Management of breeding materials

Dag L last edit 10-12-11

TBX Activity 4 D 4.2: Optimization of structure of breeding populations for long-term genetic improvement: Survey of methodological tools.

A general discussion with a rather large literature review on topics considered here is found in the text book by White et al. (2007). A recent thorough discussion focusing on the Swedish breeding program is the review by Rosvall et al. (2010).

Why long term breeding? The genetics of the forest genetic resource changes fast. Some genetic resources may vanish or be eroded in an undocumented and uncontrolled way because of Mans impact, the gene mass lost will be reduced if part of a long-term breeding program. Man utilizes the forest for different raw materials and other benefits, the value of the forest will be increase if it grows better.

What is long term breeding? Long term breeding is here defined as the continuous multi-generation improvement of a segment of a species aiming at artificial regeneration material in the future for forestry. There is not a defined end of long-term breeding in the foreseeable future. It is not only for long term conservation with a mainly botanical or biodiversity aim.

Criteria for initiating a long term breeding program

- There already exists short term activities,
- (At least) one responsible organization can be identified which is expected to fund and organize activities in the future.
- There is a reasonable chance the material coming out from the long term breeding will be the basis of forestry of some significance. Chances are higher if forestry is economically and organizationally involved. Chances are higher if seed orchards or clonal propagation works.
- Some minor reductions in immediate gain (less than most think) are tolerated to deploy a given budget so it is more profitable on some decades longer time perspective.
- It is considered a PR-value if breeding can be claimed to be sustainable and support high diversity.
- The budget may not be that large or assured continuous, ways of tackling low input breeding even on long term are indicated by Lindgren and Wei (2007).

The aim of long term breeding

- To offer options for constructing propagation (=multiplication) populations (in the near future mainly seed orchards).
- To conserve the species in an improved form.
- To preserve much of the variation of segment of the species it works with for future breeding.

Profitability of long term breeding

Profitability considerations for Sweden are summarized by Rosvall et al. (2010). Seed orchards in Sweden as supported by long-term breeding are expected to increase the timber harvest by ten percent to the end of this century (not all forest is planted and it takes long time between breeding and harvest in Sweden). The current added cost of breeding and seed orchards for a unit of wood is in the magnitude one percent of its stumpage price. Costs of seed orchards and tree breeding at current level has been estimated to less than five percent of the increase in net present value of the Swedish forest generated with 4% as interest.

Structuring the breeding population

The breeding population can be structured in strata (horizontally) of different genetic quality where the higher strata focus more on gain and invests more resources per "status number", while the lower strata have more emphasize on diversity (higher status number and usually less resources per status number).

The propagation population is mainly derived from the higher strata while the lower strata are more for maintaining diversity and raw material for continued breeding.

To invest more in the higher strata results in better options for the propagation population even if the average breeding value of the breeding population including lower strata may be slightly decreased at the same breeding effort.

It can be distinct strata (nucleus population or stratified sublining) or a continuous structure by positive assortative mating (PAM). PAM widens the genetic variation in the recruitment population, which helps both with a more efficient breeding but mainly better breeding populations. Research results indicate that there is no important advantage with distinct strata, but the same breeding population may be better managed with the mating structure (PAM).

The breeding population can also be structured in vertical strata (sublining, multi-population breeding, MPB). There can be subpopulations targeted for different areas, for sharing managerial responsibilities, for different purposes or different management strategies. For these purposes subpopulations may share founders.

Another reason for subpopulations (usually called sublines) is the option to select and mate unrelated highly bred genotypes to produce progeny/clones which does not suffer from inbreeding. It is recommended to keep the option open forever by keeping at least two unrelated segments of the breeding population targeting for the same areas, when the option to create non-inbred genotypes will remain forever. It is desirable to keep clones unrelated or to restrict the relatedness in seed orchards, but to do that with sublining requires at least 10 sublines, preferable 20, and each would when be small and that means after some generations loss of genetic variation, and inbreeding to an extent which would reduce average gain, and is not recommendable to try to keep more unrelatedness after the first generations. But for the very first generations it is an advantage if the breeding populations allow 10 or up to 20 unrelated selections to form seed orchards without inbreeding.

Initiation of long term breeding. In the first step usually plus trees are phenotypically selected. It is generally a good idea to choose more plus trees than needed to sustain long term breeding to be able to reduce the diversity in the first generation shift or shifts. In Swedish conifers the first step is progeny testing of selections and when crosses are done among those with high breeding values, thus reducing the number of potential founders with a factor of magnitude 5. It may be a good idea to start with progeny testing plus trees by open pollinated progeny in the forest and when use the progenies for additional “founders” besides using the best progeny-tested trees, but infusing fresh unrelated material into the breeding population after some generations will sacrifice much gain. Goals of long-term breeding should be general as environments, silvicultural methods, markets, industrial processes and customers will change before the improved trees are harvested.

Management of breeding populations.

Cycling of breeding population (recombination). Swedish breeding often applies field measurement and selection of advanced generation trees at around 3-5 m height at typically 20 % of foreseen rotation time. It is often not good breeding economy to cycle the whole breeding population at the same time as it may not develop synchronously, it may be more profitable in the long run to keep it asynchronous. The suitable stage of tree development for field test measurement and selection for breeding has been found to be at about 3-5 m height, which is typically 20 % of the rotation time. It is often more practical to do crosses on convenient places (e.g. clone archives) than in the field. It seems probable that identification of parents by molecular markers in open pollinated or polycross progenies will play an increasing role in cycling breeding populations in the near future. It gives a better preparedness for environmental change if the breeding stock is tested over a wider environmental range of sites than it will be finally deployed at.

The balance between gain and diversity in long term breeding

Diversity is usually desired in the forest. Lack of diversity in the regeneration material probably reduces the expected biological propagation somewhat. A genetic diverse material is expected to be more able to utilize variable sites somewhat better; the risk of biotic and abiotic calamities seem likely to increase if there is no diversity and it is very politically correct and has a large PR value if it can be claimed that there is sufficient biological diversity. The set up of clonal mixtures or seed orchards from available breeding stock considers both breeding value and gene diversity. The genetic gain of the propagation population is considerable higher than the average genetic gain of the breeding stock, as propagation populations benefit on the genetic variance in the breeding population.

Gene diversity decreases in the long term breeding because of genetic drift in a limited breeding population. That means that relatedness increases annual genetic gain decreases. Thus the founder population and the breeding population must be sufficiently large in long time breeding and the selection should consider maintenance of diversity. In the Swedish breeding population this has been considered and the breeding program is sustainable at least 10 generations ahead. The future tools of breeding to counteract gene diversity losses are difficult to predict and the models used have limitations and probably overestimate the long term erosion of gene diversity, thus it seems enough to demand from a long term breeding program that it is sufficiently diverse after 5 generations and a century ahead (preserves more than 95% of the gene diversity for the breeding population serving some an area with similar adaptedness requirement, which is larger than a Swedish subpopulation).

Future clonal mixtures and seed orchards must be sufficiently diverse, thus the breeding stock must be sufficient diverse. Excess diversity in the breeding population can be converted to gain when constructing propagation populations which is a reason for diversity in long term breeding stock. The conditions served by specific propagation populations may not be exactly what long term breeding is heading for, but if there is a diversity special demands can be efficiently met. If gain is bought in the long time breeding by low diversity, almost most of the advantage will be lost by its decreased potential for constructing sufficiently diverse breeding populations.

The breeding stock serves an uncertain future. The environment where it will be used is highly uncertain from many aspects; geographically, environmentally, biotical, silvicultural and economically. Diversity makes it easier for long term breeding to adapt to these changing conditions.

Breeding population size

To avoid:

- genetic drift,
- accumulation of inbreeding and relatedness,
- random changes in genetic set up,
- decrease of genetic variance later reducing the response to selection,
- random changes in allele frequencies,
- loss of alleles,
- that variable desires and propagation populations can be not be well served

It seems desirable to have breeding populations in magnitude of hundreds. This will not be enough to preserve the most rare alleles for long time (frequency <0.03), but this is probably not important. The requirement is lower the more equally the founders are represented in the breeding population. The requirement is higher without controlled crosses or at least controlled seed parent contributions.

Breeding population size in a number of important tree breeding programs were listed by Johnsson et al. (2001, Table 3, mainly “per unit” figures) and White et al. 2007. Most programs have between 200 and 400. Only one European program (Swedish Norway spruce) was in their lists. The Swedish breeding program maintains breeding populations of more than 1000 for Scots pine and Norway spruce. The Swedish subpopulations are only 50, but several can serve the same propagation population and it seems fair to set the Swedish 200 at such context, and it should be remembered that it is more balanced than most other programs. Arguments which may justify a lower breeding population size are that many of the trees of the species are not predicted to origin from the breeding population (natural regeneration); that the species or population is an exotic (and thus the diversity is less of a domestic problem and more a problem for the country where it is natural) and that there are overlapping breeding populations (e.g. in neighbour countries, competing organizations or adjacent breeding populations).

The breeding population size of a subpopulation can be regarded as a breeding economic problem, Danusevicius and Lindgren (2005) calculated optimal breeding population size in a setting like the Swedish program considering budget, gain, gene diversity and time; and found optima in the range 30-70, which can be said to agree with the Swedish 50. High heritability, more precise testing (clonal or progeny), small additive variance at mature age and the diversity maintenance time horizons of less than some hundred years favor low breeding population size. The rather low optimum reflects that disadvantages with low breeding population size can be more than compensated by higher gain if resources are spread on fewer breeding population members. It seems favorable to increase the breeding population size considerable above the number needed to minimize the decrease in diversity in a balanced breeding to allow short term unbalances while maintaining the a higher degree of long term balance (Lindgren, Danusevicius and Rosvall (2009).

Calculations on experimental data For the recruitment population prediction of breeding values of candidates for selection and pedigrees are needed. Tools for pedigrees become more complicated, when multi-generation breeding makes the pedigrees more complicated, but the largest part of forest tree breeding material is unfortunately not more advanced to make handling pedigrees very complicated. To use the full information from experiments to evaluate breeding values is complicated and demanding, but reasonable approximations are possible with more simple tools disregarding the full information. Multi character breeding can be simplified to single character breeding by using relevant indices and weights, but again a full consideration is complicated. Pedigrees including open pollination later than unidentified pollen parents on the founders as seed parents instead of controlled crosses make calculations difficult and depending on highly unreliable assumptions, thus highly unsophisticated and unreliable breeding and is recommended only for low-input breeding of minor species with low budget and little economic importance for forestry.

Simulations and calculations on strategies for breeding population management

Predicting breeding values is always rather uncertain. Trials the selections are based on are small, young, sample just a few environments and replications in time, and are silvicultural different from future forest. The character selected for should be something like economic value for forestry evaluated at harvest, but nobody knows with some degree of certainty how characters and "gain" will get be given values in a far future with unknown end uses. Calculated breeding values tend to regress to the mean if used for selection.

Tools for long-term breeding

Strategies used by TREEBREEDEX participants
Danusevičius et al. (2010) have analyzed this.

Testing strategies. The favored testing strategy for selection to the breeding population is a two stage selection: pre-selection based on the trees own phenotype besides information from relatives followed by progeny testing and final selection guided by the performance of the progeny. Selection based on single stage testing on the phenotype or the progeny is less common. Clone testing (for selection to the breeding population) for species where cloning is easy is surprisingly rare compared to how favorable studies on its use in Swedish Norway spruce breeding have found it. In particular low input programs could benefit from more use of phenotypic selection.

Nucleus breeding. Only 10% of the programs used the nucleus or similar concept.

Open/closed population. Of the long term programs almost half counted on infusion of fresh unimproved material, probably this will retard the breeding progress if going on longer than the first generations and more than marginally. The long term breeding programs must assure that they have a sufficient base before closing the population or keep it open longer. To preserve the diversity in a closed population there are good arguments to focus on within family selection but few closed programs focus on that.

Controlled crosses/open pollination to create recruitment population. In long term breeding coancestry cannot be controlled if controlled crosses are not used. Diversity will decay faster and not in a controlled fashion and there are risks the program will collapse. It seems to be remarkably few programs, which use controlled crosses, but that may reflect that not much breeding has reached the advanced generation stage.

Selection within or between families. Mainly within family selection (as in the Swedish programs)

can be regarded as essential in the long run to avoid erosion of genetic diversity, but it is used in on a low share of the programs, not even in the long term high intensity programs with closed breeding populations. But many programs use both types and only for short-term programs most are between family.
Different testing strategies for different characters. A minor part of the programs used different testing strategies.
Time and cost components. Programs focus on gain per generation rather than gain per year and Euro. That has probably led to inoptimal programs, like too much focus on long time strategies like selection backwards after progeny-testing.
Breeding vs propagation population. Most breeding programs do not separate the two types of population, not even the long term programs. The propagation population should be the best share of the breeding stock as propagation population harvests gain for the forest, while breeding populations can preserves more diversity for future breeding and flexibiliy.
Simulations. Simulations are used rather little to optimize breeding (10 partners of 28, but some only limited uses, and only 7 partners apply it to practical breeding), more use of simulations would benefit tree breeding.
MAS (Marker Assisted Selection, molecular tools) 4 breeding programs of 114 used it for practical breeding, but it is doubtful if any used it as a well-established routine.

Simulation and mathematical tools are more for optimization and the results are depending on the input and the input are usually not exactly or even roughly known even when it appears so.

Tools for experimental evaluation and breeding value estimation

Databasis (Oracle,

ASReml Statistical package fitting linear mixed models with residual maximum likelihood. Commercially marketed. Can evaluate breeding value and other results as a function of results on many places, many measurement criteria, many sites, unbalanced, BLUP, spatial considerations, consider relatedness and use economic weights. download a free trial from http://www.vsni.co.uk/downloads/asreml/ . Cookbook at http://uncronopio.org/ASReml/HomePage

You could get started with the manual (included in the download) and the asreml (http://uncronopio.org/ASReml/HomePage)

CycDesigN is a computer package for the generation of optimal or near-optimal experimental designs.

SAS/STAT general purpose commercial (processes MySQL, GLM, MIXED, LSMEANS, LATTICE)

TREEPLAN® BLUP breeding value estimation. Commercial. It comprises an integrated database system where all measurements and trial information from the genetic tests can be stored and analysed, together with the pedigree data including all genotypes from founder trees and onwards. Using TREEPLAN® put light on experimental design, spatial analysis, connectedness, site selection, correction for competition, economic weights, data administration, efficient measurement of traits and breeding value reporting.

warehousingR statistical general purpose. free

Diogene Plant breeding software, including population genetics, compromise between expected gain and relatedness in seed orchards, selfing rate and contamination

MTGSAM and MTDFREML is a package fitting models via Gibbs sampling. Estimation of (co) variance components and resulting genetic parameters and BLUPs.

Genstat

Tools for calculating **group coancestry (status number)** on http://www-genfys.slu.se/staff/dagl/Breed_Home_Page/StatusNumberCalc/StatusNumberCalculationMenu.htm

Simulators.

It is not difficult to run simple stochastic simulations from scratch in standard programs like SAS, AsREML and EXCEL. But if many and complicated features are considered, it may be better to use programs which controls many features. Even programs which are deterministic formula driven can be called simulations (

POPSIM (developed by Tim Mullin et al.). A stochastic quantitative simulator based on the cumulative action of many genes

Allele dropping. (developed by Leopoldo Sanchez) drops an allele from a founder through a pedigree and notes its destiny.

Tree Breeding Tools including Breeding cycler, Orchard Manager etc (developed by Dag Lindgren, Darius Danusevičius at al.)

Literature cited

Danusevičius D & Lindgren D 2005. Optimisation of breeding population size for long-term breeding. Scandinavian Journal of Forest Research, 20:18-25.

Danusevičius D, Pliura A, Jansson G & Lindgren D. 2010. Efficiency of tree breeding strategies in Europe. Report from the Questionnaire “Testing strategies in tree breeding”, FP6 project “Treebreedex”, 89 p. (in preparation).

Johnson, R., St. Clair, B., & Lipow, S. 2001. Genetic conservation in applied tree breeding programs. In Proceedings of the ITTO Conference on in situ and ex situ conservation of commercial tropical trees , Yogyakarta, Indonesia, June 2001 (pp. 215/230). Yogyakarta, Indonesia: Gadjan Mada University.

Lindgren, D & Wei RP 2007. Low-input tree breeding strategies. In Proceedings of the IUFRO Division 2 Joint Conference: Low Input Breeding and Conservation of Forest Genetic Resources: Antalya, Turkey, 9-13 October 2006. Edited by Fikret Isik. p 124-138.

Rosvall O, Ståhl P, Almqvist C, Andersson B, Berlin M, Ericsson T, Eriksson M, Gregorsson B, Hajek J, Hallander J, Högberg KA, Jansson G, Karlsson B, Kroon J, Lindgren D, Mullin T & Stener L-G 2010. Swedish tree breeding program. Skogforsk. Arbetsrapport in preparation, In English expected to be official before end of 2010.

White, T.L., Adams, W.T. and Neale, D.B. 2007. Forest Genetics, CABI. ISBN 978-0851993485

Comments which will be removed. TREEBREEDEX has been very descriptive in its actions. Personally I am disappointed with the outcome on TREEBREEDEX and probably it is disappointed with me,