

alleles, and all their variation. They include populations and individual genotypes resulting from artificial selection and breeding efforts. They constitute an inter-generational resource for all forest-based demands of products and services. The various benefits sought by humankind are controlled to different extents genetically and information on this variability is fundamental to obtaining genetic advance from selection and breeding. This wide diversity of resources requires a range of methods for its exploration, evaluation, conservation, improvement, and dissemination. Modern tree improvement programs deliberately target the conservation of representative natural diversity in addition to the production of genetically restricted populations for high productivity of benefits.

Conservation of natural forest populations is traditionally undertaken through the establishment of parks and reserves (*in situ*) but it is also effected by exotic plantings (e.g., arboreta, botanic gardens, conservation stands, *ex situ*). Many of the international trials of species and provenances have been used for *ex situ* conservation. Temporary but relatively long-term conservation is also practiced through the storage of seed under appropriate conditions (commonly low temperature and moisture, depending on the species requirements). Tree breeders are now well aware of the values, needs and methods of the conservation of forest genetic resources.

See also: Genetics and Genetic Resources: Cytogenetics of Forest Tree Species; Forest Management for Conservation; Geneecology and Adaptation of Forest Trees; Genetic Aspects of Air Pollution and Climate Change; Genetic Systems of Forest Trees; Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics; Propagation Technology for Forest Trees; Quantitative Genetic Principles. **Tree Breeding, Practices:** Breeding and Genetic Resources of Scots Pine; Breeding for Disease and Insect Resistance; Genetic Improvement of Eucalypts; Genetics and Improvement of Wood Properties; Genetics of Oaks; Nitrogen-fixing Tree Improvement and Culture; *Pinus Radiata* Genetics; Southern Pine Breeding and Genetic Resources; Tropical Hardwoods Breeding and Genetic Resources. **Tree Breeding, Principles:** Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tropical Ecosystems:** Tropical Pine Ecosystems and Genetic Resources

Further Reading

- Adams WT, Strauss SH, Copes DL, Griffin AR (eds) (1992) *Population Genetics of Forest Trees*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Barnes RD (1995) The breeding seedling orchard in the multiple population breeding strategy. *Silvae Genetica* 44(2-3): 81-88.

- Burley J and Styles BT (eds) (1976) *Tropical Trees: Variation, Breeding and Conservation*. Linnean Society Symposium Series no. 2. London: Academic Press.
- Eldridge K, Davidson J, Harwood C, and van Wyk G (1994) *Eucalypt Domestication and Breeding*. Oxford, UK: Clarendon Press.
- Fins L, Friedman ST, Brotschol JV (eds) (1992) *Handbook of Quantitative Forest Genetics*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Kanowski PJ (1993) Forest genetics and tree breeding. *Plant Breeding Abstracts* 63(6): 719-726.
- Larsen CS (1956) *Genetics in Silviculture*. Edinburgh, UK: Oliver & Boyd.
- Mátyás C (1999) *Forest Genetics and Sustainability*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Namkoong G, Barnes RD, and Burley J (1980) *A Philosophy of Breeding Strategy for Tropical Forest Trees*. Tropical Forestry Papers no. 16. Oxford, UK: Commonwealth Forestry Institute.
- Namkoong G, Bawa K, Burley J, and Shen SS (1991) *Managing Global Genetic Resources: Forest Trees*. Forest Genetic Resources Work Group, Committee on Managing Global Genetic Resources, National Research Council. Washington, DC: National Academy Press.
- Simons AJ (1992) Genetic improvement of non-industrial trees. *Agroforestry Systems* 18: 197-212.
- Thielges BA (1975) *Forest tree improvement: the third decade*. Baton Rouge, LA: School of Forestry and Wildlife Management, Louisiana State University.
- Wright JW (1976) *Introduction to Forest Genetics*. New York: Academic Press.
- Young A, Boshier D, Boyle T (eds) (2000) *Forest Conservation Genetics: Principles and Practice*. Canberra, Australia: CSIRO Publishing.
- Zobel BJ and Talbert J (1984) *Applied Forest Tree Improvement*. Caldwell, NJ: The Blackburn Press.
- Zobel BJ and van Buijtenen JP (1989) *Wood Variation: Its Causes and Control*. New York: Springer-Verlag.
- Zobel BJ and Sprague JP (1993) *A Forestry Revolution: The History of Tree Improvement in the Southern United States*. Durham, NC: Forest History Society and Carolina Academic Press.

Forest Genetics and Tree Breeding; Current and Future Signposts

R D Burdon, New Zealand Forest Research Institute Ltd., Rotorua, New Zealand

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Introduction

The context of forest tree improvement is changing and will continue to change. Upgraded processing

technology, the development of new products, global economic changes and associated changes in markets, biotic events, plus changes in crop management systems, will all tend to change breeding goals. The classical breeding methodology is likely to undergo basically incremental changes made possible by a combination of more refined algorithms, upgraded software, and continued increases in computing power. Advances in propagation technology, some more or less classical, some much more radical, will favor updating of both breeding goals and crop management systems. Management of the populations used in total breeding programs will become a more pressing issue as genetic advances continue, with the associated tendency to narrow genetic bases. Novel gene technology, directed at identifying existing genes or at introducing new ones, is being widely explored, yet remains unproven. Genetic modification has many attractions, including reducing lead times and expanding the range of prospective breeding goals, but in forest trees poses some special risks and requires prolonged testing of transformants. While new biotechnology promises much, it is widely seen as a powerful supplement to classical breeding rather than a substitute for it. Institutional and economic changes, along with rapid changes in technology, are changing the ways in which forest genetic improvement is pursued. Collaborative structures are coming under severe pressure, planning horizons are becoming shortened, and field-based work is tending to lapse in the face of stagnant funding combined with a shift towards biotechnology.

At the same time, and counter to the genetic improvement that is a key part of intensive domestication, there is a movement away from interfering with natural genetic processes and towards management of natural ecosystems. Yet to retain this option may require the productive capacity of intensive, highly domesticated plantations; and to implement it effectively may require research information from modern gene technology.

Plantation Crop Improvement

Evolution of Breeding Goals

Breeding goals initially tended to focus on growth rate and tree form, with general health and adaptation as prerequisites. However, the goals have almost always evolved as breeding has progressed, with new information on biotic factors, genetic parameters, market demands, and the underlying wood characteristics that meet those demands. The goals will surely continue to evolve.

Disease and pest resistance Intensive plantation culture, plus increased and more rapid global travel, make diseases and pests more of a risk. So too will the favored status of a few intensively domesticated species that people may seek to grow over extended ranges of environments. Thus increased emphasis on improved pest and disease resistance is likely.

Wood properties Impetus for achieving genetic improvement of wood properties can be expected from several directions. On the one hand, there is greater sophistication among wood processors and in the markets. On the other, there is a widespread tendency for practices that reduce the effective growing costs, notably use of fertilizers and lower stockings in order to shorten rotations, plus genetic gains in growth rate, to militate directly and indirectly against wood quality. Thus there is a call both to tailor wood properties better to market needs and to offset adverse impacts of reducing growing costs, to improve net value.

Portfolio approach Despite the greater sophistication, market requirements will remain uncertain, especially for species that are unsuited to extremely short rotations. One way of addressing such uncertainties is to deliberately grow a 'portfolio' of well-characterized but differentiated breeds in the hopes that one or more may eventually command a high premium in a market niche while the others are all routinely marketable by virtue of being well characterized.

Targeting by hybridization Early on in tree breeding, interspecific hybridization was pursued widely and somewhat uncritically, probably because many poplar hybrids gave strong, often almost unconditional heterosis (superior hybrid vigor) and were readily amenable to mass vegetative propagation. Many species hybrids, however, show no clear heterosis, and/or pose major problems of mass propagation. More recently, it has become appreciated that careful choice of parental populations or genotypes can strongly influence the merit of hybrids, that there are specific situations where heterosis can result from complementarity of site tolerances or pest or disease resistance, and that economic advantages can accrue from certain combinations of attributes even in the absence of actual heterosis, while advances in propagation technology can overcome the historic difficulties in mass propagation. Even with past difficulties, some nonpoplar hybrid combinations have proved successful, and there is likely to be a resurgence of experimental hybridization, both interspecific and interprovenance.

Impacts of new propagation systems and other biotechnology Improved vegetative propagation systems are making possible mass propagation of individual clones in a wider range of species. The consequent clonal systems can change breeding goals in several ways. They will facilitate the selection of ideotypes that may not be strong competitors but can, as pure crops, be especially productive. This would be matching long-term trends in much crop breeding, whereby certain features that can militate against competitive ability can actually favor high economic productivity. Thus some long-term gains in production may stem from exploiting divergences between competitive ability and productivity, although the scope for this is necessarily relatively limited when trees are grown for stemwood production. Yet in future the divergence that exists may become the basis for wringing out further gains in productivity. Moreover, various features of stem architecture that favor competitive ability also represent highly undesirable within-log variation in wood properties. For some traits, like resistance to climatic damage, clonal selection may be much more powerful, since much wind damage may reflect physical interactions among neighboring genotypes rather than the inherent susceptibility of each and every genotype to such damage. Routine screening of large numbers of candidate genotypes for such crop-performance traits is prohibitively costly and time-consuming, so a major challenge is to develop the capability to characterize the appropriate ideotypes for improving such traits.

Less radical is the potential for clonal forestry to target ideotypes that represent intermediate expression of traits, since use of clonal material avoids the variation arising from genetic segregation. This, however, will only be worthwhile for traits of high heritability.

Genetic engineering, which is addressed later, can of course make it possible to address breeding goals that are basically inaccessible when using naturally occurring material. It can also be used as a research tool, to provide information with a range of applications.

Classical Breeding

Quantitative methodology

Selection Algorithms for estimating (or predicting) genotypic values from data are likely to undergo some incremental refinement. However, the limiting factors may remain information on economic-worth functions and genetic intercorrelations, poor economic information being a major problem in the presence of adverse genetic correlations; this calls for

good understanding of cost and price structures in production systems, although uncertainty concerning future markets will bedevil longer-rotation species. To some extent, this problem can be finessed by deploying differentiated breeds, which exploit differences between environments and end-uses in the comparative economic weights of different traits. In effect, this is a means of exploiting global nonlinearities in economic-worth functions for different traits. However, with clonal forestry systems there is the prospect of exploiting various nonlinearities to a greater degree.

Trial layout Theoretical efficiency of experimental layouts for selection has been widely studied, but often in relation to fixed total numbers of individuals planted. Optimality in terms of cost-efficiency of genetic gain, however, remains the ideal. While it is almost always the subject of operational guesses, explicit quantitative analysis has seldom, if ever, been published.

Data analysis While experimental layouts can be refined, the efficiency of selection therefrom may remain limited by the inherent effectiveness of block layout schemes for partitioning environmental effects. Another approach is to use the data to estimate both the local environmental effects and the genotypic effects, in order to achieve better estimates of genotypic values. Such neighborhood-adjustment or spatial analysis has already been significantly developed, but guidelines as to optimal algorithms in given situations remain to be established with any high degree of confidence. Establishment of better guidelines and more extensive use of such analysis are foreseen, especially with continued improvements in software and computing power.

As tree-breeding programs progress, population structures are typically becoming more complex, with overlapping generations and multiple classes of relatives. This increases the call for sophisticated data analysis for selection, thus strengthening the traditional affinities with animal-breeding methodology.

Stochastic simulation For general optimization studies, increased stochastic simulation is foreseen, since it is a powerful tool not only for predicting outcomes but also for assessing associated risks by characterizing distributions about the most likely outcomes.

Genotype–environment interaction ($G \times E$) Genotype \times environment interaction, whereby the comparative performance of different genotypes will vary according to the environment, remains an important

issue for genetic management of forest trees. It involves: (1) geographic transference rules for deploying material; (2) possibly structuring breeding populations into units to serve different environments; and, (3) even without such differentiation of breeding populations, selective deployment of planting-stock genotypes in different environments. A challenge remains to characterize the roles of environments in generating interaction, so that candidate genotypes can be tested more efficiently by choosing near-optimal subsets of environments for testing. In that way, it should be possible to maximize the efficiency of screening candidates for performance across the range of environments over which the species may be grown. Such an approach will contrast with much of the traditional methodology for studying $G \times E$ in crop plants, which has focused on the interactive behavior of finite numbers of stabilized cultivars and is the subject of a voluminous literature. More specifically, a challenge exists to make joint use of data on both test performance and environmental particulars for characterizing the roles of environments in generating interaction.

Forwards versus backwards selection The term 'backwards selection' is classically applied to selection on the basis of progeny-test performance, as in roguing or reconstituting seed orchards. Forwards selection applies classically to selection of seedling ortets within families created by crossing between superior parents, as in turning over generations in a long-term breeding population. While backwards selection gives high confidence in individual selections, it may sacrifice too much in terms of the genetic gain that can be virtually assured from forwards selection. Moreover, the distinction between forwards and backwards selection can become blurred in clonal selection, where either there can be dedicated clonal trials or seedling offspring in the breeding population can be clonally replicated. The latter case effectively allows forwards selection while reducing exposure to $G \times E$.

Population management

The status of controlled pollination Controlled pollination and the associated control of pedigree have been cornerstones of many existing breeding programs. However, full control of pollination can either limit the number of combinations in which parents can be crossed or incur excessive cost. Full control of pedigree, while it maximizes control of nominal inbreeding, effectively limits the manageable size of a breeding population, which can lead to loss of low-frequency alleles and severely limits the

chances of capturing the infrequent to very rare favorable mutations. Sacrifice of full pedigree, however, need no longer be the irreversible step that it has been, thanks to DNA marker technology.

Refining of population structure Management of domesticated genetic resources has not usually reached the stage at which appreciable inbreeding is unavoidable. Neighborhood structures make mild inbreeding a natural feature of the genetic systems of many, if not most, forest tree species, so such inbreeding should be easily enough accommodated. However, there are signs of rekindling interest in some quite close inbreeding as a breeding tool, in order to purge genetic load and to build up frequencies of desired alleles more rapidly — only by selfing is it possible to achieve perfect assortative mating for all traits.

Breeding populations, where programs have elaborated beyond relatively simple variations of mass selection, have basically been structured around the production of seed orchards. However, where clonal forestry systems are the norm, the tendency has been for little to be developed in the way of formally structured breeding populations. In future, we must look to structuring breeding populations in the expectation that they will provide clonal material. Two likely implications are: (1) that individual offspring genotypes may be clonally replicated, particularly across sites; and (2) that some inbreeding may be more readily tolerated, because associated bias in family-mean information may matter less for selection.

In any event, a breeding population with clonal replication allows a closer integration of elements of both forwards and backwards selection.

Allowing for climatic change Since climatic change is a near certainty and, from latest knowledge of quaternary history, an ever-present risk, any management of genetic material should make some provision to accommodate such change. Even without the human influences that are currently driving global warming, recent climatic changes have sufficed to create widespread suboptimality of local populations. While most natural populations, with high rates of natural mortality and the consequent 'soft,' density-dependent selection, are sufficiently heterogeneous to allow considerable natural wastage of maladapted segregants, plantation forestry which is based on low ratios of final-crop trees to trees planted will not accommodate such wastage so readily. It seems logical to anticipate likely climatic change in locating at least some of the breeding-population and gene-resource material.

Deployment Issues

Family and clonal forestry Genetic uniformity has in principle enormous advantages for growing and utilization, although clonal monocultures are subject to notorious biotic and bioclimatic risks. For many species, therefore, single clones cannot safely be regarded as crop cultivars in their own right; rather, they should be components of a composite cultivar population, akin to the multiline cereal cultivars that have been synthesized to provide durable disease resistance in the face of mutation and adaptive shifts in pathogen populations. It remains to be seen what proportions of such clonal assemblages in forest trees will be deployed in mosaic or mixture respectively. For clonal material, management regimes can be precisely tailored to individual clones, or even to mixtures of clones that may be silviculturally similar but diverse with respect to ancestry and cryptic traits such as resistance to new pathogens.

Short of deploying specific clones, specific families are already used in some cases to match the management and utilization of crops to genetic composition but, with the genetic segregation that can even occur within pair-crosses, such matching is likely to fall well short of what is possible with clones.

Application of Molecular Biology

Molecular biology, involving DNA technology, has already reached initial applications in tree improvement. Most of the major potential applications and the basic underpinning science, however, are still being researched. Some of that work is being done with new sources of funding. However, with stagnant funding levels, much of it is being done at significant opportunity costs in terms of gains available from conventional breeding. Yet the successful application of much of the DNA biotechnology will be strongly dependent on the field plantings of the genetic material of conventional breeding programs. Using such biotechnology will intensify the domestication process that begins with plantation forestry and continues with classical breeding, and the essence of domestication is increasing inputs in order to obtain better returns. While biotechnology can substitute for some classical breeding measures, no prospect is seen of satisfactory net overall substitution within the short term.

Markers and expressed sequences

Verification/determination of genetic identity Use of simple sequence repeats (SSRs), also called microsatellites, has enabled verification of both clonal identity and pedigree. It has also revealed an embarrassing rate of errors in genetic identity, such errors becoming more and more crucial as a breeding

program advances, on account of the increasing levels of genetic gain that are dependent on correct identity.

Determination of population origins While verifying an intended pedigree may now be relatively straightforward, there can be much greater challenges in identifying population origins of material, because the polymorphisms (presence of different alleles or forms of genes at individual loci within the genome) that differentiate individual genotypes or pedigrees represent noise variation in trying to differentiate populations. Such a capability, however, may be crucial for addressing problems of genetic contamination, which may be acute in the gene resources that underpin breeding populations.

Pedigree reconstruction Pedigree reconstruction, as opposed to the verification of a specific pedigree, has been proposed in respect of paternity as a means of saving on the costs associated with multiple pair-crosses per parent. However, there are likely to be situations where reconstruction of pedigrees, from large numbers of possible parents, may yet be needed, as in a biotic crisis when it may be necessary to select for disease resistance in unpedigreed commercial stands. For that, it appears that much more powerful marker systems will be needed in order to give essentially unambiguous answers.

Use of DNA markers for selection Use of neutral genetic markers to locate and characterize quantitative trait loci (QTL) in the genome (see below), as an aid to selection, has already been the subject of much experimental and theoretical research. Such information may be used in conjunction with phenotypic information on the trait(s) concerned, in true marker-aided selection (MAS) or, if practiced before phenotypes can be expressed, can be done entirely on marker information. Even after some theoretical pitfalls have come to light it appears promising, and it has worked well in some crop plants but not others. However, its efficacy in forest trees remains to be demonstrated. Because forest trees are outbreeders the general linkage disequilibrium (LD) that forms the ideal condition cannot be expected, except perhaps in hybrids between species that are fixed (having zero or 100% gene frequencies) with respect to different QTL and linked markers.

Genomics Genomics, the study of the physical arrangement of genes and noncoding DNA in the chromosomes, and the base sequences and gene functions, has become the focus of major research efforts.

Comparative The close genomic similarities between genomes of various important forest trees will favor collaborative efforts, since findings in one species can often be applied, in various possible ways, to one or more other species. The very high degree of synteny among certain species, e.g., within the genus *Pinus*, with the same genes at the same genetic loci having the same function, allows information to be readily applied from one such species to another. Quite remarkable, however, are the orthologies between very distantly related organisms, whereby very similar DNA sequences can code for closely homologous gene action despite wide differences in general plant structure and organization. Commonalities between the roles of the same genes (or close homologs) in different organisms can provide the basis for what S.H. Strauss refers to as genomics guided transgenes for exploratory use in genetic engineering.

Functional Study of pathways of gene action, based on expressed sequence tags, can, apart from yielding fundamental knowledge, help identify the effects of particular genes, and the feasibility of various prospective breeding goals. Genetic modification can be a powerful research tool, allowing the study of the metabolic and phenotypic impacts of altering the expression of existing genes or introducing alien genes.

Targeting breeding goals While there may arise some conditions that allow general LD in out-breeders, these conditions are often unlikely to obtain. This creates an additional call for the ideal situation of being able to identify readily the genes of interest by the base sequences, which would allow true gene-assisted selection (GAS).

Applications of genetic engineering Genetic engineering, or genetic modification (GM), entails inserting DNA sequences to modify the activity of existing genes, or introduce new functional genes. Much of the research to date has aimed at proving the concept for the species concerned. Several operational applications are being widely pursued, notably pest resistance, herbicide resistance, and reproductive sterility. GM is also being explored as a means of improving certain wood properties. It promises certain gains that may substantially exceed those already promised by the typically high heritabilities of wood properties. However, there remain great attractions in using GM essentially as a research tool, using the insertion of DNA sequences to probe the roles of certain genes and their pathways of action. Indeed, this could yield some information that may eventually be applied in conventional

breeding. GM, however, is intensely dependent on *in vitro* culture systems.

While all technologies have their own risks, the risks of GM attract special public attention, and in the case of forest trees they have some special features. They must therefore be addressed as part of the research on developing GM technology for forest trees, and be seen to be so.

Propagation Technology

Seed propagation will remain necessary, at least to produce the genetic recombinants that provide the candidates for the next cycle of recurrent selection. For many species, however, seed production will continue to be needed for mass production of commercial stocks, either directly or as a platform for mass vegetative multiplication. Pending, or failing, the development of mass vegetative multiplication, incremental improvements can be expected in seed-orchard technology, to improve yields and physical quality of seed and to avert unwanted external pollination. Care may be needed, however, in the choice of environment for seed production. In some spruces, in particular, the inherent growth rhythms and climatic tolerances of seedlings have been found to be affected by climatic conditions during a particular phase of seed production. Thus the choice of a congenial climate for producing seed may compromise adaptation to the harsher climates for which the seedlings are intended.

Rooting of cuttings has become a mature technology for mass-producing planting stock in many species, including some that were traditionally propagated as seed. Its development will surely continue in some quarters. Micropropagation, or tissue culture, will be refined further in many cases and developed for additional species, often for initial rapid multiplication to complement cuttings production. Embryogenesis, the other *in vitro* system, offers even higher multiplication rates, and has special promise as a means of providing recipient material for GM. Often, however, *in vitro* systems need to be refined in order to work with any genotypes of choice within a species.

Full control of maturation state in clonal material is extremely desirable, if only to allow clones to be mass-propagated after their merit has been proven. Several technologies exist to check the process of maturation (or physiological aging), with cryogenic storage looking increasingly promising. However, achieving true reversal of maturation, or rejuvenation, in somatic tissue would have enormous strategic significance. Still unrealized for a great many species that do not sprout from stumps, it

remains perhaps the biggest single challenge in propagation technology.

Technology Portfolios

New biotechnologies are developing rapidly, and the many prospective technologies for individual steps in the process of genetic improvement can lead to large numbers of potential technological pathways for delivering enhanced genetic gains. Individual technologies typically have risks, of not performing as hoped, at least for the species in question. Even if a technology succeeds in itself, it may fail because it belongs in a pathway that is outflanked by another pathway. The problem is that, while each technology needs a concerted research effort, there needs to be a portfolio of alternative and complementary technologies under investigation in order to spread risks.

Interactions with Other Disciplines

Wood science, processing technology, and product development Increasing emphasis is being placed on genetic improvement of wood properties, for a number of reasons. Easily obtainable genetic gains have often been already captured for traits involving silvicultural performance and tree form. At the same time the pursuit of shorter rotations, fertilizer use, and lower stockings, all to reduce effective growing costs, call for genetic improvement to offset consequent declines in wood quality. Furthermore, wood processors and end-users are often demanding tighter quality specifications. Wood properties often appear to be very amenable to conventional breeding, but can be very expensive to evaluate (especially product-performance properties), while the role of specific basic properties in governing product performance is often little known. Major research efforts are afoot to study wood chemistry and ultrastructure in relation to product-performance properties, and the developmental pathways in expression of genes significantly affecting wood properties, with comparative genomics and genetic modification as research tools. Such work is directed at the full range of existing wood products, and the possibilities of new products.

Pathology Improved disease resistance is often needed for plantation crops, in the face of additional hazards posed by monocultures and growing preferred species over a range of sites. Such resistance often needs to be durable against genetic shifts in pathogen populations. Use of DNA markers promises to detect the various genetic resistance factors in the host, to help aggregate the multiple resistance factors needed to assure durability.

Other disciplines Of note are the overlapping areas of physiology and biochemistry, as essential adjuncts of functional genomics.

Impacts of Institutional Changes

Forest genetics research and tree breeding have historically been done largely under government agencies, or else multiparty cooperatives. Governments have tended to withdraw from such activities, with global pressures to reduce taxes. The development of biotechnology, particularly relating to DNA, has encouraged much more proprietary attitudes towards intellectual property. That in turn, along with many recent changes in forest ownership, is placing tree-breeding cooperatives under pressure. All these factors are also exerting pressure on the long-term strategic management. Also discouraged by proprietary attitudes toward individual technologies, which militate against collaboration, are adequate risk-spreading technology portfolios.

Species for Domestication

The list of forest tree species that have been subject to intensive domestication, including elaborate breeding programs, is relatively short, rather like the main food crops. The cost of intensive breeding will tend to focus domestication on a limited number of forest tree species. On the other hand, the perenniality and lifespan of forest trees make environmental adaptation much less flexible, which may tend to stop the list of domesticated forest tree species from remaining extremely short. Nevertheless, pines, eucalypts, and acacias seem likely to predominate among the intensively domesticated species.

Management for Conservation

Plantation forests have assumed great economic importance, despite occupying only a small area relative to native forests. They also have potentially great ecological importance, in that they may serve to relieve exploitation pressures that might otherwise affect natural forests (although clearance for agriculture is another matter). However, preserving and managing native forests, either for controlled exploitation or pure conservation, is often far from straightforward. Monitoring breeding systems and measures of genetic diversity can help indicate the likely impacts of population size and of cutting and regeneration regimes on long-term viability of populations. For this, information on reproductive biology will be very important. Some indications are being obtained of the impacts of certain exploitation

regimes on the structure and diversity of populations. However, the most appropriate measure of genetic diversity is problematic. Diversity reflected in neutral genetic markers is often poorly correlated with the functional diversity that is often crucial to site adaptation and to response to artificial selection, such that common-garden field trials are often needed to relate functional diversity to marker diversity as well as elucidating genecology and within-species taxonomy. Common-garden experiments, however, while they can reveal much, will often need to be complemented by ecophysiological studies. Such studies can identify the specific environmental factors that cause stress, and the ways in which stress arises. As such, they can be powerful tools for applying results of the common-garden experiments beyond the particular environments where they are located. Of interest are indications that major functional diversity can be governed by promoter regions rather than coding regions of genes.

The genetic component of conservation management is likely to depend on the ecological validity of management regimes. Misguided exclusion of fire has often proved very counterproductive. Questions must now arise concerning the appropriateness of trying to impose uneven-aged and essentially continuous canopy structures on each and every species.

See also: Genetics and Genetic Resources: Genetic Systems of Forest Trees; Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics. **Tree Breeding, Practices:** Breeding for Disease and Insect Resistance; Genetics and Improvement of Wood Properties. **Tree Breeding, Principles:** A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Economic Returns from Tree Breeding. **Tree Physiology:** Stress.

Further Reading

- Burdon RD (2003) Genetically modified forest trees. *International Forestry Review* 5(1): 58–64.
- Dutkowski GW, Costa e Silva J, Gilmour AR, and Lopez GA (2002) Spatial analysis methods for forest trials. *Canadian Journal of Forest Research* 32: 2201–2214.
- Kibblewhite RP and Shelbourne CJA (1997) Genetic selection of designer trees for different paper and pulp grades. In: *Transactions of the 11th Fundamental Research Symposium Fundamentals of Papermaking Materials*. Cambridge, UK, pp. 439–472.
- Lambeth C, Lee B-C, O'Malley D, and Wheeler N (2001) Polymix breeding with parental analysis of progeny: an alternative to full-sib breeding and testing. *Theoretical and Applied Genetics* 103: 930–943.
- Lambeth C, Lee B-C, O'Malley D, and Wheeler N (2001) Polymix breeding with parental analysis of progeny: an

alternative to full-sib breeding and testing. *Theoretical and Applied Genetics* 103: 930–943.

- Mátyás C (ed.) (1999) *Forest Genetics and Sustainability*. Dordrecht The Netherlands: Kluwer Academic.
- Muller-Starck G and Schubert R (2001) *Genetic Response of Forests to Changing Environmental Conditions*. Dordrecht, The Netherlands: Kluwer Academic.
- Plomion C (2001) Wood formation in trees. *Plant Physiology* 127: 1513–1523.
- Skårøppa T and Johnsen Ø (1999) Patterns of adaptive variation in forest tree species: the reproductive environment as an evolutionary force in *Picea abies*. In: Mátyás C (ed.) *Forest Genetics and Sustainability*. Dordrecht, The Netherlands: Kluwer pp. 49–58.
- Strauss SH (2003) Genomics, genetic engineering, and domestication of crops. *Science* 300: 61–62.
- Strauss SH and Bradshaw HD (eds) (2004) *The Bioengineered Forest: Challenges for Science and Society*. Washington, DC: RFF Press.
- Stroup WW (2002) Power analysis based on spatial effects mixed models: a tool for comparing design and analysis strategies in the presence of spatial variability. *Journal of Agricultural, Biological and Environmental Statistics* 7: 491–511.
- Unifying perspectives of evolution, conservation and breeding (2001) Proceedings (eight papers), Symposium in Honour of Dr Gene Namkoong. *Canadian Journal of Forest Research* 31: 561–632.
- Walter C and Carson MJ (eds) (2004) *Plantation Forest Biotechnology for the 21st Century*. Trivandrum, Kerala, India: Research Signpost.
- White TL, Neale DB, and Adams WT (2003) *Forest Genetics*. Wallingford, UK: CAB International.
- Yanchuk AD (2001) The role and implications of biotechnological tools in forestry. *Unasylva* 204(52): 53–61.

Conifer Breeding Principles and Processes

A D Yanchuk, British Columbia Ministry of Forests, Victoria, BC, Canada

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Introduction

Conifers or gymnosperms occupy many important forest ecosystems and are some of the oldest known species on the planet. Of the thousands of conifer species known to exist on earth, probably fewer than 100 have received even preliminary genetic studies, and only a dozen or so are under any kind of intensive tree improvement and breeding efforts. Some of these species, such as Monterey pine (*Pinus radiata*), have provided some of the most successful