enhance gains from tree breeding, but must be tested for effectiveness, safety, and public acceptance.

See also: **Genetics and Genetic Resources**: Genecology and Adaptation of Forest Trees; Genetic Systems of Forest Trees; Propagation Technology for Forest Trees; Quantitative Genetic Principles. **Tree Breeding, Practices**: A Historical Overview of Forest Tree Improvement; Breeding for Disease and Insect Resistance; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts; *Pinus Radiata* Genetics.

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Economic Returns from Tree Breeding

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Introduction

The economic returns from tree breeding can be estimated over time-frames ranging from the short to the long term, on scales varying from that of an individual enterprise to the entire extent of a species' use, in terms of each individual strategic and technical decision or of their cumulative effect, and in purely financial or in wider economic terms. The gains realized by particular stages or elements of tree breeding can be so dramatic that only the most cursory economic evaluation is necessary to substantiate them; conversely, strategic and technological options may be so complex, and realization of benefits so contingent on particular assumptions, that sophisticated economic analyses are necessary to inform investment decisions.

As for many forestry activities, economic analyses of tree breeding investments are variously complicated by long investment and rotation cycles, uncertainties about costs and benefits over these long time horizons, and by the challenges of accounting for nonmarket benefits and costs. However, there is both a long history of, and an increasing focus on, economic analyses of tree breeding investment decisions, which have contributed significantly to the design and development of tree breeding strategies and programs.

Economic returns from tree breeding are determined by species- and program-specific combinations of the following key parameters:

- the genetic characteristics of the population subject to breeding–reflecting inherent levels of genetic variation in a species, the extent to which that variation has been sampled in the population subject to breeding, and the stage of breeding of the population
- the breeding strategies and technologies employed, and the breeding objectives specified
- the value of the products and services, and the scale of deployment, of improved populations
- the institutional arrangements for breeding and benefit sharing.

Our discussion of the topic is structured around these parameters. In general, they are better characterized for longer-established, advanced industrial tree breeding programs, such as those for loblolly pine (*Pinus taeda*) in the southeast USA, radiata pine (*P. radiata*) in the southern hemisphere, or *Eucalyptus* species in continents other than North America. Industrial tree breeding programs are typically more advanced and data-rich, and have markets and benefit regimes that are generally better defined, than are programs for the breeding of trees for nonindustrial uses. Consequently, while the latter also have the demonstrated potential to make very significant economic contributions to people's livelihoods and to environmental services, they are not necessarily easily evaluated by conventional economic analyses applied to investment decisions.

Realization of returns from any tree breeding is dependent on appropriate silviculture and management of genetically improved trees, and appropriate processing of their products. There are many cases where predicted or potential gains from tree breeding have not been realized because one or more of these technologies has not been optimized or implemented for genetically improved trees or products. An example of the profound impact of silviculture on the capture of economic returns from breeding is illustrated by **Figure 1**.

Figure 1 Economically significant differences due to silviculture in first-generation Caribbean pine (*Pinus caribaea* var. *hondurensis*) performance in coastal central Queensland, Australia. Trial age is about 20 years; the researcher stands in an experimental plot which received neither preplanting site preparation nor postplanting fertilizer application; a plot of the same genotypes, which received both site preparation and fertilizer, is in the background. The experiment was established by the Queensland Department of Forestry. Photograph by Peter Kanowski.

Evaluating Economic Returns from Tree Breeding

Like evaluation of many other forestry investments, the relatively long time intervals between investment and returns both dominate and complicate economic analyses of returns from tree breeding. Historically, most industrial tree growing rotations have been more than 25 years, complicating direct comparisons of more-improved and less-improved material. While many industrial plantations and nonindustrial species are now managed on much shorter rotations, significant practical problems remain in making accurate comparisons. Improved genotypes seldom grow in an environment identical to that of earlier tree crops, as both environments and management practices change. Technological changes in all aspects of tree growing – in the nursery, in silviculture, and in product processing – have profound and interconnected impacts on tree performance and on product recovery, value and economic returns.

Economic returns from breeding may also be evaluated from perspectives of different interests, as follows.

1. Those who have invested, or are considering investment, in tree breeding activities. Typical investment criteria are those such as the internal rate of return, present net worth, or benefit–cost ratio of funds invested, or the minimum scale of deployment of bred material required to break even. These assessments may be applied to whole breeding programs, or to particular separable aspects of them, such as the decision to invest in a new seed orchard or in vegetative rather than seedling propagation.
2. Tree growers, who vary in scale from corporations or public sector agencies with annual planting programs on the order of millions of plants, to small-scale resource-poor farmers who, at the extreme, may be making decisions about individual trees. In both cases, however, decision criteria are likely to reflect an assessment of likely net gain, perhaps including nonmarket values, over the investment period. Criteria may include implicit or explicit assessment of the risks of not investing – for example, in terms of poor adaptation of unimproved material or potential loss of market share – as well as the anticipated direct financial gains from the investment. For those with limited access to financial resources, such as poor farmers, the immediate cost may be a more significant determinant of the investment decision than the ultimate returns on investment.
3. Purchasers of forest products and services, ranging from governments or communities willing to pay for environmental services, to large-scale industrial wood-processing enterprises, to individuals

purchasing individual products (e.g., fruit or poles) at a local market. Ultimately, their decisions provide the market signals on which the decisions of the preceding two groups stand or fall. Their decisions may be expressed through a price differential, or simply through giving preference to particular genotypes, leaving those without such genotypes as residual suppliers with more limited market access.

For these reasons, there is no single economic criterion against which tree breeding investments are or should be judged. The balance of benefits between private interests and public good may also change over time, necessitating evaluation against different criteria. As in other areas of innovation, there is often a phase in which the benefits of tree breeding are captured principally by a few breeders, tree growers, or product processors who have access to new material or technologies. As these materials or technologies become more widely adopted, there is no longer a comparative advantage for the innovators, and the economic benefits from tree breeding will accrue to society more generally rather than to those leading the innovation.

The Genetic Characteristics of Tree Populations

Forests and woodlands are the most biologically diverse terrestrial ecosystems. With some notable exceptions, the tree species which are the defining feature of these ecosystems have been little domesticated relative to the crop plants or animals upon which agricultural production is based. Although their gene pools have been altered, sometimes profoundly, by a wide range of human activities, the genetic resources of most tree species remain rich, a consequence of the longevity of individual trees, their outcrossing breeding system, the extensive geographic distribution of many species, and the high proportion of genes common across most populations in most species. Even for those species that have been the subject of informal domestication or of organized breeding, tree breeders still have – in general – relatively easy access to extensive gene pools which are highly diverse compared to those of other plant species, although some of these genetic resources are now threatened by the unprecedented global rate and scale of forest loss and degradation over the nineteenth and twentieth centuries.

Consequently, there are few tree species for which levels of genetic variation are insufficient to expect significant genetic gains from breeding, although the extent to which these genetic gains translate to economic gains depends on the factors discussed below. *Pinus torreyana* is one such example, as a consequence of a genetic bottleneck in its evolutionary history. Another example is the Australian Gondwanan relic species Wollemi pine (*Wollemia nobilis*), represented by only a few individuals in the wild. Even in such cases, where the species has a commercial value, significant economic returns may be possible simply from propagation. This is the case for Wollemi pine which, although discovered only in 1994, is now being vegetatively propagated on a scale sufficient for large-scale commercial release as an ornamental in 2005, using propagation technologies developed for the related Australian industrial plantation species *Araucaria cunninghamii*. The economic returns from this venture are anticipated to be both commercially attractive and sufficient to contribute significant funds towards conservation efforts for the species.

Stages of Tree Domestication and Breeding

Some tree species have a long history, often of millennia, of informal domestication. These are species important for food and in traditional land use systems: e.g., those of the genera *Artocarpus*, the jakfruits and breadfruits of Asia, or *Mangifera*, the tropically widely distributed mangoes; the leguminous genera *Faidherbia* and *Leucaena* of, respectively, Africa and the New World; or *Fraxinus* and *Quercus*, the European ashes and oaks. The situation of these species, subject to many generations of informal selection and often to induced or spontaneous hybridization, parallels that of other long but extensively domesticated crops, with an often imprecise distinction between natural and naturalized populations. Consequently, the genetic resources available for breeding comprise a highly heterogenous mixture, ranging from highly selected individuals with significant immediate economic value to wild relatives whose value has yet to be established and which may take many cycles of breeding to realize.

Relatively few tree species (around 500 of the presumed more than 50 000) have been subjected to any level of deliberate selection or breeding. The breeding histories of these species are quite contrasting, with contrasting implications for breeding options and associated economic returns.

1. A small group of tree species is of high significance in cultivation in horticultural or estate systems, or in arboriculture. Examples include apple (*Malus* spp.), coffee (*Coffea* spp.), coconut (*Cocos nucifera*), rubber (*Hevea brasiliensis*), and numerous ornamentals. While the principles of assessment of economic returns from these species do not differ

from those for other trees, and tree breeders have much to learn from these industries, the associated body of literature is sufficiently distinct and well addressed elsewhere to not be the subject of this review.

2. Around 200 species have been subject to at least one cycle of breeding (i.e., selection, mating, and testing); a similar number have simply been included in genetic tests. Those subject to the most intensive breeding efforts are the 60 or so species, principally of the genera *Acacia*, *Eucalyptus*, *Picea*, *Pinus*, *Pseudotsuga*, *Populus*, *Larix*, and *Tectona*, that have been improved for industrial wood production (i.e., for solid or reconstituted wood and for pulp) over typically not longer than some fraction of the past 50 years. These populations provide the bulk of our experience and information about the tree breeding and its economic returns, and a few of them provide our only experience of returns associated with advanced generations.
3. Another 60 or so more taxonomically disparate species, amongst them some of the long-domesticated species, have become the subject of breeding for nonindustrial objectives in the past few decades. Examples include species of the tropical and subtropical *Acacia*, *Azadirachta*, *Calliandra*, *Calycophyllum*, *Casuarina*, *Dalbergia*, *Faidherbia*, *Gliricidia*, *Grevillea*, *Irvingia*, *Leucaena*, and *Prosopis*, and the temperate *Acacia*, *Alnus*, and *Salix*. Breeding objectives and strategies, and management regimes, for these species are typically more diverse than for those bred for industrial wood production, and most of the economic returns realized to date are associated with the early stages of breeding.

Figure 2 Economically significant variation in a Douglas-fir (*Pseudotsuga menziesii*) provenance trial, Limousin region, France. Trial age is about 10 years; the student stands between blocks representing an Oregon (background left) and northern British Columbia (foreground and right) provenances. The experiment was established by Office National des Fôrets. Photograph by Peter Kanowski.

Economic Returns from Early Stages of Breeding

The early stages of tree breeding typically involve species and provenance selection, the selection of individual trees within these populations, and the establishment of seed orchards to provide improved material for both production and for further breeding. Given the undomesticated or little-domesticated status and genetic richness of most tree species, substantial genetic gains are possible from the basic first step of species and provenance selection; further substantial gains can be achieved from subsequent individual tree selection and the establishment of seed orchards. The economic gains associated with these genetic gains depend on both the cost of undertaking the breeding activities and on the economic value of the improved material.

The genetic gains achieved at these stages in most tree breeding programs have, almost invariably, been large and cost-effective; they are typified by **Figure 2** which, for a striking but not atypical case, illustrates the extent to which simple provenance selection influences the viability of a species for economic use. Selection on this fundamental basis, for both immediate gain and as the foundation for subsequent breeding, remains the basis of economic returns for new programs, exotic environments, or new breeding objectives. The gains from these early stages of selection can be enhanced by judicious use of any a priori knowledge of patterns of variation and environmental adaptation over a species' range in both natural and exotic environments.

Almost all quantitative data describing genetic and economic gains from this stage of breeding originate from industrial tree improvement programs, many programs now have sophisticated systems for updating breeding and genetic values for individuals, such as Australia's 'Treeplan' or New Zealand's 'GF-Plus' scheme. The gains realized in commercially utilizable stem volume, the initial focus for most industrial programs, from provenance and the first generation of individual tree selection have typically been at least 10% (where provenance differences are small), and often up to 30–50% (where provenance differences are great), over unimproved population means. Gains realized have reflected, to varying extents, selection of well-adapted provenance(s), effective within-provenance selection, and in some cases the release from inbreeding depression associated with natural or small populations. In the most straightforward and historically typical case, where growers' returns for a particular industrial species were dependent simply on the value of wood produced in large-scale afforestation, these genetic gains corresponded to very favorable returns on investment; benefit–cost ratios greater than 5, and internal rates of return of 10–15%, are commonly reported.

Data for nonindustrial species are scarce, reflecting the more recent origins of formal improvement programs. However, nonindustrial tree species appear to be no less genetically variable than industrial species, suggesting that expectations of realized gains should be comparable. The attribution of costs and benefits does, however, differ significantly between many industrial and nonindustrial species; in the former case, benefits typically accrue to an industrial-scale enterprise, whereas in the latter, the intended beneficiaries are typically resource-poor small-scale farmers. The increasing scale of 'outgrower' schemes, under which small-scale farmers grow industrial tree crops under contract to forest products enterprises, blurs this distinction and provides another perspective on the evaluation of economic returns. Where outgrower schemes are well established and offer the option of access to genetically improved material at additional cost, such as for some eucalypts in South Africa, high levels of uptake of advanced material suggest that growers judge the additional cost per plant to be a good investment.

Economic Returns from Advanced Cycles of Tree Breeding

Economic returns from advanced (i.e., later) cycles of tree breeding are founded on the populations established and selections made in the initial stages. As breeding advances from initial stages to subsequent cycles, strategic objectives and breeding options have generally become more focused–for example, through the clearer definition of breeding objectives, more efficient approaches to genetic testing and selection, the better use of genetic information and advanced statistical methods, and sharper analysis of the options amongst various mating designs and multiplication options. Each of these has implications for economic returns, as we discuss below.

In general, the evidence from 'advanced' generations of tree breeding, represented by only a small number of species to date, suggests that it is possible to continue to achieve high rates of economic return over at least a few generations. The capacity to deliver continuing genetic gains and economic returns depends on:

- the clearer definition of breeding objectives and their relation to economic returns
- the better understanding, as a result of accumulating species-specific genetic information over generations, of the genetic structure and parameters of populations
- the efficient design and conduct of breeding activities, to optimize investments amongst alternative breeding strategies, and amongst the elements of tree breeding activities such as selection, mating, and multiplication
- advances in technologies, ranging from simple propagation methods to advanced biotechnologies, and including forest management and product processing technologies
- the optimization of forest and tree management regimes and product processing systems.

Each of these advances helps the breeder, grower, and processor improve the efficiency of and return from their efforts. Economic analyses of returns on investment for various individual elements of advanced generation breeding are encouraging, but analyses of actual gains realized from the overall package of advanced breeding activities await the further progress of these programs.

Breeding Strategies, Technologies, and Objectives

From the 1990s, tree breeders began to follow the lead of their animal-breeding colleagues in defining breeding strategies and objectives more explicitly and formally. Increasing sophistication and competition in markets for forest products and services, and in those for growing trees, have encouraged breeders to focus more sharply on maximizing value gain and optimizing investments – a process that requires both explicit definition of the breeding objectives and assessment of strategic options to achieve them. Technological advances in many aspects of the biological sciences and breeding operations have allowed options that were not previously possible, or enhanced the efficiency of existing options. At the same time, the large scale of deployment in some plantation forestry systems has allowed levels of investment in breeding that would otherwise not be possible, and has helped develop and prove new technologies with wider relevance, such as those for cuttings production of species previously propagated only by seed, or the many applications of molecular genetics.

Breeding Strategies and Technologies

Breeding strategies provide both the conceptual and operational frameworks for tree breeding activities, and comprise both an overall plan and its particular elements – principally selection methods, mating and testing designs, and multiplication processes. They are enabled, and constrained, by technologies relevant to breeding activities. Breeding strategy options are determined principally by the breeding objectives specified, the species' biological and genetic characteristics, the available technologies, and the human and financial resources invested. These factors depend at least in part on the value of products and services, and the likely scale of deployment, of improved populations. Strategies and technologies that deliver outcomes more quickly, by reducing the time associated with breeding activities, are generally most appealing in terms of economic criteria.

An array of breeding strategies, from simple to sophisticated, is available to the breeder. Experience in tree breeding demonstrates the economic importance of designing and implementing strategies appropriate to the species, its scale of deployment, and the production system. In general, simple strategies and technologies, such as those based on mass selection and seedling seed orchards, can be very cost-effective for species for which only limited resources can be found or justified. As the level of available investment increases, reflecting the relative economic importance of a species or judgements about its potential, more sophisticated strategies and technologies become economically accessible and justified.

Decisions to adopt, or not adopt, particular strategic options and technologies reflect an economic assessment of their benefits relative to their costs; there are many examples of how such decisions, ranging from the use of biotechnologies to the choice of propagation system or the decision to incorporate a particular trait in a breeding objective, have been informed by various forms of economic analysis. Estimation of break-even thresholds, in terms of the extent of deployment or level of gain required to justify an investment, or of the investment's likely internal rate of return, are common means of economic analysis of strategic and technological breeding decisions.

Specification of Breeding Objectives

A breeding objective is the specific combination of traits that a breeder seeks to improve, weighted according to their relative economic worth. In the first phase of tree breeding, breeding objectives were typically defined (often necessarily) subjectively and imprecisely. However, both theoretical and empirical evidence demonstrate that, as in plant and animal breeding more generally, progressing to less subjective and more accurate definition of breeding objectives is one of the most significant means of enhancing economic returns from tree breeding. Even preliminary economic information about particular production systems can considerably clarify breeding objectives, which also depend on genetic information generated by a breeding program. Consequently, the refinement of breeding objectives usually proceeds in conjunction with the progress of breeding into advanced generations.

Definition of breeding objectives has to consider both costs and income associated with the production system under consideration, which may vary for example from that for multipurpose trees grown on small-scale farms for fodder, fuelwood, and fruit to that for industrial-scale pulpwood plantations. In terms of the breeding objective, economic returns can be maximized by increasing income (e.g., from achieving higher growth rates without prejudicing wood quality), decreasing costs (e.g., reducing processing costs by altering wood properties), or both. Retirement of the breeding objective for eucalypt pulp production in Portugal offers a typical example; two generations of selection were expected to increase income by 1.5% and decrease production costs by 16%, saving $US7.2 million per annum for a 250,000 tonne pulp mill.

The economic returns associated with clearer definition of breeding objectives are dependent on the characteristics of the species being bred, the costs and income associated with particular production system and suite of products, and the scale of deployment. Notwithstanding this heterogeneity, empirical results over the past decade suggest that investment in the clearer definition of breeding objectives generates substantial economic returns to both the breeder and grower of forest products.

The Value and Scale of Deployment of Improved Populations

The economic returns from tree breeding are ultimately dependent on the value of the products and services, and the scale of deployment, of improved populations. As each of these increases, so do the capacity for investing and the potential for generating returns from investments in breeding. The value of improved populations has historically depended only on their physical wood and/or non-wood products. However, value might also be reflected in terms of the opportunity costs avoided, and expanded by the services as well as the products of trees. Breeding for disease resistance exemplifies the former, and has been demonstrated to generate very favorable benefit–cost ratios; an example is that of fusiform rust resistance in southern pines in the USA, which is expected to return benefits at least four times greater than costs. The emergence of environmental services markets, such as those for carbon or ecosystem restoration, offers additional opportunities for the definition and delivery of breeding objectives, and consequent income generation.

The scale of deployment of improved populations is a significant determinant of the income stream against which the fixed costs of breeding will be offset. For these reasons, assessment of threshold levels of deployment or uptake are a common means of economic evaluation of breeding options. The role that many governments assume, of helping to foster new industries, is one reason why many tree breeding programs worldwide began with significant public-sector involvement, often transferring progressively to the private sector as industries became established on a scale sufficient to support commercial ventures. It is also one of the reasons that the public sector retains a substantial role in breeding of many nonindustrial species.

Institutional Arrangements for Breeding and Benefit Sharing

Institutional arrangements for breeding and benefit sharing impact on the distribution of costs and benefits associated with tree breeding. Historically, access to genetic resources of tree species has seldom been restricted; more usually, access has been facilitated by strong cooperation between countries and between public and private sectors. For reasons outlined above, most tree breeding programs began, and many remain, in the public domain, and have been judged against broader economic, rather than narrower financial, criteria. However, tree genetic resources and breeding activities are becoming increasingly proprietary, mirroring more general trade and intellectual property regimes. These changes challenge some of the important assumptions on which public investments in tree breeding have been made, and are likely to make breeding of some species more economically attractive and that of others less so.

Public-sector entities investing in breeding are likely to have different performance criteria than private investors, leading to different forms of economic evaluation. They may, for example, be willing to incorporate consideration of externalities, such as the potential for industry development or employment generation, the maintenance of rural livelihoods, or the delivery of environmental services, into evaluations; they are also likely to have access to lower-cost capital, and have a longer time horizon, than private sector investors. Where the investment is part of a development assistance program, as has been the case for both industrial and nonindustrial tree species, economic criteria may be very broadly defined, for example, the potential to contribute to sustainable livelihoods, or to address environmental degradation. However, in such cases, it is likely that investment in tree breeding will still need to be justified against alternative investment options.

Conclusions

Prudent investments in tree breeding offer the prospect of good economic returns, frequently greater than those from alternative forestry investments. Their realization is, however, contingent on good silviculture and management and appropriate product processing, which themselves also demand astute investments. High returns can be achieved most easily in the early stages of breeding, but evidence suggests that they can be sustained over subsequent generations through more focused, informed, and efficient breeding. Simple breeding strategies can yield relatively good returns, and may have advantages over more sophisticated strategies in terms of lesser risk and opportunity cost. However, more sophisticated strategies are likely to be necessary to optimize returns from advanced generations of breeding. The value of forest products and services, and the scale of deployment, of improved populations have significant influence on the magnitude of economic returns from tree breeding. The institutional arrangements for breeding and benefit sharing impact on the distribution of costs and benefits associated with tree breeding, and thus on the economic returns to different parties. The criteria against which the economic returns from tree breeding are assessed are also likely to depend on whether the evaluation is undertaken from the perspective of the breeder, the tree grower, or the purchaser of forest products and services.

See also: **Genetics and Genetic Resources**: 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; Nitrogen-fixing Tree Improvement and Culture; *Pinus*

Radiata Genetics; Southern Pine Breeding and Genetic Resources; Tropical Hardwoods Breeding and Genetic Resources. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources.

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TREE PHYSIOLOGY

Contents

Physiology and Silviculture

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Introduction

Physiology is the study of how plants function. Ecophysiology is the study of how a community of plants, animals, and microorganisms function together. Environmental ecophysiology is the study of how factors such as light, temperature, atmospheric carbon dioxide concentration, wind, relative humidity, soil water, and nutrients affect community function. Silviculture is the science and art of using environmental ecophysiology, wittingly or unwittingly, to manage forests.

The physiological processes observed in trees are common to most plants. As with other species in the plant kingdom, trees are found across a range of environments and therefore display a very wide