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BENEFITS FROM TREE IMPROVEMENT

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1 INTRODUCTION

Genetic improvement consists in the manipulation of existing natural variation. Because most tree species are predominantly outbreeding, the forests of the world have over the millennia developed an awe-inspiring fund of genetic variation. The tree breeder must select from this variation to improve the quality of new forests, while at the same time conserving for future generations as much as possible of the total genetic variation, now threatened by man's activities as never before.

Phenotypic variation may be a combination of:

1) Developmental variation (e.g. a mature tree is bigger than a young seedling of the same species).
2) Environmental variation (e.g. a tree on a good site is bigger and healthier than one of the same species and age on a poor site).
3) Genetic variation (e.g. one tree may be bigger or straighter than another of the same species and age growing on an identical site).

The art of the tree breeder is to identify the element of genetic variation, which will be passed on from parent to progeny, and isolate it from the more random effects of development and environment. This may be a difficult and time-consuming process, involving a whole system of species, provenance and progeny trials, but the basis of tree improvement lies in the possibility of selecting trees which possess **heritable**, rather than non-heritable, superiority in desirable characteristics.

Stages in the selection and breeding process are:

1) Selection between species,
2) Selection between populations within a species (varieties, races, provenances, seed sources etc.),
3) Selection between individuals within superior populations,
4) Controlled breeding, including recombination and hybridisation between selected species, populations, parents or progeny.

Selection and breeding need to be supplemented by the development of successful techniques for mass propagation, either sexual or vegetative, to ensure that superior genotypes are available for large-scale planting.

In general, wood is the most important material produced by trees. For wood production, growth rate, whether in height, diameter, basal area or volume, is the trait most commonly considered for improvement. It has the advantage of being easily measured in quantitative terms. Volume is often used for older stands, height and diameter for young ones.

Measurement of a sample of trees for specific gravity enables volume production per hectare to be converted to weight production per hectare. In the case of pulpwood, important additional components of wood quality include fibre length, cell width, cell-wall thickness and proportion of reaction wood.

Stem straightness and degree of branchiness (including incidence of forking) affect both handling costs and percentage conversion loss for industrial wood. Volume production can be converted easily into value production, whereas conversion into monetary terms of quality estimates, which are usually assessed on a scoring scale, often presents a problem. This is compounded if local timber markets have not yet developed clear price gradients dependent on diameter of log and degree of defect.

Security/risk is closely linked with adaptability to local climate and soils, and with susceptibility to local pests and diseases. In some species, discovery and breeding of disease-resistant genotypes may be critical to the success or failure of major planting programmes. A particular problem in adaptability is the need to survive abnormally severe climatic conditions which may recur after only long intervals. In some cases a non-indigenous provenance may grow best for a number of years but suffer catastrophic losses in an exceptionally cold or an exceptionally dry year.

Little is known about patterns of variation in the traits which characterise social forestry species, e.g. fodder production, chemical content, shade or soil improvement, but there is no reason to doubt that their potential for improvement in yield and quality is just as great as that of wood-producing species.

Probably the most essential single benefit of forests is their protective function; protection of watersheds and catchments, control of soil erosion and flooding. On steep slopes, the conservation of inviolate natural forest is more important than any attempt to 'improve' it. On mismanaged and degraded areas, where reforestation is often the most effective means of restoring the site, rate of growth is again of universal importance; in this case, however, rapid growth of root and crown, rather than of stem, are the essential criteria for success.

2 SELECTION BETWEEN SPECIES

It is self-evident that species vary greatly in many characteristics. To take some extremes, no teak tree could survive outdoors in northern Europe, and no Norway spruce tree on the equator. Even when climate and soil conditions are ideal, inherent potential for growth may vary enormously between species of a single genus. As an example we may compare *Eucalyptus regnans*, capable of exceeding 90 m in height and with a straight cylindrical stem, and *E. pyriformis*, a multi-stemmed species, seldom exceeding 6 m. Volume yields can also vary greatly between species which are equally well-adapted to the site and which survive and remain healthy. Mean annual increment on highest quality sites in Denmark averages 7.5 m^3 for oak compared with 11.0 m^3 for beech and 19.0 m^3 for Norway spruce.

Type and quality of wood also vary enormously. Teak and oak are better suited to cabinet making than spruce or pine, eucalypts better suited for firewood than tropical pines. Trees are of great value for purposes other than wood production and species best suited for forage production, soil amelioration or shade and shelter will seldom be the same as those for production of sawlogs.

It follows that choice of species is an essential pre-requisite for all subsequent stages in tree improvement and should be guided by the following principles.

1) Define the object of production or service before embarking on a programme of species selection. Superior health and growth-rate are valueless if the end product is inappropriate. Truly 'multi- purpose' species are few and most planners of species introduction trials will need to identify a range of species for a range of purposes.
2) By definition locally indigenous species should be best adapted to the site. One or more should always be included in a programme of trials.
3) Exotics originating from a different country or continent may, if sites in the country of origin are similar to those of the introducing country, prove no less well adapted than the local species.
4) Some species have performed much better as exotics than in their native habitat, possibly because seed introductions were made without any of the natural pests. *Pinus radiata* is an example of a species of little account in its native range but of outstanding global importance as an exotic.
5) Although some species are less site-specific than others, no species can be best on all sites in all climates. Selection and testing should therefore be aimed at assessing the performance of each species on an identified site type and care must be taken not to extrapolate results to other sites with very different characteristics.
6) Selection of provenances is considered below. Its importance is now realised by foresters much more than it was 50 years ago. Therefore even in species elimination trials the source of the seed of each species being tested must be known and recorded. The trials then become not just the comparison of species A with species B, but the comparison of seed source X of species A with seed source Y of species B when both are planted on site type No. 1.

3 SELECTION BETWEEN PROVENANCES

Many tree species cover a large geographical area, within which climate may vary considerably. Examples are *Pinus taeda* in the USA (a range of 10° in latitude and 21° in longitude, with mean minimum temperatures in the coldest month of -2.5°C at the northern limit and +7°C at the southern) and *Eucalyptus camaldulensis* (a range of 25° in latitude and 36° in longitude, with mean minimum temperatures in the coldest month varying from +4° to +13°C and percentage of total rainfall received in the six summer months varying from 95% to 17%). To the broad variations of climate associated with latitude and longitude must be added more local environmental variations caused by topography, geology and soil.

The Darwinian evolutionary law of natural selection and the survival of the fittest, working upon the Mendelian laws of heredity, leads us to expect that local populations should be adapted to their environment. The degree of adaptation may vary with the relative rates of environmental change, genetic mutation and dispersal/migration by seed or pollen, but the tendency towards local adaptation is universal. Where the environment varies, we can thus expect some corresponding genetic variation in a species, even though there may not be morphological changes sufficient for the taxonomist to concede separate status as species or variety. The mass of evidence obtained from the collection of seed from different sources or provenances within a species, and the comparison of the next generation grown together on the same site, confirms that this is so. Environmental variation between sites is commonly associated with heritable variation between the respective populations which occupy these sites.

It follows that a species with a very wide range is likely to show more genetic variation than one with a smaller range. This has been demonstrated in a number of cases. *Pinus elliottii* partly overlaps with *P. taeda* but has a much smaller distribution, approximately half the latitudinal and half the longitudinal range. Provenance trials have shown that it also has less overall genetic variation. A similar comparison has been made between *Picea glauca* (wide range, high degree of genetic variation) and *Pinus resinosa* (less extensive range, lower degree of genetic variation). We can predict with some confidence that in Australia *Eucalyptus nesophila*, with a latitudinal range of 1° and a longitudinal range of 3°, will exhibit much less genetic variation than *E. camaldulensis*.

The total area of distribution is not, of course, the only cause of genetic variation. Relatively sudden changes in topography, aspect and soil may cause greater genetic variation than occurs over much wider areas of uniform plain. Isolation is another factor which can accelerate the rate of differentiation between populations, through the elimination of seeds or pollen migrating from adjacent populations. Distinct marine island populations, especially in animals and birds, have figured prominently in ecological literature, but similar isolation effects may operate in the case of mountains in a 'sea' of desert or relict forest in a 'sea' of agriculture.

An important stage in the identification of superior provenances for a given site is the conduct of replicated provenance trials as described e.g. by Burley and Wood, 1979. Comparisons may include growth of the most productive compared with the least productive (three times as great in trials of species as diverse as *Picea excelsa* and *Eucalyptus camaldulensis*).

A more useful comparison, however, is between the best provenance and the mean of those under test. Where a species is indigenous, comparison of the best with the local provenance is valuable, while for an exotic species of which seed has been difficult to obtain in the past, comparison of the best 'new ' provenance with the hitherto most readily available 'standard' provenance (e.g. Mountain Pine Ridge, Belize for *Pinus caribaea* var. *hondurensis*) is also of great interest.

In recent years increasing concern has been expressed about the long- term effects of narrowing the gene-pool of plantation species which may result from the use of a few improved genotypes within a single provenance. For this reason a wise precaution is to maintain a broad gene-pool by using a proportion of each of several superior provenances (say the best three) revealed by trials, rather than concentrating on the single best provenance. The immediate overall improvement may be slightly reduced, but this is compensated by the reduced risk of an excessive narrowing of the gene-pool.

Well-designed provenance trials in the tropics are, in general, much more recent than those in the temperate zone. However examination of some recently published results of trials of tropical and sub-tropical species suggests that provenance differences can be expected to be at least as great as those in temperate species. Because growth rates are usually a lot faster and rotations shorter in the tropics than in the temperate zone, a given percentage gain is worth a good deal more in terms of both volume production per hectare and net discounted revenue (net present value).

One of the oldest series of temperate trials is the IUFRO series on *Picea abies*, conducted in a number of countries and dating since 1938. Results of the trial at Donjelt in Sweden at 41 years (Ståhl 1986) have shown that the improvement in total volume production of the best provenance over the average of all provenances was 46%, while improvement over the local unimproved provenance was 39%.

Other conclusions from this trial were that:

1) The better provenances could be selected on a basis of height growth from about 8 years, or about one eighth of the usual rotation, in this species.
2) A difference in height of 0.5m (13% of the mean) at an age of 14 years corresponded to a difference in volume production of 100 m^3 solid stem wood (21% of the mean) at an age of 41 years. However, the differences in volume production would have been somewhat exaggerated by the small plot size and the good site quality.
3) Good provenances continuously produced higher volumes than average provenances. Thus the effect of correct provenance selection may be compared to an increase in site quality.

4) Planted stands and so-called 'land races' figured prominently among the most productive provenances.

Most tropical provenance trials are still comparatively young and early height growth is the trait most commonly measured. Examination of results in a number of trials (Willan 1988) suggests that the improvement in early height growth to be expected **from the mean of the three fastest provenances** compared with the mean of all provenances under test is:-

(1) 'Very variable' species: 15-30%
(2) 'Moderately variable' species: 5-15%
(3) 'Slightly variable' species: 1-5%

The above classification is admittedly arbitrary and, for many tropical species, it is not yet possible to evaluate genetic variability. But it does serve to emphasise the fact that the benefits from provenance selection are much greater in some species than in others. In the trials examined, *Cedrela odorata, Cordia alliodora, Eucalyptus camaldulensis, E. cloeziana* and *Pinus taeda* figured as 'very variable' species, while *P. patula* and *P. caribaea* var. *hondurensis* appeared to be 'slightly variable'.

The question remains to what extent the actual differences recorded in trials can be repeated when it comes to large-scale planting. Extrapolation of trial results to commercial plantations depends on a number of factors:

1) Availability of seed from the same source(s) as the original provenance(s) which proved superior in the trials. Some variation is inevitable between the collection of small research quantities of seed from a few (25-100) trees and the collection of larger quantities from more trees spread over a wider area. In some cases the latter operation may present positive advantages in subsequent generations, if mixture of seeds from over a wide area reduces the degree of inbreeding in the offspring. Such effects may contribute to the improved performance of 'land races' and stands raised from seed collected in plantations, in comparison with those raised from seed collected in natural stands, which has been reported from a number of trials. But it is important that collection is carried out in the same seed zone as the original (similar latitude, altitude, rainfall, aspect and soil type).
2) The extent to which apparent phenotypic superiority in the trials is due to genetic superiority which will be repeated in other plantings, or to environmental differences which may not be repeated. Well-designed experimental layouts should enable an estimate to be made of the proportion of phenotypic differences which can be ascribed to genetic differences, i.e. the heritability (h^2) of the observed differences. In the series of teak and gmelina trials (Keiding et al. 1986; Lauridsen et al. 1987), h^2 was calculated for each experiment and, for mean diameter, commonly lay within the range of 0.5 - 0.9. The product of h^2 times phenotypic differences were then used as the estimate of genetic differences.

   A particular example of environmental effects is the fact that genuine differences in the trials may be exaggerated by edge effect between small (including line or single-tree) plots. By definition trees of the best provenance must be growing alongside less vigorous provenances and so suffer less competition than when growing alongside other trees of the same provenance in large plantations. Such edge effects can be expected to increase with age and to affect diameter and volume growth more than height-growth; to some extent they can be reduced by the use of larger plots surrounded by one- or two-row unmeasured strips.

3) The correlation between height differences in the trials at the date of measurement and height differences to be expected in operational plantations at rotation age. If the trials are measured at rotation age, correlation will of course be equal to 1.0, but in most cases it is necessary to take a decision on what to plant when the trials are still comparatively young. One series of studies made in North America (Lambeth 1980) examined the correlations of juvenile/mature height demonstrated for several species of conifer at different ages of juvenile selection and of rotation and found that they increased from about 0.5 for an age/age ratio of 20% to about 0.8 at age/age ratio of 50%. A possible compromise between delaying too long and making premature and inaccurate forecasts by selecting the best provenances too early would be:

   a) Base the decision on a final assessment made at a minimum of one third rotation age or (for very short rotation crops) four years, whichever is the greater. An age/age ratio of 33% gave a correlation of about 0.7 in Lambeth's studies, but their applicability to tropical crops has yet to be demonstrated.
   b) If possible, stability of provenance ranking should be demonstrated by consistent results over at least two successive assessments.
   c) As previously recommended, select several of the best provenances for seed production, not the single best, and establish seed stands of total area in excess of anticipated needs. Some modification in selection can then be made, if necessary, before the first seed is collected for commercial plantations. For example in a tropical pine, if initial provenance selection is made when the trials are 8 years old, they could be 23 years old by the time seed for commercial plantations is collected from the later planted seed stands. At that time, if early promise in one provenance had not been maintained, it would be possible still to reject it and collect seed from the remaining selected provenances.

4) Conversion of mature height differences to differences in total productivity at rotation age. Examination of yield tables for different site quality classes (to which stable provenance differences may be considered analogous) suggests that mature **height** differences between adjacent site classes of say 10% are commonly associated with differences in **volume** production of 15- 20%. If there is a premium on larger diameter classes, the increase in **value** production would be still higher.

5) Correlation of expected productivity at rotation age of the best provenances in the trial plots with their expected productivity when planted over areas of many thousands of hectares. This depends on how representative of the planting area as a whole are the sites used in the provenance trials. For example, results of perfectly conducted trials on a heavy clay soil will be of limited value if the planting area is later discovered to comprise 80% of free-draining sandy soils. The most efficient distribution of provenance trials to sample the major site types present in the planting area is itself dependent on the efficiency of preliminary edaphic and topographic survey. Often the survey will reveal several representative site types within the planting zone. These need to be sampled separately and the trials may indicate different preferred provenances according to site. Extrapolation of trial results to strongly contrasting sites or climates, without further testing, can never be justified, but satisfactory correlation within a reasonably homogeneous planting zone can often be expected. With Norway spruce in southern Sweden, a correlation coefficient of r = about 0.8 was obtained within a representative planting zone (Wellendorf *et al.* 1986).

No studies of all the above factors have been made, as far as is known, for tropical species. In their absence, it is considered that a conservative estimate of the improvement levels to be expected from programmes of tropical provenance research (value differences in operational plantations at rotation age of the mean of the three fastest provenances compared with the mean of all provenances) is:-

(1) 'Very variable' species 10-20 %
(2) 'Moderately variable' species 5-10 %
(3) 'Slightly variable' species 1-5 %.

The above discussion considers only the quantity and size of logs produced. It is also possible to improve the quality of the stem (straightness, incidence and size of branch knots) and of the wood (specific gravity, fibre length etc). Growth and vigour traits may sometimes be negatively correlated with traits for stem and wood quality, hence it is realistic not to allow any general addition in improvement for these traits. For individual species, however, improvement in the ultimate value of the crop may depend on improving quality rather than volume production. In *Pinus kesiya*, for example, provenance selection for stem straightness should lead to a greater increase in crop value than selection for the much less variable traits of height and diameter growth in that species.

Although a single provenance is rarely the best on all sites, some international trials have identified certain provenances which are consistently among the best few over a wide range of site conditions. Examples are some Ontario provenances of *Picea glauca*, some Romanian provenances of *Picea abies*, and the Guanaja, Alamicamba and Santa Clara provenances of *Pinus caribaea* var. *hondurensis*. The Albacutya provenance of *Eucalyptus camaldulensis* has performed outstandingly throughout the Mediterranean region, while the Katherine and Petford provenances have been consistently among the superior provenances in, respectively, dry tropical and semi-humid tropical (summer rainfall) regions.

A number of provenance trials have, incidentally, provided evidence of the superior performance of land races (plantations managed and improved for one or more generations) over the original, unimproved, natural source. Where these have been included in the trials, they usually figure among the best performers over a range of sites. A good example is the Byfield (Queensland) clone bank of improved clones of *Pinus caribaea* derived from the original source of the Mountain Pine Ridge in Belize. In international trials this produced an average of 12% greater volume than the unimproved MPR source. Superiority of local land races has also been demonstrated for *Eucalyptus cloeziana* in Ivory Coast, *Pinus patula* in Zimbabwe, *Pinus taeda* in Malawi, and *Tectona grandis* in Nigeria and Papua New Guinea. This does not alter the fact that the most valuable long-term gains are likely to be made by combining the identification of provenances best adapted to local conditions, through well-designed comparative trials, with subsequent selection, propagation and breeding of the best genotypes within them.

4 SELECTION WITHIN PROVENANCES

Research has shown that, in many species, there is considerable variation within provenances or populations, as well as between them. After one or more provenances have been identified which show superior performance under local conditions, the next stage therefore is to select superior stands within the superior provenances and manage them as seed stands (seed production areas) and/or to select superior individuals and to concentrate genetic material from them into clonal or seedling seed orchards.

Some genetic gain may be obtained by the selection of superior stands and their management for seed production. This involves early and heavy thinning to remove the poorer phenotypes and to develop large crowns on the remaining good phenotypes for heavy seed production. The selection intensity involved would be about 1 in 10 trees retained out of those originally planted, four or five times the intensity of selection in commercial timber stands at the same age, but still a low intensity compared with the 1 in 1000 commonly advocated for plus-tree selection for seed orchards. Where the area of seed stand needed is only a small proportion of the total plantation area available, the selection of the stand itself will confer some additional improvement; the improvement of say the best 20 ha over the average of a total plantation area of 1000 ha should be significantly better than that of the best 20 ha out of a total of 50 ha. However, the improvement from selected and managed seed stands is unlikely to exceed one quarter to one half of that expected from an initial cycle of improvement from seed orchards. Its main advantages are its simplicity and cheapness and the possibility of harvesting improved seed within a few years of the application of treatment.

Most of the evidence on the genetic improvement to be obtained from seed orchards refers to temperate conifers. There is much less on tropical conifers or on broadleaved species. Even for temperate conifers, most comparisons of the growth of stands from 'improved' and 'standard commercial' seed sources are from measurements made over half or less the rotation length. Nevertheless, the available evidence is fairly consistent. Carlisle and Teich (1978) have summed it up as follows: 'In most tree species we can expect at least 10% gain in growth and, in some, 15-25% growth gains'. Additional gains may be obtainable in stem and wood quality and in disease resistance. Gains of this order can be expected from the first cycle of selection and the first generation of seed orchards. Additional gains of the same order can be expected from subsequent selection on the basis of progeny trials and the establishment of the selected genotypes in a second generation orchard.

Although evidence on the effects of individual selection in tropical and subtropical species is sparse, it suggests that improvement will be no less than that for temperate species. On the basis of results in *Eucalyptus grandis, Pinus caribaea var. hondurensis, P. patula, P. elliottii* and *P. taeda*, it seems likely that we can expect the following gains from the relatively simple initial stage of individual selection i.e. phenotypic selection of plus trees within a given population at an intensity of about one tree in a thousand (approximately 3 standard deviations from the population mean) and either concentrating the phenotypically superior genotypes in a grafted seed orchard or collecting wind-pollinated seed from them and establishing a seedling seed orchard:

1) **Provenances with 'high' within-provenance variation** are likely to show an improvement in total value production in the range of 15- 30%.

2) **Provenances with 'moderate' within-provenance variation** are likely to show an improvement in total value production in the range of 5-15%.

3) **Provenances with 'low' within-provenance variation** are likely to show an improvement in total value production in the range of 1- 5%.

In some species, e.g. *Pinus kesiya*, most of the value improvement is likely to be due to an improvement in stem straightness. In species which are naturally of excellent form, e.g. *Eucalyptus grandis*, most of the value improvement will be due to improved vigour and volume production.

Davis (1970) pointed out that harvesting costs in South-eastern USA constituted 60-75% of total costs of wood delivered at mill, therefore a given percentage of increased harvesting efficiency may be 2-3 times as effective in increasing profitability as the same percentage increase in stumpage volume production. Stem straightness is a big factor affecting harvesting efficiency. He also calculated that a relatively small percentage increase in milling efficiency (5% reduction in processing time plus 5% higher conversion rate) should raise mill profits by 15-4l%. Here again log form and wood quality exert a preponderant influence and it is likely that both traits have been underestimated hitherto in evaluating tree improvement benefits.

5 SUMMARY OF EXPECTED GAINS FROM EARLY STAGES OF TREE IMPROVEMENT

In summary, the gains in total crop value over a rotation to be derived from tree improvement should, on average, be no less in tropical than in temperate species. For the early stages of within- species selection (provenance research followed by first cycle individual selection and seed production in managed but unrogued seed orchards) average gains may be conservatively estimated as follows:-

Degree of variability between provenances	**Value gain expected from provenance selection %**	**Degree of variability within provenances**	**Value gain expt. from individual selection (first cyclæe managed but unrogued seed orchards %**	**Total value gain expected %**
High	10-20	High	15-30	25-50
	"	Moderate	5-15	15-35
	"	Low	1-5	11-25
Moderate	5-10	High	15-30	20-40
	"	Moderate	5-15	10-25
	"	Low	1-5	6-15
Low	1-5	High	15-30	16-35
	"	Moderate	5-15	6-20
	"	Low	1-5	2-10

Further gains from later stages of selection and breeding (progeny testing, controlled pollination, vegetative propagation etc.) are likely to be of the same order as those expected from the first stage of within provenance selection.

6 ECONOMIC ASPECTS

The expected value gains discussed previously needs to be related to the costs incurred in the research and development needed to achieve them. One method which has been used in a number of economic analyses of tree breeding programmes is that of the Internal Rate of Return (IRR) or Financial Yield, i.e. the rate of interest at which total returns exactly equal total costs, when all are discounted to a common point in time.

Results of several economic studies of individual tree selection and seed orchard establishment and management have recently been summarized by Stier (1986). Most of them refer to work in North America and the range of IRR, for all except one report, is between 6% and 20%. The trend was from lower IRRs (<10%) for slower growing species in cool to cold temperate conditions, e.g. *Picea glauca* and *Pinus resinosa*, to higher IRRs (>15%) for *P. taeda* and *P. elliottii* in warm temperate or sub-tropical conditions. As a general rule, any IRR over 8% may be considered satisfactory and anything over 12% highly satisfactory when assessing projects at the national economic level.

There is very little information on the economic benefits and costs of tree improvement in tropical species, nor on those of provenance selection, considered in isolation, for any species. An attempt to evaluate provenance research in the hypothetical case of a tropical pine, such as *Pinus caribaea* var. *hondurensis*, showed that, for conditions and assumptions of the case study, the IRR varied from 9.7% for a value improvement of 2.5% to 15.2% for a value improvement of 20% (Willan 1988).

Reilly and Nikles (1978) analysed costs and benefits of improved yields, through unrogued clonal seed orchards, in *Pinus caribaea* var. *hondurensis* in Queensland. They based costs on those actually incurred in the Kennedy Seed Orchard. They estimated that the IRR would fall between 9.9% (improved straightness with no improvement in basal area increment) and 15.2% (improved straightness plus 10% increased basal area increment plus improved height growth).

The authors found that, for a discount rate of 8% the initial selection of plus trees accounted for 36% of the discounted cost of improvement, seed orchard establishment 30% and seed orchard maintenance 34%. Whereas the total costs of establishing and maintaining seed orchards are proportional to the area of orchard needed to supply improved seed and hence to the area of commercial plantations to be established annually, the cost of searching for and selecting plus trees is largely independent of the areas to be planted. This accounts for the important fact that the profitability of a tree improvement programme depends not only on the percentage increase in value of the crop but on the scale of planting. To take a hypothetical example, assuming the same proportion of costs (36% - 30% - 34%) as experienced in the above Queensland example;

Annual planting area (ha)	10,000	1,000	100
Total discounted cost ($) of:			
- plus tree selection	18,000	18,000	18,000
- seed orchard establishment	150,000	15,000	1,500
- seed orchard maintenance	170,000	17,000	1,700
Total discounted cost ($) of:			
- improvement operations	338,000	50,000	21,200
Discounted cost/ha ($) of:			
- plus tree selection	1,8	18	180
- seed orchard establishment	15	15	15
- seed orchard maintenance	17	17	17
Total discounted cost/ha ($)	33,8	50	212
Discounted additional revenue/ha ($) derived from tree improvement	100	100	100
Discounted profit or (loss)/ha ($)	66,2	50	(112)
Total discounted profit or (loss) of tree improvement enterprise ($)	62,000	50,000	(11,200)

It can be seen that only a substantial annual planting area can justify the initial rather heavy outlay on plus tree selection. Very small planting programmes cannot carry out their own selection programme economically. Their appropriate course of action is to purchase the relatively small quantities of improved seed which they require from bigger tree improvement enterprises, whether these are conducted by national forest services, cooperatives or large private companies. A prerequisite of such purchases is good information on the degree of improvement expected (selection intensity of plus trees, results of progeny tests if available) and the suitability of the populations from which the selections were made for the planting region in question. Since the cost of seed is a small part of total establishment costs, a relatively modest increase in productivity justifies paying a considerably higher price for the improved seed from which the plantations will be raised.

The genetic improvement to be obtained from a first stage seed orchard can be further increased by roguing, i.e. by the removal of those clones or families in the orchard which have shown themselves as inferior in progeny tests. Several authors have shown evidence that intensive roguing (50% - 70% poorest families/ clones removed) can yield an added genetic gain of about half the original gain from the unrogued orchard. This has to be set against the additional cost of the progeny tests and the roguing operation, and the reduced quantity of improved seed which will be produced, at least temporarily, from the remaining trees in the orchard. It may be considered preferable to maintain an orchard producing say 100 kg of seed a year having 10% genetic improvement than to rogue it and be left with an annual seed yield of 50 kg having 15% genetic improvement. For these reasons van Buijtenen and Saitta (1972) concluded that, in the local conditions of *Pinus taeda* orchards, roguing a first stage orchard was of doubtful value, but that progeny tests were still an essential tool for selecting clones or families for a new second stage orchard. For other species and with careful choice of initial spacing and the timing of the roguing operation, it may more than pay for itself.

Some authors have evaluated tree improvement projects not in terms of the IRR but of the Net Present Value (NPV), sometimes referred to as Net Present Worth or Net Discounted Revenue. With this method a realistic rate of interest is assumed (usually the 'Real Rate' which equals the nominal rate less the rate of inflation) and the NPV represents the total value of returns less the total value of costs, all discounted to a common point in time, which is usually the start of the project. The NPV method is now generally preferred.

With the NPV method, the result clearly depends on the size of the annual planting area as well as the genetic gains obtained. In the case of a fast-growing tropical pine, planted at a rate of 1000 ha a year, with a rotation of 16 years, 10% genetic improvement and 6% interest, the project could show a NPV of around $0.6 million by year 58 of the project (when the youngest of the 16 annual 1000 ha blocks of improved commercial plantations is harvested) (Willan, 1988). If the same degree of improvement could be applied to the global area of tropical pines being planted each year, the NPV would amount to over $50 million.

In most cases, the additional benefits to be gained in processing and marketing wood products are likely to be several times the increase in value of unprocessed logs. Where large planting areas are concerned, it is clear that relatively modest inputs of research and development can produce very large financial benefits.

Increased production from tree improvement offers several alternative courses of action. For example a 15% increased yield per ha would enable forest planners to fulfil a 15% increase in demand. If demand is expected to remain static, on the other hand, it could be fulfilled by a 15% smaller plantation area. The reduced area could be obtained by rejecting the lowest quality sites and so increasing the average yields on the area retained, or by rejecting the least accessible planting sites and thus reducing average logging and transport costs. Either choice provides further economic benefits. Alternatively, the full area could be retained and the rotation reduced. Any reduction in the period, over which the returns from final felling must be discounted will improve the IRR of the project, but this advantage may be lost if wood quality and hence value is inferior at the lower age. Detailed knowledge of species characteristics is needed to appraise the various alternatives offered by tree improvement benefits.

In addition to increasing returns, tree improvement may reduce costs. If improved provenances and genotypes grow faster from the start, they will close canopy and cease to need tending at an earlier age. Reduction in the number of weedings from say 5 to 4 may be possible and the saving of cost so early in the rotation could have a significant effect on the economic success of the project. At the same time improvement in crop uniformity may make it possible to change from selective thinning methods to a cheaper system of line thinning. Quantitative assessment of reduction in management costs as a result of tree improvement is usually not included in economic analysis, but the savings may be substantial.

The evidence seems overwhelming that, wherever there is a substantial afforestation programme, tree improvement (both provenance research and individual selection) in the tropics will more than pay for itself. Economic returns are likely to be excellent in most species. Looked at another way, no one can afford the substantial **losses** which will result from **not** implementing a realistic improvement programme.

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