THE TREE BREEDER AND THE GENE CONSERVATION 'BOGEYMAN''

Alvin D. Yanchuk2

lNTRODUCTION

Over the past two decades, tree breeders have struggled with ways that meaningfully integrate breeding and gene conservation populations. Previous efforts have adequately outlined the conceptual roles of both *in situ* and *ex situ* populations, but more quantitative structure was necessary in order to establish practical planning targets. This gene conservation 'bogeyman' has undermined our ability, in many ways, to address the concerns of critics of tree breeding programs around the world.

Successful strategies to conserve genetic variation over time and space will depend upon many genetic details, such as gene action and gene frequencies. Although we will remain largely ignorant of these genetic details, we present some general approaches and sampling targets which should help quantify gene conservation and work towards integrating breeding and conservation populations into more of a genetic continuum.

Conservation of Rare Alleles: *in situ and ex situ*

It is proposed that capturing one copy of an allele is of limited value, and sampling targets should be set around 20 (Namkoong et al., 1988). This is necessary to avoid potential problems of inbreeding at later stages. Also, it seems important to differentiate between gene action (i.e., recessive or dominance) as it will affect our ability to locate phenotypes with desirable alleles. Using the normal approximation of the binomial (Namkoong, pers. comm.), one can construct a sampling scheme for the number of individuals required (by gene action), to ensure at least 20 individuals will he present (for more details see Yanchuk, 2000). Agencies are free to choose numbers larger or smaller, but the important point is that sampling guidelines emerge. Figure 1 shows the approximate numbers of individuals that would be necessary in a sample (i.e., a reserve population, or that present in a test or breeding population), by the two types of gene action we are interested in.

From Figure 1, it is clear that it will be difficult to conserve recessive alleles at frequencies less than 1.0%, as approximately 300,000 individuals are required. For dominant alleles at frequencies of 0.5%, approximately 3000 individuals are required, which suggests that even a small *in situ* reserve network would be adequate. In a survey of the protected status of conifers in British Columbia (Yanchuk and Lester, 1996) we suggested that a population would only be adequately protected if approximately 5000 individuals were in the reserve, but this is a choice open to the agency. Persistence of *in situ* populations remains a planning and management issue (Aitken, 1999; Yanchuk and Lester, 1996).

Large *ex situ* 'breeding' or test populations, in the order of —700 individuals, would conserve recessive alleles at frequencies of — 20%, but dominant alleles as low as —2% frequency would be easily maintained. Breeding populations of small to moderate size (-80) will contain adequate amounts of quantitative genetic variation (discussed later), but should also contain dominant genes at frequencies of — 0.20.

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[2] Forest Genetics Section, Research Branch, British Columbia Ministry of Forests, 3rd floor, 712 Yates St., Victoria, B.C. Canada V8W 9C2

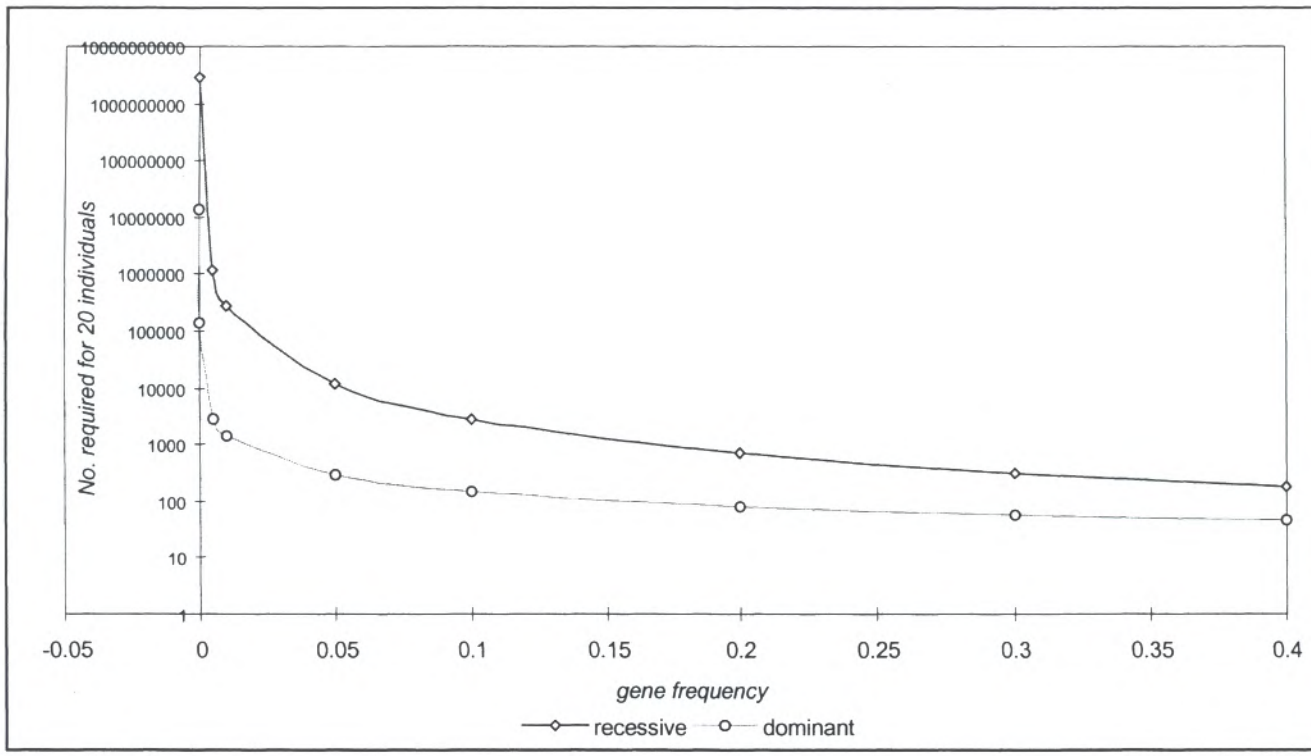

Figure 1. The number of individuals needed to insure that 20 individual genotypes will have a copy of an allele at an alpha of 0.05.

If the species in question has substantial outplantings from an improvement program, then might we be able to rely on mutations in commercial plantations as a way of providing a new source of low frequency alleles (e.g, Burdon, 1995; Yanchuk and Lester, 1996)? If we assume commercial plantations contain approximately one new useful mutant for every one million individuals (e.g., Lande, 1995), finding 20 unrelated trees homozygous for the recessive gene would likely be difficult or next to impossible with 2.89^{+13} individuals required. Even assuming about 400 trees/ha at maturity (for an average plantation situation), this would translate into billions of hectares. With plantation establishment numbers in the order of 1500/ha, and considering losses due to stand competition over time, the number of trees needed is likely even larger. Some mutants may be found, but would only be for dominant alleles, as –14 million trees would be required (which may translate into – 35,000 hectares of commercial plantation). For a few species in the world (e.g., loblolly pine, radiata pine, coastal Douglas-fir) the number of trees available may actually be large enough to consider. However, it seems best to consider this only as a last resort, and in fact may not be necessary for us meet our objectives.

Conservation of Quantitative Genetic Variation: *in situ*

Most *in situ* populations will have to be large enough to persist on their own over several generations, so the more recent population size number proposed by Lynch (1996)(i.e., effective population sizes of 1000) seems appropriate.

If these values are operationally feasible to attain, then it seems these two issues numerically converge for two important conservation purposes. First, for conservation of rare alleles, a census number of 5000 in most situations may be adequate to attain an N_e of 1000 for *in situ* populations in natural or wild situations, for most types of low frequency alleles. However, low frequency recessive alleles (<0.07) are

likely not going to be conserved in adequate numbers, but at least this can be stated. Second, for the maintenance of adaptive genetic variance, populations require a size large enough for long-term persistence and values of approximately 5000 appear adequate as well.

Conservation of Quantitative Genetic Variation: *ex situ*

Breeding populations, on the other hand, are subject to strong directional selection, and the management of genetic variance in breeding populations is a very different issue. For loci not under direct selection, the expected loss in heterozygosity, or purely additive genetic variance, in quantitative characters, is predicted by 1/2N
genetic variance of the initial base population, and even after 10 generations, approximately 60% should remain. The main question for breeders, then, is when will genetic variances be depleted for polygenic traits of interest, and how should this depletion be managed? It is clear that random fixation of undesirable alleles is something to be minimised, but with *in situ* conservation targets more clearly quantified, we now may be able to evaluate how large breeding populations should actually be.

Integration of *In Situ* and *Ex Situ* Populations

With conservation targets better quantified for *in situ* populations, we should be able to evaluate more clearly how large *ex situ* (breeding populations) really need to be. Some trade-offs will be necessary (in short vs long-term gains), but the long generation time of most forest trees may suggest we not focus on more than 10 generations (Carson, 1995). Other agencies may not be comfortable with this target, but it should no longer be an undefined planning horizon.

Many examples are now present in the literature that show long-term response is possible even in populations that originate from relatively few parents (see Rasmusson and Phillips, 1997). This article, and many other in the literature (e.g., see Hill and Caballero, 1992; Namkoong *et al.,* 1988; Eriksson *et al.,* 1993; White, 1992), should challenge our assumption that large breeding populations are necessary. This is particularly true if effective gene conservation plans are in place. Breeding population size and structure ultimately needs to factor in the biology, importance and economic capabilities of breeding agency; however, in British Columbia, the number of species and breeding zones under development is so large that traditional breeding populations in the 100's cannot be maintained.

Considering the above arguments, population sizes in the range of 40-80 seem appropriate. At this size, the criteria of '20 copies of an allele' will only be met for recessive alleles at mid-frequency or higher and for dominant alleles at 0.2 to 0.4. It is important to note that doubling these numbers does little to increase the probabilities of capturing more low frequency alleles, or for increasing quantitative genetic variation. Moreover, major genes of interest, at these low to mid-frequencies, are already at frequencies that provide near maximum expression of additive variance in the population (Falconer, 1989).

This suggests that a better strategy for maintaining alleles at lower frequencies (say those ranging between 20-50% for recessive alleles and 1-10% for dominant alleles) is needed. *In situ* reserves will contain alleles in this frequency range in more than adequate numbers, but the same argument applies to *in situ* reserves, in the long term; i.e., undesirable genetic backgrounds after a few generations. Burdon (1995) proposed the establishment of 'conservation blocks' (e.g., open-pollinated plantings originating from *in situ* populations) to enhance and rejuvenate populations, and these might well suit our needs for low frequency alleles. However, the fate of these populations may be similar to large main populations, and the costs may be substantial.

A new approach, in some ways similar to that proposed by Burdon (1995) as well as that proposed by Cotterill (1984) for a 'gene pool population' in radiata pine, may address this concern. For example, a breeder decides on a structure and size for the initial breeding populations, as discussed earlier, in the range of N_e =20-80, and then assesses the situation with rare and low frequency alleles in the population of interest (i.e., in appropriate *in situ* reserves). If these are not present, then the breeder would have to rely on other experimental populations (sec below) or make speciality collections that will include a few hundred individuals.

Moreover, many tree breeding programs have invested heavily in initial screenings of wild or non-native germplasm, and even in large F1 'main populations.' These populations could have a more prominent role in forest tree gene conservation; not for providing a population for recurrent selection, but for providing an intermediate size population for low to mid-frequency alleles in more desirable genetic backgrounds. Conservation programs for other species have identified these types of populations as being potentially more 'dynamic' (Bretting and Duvick, 1997), and could be called *inter situ* (Blixt 1994) to reflect them being an intermediate type of population.

It appears, then, that the gap between elite breeding populations and the more traditional *in situ* reserve systems (e.g., parks, ecological reserves) is in the range of *Ne* >80 and <1000. Recently, the Western Gulf Tree Improvement Co-operative established approximately 3000 of its first generation selections in clone banks (Byram, *et al.*, 1998). Intact progeny test populations could well serve a similar function, and in fact may have several better features (e.g., open-pollinated trials may have larger effective population sizes, and planted in multiple-locations). Identifying candidate test populations and developing maintenance programs for *inter situ* populations, over time and space, is an additional challenge for tree breeders. Conservation with continued exposure to current and future environmental challenges with the potential of more directed selection is an important feature.

CONCLUSION

Breeding and gene conservation need to be moved from the conceptual stage, to a stage where agencies can state what types of genes or genetic variances they are expecting to conserve, and what vehicles they will use to conserve them over space and time. This approach, of quantifying the maintenance of genetic variations at different levels, should help convince professional and non-professional foresters that both gene conservation and tree breeding are compatible and are simply a continuum necessary for proper genetic resource management.

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