60	51,44	9,90	9,79	5,21	4,31	-0,19	4,54
																	69,49	0,0812	66,78	61,37						
	0,1	BP 50	0	12,35	0,0000	12,35			19,02	0,0000	19,02	19,02	6,68	6,68												
			1	23,08	0,0100	22,08			29,77	0,1072	26,20	19,05	6,69	4,12			27,82	0,0181	27,22	26,01	4,74	5,13			1,02	6,96
			2	33,98	0,0200	31,98			41,52	0,1279	37,26	28,73	7,55	5,28			40,56	0,0390	39,26	36,66	6,58	7,28			2,00	7,92
			3	44,77	0,0297	41,80			53,73	0,1428	48,97	39,45	8,95	7,16			51,83	0,0682	49,55	45,01	7,05	7,75			0,59	5,56
			4	55,94	0,0395	51,98			66,19	0,1596	60,87	50,23	10,25	8,88			63,93	0,0764	61,38	56,29	7,99	9,40			0,52	6,06
																	74,97	0,1033	71,52	64,64						
		BP 100	0	12,98	0,0000	12,98			20,89	0,0000	20,89	20,89	7,91	7,91												
			1	23,41	0,0149	21,92			32,16	0,1286	27,88	19,30	8,76	5,96			29,70	0,0222	28,96	27,48	6,29	7,03			1,08	8,17
			2	35,47	0,0249	32,98			43,57	0,1374	38,99	29,83	8,10	6,01			40,80	0,0517	39,07	35,62	5,33	6,09			0,08	5,79
			3	47,18	0,0346	43,72			54,39	0,1447	49,57	39,92	7,21	5,85			53,11	0,0686	50,82	46,25	5,93	7,10			1,25	6,33
			4	58,79	0,0445	54,34	2,85	2,36	67,61	0,1558	62,42	52,03	8,82	8,08	1,43	1,55	66,06	0,0772	63,48	58,34	7,27	9,15	2,13	2,10	1,07	6,31

[1] using pwC = *F*, and inbreeding depression being -1 per 0.01 *F*.

Table 1-2.
Per-cycle rate of increase for pwC in the BP and PPs. The average does not include the jump in cycle 1 and will therefore represent the long-term increase.



Rate of pwC increase												
	GC increase 0,005						GC increase 0,01					
	BP 50	BP 50	BP 50	BP 100	BP 100	BP 100	BP 50	BP 50	BP 50	BP 100	BP 100	BP 100
Cycle	BP pwC	Seed PP p	Clone PP	BP pwC	Seed PP p	Clone PP	BP pwC	Seed PP p	Clone PP	BP pwC	Seed PP p	Clone PP
1	0,005	0,021		0,010	0,131		0,010	0,107		0,015	0,129	
2	0,005	0,007	0,007	0,005	-0,009	0,027	0,010	0,021	0,021	0,010	0,009	0,030
3	0,005	0,011	0,011	0,005	0,009	0,017	0,010	0,015	0,029	0,010	0,007	0,017
4	0,005	0,011	0,011	0,005	0,017	0,013	0,010	0,017	0,008	0,010	0,011	0,009
5			0,007			0,004			0,027			0,022
average 2	0,005	0,010	0,009	0,005	0,006	0,015	0,010	0,017	0,021	0,010	0,009	0,019

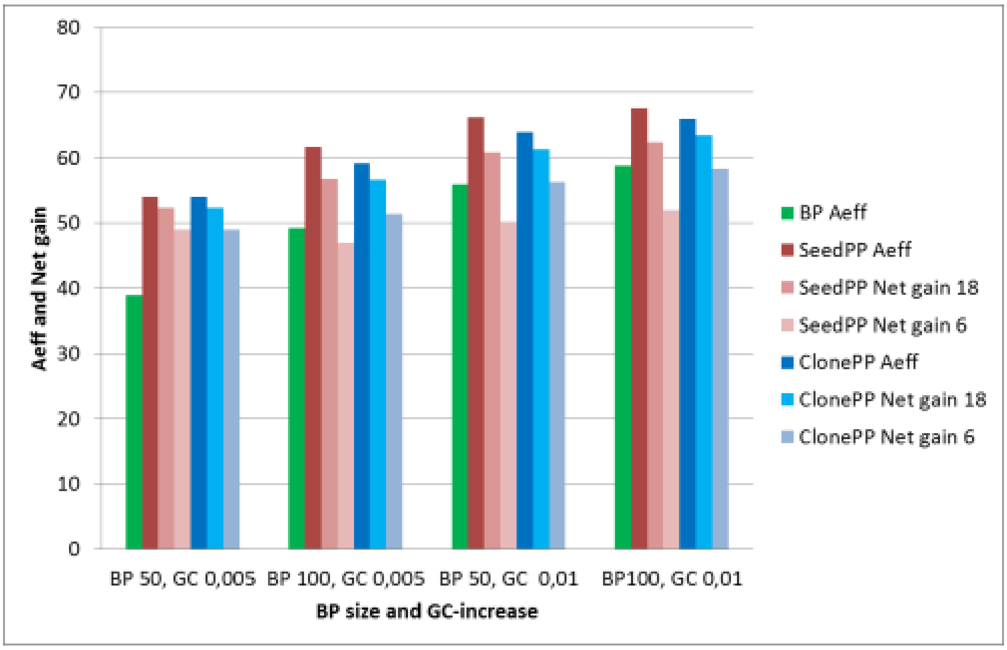
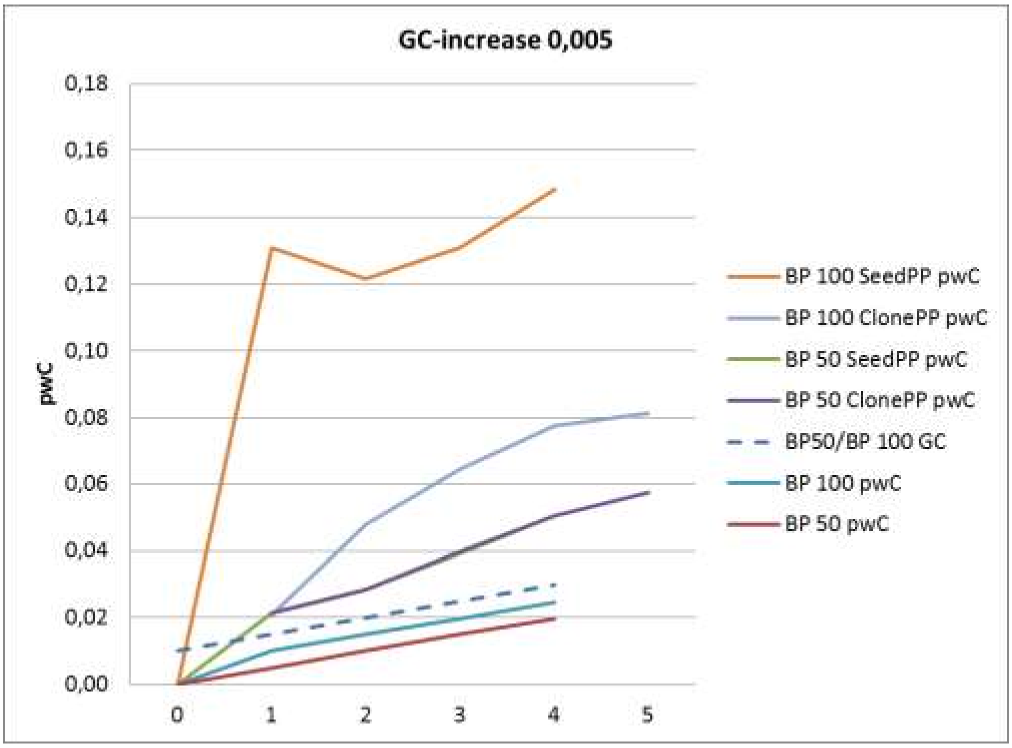


Figure 1-1.
Aeff in the BP and PP, and corresponding PP net gain for BP of size 50 and expanded to 100, with GC increasing at 0.005 and 0.01 per cycle.



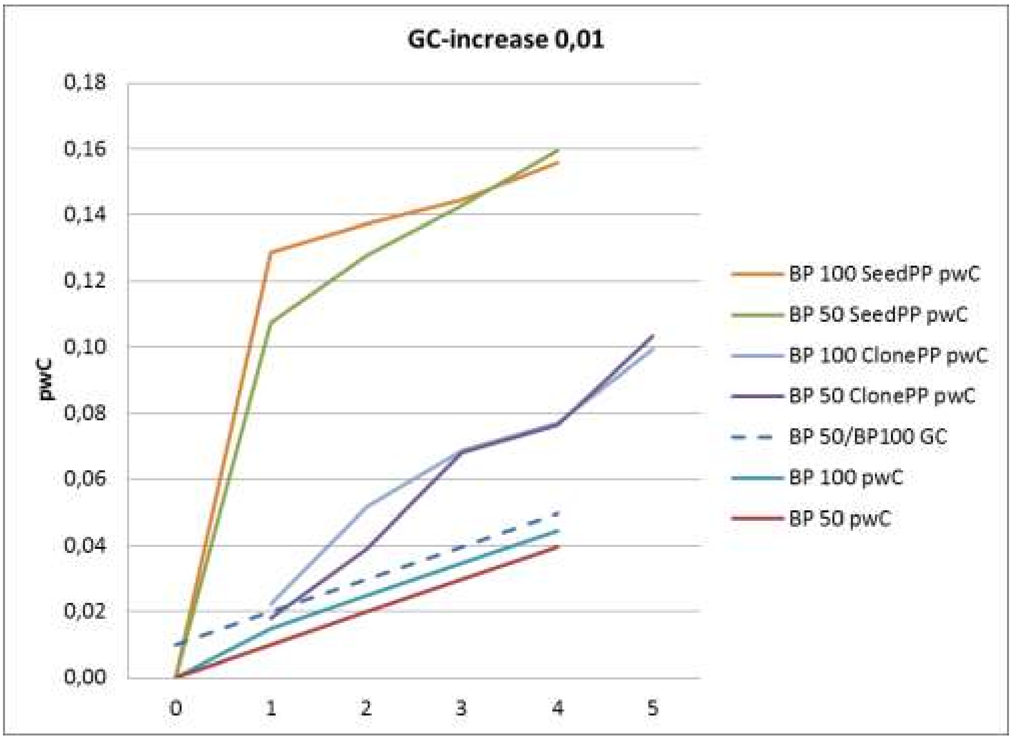


Figure 1-2.
Development over cycles for GC in the BP and pairwise coancestry (pwC) of the BP and PPs, with and without expansion of the BP (size 50 and 100) and two rates of increase in GC (0.005 and 0.01 per cycle). The SeedPP is the 6 top-ranked trees of the BP, while the ClonePP is 6 top trees avoiding common parents.

DISCUSSION

While using net gain as one way to incorporate the effect of increased relatedness in the evaluation, this is likely a “worst-case” outcome. There might be a danger in trying to predict the behaviour of a gamete pool during mating and fertilization, when there are various ways that the frequency of less-fit zygotes can be reduced.

Since we assume that the top trees are used together with other unrelated groups of trees, the pwC is reduced and the inbreeding depression becomes less pronounced. Nevertheless, by using net gain in the analysis, we can account conservatively for unforeseen problems due to close relatedness.

Comparing the 6 trees selected with different restrictions (SeedPP and ClonePP) helps to understand the trade-off between gain and diversity; however, the way selection is restricted is crude and the 6 trees from different strategies will differ in diversity, complicating the comparison. It will be useful to incorporate OPSEL for selecting the 6 PP trees at a pre-set value of coancestry so that results will be comparable.

When using OPSEL in our simulations or in real life, one must decide on an acceptable level of coancestry in the PP. For a managed single forest stand there is generally a lower requirement for genetic diversity in terms allele-carrying capacity and adaptive genetic variance, than there is for a truly sustainable breeding population (or all stands across a landscape). These single stand-level requirements are easily met. It is the reduction in heterozygosity due to inbreeding and the resulting inbreeding depression that is the limiting factor for a forest stand. In spite of not knowing how selection against inbreeding depression take place, it is the pwC of the orchard trees that can best be used to estimate possible depression from relatedness.

When GC increases at a rate of 0.005, the pwC for the BP of size 50 and for the expanded BP of 100, are about 0.02 and 0.025, respectively. The top 6 trees in the SeedPP of the unexpanded and expanded BPs had pwC of 0.05 and 0.15, respectively, and pwC in the ClonePP as 0.05 and 0.08, respectively. When GC increases at the rate of 0.01, the pwC of the BP 50 and 100 both reached to about 0.04, as well as both SeedPPs and ClonePPs reaching 0.16 and 0.08, respectively, corresponding to levels of F of about 0.05 and 0.025, respectively, for 18 trees from 3 BPs.

The level of inbreeding was discussed for the case of seedling seed orchards by Rosvall and Lindgren (2012). Using 5-10 unrelated full-sib families (10-20 parents) gave pwC in the range of 0.025 to 0.05. That interval may be acceptable. In our study here, the lowest-possible pwC in cycle 4 for all 50 trees with balanced selection (rate of GC increase of 0.005 per cycle) in an unexpanded BP of size 50 is 0.02, and for the 6 best trees is 0.05. Taking 18 trees from 3 BPs would reduce the pwC in the orchard to 1/3 = about 0.02. Assuming a 1 unit reduction per 0.01 units of F, this inbreeding depression will reduce gain by about 2%. At the 0.01 rate of GC increase per cycle, the BP pwC is 0.04 and in the 6 top trees pwC in the SeedPP and ClonePP is 0.16 and 0.08, respectively, if selection is restricted. For 18 trees from 3 BPs, this corresponds to F about 0.05 or 0.025 reducing gain by about 5 or 2.5 %, respectively.

If relatedness among the top trees is found to be too great, there may be alternatives to avoid selecting too many trees from the same family. Under DPM, the short list of candidates used by OPSEL can be reduced from the 5 used in our study to maximize BP gain, to perhaps only 2 or 3 per family. Using the 3:2:1 mating scheme and a low increase in GC may enhance gain by increased selection intensity without increasing relatedness among the best trees (has to be studied more). Restricting on grandparents will have a large effect. To better understand what is happening in the first cycle when expanding might crucial.

Appendix 2.

Truncation of candidate list for OPSEL

INTRODUCTION

The short list of candidates used by OPSEL is prepared by POPSIM, including only the best full-sibs from each cross (NBPFS). Generally, the shorter the list, the faster will OPSEL confirm an optimum solution. The minimum number is set by the required number of full-sibs to be selected in the very best families to reach the desired diversity.

The greatest diversity is obtained through balanced selection. In general, for double-pair mating, balanced selection is achieved by selecting exactly 1 per family. Thus for unbalanced selection 2 or more per family are needed for the short list. When expanding the BP from 50 to 100 parents in cycle one, there must be more than 2 per family in the short list to allow unbalanced selection, as the expansion itself requires 2 selections be crossed to be fully balanced.

METHOD

We first conducted preliminary simulations comparing short lists composed of the best 2, 3, 4 and 5 full-sibs per family for BP size 50 and for expansion factor of 2, giving BP size 100 after cycle 1. Resource size, increase in GC per cycle and h^2 were fixed at 26 000, 0.01, and 0.2, respectively, while numbers of ramets used for field testing were 1 and 10. A total of 16 scenarios were required to cover all combinations of these factors. In Appendix 3, the analysis was expanded also considering net gain.

RESULTS

The development over cycles of BP N_s is shown in (Table 2-1), while that for GC over cycles and per cycle is given in (Table 2-2 and Figure 2-1), and that for A-eff in (Table 2-3 and Figure 2-2). The development of SeedPP N_s and GC is given in (Tables 2-4 and 2-5), respectively.

For a constant BP size of 50 using simple forward selection and a GC constraint of 0.01 per cycle, identical results were achieved for all sizes of short lists, regardless of whether truncation included the best 2 or the best 5 per cross, thus a short list of 2 per family totaling 100 trees to select the 50 best was enough. When expanding the BP size 50 to 100, a short list of 5 trees per family or 250 trees is required to achieve the same increase in GC.

Allowing a GC-increase of 0.01 for BP size 50 resulted in BP $N_s = 25$ in cycle 1, as compared to $N_s = 40$ for the expanded BP if the truncation list allowed just 2 selections per family (Table 2-1). This room between N_s 40 and 25 generated by expansion requires selecting up to 5 full-sibs per family.

At $h^2 = 0.2$, it is evident that the constant BP of size 50 always produces more gain than expanding the BP to 100, and cloning is always beneficial at both BP sizes (Table 2-3).

DISCUSSION

Balanced selection (1 per family) for BP size 50 would result in BP N_s = 33 in cycle 1 (not shown) as compared to BP N_s = 25 for BP size 50 and BP N_s = 40 when expanding BP size to 100, allowing 2 selections per family (Table 2-1). Up to 5 full-sibs are selected (at least in the first cycle) when the BP is expanded to reach the diversity target (0.01 per cycle, N_s = 25 in the first cycle). In both cases the structure of the BP results in close relatedness among the 6 top ranking trees, as seen for the SeedPP (Tables 2-4 and 2-5). It seems that a GC increase of 0.0075 rather than 0.01 would be of interest for further study.

Table 2-1.
Development of BP Ns over cycles.

	BP Ns															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	50,00	50,00	50,00	50,00	50,00	50,00	50,00	50,00	50,00	50,00	50,00	50,00	50,00	50,00	50,00	50,00
1	25,11	25,18	40,00	40,00	25,03	25,02	31,71	32,79	25,07	25,02	26,21	27,80	25,03	25,04	25,16	25,45
2	16,75	16,78	24,31	25,05	16,69	16,70	17,15	17,83	16,70	16,68	16,79	16,91	16,68	16,69	16,75	16,80
3	12,57	12,62	16,30	16,39	12,52	12,54	12,67	12,89	12,52	12,53	12,61	12,65	12,54	12,52	12,59	12,64
4	10,06	10,09	11,98	12,30	10,01	10,05	10,12	10,20	10,03	10,05	10,09	10,14	10,02	10,03	10,06	10,12

Table 2-2.
Total and per cycle BP increase in GC over cycles.

	BP GC															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	1
0	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	
1	0,020	0,020	0,012	0,012	0,020	0,020	0,016	0,015	0,020	0,020	0,019	0,018	0,020	0,020	0,020	
2	0,030	0,030	0,021	0,020	0,030	0,030	0,029	0,028	0,030	0,030	0,030	0,030	0,030	0,030	0,030	
3	0,040	0,040	0,031	0,031	0,040	0,040	0,039	0,039	0,040	0,040	0,040	0,040	0,040	0,040	0,040	
4	0,050	0,050	0,042	0,041	0,050	0,050	0,049	0,049	0,050	0,050	0,050	0,049	0,050	0,050	0,050	
	Increase															
0 t 1	0,010	0,010	0,002	0,002	0,010	0,010	0,006	0,005	0,010	0,010	0,009	0,008	0,010	0,010	0,010	
1 t 2	0,010	0,010	0,008	0,007	0,010	0,010	0,013	0,013	0,010	0,010	0,011	0,012	0,010	0,010	0,010	
2 t 3	0,010	0,010	0,010	0,011	0,010	0,010	0,010	0,011	0,010	0,010	0,010	0,010	0,010	0,010	0,010	
3 t 4	0,010	0,010	0,011	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	0,010	

Table 2-3.
BP A-eff over cycles.

	BP Aeff															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	12,35	12,40	12,98	12,17	12,35	12,40	12,98	12,17	12,35	12,40	12,98	12,17	12,35	12,40	12,98	12,17
1	22,68	26,53	19,48	20,80	23,17	26,66	21,91	22,98	22,87	26,55	23,01	23,76	23,08	26,55	23,41	24,20
2	33,42	40,31	31,15	34,50	33,87	40,51	34,33	36,85	34,21	40,46	34,87	37,35	33,98	40,48	35,47	37,61
3	44,20	54,04	42,32	47,99	44,76	54,11	45,93	50,24	45,11	54,10	46,51	50,67	44,77	53,99	47,18	50,84
4	54,75	67,05	53,15	60,79	55,63	66,98	57,43	62,99	56,06	67,44	57,90	63,56	55,94	67,19	58,79	63,77

Table 2-4.
SeedPP (6 BP top trees) Ns over cycles.

	Seed PP Ns															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00
1	3,51	3,71	3,45	3,86	2,91	3,48	2,93	3,44	2,78	3,38	2,69	3,31	2,71	3,26	2,47	3,25
2	3,17	3,31	3,14	3,54	2,71	3,04	2,67	3,28	2,47	2,98	2,47	3,10	2,47	3,07	2,36	3,20
3	3,10	3,01	2,92	3,05	2,60	2,71	2,64	2,97	2,33	2,93	2,36	2,92	2,25	2,82	2,30	2,81
4	2,76	2,78	2,68	3,10	2,38	2,41	2,31	2,70	2,13	2,37	2,11	2,59	2,10	2,24	2,16	2,58

Table 2-5.
SeedPP (6 BP top trees) GC over cycles.

	Seed PP GC															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	0,08	0,08	0,08	0,08	0,08	0,08	0,08	0,08	0,08	0,08	0,08	0,08	0,08	0,08	0,08	0,08
1	0,15	0,14	0,15	0,13	0,18	0,15	0,18	0,15	0,18	0,16	0,19	0,16	0,19	0,16	0,21	0,17
2	0,16	0,16	0,16	0,15	0,19	0,17	0,19	0,16	0,21	0,17	0,21	0,17	0,21	0,17	0,22	0,16
3	0,16	0,17	0,17	0,17	0,20	0,19	0,20	0,18	0,22	0,18	0,22	0,18	0,23	0,19	0,23	0,19
3	0,19	0,19	0,19	0,16	0,22	0,22	0,22	0,20	0,24	0,22	0,25	0,21	0,25	0,23	0,24	0,21

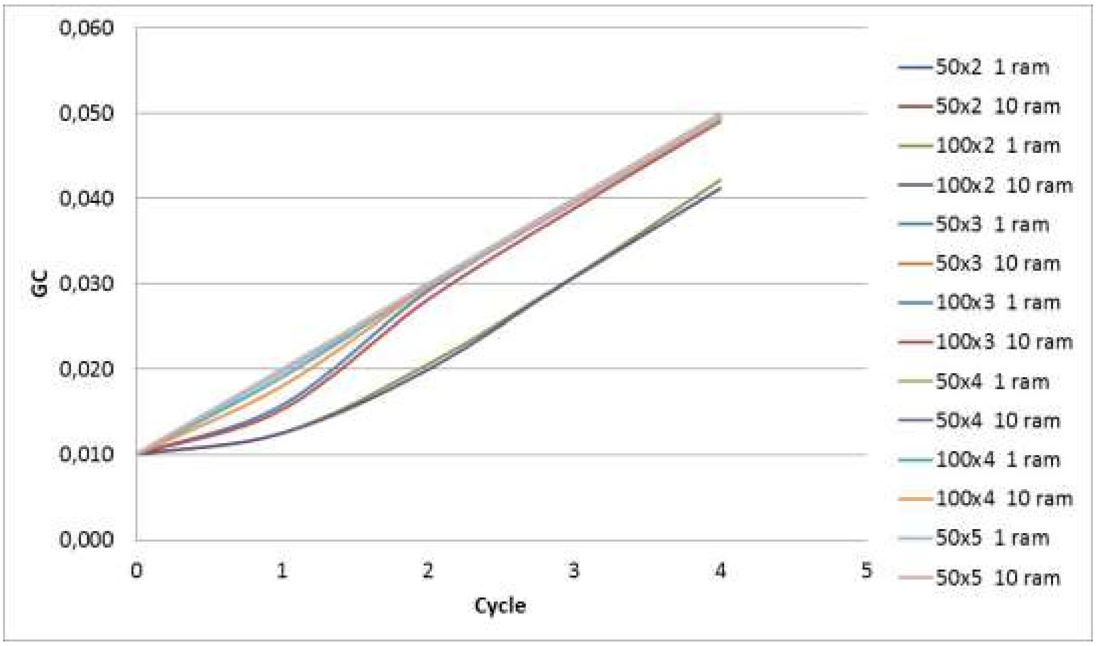


Figure 2-1.
BP GC over cycles.

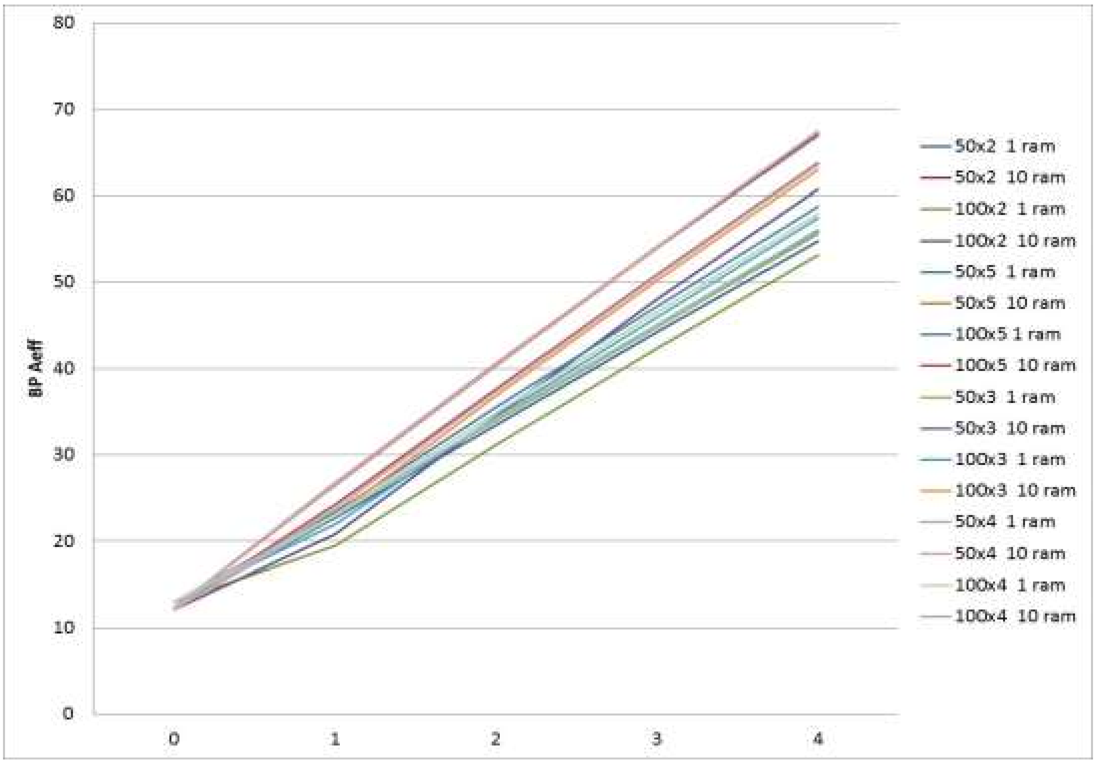


Figure 2-2.
BP A-eff over cycles.

Appendix 3.

Effect of list truncation on PP diversity and Net gain

INTRODUCTION

Gain in the BP is increased by easing restrictions on relatedness so that more selections are made in the high-ranked families and less in the low-ranked, resulting in more relatedness among the top trees. These can be full-sibs and half-sibs. Increased relatedness results in loss of diversity and greater inbreeding depression. In this case, there is a risk that too much gain will be lost when additional restrictions are applied to reduce inbreeding when selecting a seed orchard. This might change the rank order of breeding strategies. The issue of net gain in this is section is later dealt with also for other runs and presented in Appendix 1: BP and PP Aeff and net gain as evaluation criteria.

METHODS

We used two options in POPSIM to select orchards to understand the structure among the top trees in the BP. The SeedPP was selected without restrictions on relatedness and represents the very top 6-trees subset from the BP. The selection of the 6-tree for the ClonePP was restricted to one per parent.

Both the SeedPP and ClonePP were selected using BLUP-predicted breeding values; the Aeff should therefore be comparable. The ClonePP comes from the F_{n+1} generation of the BP and can be compared using its F_n-generation results.

Assuming no selfing in the seed orchard and otherwise random mating, the pair-wise coancestry (pwC) of the orchard trees becomes the inbreeding of the seed progeny. Often, the inbreeding coefficient F is directly translated to inbreeding depression in percent, i.e., F of 0.05 correspond to 5 % reduction of gain. This is presented here to give an understanding of what effects relatedness involve. F in the BP also reduces additive variance by $1-F$.

RESULTS

PP N_s, PP GC and PP pwC are presented in (Tables 3-1, 3-2 and 3-3), respectively. The increase over cycles of PP pwC is given in (Figure 3-1). The additional gain from the SeedPP over the ClonePP is shown in (Table 3-4).

Step-by-step lengthening of the truncated short list (2, 3, 4 or 5 per family) results in selection of more and more sibs from the best families, making the top 6 trees of PPs increasingly related. Except for the balanced case (exactly 2 per family), the least relatedness was found for the expanded BP 100 and cloning (Tables 3-1 and 3-2). In general, cloning increases h^2 and the BLUP values are less influenced by the family mean (and other relatives) and more by the individual information, so that trees are selected from more families.

The highest ClonePP N_s (lowest GC) was found when using the shorter short-lists (2 candidates per family), but the largest increase compared to N_s of the SeedPP was from longer short lists (4 or 5 candidates per family) (Tables 3-2 and 3-3). The greatest increase was also found when the recruitment population was not cloned. The increase in GC by 0.07 for 4 and 5 candidates per family can be compared to the per-cycle increase for all BPs, which was 0.01, resulting in BP N_s = 0.05 in cycle 4.

The restrictions on selecting 6 trees to the ClonePP (one per parent) decreased pwC in cycle 4 to 0.06-0.08 in the ClonePP, compared to 0.10-0.15 in the SeedPP (Table 3-3). The increase of pwC over cycles is faster for the PP than for the BP, and faster for the SeedPP than the ClonePP, which develops at a lower level (Figure 3-1 and data not shown).

The 6 top trees forming the SeedPP have on average about 10 units additional gain over the BP average, at best reaching 75 (Table 3-4). With restrictions on relatedness among the 6 trees, as shown by the ClonePP, the additional gain is about 8, only 2 units lower.

The greatest gain in the SeedPP and ClonePP was for the unexpanded BP 50 with cloning. Except for the balanced expanded BP of size 100, the greatest increase for the SeedPP gain over the average BP gain is for the unexpanded BP of size 50 without cloning. This tendency is less obvious for the ClonePP (Table 3-4).

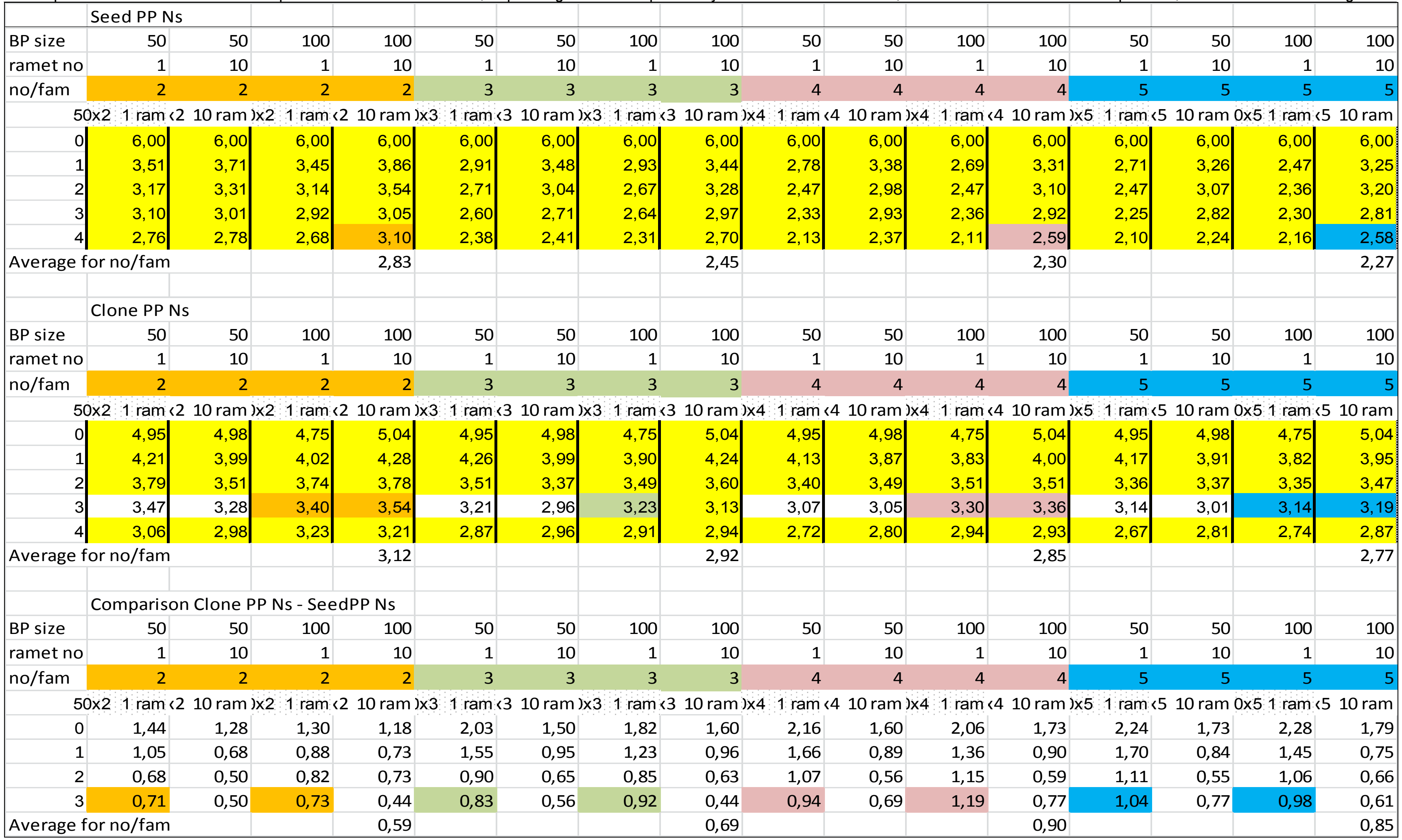
The difference between the gain in the SeedPP and ClonePP is large (2–3 units) for the BP of size 50 without cloning, and small (only 0.1 – 0.7) for the BP of size 50 with cloning. It is intermediate (1 unit) for the expanded BP of size 100 (Table 3-4).

DISCUSSION

In conclusion, the restrictions used when selecting the best 6 trees in the ClonePP result in a substantial decrease of relatedness from GC 0.18 – 0.23 down to 0.15 – 0.17, with little reduction in gain. The pair-wise coancestry of the SeedPP is 0.10-0.15 and for the ClonePP is 0.06 – 0.08. This corresponds to the expected inbreeding in the progeny corresponding to an inbreeding depression reducing gain by 6 to 8%. It is obvious that it is possible to decrease relatedness among selections without much loss of gain. We have a feeling that pwC of the 6 trees is at the upper end of what is acceptable, i.e., decreasing from N_{eV} 100 to N_{eV} 50 might be too much. Using a per-cycle increase of 0.075 instead of 0.01 reaching N_{eV} 75 might be better, even if a stronger restriction than using one per family, as was used here, might give a more suitable PP diversity.

Table 3-1.

Development of N_s in the SeedPP compared to that in the ClonePP, depending on number per family in the candidate shortlist, under different levels of BP expansion, with and without cloning.

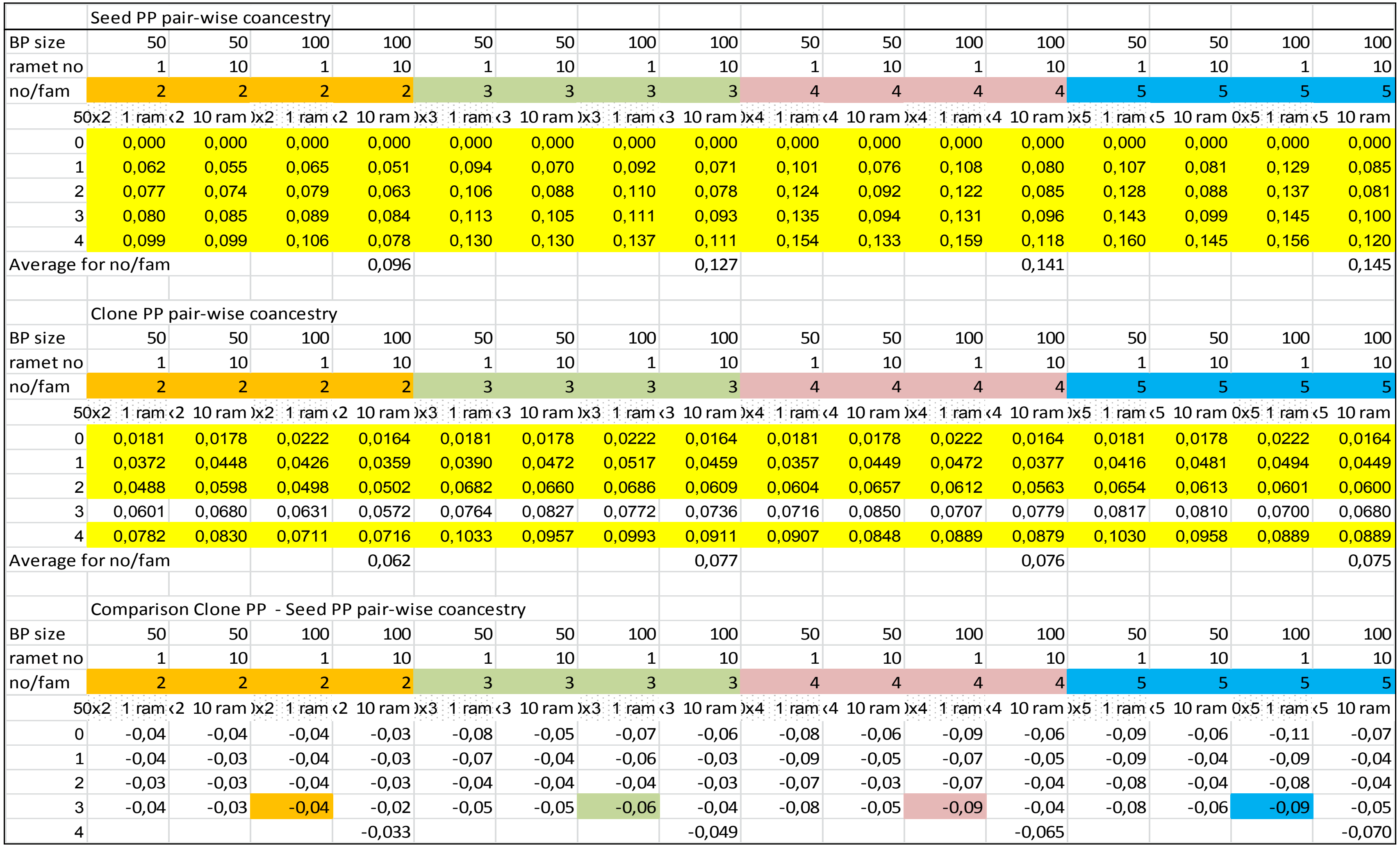


	Seed PP Ns															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00	6,00
1	3,51	3,71	3,45	3,86	2,91	3,48	2,93	3,44	2,78	3,38	2,69	3,31	2,71	3,26	2,47	3,25
2	3,17	3,31	3,14	3,54	2,71	3,04	2,67	3,28	2,47	2,98	2,47	3,10	2,47	3,07	2,36	3,20
3	3,10	3,01	2,92	3,05	2,60	2,71	2,64	2,97	2,33	2,93	2,36	2,92	2,25	2,82	2,30	2,81
4	2,76	2,78	2,68	3,10	2,38	2,41	2,31	2,70	2,13	2,37	2,11	2,59	2,10	2,24	2,16	2,58
Average for no/fam				2,83				2,45				2,30				2,27
	Clone PP Ns															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	4,95	4,98	4,75	5,04	4,95	4,98	4,75	5,04	4,95	4,98	4,75	5,04	4,95	4,98	4,75	5,04
1	4,21	3,99	4,02	4,28	4,26	3,99	3,90	4,24	4,13	3,87	3,83	4,00	4,17	3,91	3,82	3,95
2	3,79	3,51	3,74	3,78	3,51	3,37	3,49	3,60	3,40	3,49	3,51	3,51	3,36	3,37	3,35	3,47
3	3,47	3,28	3,40	3,54	3,21	2,96	3,23	3,13	3,07	3,05	3,30	3,36	3,14	3,01	3,14	3,19
4	3,06	2,98	3,23	3,21	2,87	2,96	2,91	2,94	2,72	2,80	2,94	2,93	2,67	2,81	2,74	2,87
Average for no/fam				3,12				2,92				2,85				2,77
	Comparison Clone PP Ns - SeedPP Ns															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	1,44	1,28	1,30	1,18	2,03	1,50	1,82	1,60	2,16	1,60	2,06	1,73	2,24	1,73	2,28	1,79
1	1,05	0,68	0,88	0,73	1,55	0,95	1,23	0,96	1,66	0,89	1,36	0,90	1,70	0,84	1,45	0,75
2	0,68	0,50	0,82	0,73	0,90	0,65	0,85	0,63	1,07	0,56	1,15	0,59	1,11	0,55	1,06	0,66
3	0,71	0,50	0,73	0,44	0,83	0,56	0,92	0,44	0,94	0,69	1,19	0,77	1,04	0,77	0,98	0,61
Average for no/fam				0,59				0,69				0,90				0,85

Table 3-2.
Development of GC in the SeedPP compared to that in the ClonePP, depending on number per family in the candidate shortlist, under different levels of BP expansion, with and without cloning.

	Seed PP GC															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	0,083	0,083	0,083	0,083	0,083	0,083	0,083	0,083	0,083	0,083	0,083	0,083	0,083	0,083	0,083	0,083
1	0,145	0,139	0,149	0,134	0,177	0,154	0,176	0,155	0,184	0,159	0,191	0,163	0,191	0,164	0,212	0,169
2	0,161	0,158	0,162	0,146	0,189	0,172	0,193	0,161	0,207	0,175	0,206	0,169	0,211	0,172	0,221	0,165
3	0,165	0,172	0,174	0,170	0,199	0,191	0,198	0,179	0,221	0,181	0,219	0,183	0,229	0,185	0,232	0,187
3	0,186	0,186	0,193	0,165	0,217	0,218	0,225	0,199	0,242	0,221	0,246	0,206	0,248	0,234	0,244	0,208
Average for no/fam				0,183				0,215				0,229				0,234
	Clone PP GC															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	0,101	0,101	0,106	0,100	0,101	0,101	0,106	0,100	0,101	0,101	0,106	0,100	0,101	0,101	0,106	0,100
1	0,121	0,128	0,126	0,119	0,119	0,128	0,131	0,121	0,125	0,131	0,133	0,128	0,122	0,130	0,135	0,129
2	0,134	0,146	0,135	0,136	0,146	0,152	0,148	0,142	0,151	0,148	0,147	0,147	0,154	0,153	0,156	0,148
3	0,147	0,155	0,150	0,144	0,159	0,173	0,159	0,166	0,170	0,169	0,158	0,156	0,164	0,171	0,165	0,162
4	0,166	0,171	0,159	0,159	0,180	0,174	0,179	0,178	0,193	0,185	0,178	0,178	0,193	0,185	0,189	0,181
Average for no/fam				0,149				0,164				0,163				0,166
	Comparison Clone PP GC - Seed PP GC															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	-0,04	-0,04	-0,04	-0,03	-0,08	-0,05	-0,07	-0,05	-0,08	-0,06	-0,09	-0,06	-0,09	-0,06	-0,11	-0,07
1	-0,04	-0,03	-0,04	-0,03	-0,07	-0,04	-0,06	-0,04	-0,08	-0,04	-0,07	-0,04	-0,09	-0,04	-0,09	-0,04
2	-0,03	-0,03	-0,04	-0,03	-0,05	-0,04	-0,05	-0,04	-0,07	-0,03	-0,07	-0,04	-0,07	-0,03	-0,08	-0,04
3	-0,04	-0,03	-0,04	-0,02	-0,06	-0,04	-0,07	-0,03	-0,07	-0,05	-0,09	-0,05	-0,08	-0,06	-0,08	-0,05
4				-0,034				-0,051				-0,066				-0,068

Table 3-3.
Development of pair-wise coancestry in the SeedPP compared to that in the ClonePP, depending on number per family in the candidate shortlist, under different levels of BP expansion, with and without cloning



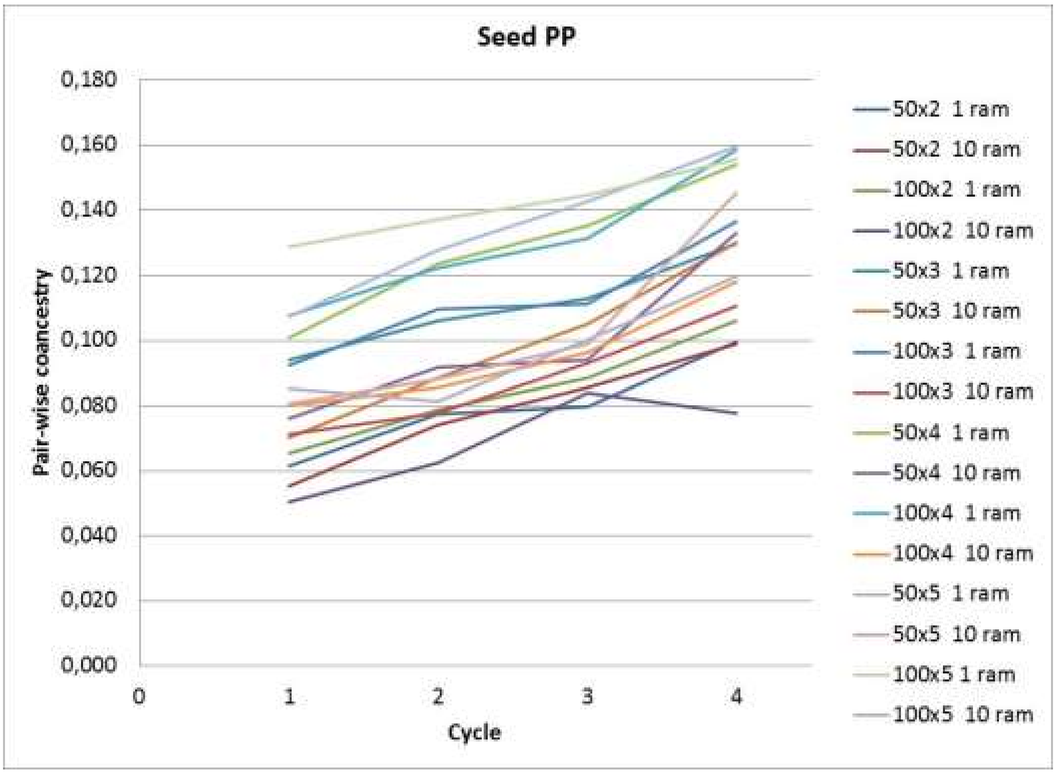
	Seed PP pair-wise coancestry															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
1	0,062	0,055	0,065	0,051	0,094	0,070	0,092	0,071	0,101	0,076	0,108	0,080	0,107	0,081	0,129	0,085
2	0,077	0,074	0,079	0,063	0,106	0,088	0,110	0,078	0,124	0,092	0,122	0,085	0,128	0,088	0,137	0,081
3	0,080	0,085	0,089	0,084	0,113	0,105	0,111	0,093	0,135	0,094	0,131	0,096	0,143	0,099	0,145	0,100
4	0,099	0,099	0,106	0,078	0,130	0,130	0,137	0,111	0,154	0,133	0,159	0,118	0,160	0,145	0,156	0,120
Average for no/fam				0,096				0,127				0,141				0,145
	Clone PP pair-wise coancestry															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	0,0181	0,0178	0,0222	0,0164	0,0181	0,0178	0,0222	0,0164	0,0181	0,0178	0,0222	0,0164	0,0181	0,0178	0,0222	0,0164
1	0,0372	0,0448	0,0426	0,0359	0,0390	0,0472	0,0517	0,0459	0,0357	0,0449	0,0472	0,0377	0,0416	0,0481	0,0494	0,0449
2	0,0488	0,0598	0,0498	0,0502	0,0682	0,0660	0,0686	0,0609	0,0604	0,0657	0,0612	0,0563	0,0654	0,0613	0,0601	0,0600
3	0,0601	0,0680	0,0631	0,0572	0,0764	0,0827	0,0772	0,0736	0,0716	0,0850	0,0707	0,0779	0,0817	0,0810	0,0700	0,0680
4	0,0782	0,0830	0,0711	0,0716	0,1033	0,0957	0,0993	0,0911	0,0907	0,0848	0,0889	0,0879	0,1030	0,0958	0,0889	0,0889
Average for no/fam				0,062				0,077				0,076				0,075
	Comparison Clone PP - Seed PP pair-wise coancestry															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	-0,04	-0,04	-0,04	-0,03	-0,08	-0,05	-0,07	-0,06	-0,08	-0,06	-0,09	-0,06	-0,09	-0,06	-0,11	-0,07
1	-0,04	-0,03	-0,04	-0,03	-0,07	-0,04	-0,06	-0,03	-0,09	-0,05	-0,07	-0,05	-0,09	-0,04	-0,09	-0,04
2	-0,03	-0,03	-0,04	-0,03	-0,04	-0,04	-0,04	-0,03	-0,07	-0,03	-0,07	-0,04	-0,08	-0,04	-0,08	-0,04
3	-0,04	-0,03	-0,04	-0,02	-0,05	-0,05	-0,06	-0,04	-0,08	-0,05	-0,09	-0,04	-0,08	-0,06	-0,09	-0,05
4				-0,033				-0,049				-0,065				-0,070

Table3-4.
Additional gain over the BP in the SeedPP compared to that in the ClonePP, depending on number per family in the candidate shortlist, under different levels of BP expansion, with and without cloning.

	SeedPP Aeff - BP Aeff															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0	6,68	7,52	7,91	8,31	6,68	7,52	7,91	8,31	6,68	7,52	7,91	8,31	6,68	7,52	7,91	8,31
1	6,75	7,89	11,65	11,41	7,09	8,23	9,80	9,51	7,24	8,47	9,07	8,77	6,69	8,67	8,76	8,60
2	6,65	7,30	9,38	10,55	7,74	7,69	7,50	8,40	7,60	7,28	7,03	8,42	7,55	7,20	8,10	8,28
3	6,31	7,86	9,30	9,53	8,23	8,19	7,96	8,52	9,65	7,49	8,37	8,33	8,95	8,45	7,21	7,77
4	8,12	7,80	9,09	10,19	9,58	8,27	8,57	8,57	12,01	8,11	8,37	8,59	10,25	8,55	8,82	9,29

	ClonePP Aeff - BP Aeff															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0																
1	5,14	6,52	10,22	10,08	4,65	6,39	7,79	7,90	4,95	6,50	6,69	7,12	4,74	6,50	6,29	6,69
2	6,44	6,73	7,67	9,46	5,78	7,04	6,70	7,95	5,91	6,49	5,52	7,36	6,58	6,38	5,33	7,75
3	6,13	7,42	8,16	9,08	7,33	7,08	6,13	8,22	8,64	7,35	4,91	7,95	7,05	7,38	5,93	7,06
4	6,12	7,67	8,19	9,14	7,67	7,88	6,85	7,92	8,90	7,87	7,11	7,27	7,99	7,85	7,27	8,27

	SeedPP Aeff - ClonePP Aeff															
BP size	50	50	100	100	50	50	100	100	50	50	100	100	50	50	100	100
ramet no	1	10	1	10	1	10	1	10	1	10	1	10	1	10	1	10
no/fam	2	2	2	2	3	3	3	3	4	4	4	4	5	5	5	5
50x2	1 ram ‹2	10 ram)x2	1 ram ‹2	10 ram)x3	1 ram ‹3	10 ram)x3	1 ram ‹3	10 ram)x4	1 ram ‹4	10 ram)x4	1 ram ‹4	10 ram)x5	1 ram ‹5	10 ram 0x5	1 ram ‹5	10 ram
0																
1	1,62	1,37	1,43	1,33	2,44	1,85	2,02	1,61	2,29	1,97	2,38	1,65	1,95	2,17	2,47	1,91
2	0,21	0,57	1,71	1,09	1,96	0,64	0,80	0,46	1,69	0,79	1,52	1,07	0,97	0,82	2,77	0,53
3	0,18	0,44	1,14	0,45	0,90	1,12	1,83	0,31	1,01	0,15	3,46	0,38	1,90	1,07	1,28	0,71
4	2,00	0,13	0,90	1,05	1,91	0,39	1,72	0,65	3,11	0,25	1,26	1,32	2,26	0,70	1,56	1,02



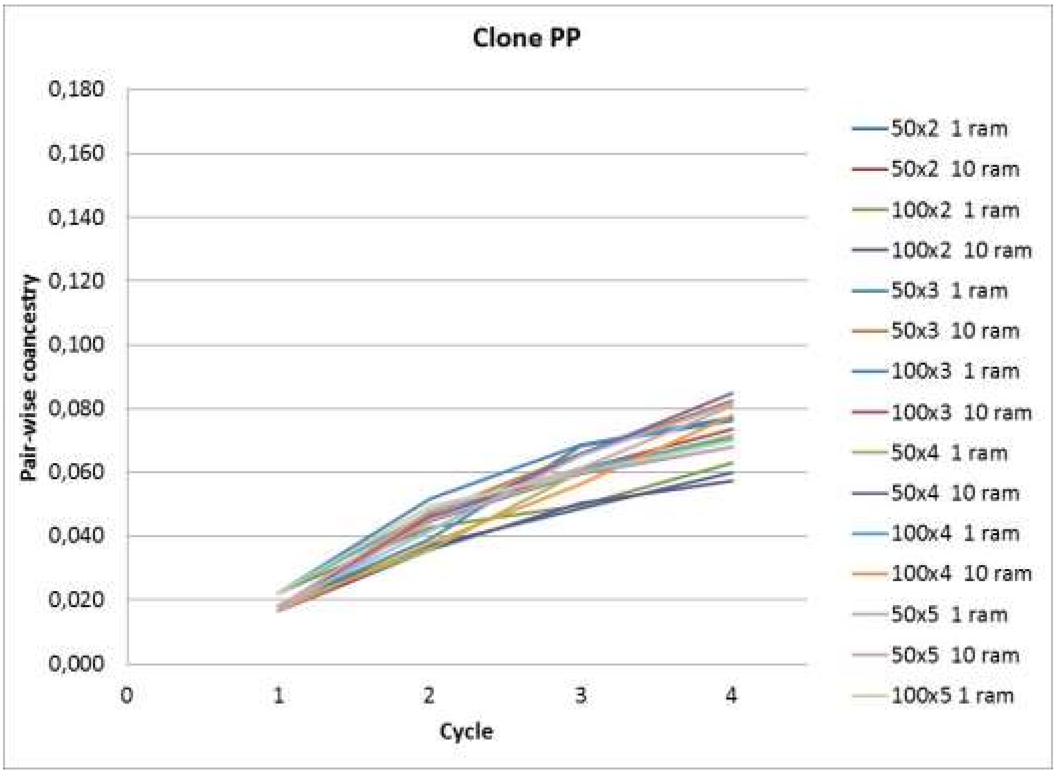


Figure 3-1.
Increase of pair-wise coancestry in the SeedPP and ClonePP over cycles (This figure involve much random variation and more runs are needed).

Appendix 4.

Expansion of the breeding population

INTRODUCTION

A greater expansion of the BP generates a larger decrease in GC and greater diversity space for selection, but it also generates a lower mean additive effect (Aeff) due to lower selection intensity. To check the earlier finding that the best results were obtained by doubling the BP using an expansion factor PSF 2, we compared different rates of expansion, allowing for comparisons among BPs expanded to 100, 150 and 200, with the unexpanded case of BP of size 50.

RESULTS

A longer candidate shortlist is needed for the more expanded case with BP 200 than with BP 100 which used 5 candidates per family (Table 4-1 and Figure 4-1). If GC increases at the rate of 0.005 per cycle, we require a shortlist with the best 7 trees per family, while increasing GC at 0.01 per cycle requires 10 candidates per family in the short-list. Cycle 1 is critical for dimensioning. There is little effect on gain by lengthening the short list and there is a little compensation in cycle 2 by the loss in cycle 1 for short short-lists. There is no increase in gain by the greater expansion as compared to BP expanded to 100.

Table 4-1.
The effect of the length of the short list for OPSEL selection on Aeff after 3 cycles of breeding for a BP expanded from 50 to 200 at two levels of GC-increase 0,005 and 0,01.

	GC-increase	
Short list Trees per family	0.005	0.01
5	42.08	44.34
6	42.09	44.72
7	42.18	45.34
8	42.57	
9	42.57	45.94
10	42.78	46.04
15	42.92	45.80

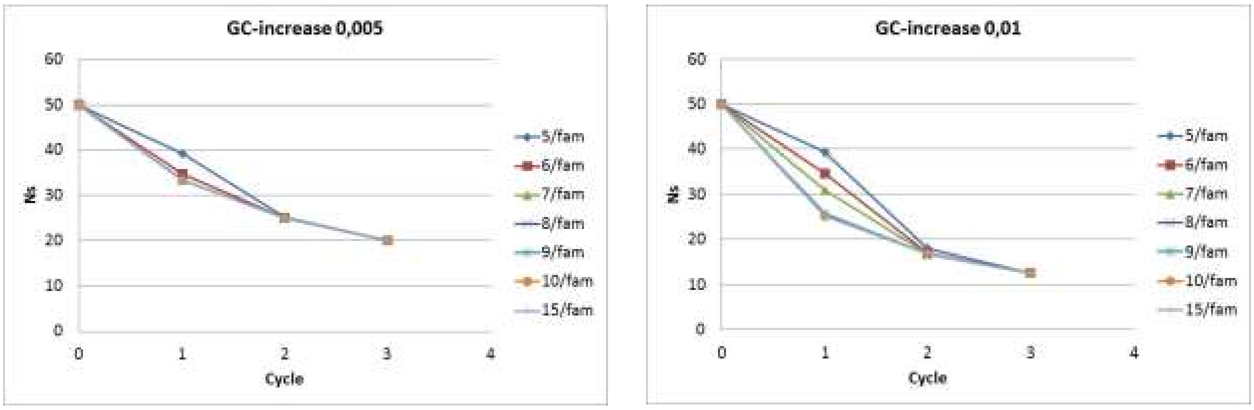


Figure 4-1.
The decrease in *N_s* over breeding cycles for expanding the BP from 50 to 200 and trying to reach an GC increase of 0.002 and 0.01 for different shortlists for OPSEL in terms of trees per family.

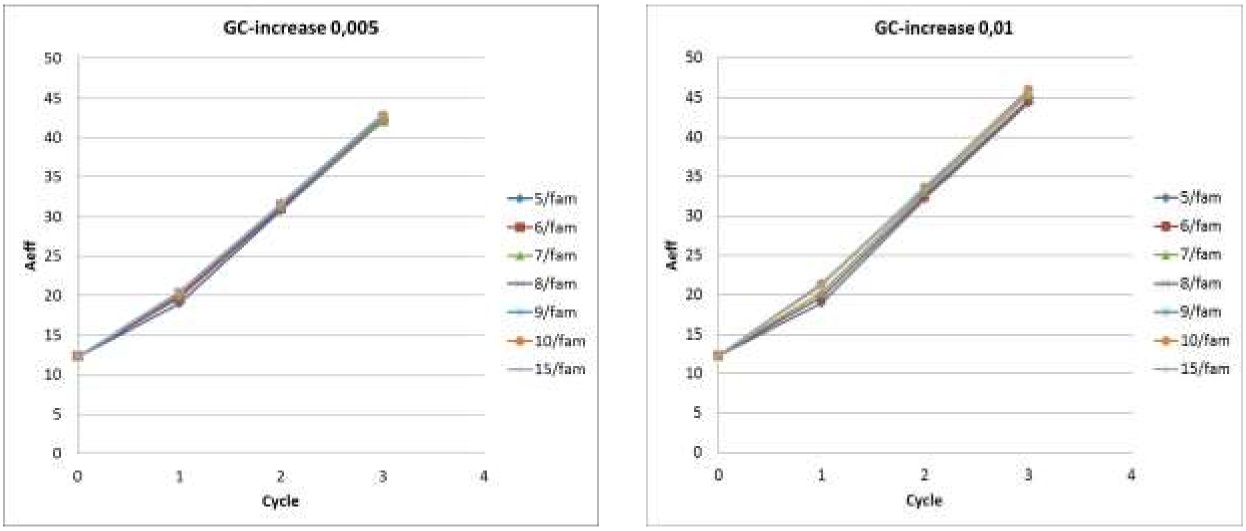


Figure 4-2.
The increase in Aeff over breeding cycles for expanding the BP from 50 to 200 and trying to reach an GC increase of 0.002 and 0.01 for different shortlists for OPSEL in terms of trees per family following the realized GC-increase in Table 4-1.

DISCUSSION

Expanding the original BP of 50 to 100, 150 and 200 by using expansion factor 2, 3 and 4 will decrease GC and increase *Ne*. The repeated sampling of sibs will increase the chance to select more of the parental alleles. In this way, the expansion creates extra "space" for selection up to the GC of a BP with constant size 50. Therefore, at the time of expansion in generation 1 (generation 0 is when the BP of 50 trees are selected from 300 for the first breeding) there is a greater extra space of GC than is generated in later generations. In later generations, the extra space just comes from the larger population size being 100, 150 or 200 instead of 50. To our understanding, it is the greater extra space of GC to be explored by OPSEL in the expansion generation that defines the level for truncation required to give the shortest short-list giving the largest optimum when selecting with OPSEL. If too few sibs per family are taken to the shortlist OPSEL is unable to increase GC to the predetermined level.

Our results indicate that for expansion factor 2 (BP size 100) 5 trees per family are needed although 4 gives almost identical results. For expansion factor 4 (BP 200), at GC-increase 0,005 and 0,010, 7 and 10 trees per family, respectively, are needed in the short-list, making a total of 350 and 500 candidates. To expand from 50 to 100, 150 and 200, 2, 3 and 4 trees per family, respectively, are used just for the expansion and the additional trees to create room for unbalanced selection.

Appendix 5.

Number of ramets per clone in field testing

INTRODUCTION

The baseline scenarios involve variation in resource levels in terms of progeny to be tested and expansion of the BP, both of which affect family size. The scenarios also involve variation in heritability, affecting test accuracy, and also variation in restrictions on selection, causing unbalance. We expect there exists an optimal distribution of ramets and clones within a family of a given size, depending on the total resource level and BP expansion factor (both affecting family size), heritability, and rate of GC increase. To find the optimal balance between selection intensity and accuracy we simulated a variety of distributions of ramet and clone numbers for the three resource levels under varied conditions.

METHOD

We used the results in Rosvall et al. (1998: page 315) as a starting point to fine tune this distribution in the interval of 1-20 ramets per clone. Balanced selection was achieved by constraining selection to one tree per family under the DPM-mating scheme. Imbalance was achieved by allowing for up to two selections per family. This simplified alternative to OPSEL was chosen to reduce computer time, even though the increase in GC was then uncontrolled. The resource levels of 6364, 12 727, and 24 455 result in family sizes 127, 255 and 509 for a BP of size 50 and 64, 127 and 255 for the expanded BP of size 100. These resources could be distributed quite differently; for example, using 1 clone with 127 ramets or 127 clones with 1 ramet (i.e., a single seedling) each.

RESULTS

The effects on the optimum number of ramets per clone resulting from imbalance in selection, heritability, and test effort are illustrated in Figures 5-1 and 5-2. Heritability has the greatest influence on the optimum number of ramets. At $h^2 = 0.4$ (corresponding to rTI = 0.63), just a few copies of a clone is optimal and, in practice, clone testing is not useful. At $h^2 = 0.2$ (corresponding to rTI = 0.45) and $h^2 = 0.05$ (corresponding to rTI = 0.22), cloning with 10 to 15 ramets is optimal. Especially at the low resource levels, the optimum numbers of ramets are lower being about 2, 7 and 10, instead of 3-4, 10 and 15 at medium resource levels.

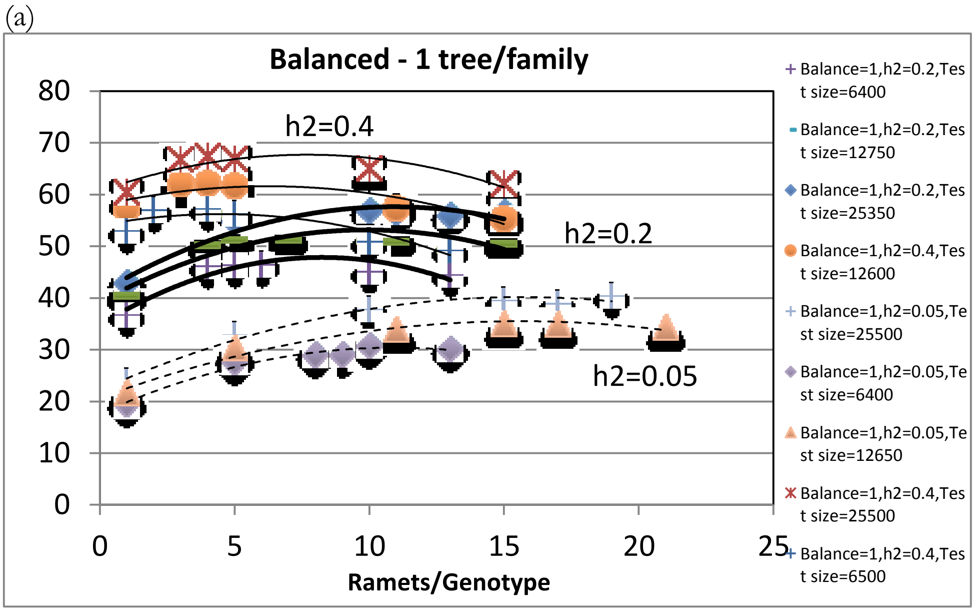
There was no effect of using unbalanced selection at a constant BP size 50 (Figure 5-1b). Expanding the BP from 50 to 100 at $h^2 = 0.2$ (Figure 5-2b) results in optimum number of ramets being about 7, 10 and 12 for the three resource levels in the balanced case and one sees no effect of expansion from the figures (other than slightly higher gain). Using expansion and unbalanced selection there might be a tendency to use a few more ramets to reach the optimum.

DISCUSSION

These runs were based on the expectation that resource levels and heritability are important for the optimum number of clones to be tested and ramets to be used. Unbalanced selection might also change heritability and therefore the optimal distribution of test effort. By expanding the population from 50 to 100, family size is halved. Smaller families give less accurate family means and therefore less selection accuracy among families, and less selection intensity within but greater selection intensity among families. All these manipulations of the BP had small effects on the optimal distribution of clones and ramets within a given resource, as compared to the greater effects of h^2 and the resource level itself.

Since we are most interested in levels of h^2 0.05 to 0.2, accepting that h^2 is not exactly known in advance, and in higher levels of resources (12 650 to 23 350), we concluded that using 10 ramets per clone is a good compromise for all conditions. It should be kept in mind that some additional gain can be achieved for specific conditions.

(a)



(b)

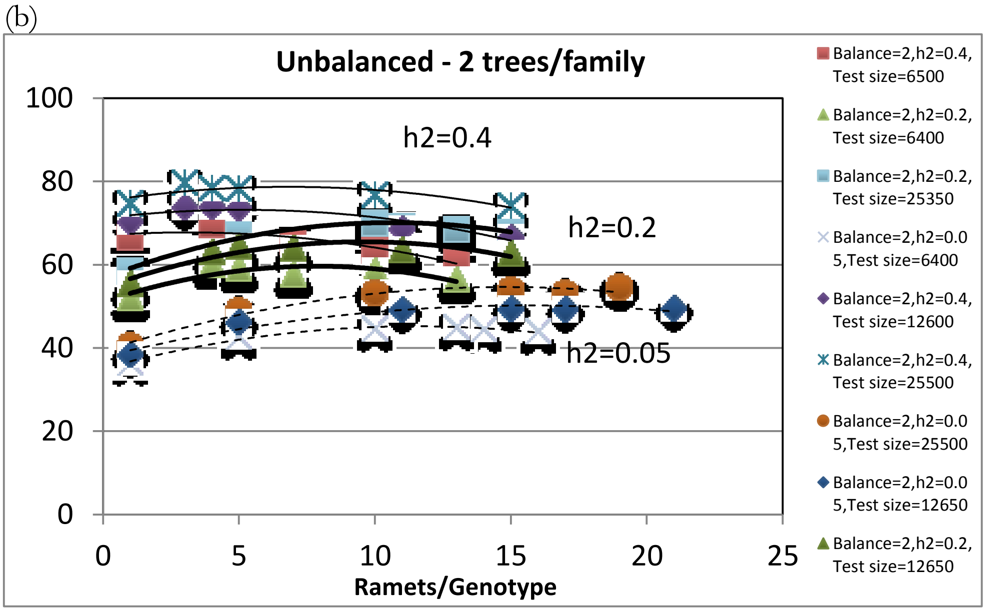


Figure 5-1.
The influence of clone and ramet numbers on Aeff after 4 cycles of breeding a BP of size 50 using (a) balanced selection under DPM (1 tree/family), and (b) unbalanced selection under DPM (up to 2 trees/family) for resource levels 6 400, 12 600 and 25 350 every 20 years and h^2 = 0.05, 0.2 and 0.4.

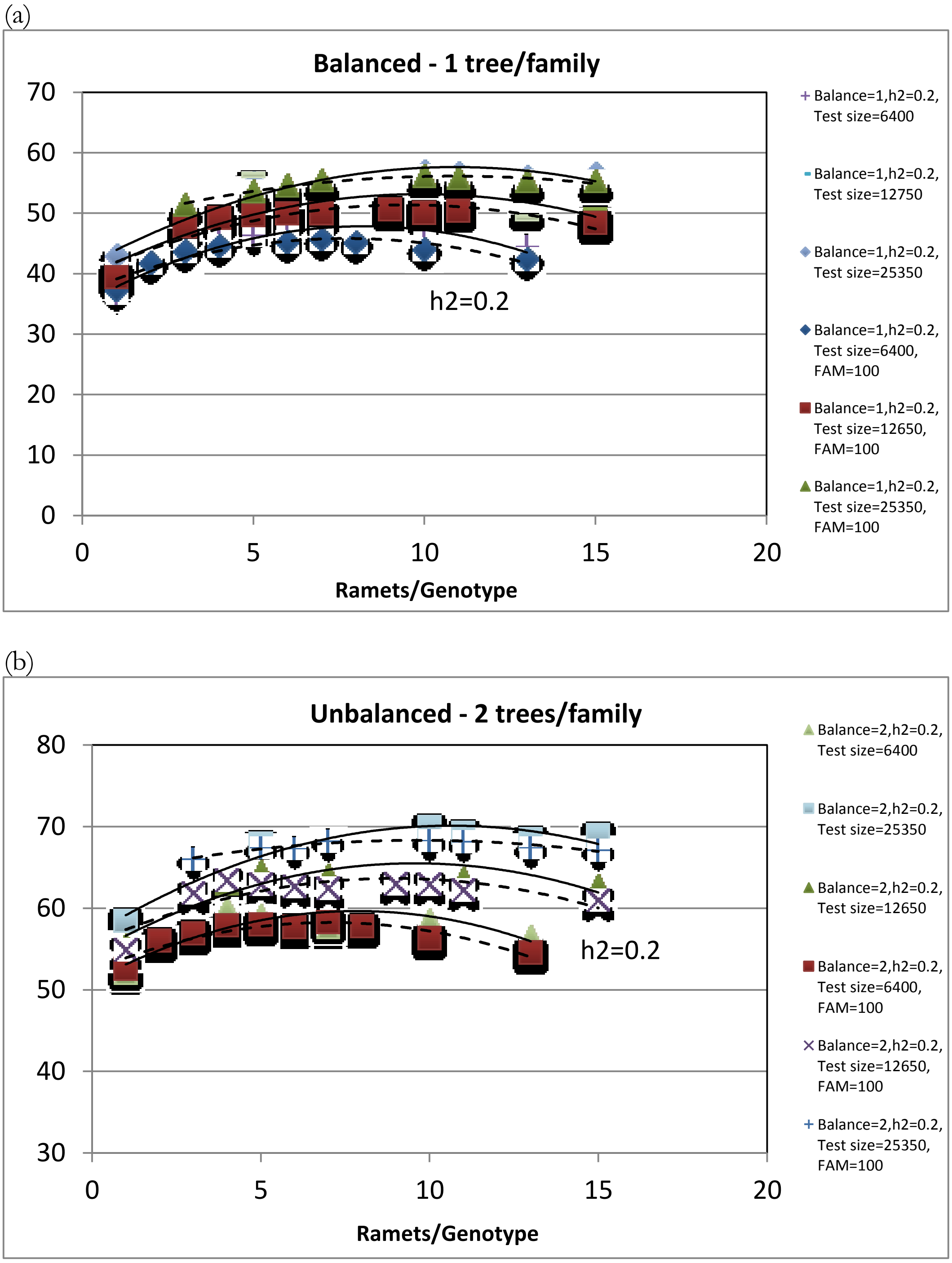


Figure 5-2.
The influence of clone and ramet numbers on Aeff after 4 cycles of breeding an expanded BP of size 100 (the continuous lines) compared to a BP of size 50 (dashed lines) using (a) balanced selection under DPM (1 tree/family), and (b) unbalanced selection (2 trees/family) for resource levels 6 400, 12 600 and 25 350 every 20 years and $h^2 = 0.2$.

Appendix 6.

Unbalanced mating using 3:2:1 schemes

INTRODUCTION

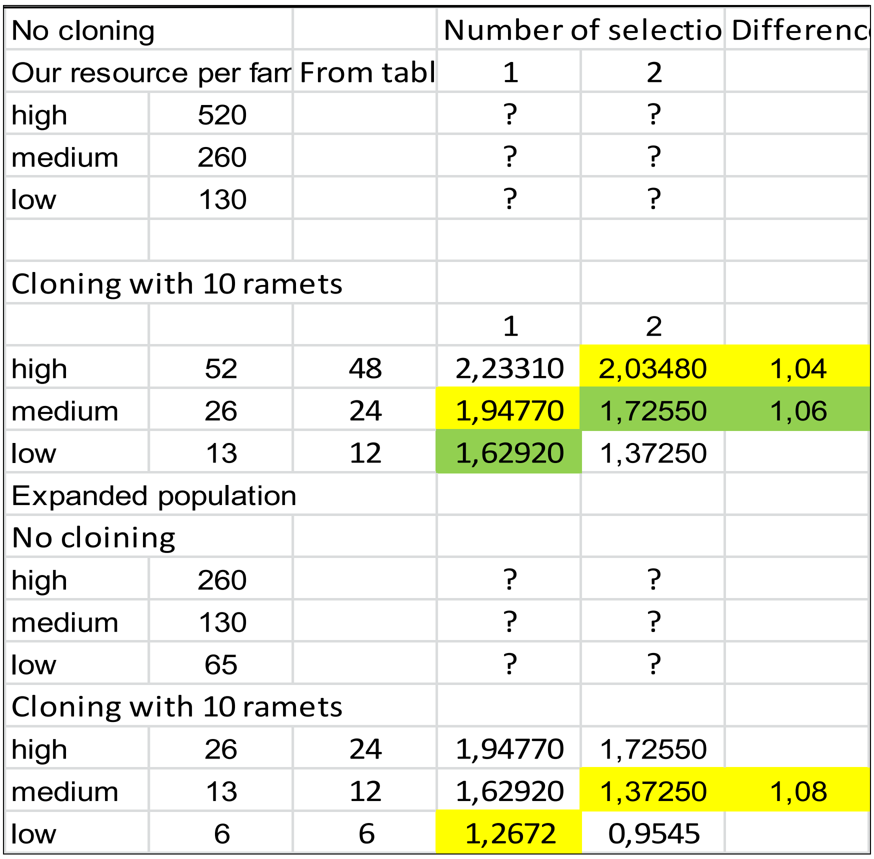
A 3:2:1 mating design produces the same number of crosses as DPM, but performs an additional cross per parent in the top part of the population, and a single cross per parent in the lower part. This unequal crossing of ranked trees will increase the effort on the higher-ranking trees by giving them larger progeny size at the expense of less effort on the lower-ranking trees. The expectation is no change in BP gain (gain at the top is traded off by loss of gain at the bottom), but an increase in PP gain for trees selected among the elite of the BP (Lstibůrek et al., 2005).

If this unbalanced mating design is combined with balanced selection (Unbalanced Mating Balanced Selection: UMBS), i.e., by selecting exactly one per full-sib family for 3:2:1, the result is increased relatedness. We saw in earlier studies (Rosvall, 1999) that this strict control of relatedness gives a good structure of relatedness for high gain and diversity in PPs compared to group merit selection GMS (Lindgren and Mullin, 1997). It is not clear if this result was specific to the case when inbreeding depression is included in the simulations, as shown by Rosvall (1999).

By using OPSEL for selection in unbalanced mating designs, we can restrict coancestry and maintain the same diversity for any number of mates swapping in the 3:2:1 design. In this way, by varying the number of crosses and using OPSEL we can vary resource allocation within the BP without changing diversity. In principle, this will isolate the effect of changing selection intensity to be high for the best and low for the less-good parents.

Generating in this way more progeny for the best at the expense of fewer for the less good is not exactly the same as increasing and decreasing family size, as was done by Lstibůrek et al. (2005). By increasing the number of crosses for a particular tree we create more progeny, but also more full-sib and half-sib relationships. Selection intensity is greater when selecting 2 in a large family as compared to selecting the 2 trees, one by one, from two families of half the size (Table 6-1).

Table 6-1.
Selection intensity is higher for selecting 2 in a large family than 1 in each of two families of half the size.



No cloning			Number of selectio		Differenc
Our resource per fam		From tabl	1	2	
high	520		?	?	
medium	260		?	?	
low	130		?	?	
Cloning with 10 ramets					
			1	2	
high	52	48	2,23310	2,03480	1,04
medium	26	24	1,94770	1,72550	1,06
low	13	12	1,62920	1,37250	
Expanded population					
No cloining					
high	260		?	?	
medium	130		?	?	
low	65		?	?	
Cloning with 10 ramets					
high	26	24	1,94770	1,72550	
medium	13	12	1,62920	1,37250	1,08
low	6	6	1,2672	0,9545	

METHODS

Here we have compared the unbalanced mating by swapping from 0 to 13 crosses in 13 different 3:2:1 schemes using balanced selection of 1 per family or by using OPSEL, with a predetermined rate of increase in GC. Simulation was for a BP size 50. The resource level was high (40 000), ramet numbers 1 (seedlings) and 10, $h^2 = 0.2$, and GC increasing at 0.01 per cycle.

RESULTS

Unbalanced mating using OPSEL to constrain coancestry

Using OPSEL and the 3:2:1 mating design resulted in the same level of BP A-eff, about 54.5, and the same BP N_s of about 10 (BP GC 0.05) for all 13 swaps, as expected (Table 6-2). Also as expected, the SeedPP A-eff increased, but the increase was low from 64 to 66 and ClonePP A-eff increased from 62 to 64, with increasing numbers of swaps. Thus, the constraint on relatedness when selecting the ClonePP gave slightly less gain, but resulted in a ClonePP pwC of about 0.12 as compared to SeedPP pwC of 0.18 (Table 6-2 and Figure 6-1).

Table 6-2.
Gain (A-eff) and diversity (GC and pwC) from using OPSEL and the mating scheme 3:2:1 with 1–13 swaps.

Swaps	BP Aeff	Seed PP	Clone PP	PP difference	BP GC	Seed PP	Seed PP	Clone PP	ClonePP
0	54,6	64,0	62,0	2,0	0,050	0,319	0,220	0,189	0,091
1	54,2	64,5	62,6	2,0	0,050	0,315	0,214	0,222	0,122
2	54,9	65,8	63,6	2,2	0,050	0,275	0,178	0,225	0,127
3	55,2	65,7	64,1	1,6	0,050	0,293	0,195	0,230	0,132
4	54,9	66,3	64,4	1,9	0,050	0,282	0,183	0,216	0,118
5	54,4	64,9	63,2	1,7	0,050	0,272	0,177	0,203	0,108
6	54,4	65,7	63,3	2,4	0,050	0,303	0,205	0,220	0,122
7	54,5	65,7	64,4	1,2	0,050	0,281	0,184	0,220	0,122
8	54,3	66,0	64,5	1,6	0,050	0,270	0,174	0,212	0,115
9	54,5	66,6	64,8	1,8	0,050	0,286	0,189	0,227	0,128
10	54,1	64,6	63,5	1,1	0,050	0,278	0,180	0,218	0,121
11	54,5	66,4	65,1	1,3	0,050	0,294	0,197	0,233	0,134
12	54,3	67,8	66,3	1,5	0,050	0,302	0,200	0,250	0,149
13	54,6	66,1	64,1	2,0	0,050	0,269	0,171	0,218	0,119
Average 1-13	54,5	65,9	64,1	1,7	0,050	0,286	0,188	0,223	0,124

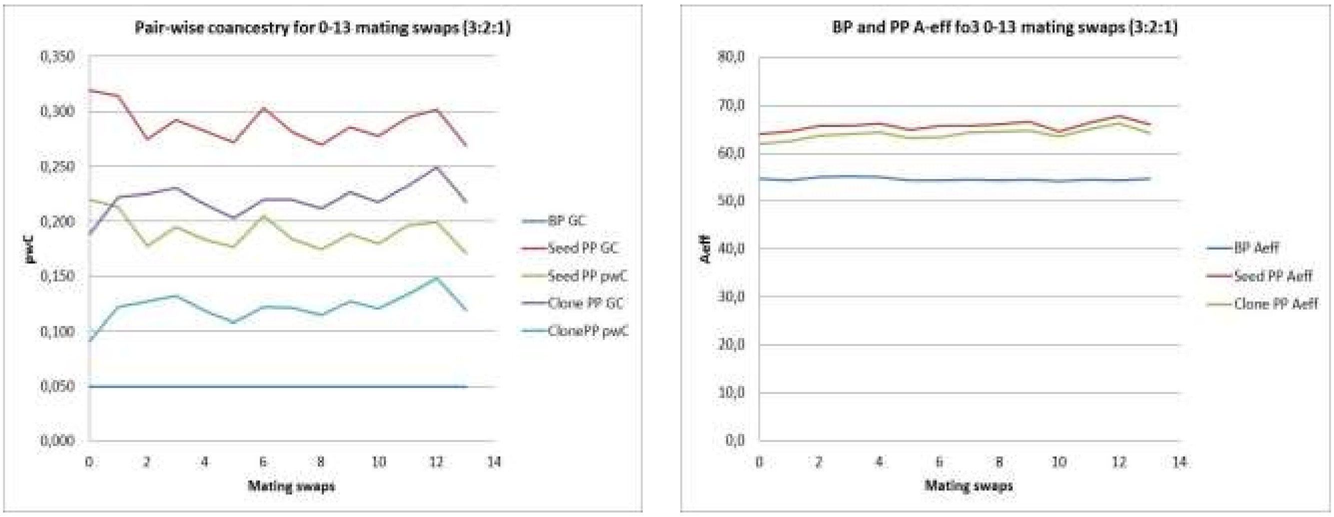


Figure 6-1.
BP and PP A-eff and diversity (pwC) from using OPSEL and the mating scheme 3:2:1 with 1-13 swaps.

Unbalanced Mating with Balanced Selection (UMBS)

The UMBS strategy increased BP gain from 42 to 50 in cycle 4 for swapping up to 13 crosses, while the BP N_s successively decreased from 16.6 to 9.7. (Table 6-3). The SeedPP A-eff increased from 56 to 62 with the SeedPP GC increasing by the first swap from 0.14 to 0.17 and with more swaps up to 0.18. The result was exactly the same for ClonePP (in cycle 3), since the selection of the BP was restricted to 1/family, resulting in the same restriction for the SeedPP as applied to the ClonePP. The corresponding PP pwC increased from 0.05 with no swaps to 0.08 to 0.09 with small or large numbers of swaps, respectively.

Compared at the same BP N_s of 10, the SeedPP GC was 0.28 under OPSEL and 0.18 for UMBS (lowest 0.14 for balanced selection). The SeedPP and ClonePP pwC were 0.18 and 0.12, respectively, for OPSEL, and 0.08 for both types of PP under UMBS (lowest for balanced selection is 0.05) (Figure 6-2).

Table 6-3.
Gain and diversity for unbalanced mating and balanced selection (UMBS) using the 3:2:1 scheme with successively 1-13 swaps. The OPSEL result from a 0.01 per-generation increase of GC, resulting in BP N_s of 10 in cycle 4.

Swaps	BP Ns	BP Aeff	d PP Aeff	e PP Aeff		Seed PP (	Seed PP p	Clone PP	ClonePP p
0	16,8	41,9	56,3	56,3		0,136	0,049	0,136	0,049
1	16,0	43,6	58,8	58,8		0,167	0,079	0,167	0,079
2	14,9	44,8	60,7	60,7		0,174	0,085	0,174	0,085
3	13,8	46,1	59,0	59,0		0,178	0,087	0,178	0,087
4	13,0	46,9	59,6	59,6		0,179	0,089	0,179	0,089
5	12,1	47,8	59,5	59,5		0,178	0,088	0,178	0,088
6	11,4	48,5	61,4	61,4		0,177	0,087	0,177	0,087
7	11,0	48,8	60,5	60,5		0,182	0,091	0,182	0,091
8	10,5	49,3	60,1	60,1		0,178	0,088	0,178	0,088
9	10,2	49,7	62,1	62,1		0,181	0,091	0,181	0,091
10	10,0	49,9	61,7	61,7		0,170	0,080	0,170	0,080
11	9,7	50,2	61,7	61,7		0,169	0,079	0,169	0,079
12	9,7	50,1	60,5	60,5		0,170	0,080	0,170	0,080
13	9,7	50,1	62,1	62,1		0,180	0,090	0,180	0,090
Average OPSEL result									
	10,0	54,5	65,9	64,1		0,278	0,180	0,218	0,121

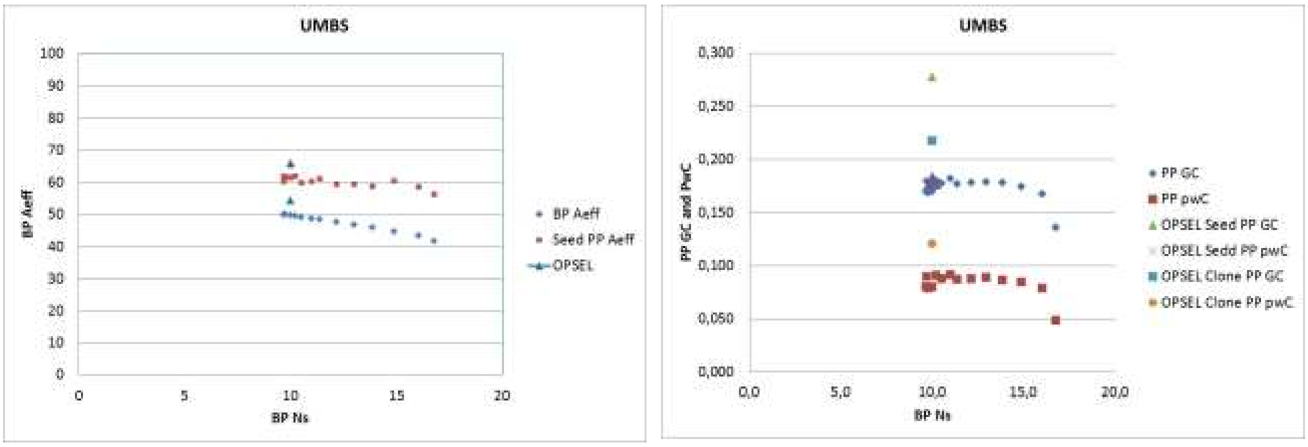


Figure 6-2.
Gain and diversity for unbalanced mating and balanced selection (UMBS) using the 3:2:1 scheme with successively 1–13 swaps plotted over BP N_s. The OPSEL result for a 0.01 per-generation increase of GC, resulting in a BP N_s 10 in cycle 4, is also shown.

Discussion

When using UMBS, most of the effect is achieved by swapping 1 or 2 crosses, which involves from 2 to 4 trees in both extremes of the rank order, or in total 4 to 8 of the 50 parents in the BP. With more swaps, BP gain is increased and P diversity eroded, but the gain and diversity for the PPs is not much changed. The reason might be that there are no more extremes than about 4 on a normal distribution of the size of our BP.

In this comparison, OPSEL was used with only one restriction, increasing GC by 0.01 per cycle. The resulting BP N_s of 10 in cycle 4, which in comparison to balanced selection is low, was achieved for all numbers of swapping crosses. At that level of BP N_s, OPSEL gives more Aeff in both the BP and PP, but at a cost of diversity lost in the PP. The most important comparison among strategies is for the restricted selection of the ClonePP, for which OPSEL results in ClonePP Aeff of 64 and pwC of 0.12, as compared to Clone/SeedPP A-eff 61 and pwC 0.09 for 2 swaps.

Continued analyses involved simulations with OPSEL at lower rates ofincrease in GC per cycle; at levels of 0.05, 0.06, 0.07, 0.08, 0.09 and 0.1, applied using just 2 to 4 swaps. These results are still to be analyzed.

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Nr	856	Widinghoff, J. 2015. Logistiklösning för delkvistat sortiment – Lätta skyddsplåtar på virkesbilar för transport av träddelar och delkvistade sortiment. – Lightweight side-shields on timber trucks transporting partly delimbed energy wood. 15 s.
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