Deployment Issues & Genetic Diversity

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Introduction

During the development of the Forest Practices Code in the mid-1990s, the Government of British Columbia recognized a need to come to terms with how much genetic variation was necessary in commercial forest tree plantations.

Seedlots registered for use on Crown land had to meet a threshold value to maintain diversity across the landscape. Furthermore, many innovative seed orchard practices were being developed to increase genetic gain, with potential reductions in diversity.

It is well known that using a few of the most elite genotypes in our reforestation programs would provide the most genetic gain. However, too few genotypes could subject plantations to unacceptable risks to currently or future biotic and abiotic threats.

The proverbial question of, "How much is enough?" has been on the mind of forest geneticists and tree breeders for decades. B.C. Government researchers developed technical standards that would reflect the best available information on an acceptable minimum level of genetic diversity for reforestation seedlots. The Chief Forester's Standards for Seed Use, mandatory standards under the *Forest & Range Practices Act of B.C.*, still maintain these technical recommendations.

Below is a brief description of the information used, the assumptions and the scientific interpretation we have made from what we believe is appropriate for most situations in B.C. In other words, this represents our synthesis of research and movement into a policy framework.

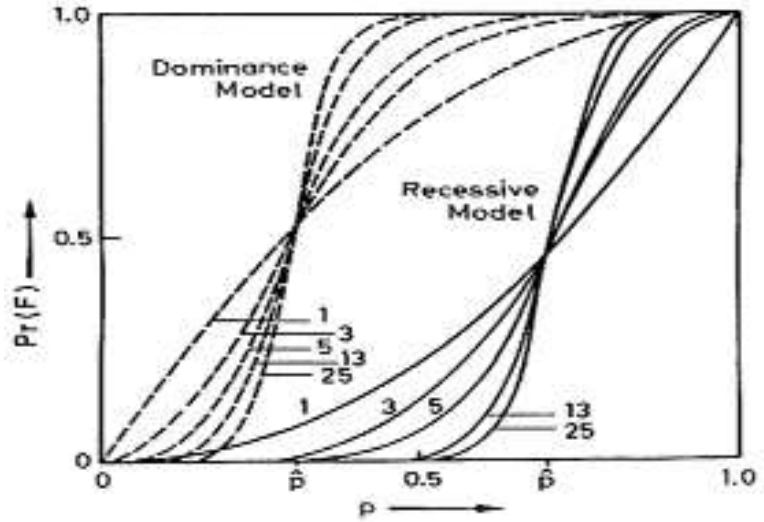
1. The "Single Gene & Risk of Plantation Failure" Approach

A landmark paper was published in 1982 by Prof. W. Libby at an IUFRO conference in the Netherlands, entitled "*What is a Safe Number of Clones per Plantation?*" This paper set the foundation for many questions relating to genetic diversity required in plantation forestry, as well as in several questions related to the larger issue in gene resource management.

Subsequent to Dr. Libby's paper, several researchers at North Carolina State University further developed the general model proposed by Libby. A useful paper that summarizes many aspects of this research was published by Roberds and Bishir in 1997 (Canadian Journal of Forestry Research, 27:425-432). The assumptions and the models are relatively simple. They typically assume:

- A single dominant or recessive gene determines the mortality of a tree in a stand, dependent on the gene action of the pest genotype virulence
- A threshold value is assumed (% of trees which die in the stand) before the stand is considered lost; most of the scenarios have been either 33% or 50% loss

The following figure, developed from Table 1 in Roberds (1990, Theoretical and Applied Genetics, 79: 841-848) indicates some of the dynamics underlying these findings:



This clearly shows that the probability of failure is very sensitive to the gene action (dominant or recessive) and to the frequency of a virulent gene in any disease or pest. Moreover, the difference between the risk levels, probability of failure (Pr(F)) is very small between 13 and 25 clones. An infinite number of clones actually falls quite closely along the N=25 line.

It is important to realize that for most situations we face in forestry, we will not know what the future risks are from unknown biotic threats in terms of the genetic system that may threaten the stand in the future (i.e., the gene action of the resistance gene or the gene frequency).

A hypothetical example will help clarify the logic of this approach. If a susceptible allele currently resides in a native species at a frequency of 0.5, and a native or exotic disease is introduced (or if the native pest or disease becomes an epidemic due to some alteration to the habitat) and it causes a successful infection and mortality to individual trees with the dominant allele, the probability of failure of the stand (Pr(F)) will be ~100% for >13 clones but somewhat less with one clone. So, in some situations, the use of one clone provided the least risk.

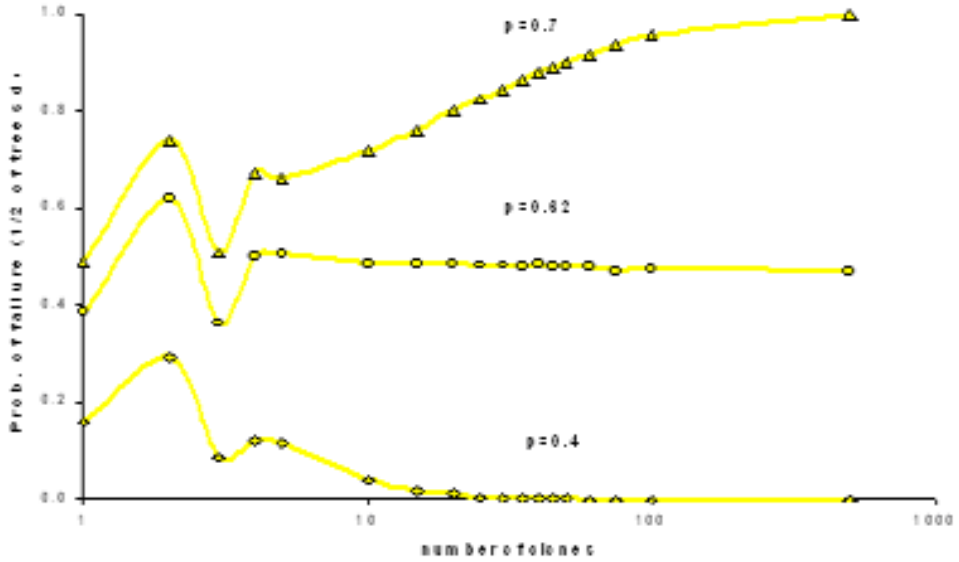
Increasing the number of genotypes simply increases the probability of capturing a susceptible allele. In this sense, wild populations are at just as great a risk as plantations, as the risk is very much related to the gene frequencies in both populations. The interesting result of this approach suggests that including more than 20 to 40 clones does not provide any greater reduction in risk.

Note that these are not evolutionary models where the pest does not evolve more virulence; they do not present volume loss per se to the stand as it matures over time, and mortality is very much determined by single gene assumptions.

Another view of this research by Bishir and Roberds (1995, Mathematics and Bioscience 125:109-125) further confirms the sensitivity of gene frequencies determining failure of a stand.

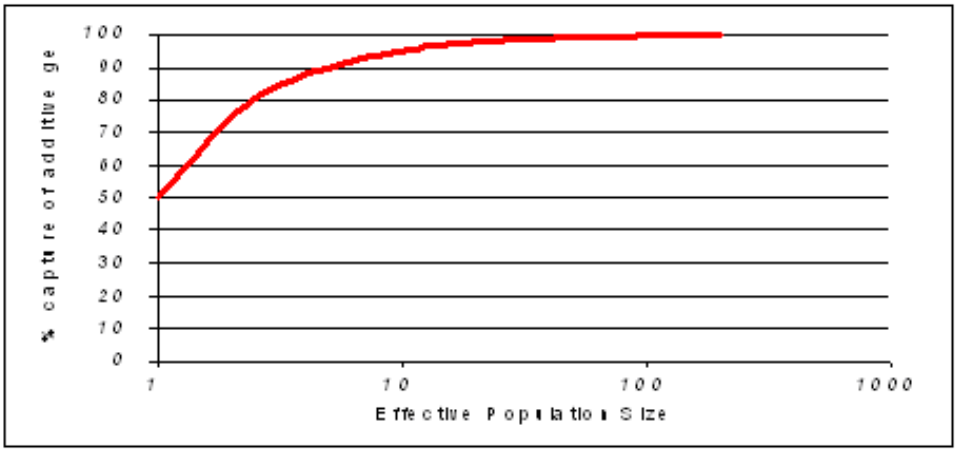
In the figure below we can see that if the gene frequency of a virulent recessive pathogen is introduced into a stand, it only has large impacts if the frequency is above 0.5 or so. More importantly, however, is the fact that after 10 clones (or an effective population size of around 10), the result is more or less the same even if the number of clones is increased substantially.

Probability of plantation failure at 50 years for 3 gene frequencies for a recessive susceptible allele

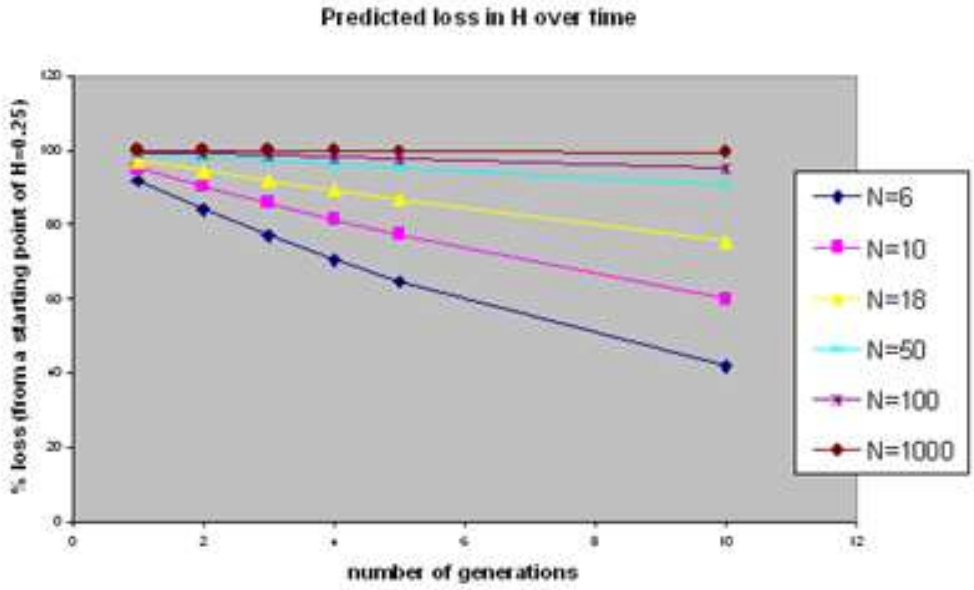


2. Genetic Sampling Theory, Loss of Adaptive Genetic Diversity & Genetic Gain

Genetic sampling theory also shows us that the loss in heterozygosity, or additive genetic variance (or the genetic variance related to adaptive genetic variation), is proportional to: Loss in H (or additive genetic variation) = 1- (1 / (2N)), where N is the number of genotypes in the sample from the original population.



The figure below further shows the general relationship between N (the number of individuals in the initial sample) and the loss in this one measure of genetic diversity, over 10 generations. The figure above is for the first generation.



We see in both figures that at generation 1, an effective size of about 10 individuals provides approximately 95% of the original genetic variation in the population. Since most quantitative traits of interest related to adaptive characteristics are largely controlled by this type of genetic variance, and most of this genetic variation is due to genes at intermediate frequencies in the population of interest, any particular stand that is established with an Ne =10 will have almost all the genes that wild populations in the same Seed Planning Zone (or unit) would have.

The small loss in genetic variance is largely due to the loss of lower frequency genes, but generally these genes are at such a low frequency they could not provide much protection to wild populations.

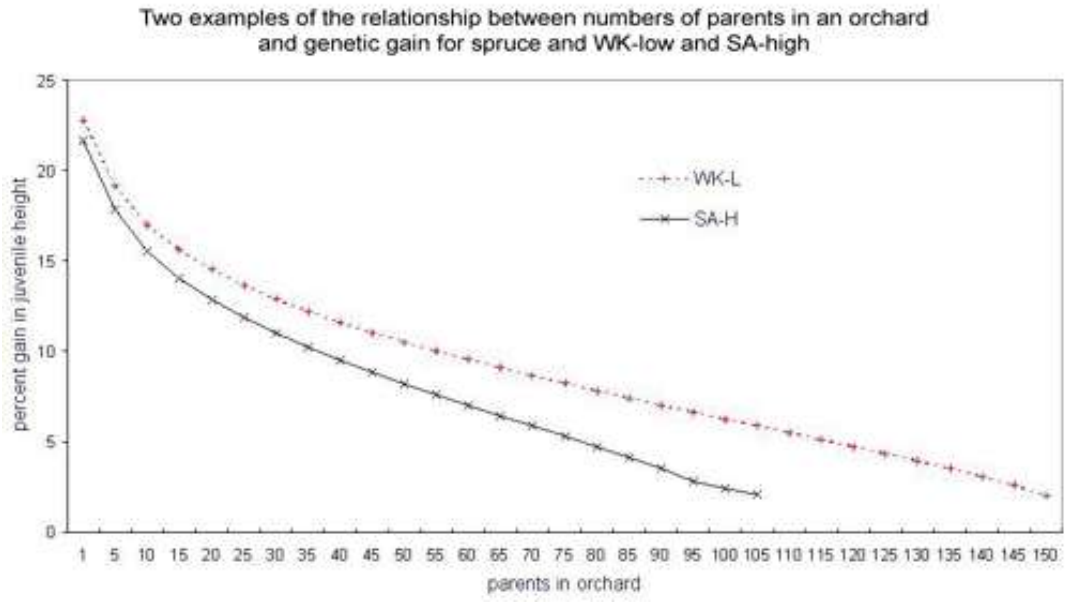
The sampling and conservation of these lower frequency genes is an important part of the genetic conservation program, and is more fully explained in a paper by Yanchuk from 2001 (Canadian Journal of Forestry Research, 31:566-576).

Over several generations, the loss of genetic variation for a population size of 10 decreases substantially, as it does for all population sizes under 100. We can also see that over the first 3 to 5 generations, from a seed orchard plantation that is left to regenerate the stand over time (i.e., the case when a plantation is initially established from seed orchard seeds with various N values in the figure above), there are small differences in the first 2 to 3 generations.

For example, after 3 generations of natural regeneration, if the initial planting from a seed orchard seedlot had an Ne=10, 86% of the original genetic variation should reside in the regenerated population, whereas 97% would reside if we started off with a population of Ne=50. By including more than 10 to 30 clones in an orchard, depending upon the structure of the breeding program, substantial genetic gain would be lost.

However, the objectives of our plantation forestry scheme is to increase productivity in the crop, so we must strike a balance between using the best several clones in an orchard population with adequate genetic diversity to minimize risks through biotic and abiotic threats.

Below is an example in spruce that shows the reduction in gain as we add more parents in the seed orchard. This relationship is surprisingly similar across many programs. We see that the top 5 to 10 parents provide most of the gain, the relationship is non-linear, and including more parents lowers the expected average value from a seed orchard. Again, this indicates that an acceptable compromise needs to be found between gain and genetic diversity, as it relates to risk.

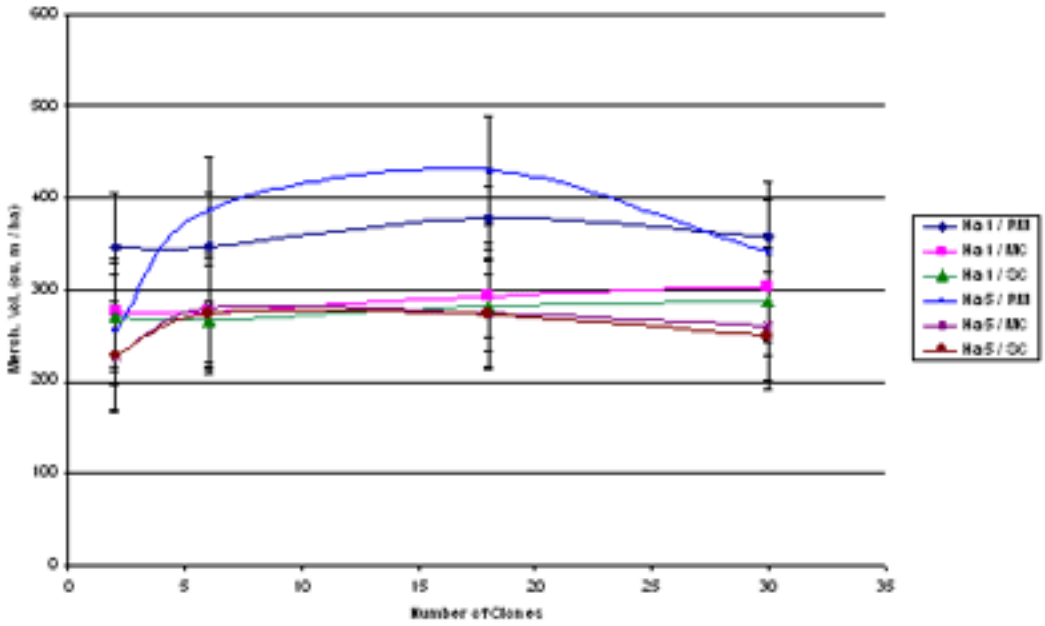


Other programs around the world have also attempted to address this question, in relation to their species, tenure conditions and the biological needs and local management circumstances.

3. Modelling & Computer Simulations of Pest Attack & Genetic Diversity

We have recently used another approach to examining this question with more local conditions in B.C. (Yanchuk, A.D., J. Bishir, J.H., Russel, and K.H. Polsson. 2006. *Variation in volume production through clonal deployment: results from a simulation model to minimize risk for both a currently known and unknown future pest*. Silvae Genetica 55 (1):25-37). It involves a more complex approach to the question of how many genotypes are required, by using new assumptions on risk and a more quantifiable measure of loss in productivity to some current or known future pest.

Figure 1



Summary

The three issues discussed above point us to the same general conclusion reached by Dr. Libby almost 25 years ago: that at some point, increasing the number of genotypes does little to reduce risk of loss.

Recent research provided significant confirmation of the results from single gene models, which suggests that even in situations of more complex resistances (multiple resistances affected by multiple genes), the results are very similar. The development of policy from this kind of information requires interpretation and synthesis into operational conditions.

- Interpreting the research in #1 suggests that somewhere between 5 and 30 clones provides as much "safety" as would be experienced in an infinitely large population (e.g., a wild stand). While the results can change, as assumptions change (e.g., one genotype can sometimes be optimal), in these models, most of the results fall into the 5 to 30 genotype range with commonly expected scenarios.

- Interpretations from theory presented in #2, suggest that a population size of 6 and a population size of 10 would retain approximately 92% and 95% of the adaptive genetic variation in a particular population, respectively. Therefore, in terms of trees succumbing to some abiotic stresses (e.g., climatic events such as drought), increasing the number of genotypes past 10 does not provide any greater reductions in potential loss due to maladaptation. However, we also expect a loss of gain of about 3% going from ~5 to ~10 genotypes in a seedlot. At this point in the distribution of breeding values and gain we must also factor in how we predict genetic gain in a population of 6 versus 10 selected genotypes. It is much better estimated, at the population or seed orchard level, with 10 versus 6 or less. Moreover, as the stands mature, normal inter-genotypic competition will be at work reducing the effective number of genotypes in the stand.

- Research from #3 suggests an optimum level of diversity might exist at around 18 genotypes. However, the differences between 6 and 18 are not large, which suggests that a minimum could be somewhere around 6. These results are applicable and derived from a more complex genetic model in both the stand and in the infectious agent.

- Results from #3 also strongly suggested there was little benefit, and in fact loss of volume production, by planting individual genotypes in blocks. Random mixtures are very much preferred and will also have other benefits, in scenarios such as climate change.

Conclusion

Based on all of the research and points described above, we have chosen a minimum level of genetic diversity of 10 for seedlots registered for Crown land reforestation. There is no absolute number that is correct, as genetic diversity is only gradually affected with increasing numbers of genotypes.

Some agencies could and will choose values different than 10, if they choose to be more conservative in their management objectives. However, a minimum effective population size of 10 incorporates our best available information from several levels of scientific findings, along with a practical knowledge of how seedlots can and will be collected and used from both wild and seed orchard populations.