THE TRADE-OFF BETWEEN GENETIC GAIN AND CONSERVATION IN A PARTICIPATORY IMPROVEMENT PROGRAMME: THE CASE OF PEACH PALM (*BACTRIS GASIPAES* KUNTH)

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ABSTRACT

Finding an equilibrium between genetic resources conservation and genetic improvement can be difficult. The problem is explored in this paper, partly through a case study of a participatory improvement programme of peach palm (*Bactris gasipaes* Kunth, Palmae), implemented in the Peruvian Amazon by the World Agroforestry Centre (ICRAF) and the Peruvian National Institute for Agricultural Research and Extension (INIEA). Peach palm, which was originally domesticated by Amerindians, produces a range of useful substance and marketable products, but today the fruit and heart-of-palm are the principal products. The characteristics of the clients (subsistence smallholders and agro-industrial plantation companies) for these crops and those of the ICRAF-INIEA project are described, and the impact on genetic diversity of future management options is explored. This is followed by a wider discussion of the relationships between genetic gain and maintenance of genetic diversity for improvement, and their implications.

The ICRAF-INIEA programme was designed to emphasize genetic conservation and timely germplasm delivery rather than genetic gain. The analysis presented here suggests that, with careful management, genetic diversity can be effectively conserved through 20 generations of improvement. Nevertheless, there is a fundamental conflict between genetic gain and genetic conservation. Consequently, no improvement programme can conserve all of the genetic diversity of a landrace or species and genetic resource management strategies must be developed to resolve these conflicts through explicit and informed decisions. Some such strategies, corresponding to different levels of emphasis on gain *versus* diversity, are presented.

Key words: Amazonia, indigenous fruits, participatory improvement, genetic conservation-through-use, genetic erosion.

INTRODUCTION

The conservation of plant genetic resources (PGR) is a common objective of development programmes and of international agreements such as the 1993 Convention on Biological Diversity (CBD 2003) and the International Treaty on PGR for Food and Agriculture (ITPGRFA 2004). However, it can be difficult to reconcile PGR conservation with development. Essentially, this is because

- within-population genetic variation tends to be positively correlated with population size and
- both domestication and improvement usually involve restriction of population size through selection.

Thus, domestication and improvement have tended to result in the genetic erosion respectively of landrace populations or improved populations. The uniformity demanded by modern markets exacerbates this problem.

Here, we analyse the trade-off between genetic gain and genetic conservation in peach palm (*Bactris gasipaes* Kunth, Palmae) improvement for Amazonian smallholders, with particular reference to a participatory improvement programme currently being implemented in the Peruvian Amazon by the World Agroforestry Centre (ICRAF), in collaboration with Peru's National Institute for Agricultural Research and Extension (INIEA). The crop, domesticated long before the European conquest (Mora Urpí *et al*. 1997), is cultivated by smallholders and by agroindustry in the lowland Neotropics, but in different production systems and for different products. Farmers generally produce fruit in agroforestry systems for subsistence and local markets, while agroindustry produces the gourmet vegetable heart-of-palm for export and regional markets in large-scale, high-input monocultures.

Peach palm makes a useful case study for two main reasons:

- conventional peach palm improvement programmes have not successfully reconciled PGR conservation with genetic gain, nor significantly enhanced fruit demand, partly because the high costs of field genebanks often impeded the improvement efforts (Clement *et al*. 2004);.
- the participatory programme described here may be suitable for wider application.

PEACH PALM PRODUCTS, PRODUCERS AND CONSUMERS

Peach palm is the only domesticated neotropical palm (Clement 1988). Although domesticated for its fruit, it is now considered an underutilized fruit crop (Clement *et al*. 2004). Its current economic importance is principally as a source of heart-of-palm. Industrial plantations, mainly in Ecuador and Costa Rica (primarily for export) and around São Paulo, Brazil (primarily for domestic markets), replaced natural populations of other palm species as the principal source of heart-of-palm in

the 1980s and 1990s, although production from natural *Euterpe* populations remains important in Brazil. Plantation size varies from 10-1,000 ha, depending upon capital availability, market-orientation and location. In Brazil, the medium and large-scale growers are often descendants of recent European immigrants. They tend to be well-educated, market-oriented and to have good access to extension agents and credit. However, they have had difficulty in keeping up with evolving consumer demands (e.g., for ready-to-eat and minimally processed products) and in complying with food safety requirements. Hence, export markets are stagnant and price-based restructuring is currently underway.

Indigenous and mestizo smallholders in Amazonia, lowland northern South America and southern Central America cultivate peach palm almost exclusively as a fruit crop in homegardens and swiddens, typically in association with numerous other crops, and occasionally in small orchards near major markets (Clement *et al*. 2004). Density in orchards is usually around 400 plants ha^{-1}. Density in homegardens and swiddens is lower and varies greatly. These producers tend to be subsistence-oriented, to have little formal education, limited or no access to extension and credit, and poor understanding of consumer demands beyond local markets. Nevertheless, they are often greatly interested in participating more fully in regional markets.

Consumers tend to prefer red-skinned fruit, with orange pulp (high in beta-carotene) and moderate oil content. However, consumer preferences vary and, consequently, in all regions fruits of varying oil content and colours (orange and yellow-skinned fruit, with orange to cream-coloured pulp) are commercialized (Clement and Santos 2002). In Costa Rica, low oil-content fruit sells well, principally because consumers associate quality with skin cracks ("rayas") that in Central America are more common on these fruits. A defect of all conventional peach palm improvement programmes has been the failure to clearly identify and respond to consumer preferences in fruit (Clement *et al*. 2004).

THE ICRAF-INIEA PARTICIPATORY IMPROVEMENT PROGRAMME

In 1995, ICRAF and INIEA initiated a participatory agroforestry improvement programme in the Peruvian Amazon. Peach palm was included in the programme after a systematic prioritization process involving farmers, researchers and marketing specialists (Sotelo Montes and Weber 1997). The programme has three principal objectives: genetic improvement (with selection criteria informed by local demand), genetic conservation and seed production for community development (Sotelo Montes *et al*. 2000, O'Neill *et al*. 2001, Weber *et al*. 2001). Seed production aims at generating income for participating farmers (particularly through supplying seed to the heart-of-palm industry) and at facilitating local planting.

The peach palm programme is active in two geographically separated (>300 km) areas in the regions of Loreto (Alto Amazonas province) and Ucayali (Aguaytía watershed). The spineless Pampa Hermosa landrace, generally considered to produce the best germplasm for heart-of-palm plantations (Mora Urpí *et al*. 1999), occurs in the Loreto region; local peach palm in Ucayali shows varying degrees of spininess

and to date has not been described as a landrace. The demand for seed of the Pampa Hermosa landrace connects smallholder producers with the heart-of-palm sector, a link that will likely persist because of low seed production in the cooler climate of the major heart-of-palm producing areas in Brazil.

Collaborating farmers selected mother trees of the Pampa Hermosa landrace, primarily based on fruit characteristics (quantity, exocarp color, oil and starch content, texture, size). Open-pollinated seed was collected from 100 mother-plants in 1997 (four localities along the Cuiparillo River, east of the city of Yurimaguas) and 302 in 1999 (12 localities along the Paranapura River, west of Yurimaguas). Selection intensities were kept low (≈1 in 20) to ensure relatively high genetic variation in all traits at programme inception. The following year, the resulting progenies were planted in two multiple-site experiments (Table 1).

A randomized complete block design was used in both experiments. The blocks, each of which constitutes an independent seedling seed orchard, are distributed on different farmers' properties. Sites were selected by farmers and by ICRAF-INIEA based on soil characteristics and distance to potential sources of extraneous peach palm pollen (minimum accepted distance was 100m). Each block consists of 150 families, planted in two-tree plots at 2.5m × 5m spacing. The area of each (around 0.5 ha) is small enough to be manageable by individual farm families. The use of two-tree plots reflects the genetic conservation objective, as the 50% thinning to the final spacing of 5m × 5m can be effected by removing one tree per family, thereby minimizing the reduction of genetic variation. It also permits preliminary evaluation of heart-of-palm productivity (i.e., on coppice shoots of thinned siblings). *Centrosema macrocarpum* Benth. was used as a cover crop because of its known performance and local economic value (Pérez *et al*. 1993). Cultural practices include manual weeding, NPK fertilizer application, and timely elimination of excessive off-shoots. Generally, growth and survival have been highly satisfactory. Flowering and fruiting began in most blocks in year three.

Farmers participate in all key decisions and effect cultural practices (Table 2), and are in frequent contact with ICRAF personnel. Quarterly meetings between ICRAF and PROSEMA (see below) allow further interchange of views and information. Farmers receive payment for weeding. As well as ensuring relatively consistent levels of maintenance between blocks, these subsidies also recognize that, in addressing wider development and conservation objectives, the programme generates public benefits, the costs of which should not be borne by the collaborating smallholders.

In 1999, collaborating farmers in Ucayali formed a civil association, the Aguaytía Watershed High Quality Seed and Wood Producers' Association (PROSEMA). More recently, PROSEMA and the Ucayali Rural Women's Association (AMUCAU) have united to form two limited companies that will supply agroforestry services and goods, including seed and plants. Although farmers' perceptions of the programme have not been formally surveyed, these developments demonstrate their interest in production of seed (for planting and commercialization) and fruit (for home consumption and commercialization).

The medium- to long-term future of the improvement programme is under discussion with farmers. In all blocks, within-family selections will be made, not

TABLE 1

Location and environmental characteristics of two multiple-site experiments of peach palm planted in the Peruvian Amazon in 1998 and 2000.

Region[1]	Zone[2]	1998		2000		Environmental characteristics
		Blocks	Families	Blocks	Families[3]	
Ucayali	Nueva Requena	5	49	5	150	Soils well-drained, highly acidic, sandy; annual rainfall ~1600 mm, pronounced dry season
Ucayali	Curimaná	4	49	4	150	Soils with varying texture (clayey loams, silty loams), drainage average, highly acidic; annual rainfall ~2600 mm
Ucayali	San Alejandro	0	0	5	150	Soils with varying texture (clayey loams, silty clays, clayey silts), drainage average to poor, slightly acid; annual rainfall >3000 mm
Loreto	Yurimaguas – Munichis	6	99	4	150	Soils with varying texture (sand to clayey loam), drainage average to good, slightly acid; annual rainfall >2000 mm
Loreto	Yurimaguas – Tarapoto road	17	99	11	150	Soils with varying texture (sand to silty clay), drainage average to good, slightly acid; annual rainfall >2500 mm

[1]Peruvian political division ('región'), geographically equivalent to former department
[2]Project designation for each spatial-environmental grouping of blocks
[3]In each region, the 150 families include 75 common to both regions; a total of 225 families were planted in the 2000 trial (the remaining families did not produce enough seeds).

TABLE 2

Farmer and institutional participation in activities and decisions of the peach palm improvement program in the Peruvian Amazon.

Activity / decision	Participation*	
	Farmer	ICRAF/INIEA
Past / present		
Selection of target landrace	1	1
Determination of selection criteria for mother-tree selection	1	1
Tree selection, seed collection	1	1
Seedling production	1	1
Experimental design	0	1
Site selection	1	1
Provision of experimental areas	1	0
Trial establishment	1	1
Daily / weekly monitoring	1	0
Monthly monitoring	1	1
Trial maintenance	1	1
Trial measurement	0	1
Statistical analysis and interpretation	0	1
Future		
Identification of thinning / roguing criteria	1	1
Thinning	1	1
Seed collection in orchards	1	1

* 1 = major participation; 0 = little or no participation

so much for genetic gain as to avoid inbreeding depression due to mating between adjacent siblings, which could occur if they flower on the same day. Subsequently, any selection will necessarily involve family selection.

GENETIC DIVERSITY *VERSUS* GAIN IN THE ICRAF-INIEA PROGRAMME

Genetic variation can be characterized using measures based on allele frequencies estimated from molecular markers, or by estimating genetic variation in observable traits (e.g., fruit size, tree diameter) in field trials. Both dominant and codominant molecular markers are useful. However, with dominant markers, heterozygosity, a key measure of genetic variation, must be inferred from frequencies of null alleles. This affects the precision of estimates of population genetic parameters (Avise 2004). For the Pampa Hermosa landrace, both molecular and morphological data exist and are relevant in defining the base line against which the effects on genetic diversity of the ICRAF-INIEA programme must be measured.

Molecular genetic variation

In the present context, the key parameters are the three types of inbreeding coefficient (F_{IS}, F_{ST}, F_{IT}). These measure different types of departure from random-mating and are related by the following equation (Hartl and Clark 1997): $(1 - F_{IT}) = (1 - F_{IS})(1 - F_{ST})$.

F_{IS} measures inbreeding as generally understood, i.e., mating between relatives, including selfing. F_{ST} reflects the degree that a population is genetically subdivided, i.e., into groups whose members are more similar to each other than to individuals drawn randomly from the whole population. For example, if a species is divided into two small, geographically separated subpopulations, then, due to random genetic drift, over time these are likely to diverge genetically. This would produce a "subpopulation structure" which is measured by F_{ST}. Seed or pollen movement between subpopulations prevents or reduces differentiation. Low levels of genetic differentiation may imply that different populations, even when spatially distant, are genetically connected through seed or pollen movement. F_{IT} is the coefficient of total inbreeding, and reflects both F_{IS} and F_{ST}.

Molecular genetic variation in the Pampa Hermosa landrace was described recently (Adin *et al.* 2004, using dominant AFLP markers). The authors found low levels of F_{ST} (0.038 among Cuiparillo River subpopulations, 0.042 among Paranapura River subpopulations, 0.025 between the rivers). They suggested that farmer-mediated seed movements among populations explains the lack of genetic subdivision. Cole (2004), using co-dominant microsatellite markers and working 500 km north of Pampa Hermosa, also found low levels of F_{ST} (0.012 among indigenous communities, 0.024 among colonist communities, 0.027 overall) and relatively high estimates of F_{IT} (0.16 and 0.21 among subpopulations in indigenous and colonist communities, respectively). Based on interviews, Cole confirmed that farmers effect significant short, medium and long distance movement of fruits/seeds, and may also use very old preferred palms on their farms as seed sources. Use of seed collected on-farm, as reported by Cole (*op. cit.*) and Brodie *et al.* (1997), could cause inbreeding (e.g., through parent-offspring or half-sib mating). The implications of farmers' practices depend on whether they have been carried out for long periods of time. If so, then this would be reflected in loss of heterozygosity and the current F-values would reflect these practices. However, if these practices are relatively new or have been intensified, then further reductions in F_{ST} but increases in F_{IS} could result.

Morphological genetic variation

The Pampa Hermosa landrace exhibits considerable phenotypic variation for fruit traits such as exocarp colour, mesocarp colour and texture, and fruit weight (36.9±12.2 g; range 21 to 57.3 g; with 89±2% mesocarp), and fruit number per bunch (177±34; range 136 to 237) (Clement and Mora Urpi, 1988). It is very likely that this phenotypic variation has an important genetic component, and reflects

variable farmer preferences. Stem spine incidence, by contrast, shows little variation, suggesting strong, unidirectional farmer selection.

In summary, there is no evidence that peach palm is under critical threat of genetic erosion in Alto Amazonas Province. However, two caveats should be noted. First, as mentioned above, the implications of current germplasm sourcing – which may differ from historical sourcing - by farmers are unclear. Second, given the current deforestation rates in the Peruvian Amazon and ongoing sociocultural change in forest margin areas, it would be unwise to conclude that the genetic resources of the Pampa Hermosa landrace will necessarily be conserved adequately under a 'do nothing' scenario. The base line with which we compare the effects on genetic diversity of the ICRAF-INIEA programme can be best described as one of short-term security, coupled with medium-to-long term uncertainty.

Immediate effects of the ICRAF-INIEA programme

The most immediate effect of the programme has probably been to increase diversity at the farm and local levels as, in effect, it has constituted a 'pooling and sharing' of the within-landrace genetic diversity. Although the importance of this effect is dependent on the degree of subpopulation structuring, the same effect has been documented in improvement programmes of conifer species (El-Kassaby 2000), which, like peach palm, tend to exhibit little subpopulation structuring. In the short term, therefore, the expected effect of the programme on genetic diversity within the range of the Pampa Hermosa landrace is positive at the local level, and neutral (because of the large overall sample size) at the population level. The blocks in the Ucayali region introduce new diversity from the Pampa Hermosa landrace. However, it should be recognized that, if the introduced material is widely planted in Ucayali, there is a risk of genetic change in local populations due to gene flow.

Future effects of the ICRAF-INIEA programme

The Fisher-Wright model (Hartl and Clark 1997) describes how genetic variation in a large population is lost by random genetic drift when it is divided into smaller and mutually isolated subpopulations. Under the model, each subpopulation of N individuals produces a large number of gametes, of which $2N$ are randomly selected to form the next generation, and so on. Due to sampling error, each sample of $2N$ is highly unlikely to have the same allelic frequency as the total population, so random change occurs (random genetic drift). Its severity depends on the subpopulation size N, with smaller population sizes constituting recurring 'genetic bottlenecks' in each generation. The effect of drift in any individual subpopulation depends on chance and initial gene frequencies and cannot be reliably predicted, unlike the overall outcome in the set of subpopulations.

The Fisher-Wright model is a reasonable approximation of the structure of the ICRAF-INIEA peach palm programme, as the spatially separated blocks can be

considered subpopulations. In the medium-long term, successive plant generations in the ICRAF-INIEA programme will be subjected to recurrent selection, and the individual blocks will be used as seed sources. We used the PopG programme (Felsenstein 2003) to illustrate the predicted loss of genetic diversity due to genetic drift under three different scenarios of possible future genetic management: relatively intensive selection, with or without gene exchange, and management for genetic conservation. PopG simulates the effect of population subdivision on genetic diversity at a single diallelic locus in a set of initially identical subpopulations. The different scenarios are described more fully below. For each, we ran 100 simulations and estimated the mean number of subpopulations (of 14 – corresponding to the number of blocks installed in Ucayali in 2000) that become fixed (i.e., become homozygous) after 3 and 20 generations, and the probability of losing all genetic diversity (i.e., all 14 subpopulations become fixed for the same allele) after 3 and 20 generations. The probability of losing all genetic diversity was estimated as the proportion of runs (i.e. out of the 100) in which all subpopulations were fixed for the same allele.

A. Management for genetic conservation – improvement without gene exchange using large numbers of propagules per sub-population

Under this scenario, no family selection is carried out, i.e., the 150 best plants (of 150 different families) are retained in each generation in each of the 14 blocks (subpopulations) in the Ucayali region. The second and subsequent generations would then consist of 150 increasingly interrelated open-pollinated families. Under this scenario, there is little risk of losing genetic diversity except for very rare alleles, and even then only over the longer term (20 generations, i.e., around 100 years) (Table 3A).

B. Selection without gene exchange using small numbers of propagules per sub-population

An alternative selection strategy would involve a relatively narrow 'bottleneck', in which the 20 best (in 20 different families) of the 300 individuals initially planted in each of the 14 blocks (subpopulations) in the Ucayali region are retained. Selections are assumed to be based on local performance (i.e., rather than cross-site performance of the families) for selection criteria decided by each farmer. The second and subsequent generations would then consist of 20 increasingly interrelated open-pollinated families. For intermediate initial allele frequencies ($p_0 = 0.5$), over 20 generations (roughly 100 years) few subpopulations would become fixed for one allele (Table 3B). For initial allele frequency of $p = 0.1$, genetic variation is lost in more than half of the subpopulations, i.e., the subpopulations become fixed for one allele, but in 100 simulations both alleles were always present somewhere in the set of 14 subpopulations. For very rare alleles $p_0 = 0.01$), however, almost

TABLE 3

Effects on genetic diversity of three different management scenarios for a peach palm improvement programme in the Peruvian Amazon.

S[1]	N[2]	P_0[3]	Estimated mean (standard error, minimum-maximum) number of subpopulations (out of 14) in which fixation occurred[4]		Esimated probability (standard deviation[5]) of loss of all diversity[4]	
			Over 3 generations	Over 20 generations	Over 3 generations	Over 20 generations
A. Improvement without gene exchange – large number of progenitors per subpopulation per generation						
14	150	0.5	0.0 (0.00, 0–0)	0.0 (0.00, 0–0)	0.00 (0.000)	0.00 (0.000)
		0.1	0.0 (0.00, 0–0)	0.6 (0.07, 0–3)	0.00 (0.000)	0.00 (0.000)
		0.01	2.3 (0.12, 0–6)	10.2 (0.14, 7–13)	0.00 (0.000)	0.00 (0.000)
B. Improvement without gene exchange – small number of progenitors per subpopulation per generation						
14	20	0.5	0.0 (0.00, 0–0)	2.0 (0.15, 0–7)	0.00 (0.000)	0.00 (0.000)
		0.1	1.1 (0.11, 0–5)	8.9 (0.16, 5–13)	0.00 (0.000)	0.00 (0.000)
		0.01	10.6 (0.15, 6–14)	13.4 (0.07, 11–14)	0.01 (0.010)	0.54 (0.050)
C. Improvement with one migrant individual per subpopulation per generation – small number of progenitors per subpopulation per generation						
14	20	0.5	0.0 (0.00, 0–0)	0.0 (0.01, 0–1)	0.00 (0.000)	0.00 (0.000)
		0.1	0.7 (0.09, 0–3)	4.8 (0.36, 0–11)	0.00 (0.000)	0.00 (0.000)
		0.01	10.6 (0.17, 5–13)	12.5 (0.21, 5–14)	0.00 (0.000)	0.51 (0.050)

[1]S = number of subpopulations; [2]N = number of progenitors per subpopulation in each generation; [3]P_0 = initial allele frequency (same in all subpopulations); [4]based on 100 sample runs; [5]i.e., $\sqrt{(pq/100)}$, standard deviation of binomial distribution.

all subpopulations tended to become fixed after 20 generations, and estimated probability of loss of all variation was around 50%. Even over 3 generations, more than half of the subpopulations became fixed, although the probability of loss of all variation was slight.

C. Management for genetic gain with reciprocal seedling exchanges – improvement with one migrant individual per sub-population per generation

Migration of alleles between subpopulations tends to mitigate the loss of genetic variation due to drift. Low levels of migration are sufficient to prevent drift under Wright's Island Model; inclusion of one migrant individual per subpopulation per generation is expected to maintain an acceptable balance of within- and between-population variation (Mills and Allendorf 1996, Wang 2004). In the present context, migration could be effected by randomly including in each group of 20 progenitors a single seedling derived from a bulked seedlot from all 14 subpopulations. For $p = 0.1$, this migration clearly mitigates the loss of diversity: around one-third of the subpopulations become homozygous over 20 generations, as against almost two-thirds for case B (Table 3B, 3C). Inclusion of a single randomly selected individual will have little impact on genetic gain. For $p = 0.01$, there is a much weaker mitigatory effect, as the probability that the migrating individual will carry the rare allele is very low.

These simulations illustrate that, in the longer-term, genetic variation could be relatively easily lost for initially rare alleles, but, except for very rare alleles, this could easily be prevented if farmers exchange seedlings among the subpopulations, as they currently do (Adin *et al*. 2004, Cole 2004). For alleles of intermediate frequency, there is little probability of loss, even without seedling exchanges. Although genetic drift is unavoidable when relatively intensive selection is carried out in small populations, selection is likely to be compatible with maintenance of genetic diversity in both the medium- and long-terms, except for very rare alleles. This outcome is acceptable when conserving crop landraces (Brown 2000).

GENETIC GAIN AND DIVERSITY IN IMPROVEMENT PROGRAMMES

White (1987) presents a framework for breeding programmes that is useful in the present context. He distinguishes four conceptually distinct components of tree breeding programmes. The 'base population' is the starting place for each generation of selection. The 'selected population' is the subset of the base population that initially is chosen to be carried forward to the next generation. The 'breeding population' is composed of those trees that are actually used to produce the next generation of the breeding programme (i.e., the following base population), and may consist of all or a part of the selected population. Finally, the 'production population' is composed of those trees used to produce propagules for commercial planting. In larger or more traditional programmes, the production population tends to constitute a relatively

TABLE 4

Comparison of seven tree improvement methods according to cost, time to delivery of germplasm, potential genetic gain and potential risk of genetic erosion. R = expected cumulative genetic gain. VPP = expected levels of genetic variation of production population. VBP = risk of genetic erosion of the base population. Methods are ranked relatively from 1 to 5, with 5 being the best (most gain, most variation, least erosion risk).

Method	Assumptions and explanation	R	VPP	VBP	Comments
			Low-cost, rapid delivery of germplasm		
1. SEED TREES: Seed collection from 100 mother-trees in farmers' fields	1. Over time, felled or dead trees replaced by new selections. 2. Seed bulked for delivery	2	5	5	1. Base population = population of trees in farmers' fields from which new selections are drawn. 2. No breeding population as such; rather a steady turnover within the production population. Production population = selected trees. 3. As successive generations of the base population are not systematically derived from a breeding population, this is not subject to cumulative gain and erosion. 4. Production population is large enough to avoid genetic erosion in commercial plantations. 5. With time, existing base population could be wholly replaced by material derived from the production population. This constitutes the main possible mechanism of genetic erosion. 6. Except for highly heritable traits, expected gain is low as (a) it depends on phenotypic selection (b) selection intensity will not generally be high. 7. Worst-case consequences of programme breakdown: return to situation before programme initiation (e.g. collections from one or few trees), i.e. no negative effect.
2. Network of seed production areas (SPAs) established from plantations or natural stands, 100 trees per stand	1. Seed bulked from each SPA for local delivery and use. 2. Subsequent generations established with seed from each SPA, with minimal 'artificial migration' to maintain diversity.	1	4	4	1. Base population in each generation is derived from breeding population of previous generation and composed of the unthinned SPA. 2. Breeding populations = production populations. 3. Breeding populations are large enough to avoid genetic erosion in the base population, particularly when artificial migration is effected. 4. Except for highly heritable traits, expected gain is low as (a) it depends on phenotypic selection, and (b) selection intensity will generally not be high.

Strategies for medium-cost, rapid delivery of germplasm

Strategy	Description	Scores	Consequences
3. MANY CLONES: Propagation of many selected clones within a network of farming communities	1. Plants of 100 clones bulked for delivery 2. Subsequently, additional clones added/substituted based on farmers' decisions.	3 4 4	5. Worst-case consequences of programme breakdown: SPAs used as seed sources until moribund; subsequently, plantations established from SPA material used as seed sources, small reductions in diversity of commercial plantations could result. 1. Like strategy 1, base population is made up of the population of trees from which new clones are selected. 2. Production population (n = 100) large enough to preclude significant loss of variation due to drift. 3. No breeding population as such; rather a steady turnover within the production population. 4. Clonal turnover is expected to maintain variation in the production population. 5. Erosion of base population can occur if this is replaced by clones of the production population. But high number of clones will confer relatively high variation. 6. Gain is likely to be relatively high because: (a) this relatively expensive strategy is only justified if selections are relatively intensive and/or selected traits are highly heritable, and otherwise is unlikely to be implemented; (b) non-additive genetic variation is captured. 7. Worst-case consequences of programme breakdown: farmers use only one or a few clones (erosion of production and base populations, higher pests and disease risk); farmers abandon vegetative propagation and begin to collect seed from one or a few clones (possible extreme erosion).
4. VILLAGE CULTIVARS: Propagation of few selected clones within a network of farming communities	1. 5–10 clones selected and used per village. 2. Subsequently, additional clones added/substituted based on farmers' decisions, possibly including clones from other villages.	4 3 3	1. Base population composed of the population from which each village's selections are drawn (similar to strategy 3, but probably with less initial variation). 2. Individual village production populations have few clones and likely to exhibit reduced genetic variation. However, the set of clones over all villages is unlikely to be genetically depauperate. 3. Like strategy 3, no breeding population as such. 4. Like strategy 3, clonal turnover expected to maintain variation in production population. 5. Gain is likely to be relatively high, for reasons indicated under strategy 3, and because clones may be better adapted to local conditions. 6. Worst-case consequences of programme breakdown: like strategy 3, but more severe as the programme is based on fewer clones per locality.

Table 4 continued

Method	Assumptions and explanation	R	VPP	VBP	Comments
Strategies for medium-cost with longer-time to delivery					
5. SSO : Network of progeny trials/seedling seed orchards (SSOs), seed derived from plus-trees	1. 50 best families selected in trials based on progeny performance. 2. Blocks thinned to the best 50 families to reproduce seed. 3. Seed bulked from each SSO for local delivery and use. 4. Subsequently generations of SSOs established by collecting seed within each SSO, with minimal 'artificial migration' to maintain diversity.	3	4	4	1. Like strategy 2, but also includes genotype selection (i.e. selection based on family performances). 2. Blocks thinned to the best 50 families to produce seed. 3. Seed bulked from each SSO for local delivery and use. 4. Subsequent generations of SSOs established by collecting seed within each SSO, with minimal 'artificial migration' to maintain diversity. 2. With artificial migration, breeding populations are large enough to prevent appreciable genetic erosion, at least in the short-term. 3. Genetic gain should be higher than strategies 1 and 2 because there are three separate selection stages (initial phenotypic, within-family, and between-family). However, gain from family selection is limited by the number of families per trial. 4. Worst-case consequences of programme breakdown: like strategy 2
Strategies for higher-cost options with longer-time to delivery					
6. CSO: Clonal seed orchards with associated progeny trials, based on large number of initial plus-tree selections (e.g. 400–500)	1. Orchards (production populations) established with grafted stock of 25 best selections, based on results of progeny tests. 2. Breeding population of 100 genotypes, maintaned in clone bank.	4	3	5	1. Base population in each generation is derived from breeding population of previous generation. 2. Breeding population is distinct from production population and large enough to avoid serious genetic erosion of base population. 3. Gain expected to be high because based on high intensity, genotypic selection. 4. Worst-case consequences of programme breakdown: farmers collect seed from commercial plantations derived from production populations, leading to significant loss of genetic variation in future plantations

High-cost options with longer-time to delivery

3. Selected and breeding populations of each generation based on selections made in progeny trials.

7. TESTED CLONES: Field tests of 500 clones to select the 25 best

Subsequently, additional clones added/substituted based on clonal testing of new candidates.

5   4   2

1. Like strategies 1 and 3, base population is made up of the population of trees from which new clones are selected.

2. Production population of 25 clones is small and likely to be less variable than the base population.

3. Like strategy 3, no breeding population as such.

4. Like strategy 3, clonal turnover expected to maintain variation in production population, but lower numbers of clones are present

5. Like strategy 3, but genetic erosion would be more serious because there are far fewer clones.

6. Like strategy 3, gain is likely to be high due to clonal selection, which captures non-additive variation.

7. Worst-case consequences of programme breakdown: like strategy 4, although more extreme due to lack of between-village variation component.

small subset of the breeding population. In less traditional programmes, the different types of populations, although conceptually distinct, may be fused. For example, in the ICRAF-INIEA programme, the individual thinned blocks simultaneously fulfill the functions of the selected, production and breeding populations.

With reference to this framework, three ways in which improvement programmes could lead to loss of genetic diversity might be identified. First, intensive selection in the breeding population will lead to loss of diversity in the base population of the following generation and, if repeated in succeeding generations, to cumulative genetic erosion. As genetic variation is proportional to population size, this can be avoided by ensuring an adequate number of individuals in the breeding population. Second, formation of production populations by highly intensive selection within the selected population will lead to loss of diversity in commercial plantations, but not to long-term erosion. Third, the use as seed sources of commercial plantations established with material from the production population – as could occur in the event of programme breakdown - would lead in the short-term to reduced diversity and possible inbreeding depression in the resulting plantations. This effect would be exacerbated if, in future generations, farmers continue to select within the populations initially derived from the production population.

In Table 4, we summarize the implications for gain and diversity of seven breeding strategies that are used or might be used in tree improvement for rural development, each classified according to cost and time to delivery of improved germplasm. It should be noted that strategies 3, 4, 6 and 7 depend on vegetative propagation, and therefore do not apply in the case of peach palm and other crops for which efficient vegetative propagation techniques have not yet been developed.

Strategies 1, 2, 5 and 6 are all based on recurrent selection, i.e., selection in successive generations. All are compatible with maintenance of genetic variation. However, for the lower cost options (i.e., 1 and 2), genetic gain is likely to be low, except for highly heritable traits. In traits with low heritability, simultaneous retention of genetic diversity and achievement of high gain is likely to require substantial investment. Growth and some form traits of timber trees, as well as traits closely related to fitness, tend to have low heritabilities (Mousseau and Roff 1987, Cornelius 1994), while fruit characteristics frequently have high heritabilities, i.e., above 0.5 (Resende 2002). Native fruit trees, such as peach palm, may therefore offer better possibilities for achieving high gain with high diversity than timber species, particularly when resource limitations preclude high investment.

In strategies 3, 4 and 7, the production population is composed of a group of clones selected from the initial base population. New clones may be added over time, but there is no sexual phase. Therefore, there is no breeding population and the base population retains its initial identity. The improvement process does not affect the base population at all, except insofar as this might eventually be displaced from farmers' fields by the selected clones of the production population. As far as the balance between gain and diversity in the production population is concerned, the considerations set out in the previous paragraph also apply here.

In the case of programme breakdown, different conclusions apply. Misuse of the production population may occur. The consequences for genetic diversity will be

most serious in the case of the most intensively selected production populations. For example, collection of seed from a few superior clones, and use of the trees thus produced as progenitors of future generations, could have severe effects on genetic diversity, although in many situations gene flow (i.e., pollen and/or seed movement) from wild and other populations would mitigate the resulting bottlenecks. In the case of the less intensive strategies, programme breakdown would lead to reversion to a situation similar to that before programme initiation and therefore its effects on diversity would not be a major concern.

From the perspective of programme success, lack of institutional continuity poses a greater threat than does loss of genetic diversity. For example, in the case of the peach palm programme, funding availability could limit ICRAF's or INIEA's involvement long before inbreeding becomes a serious concern. Similarly, farmers' priorities may change, as may farm ownership, and subpopulations may be lost or abandoned as a result. The full challenge in such programmes lies not only in balancing genetic gain and genetic diversity, but also in ensuring that medium to long-term benefits can accrue from such programmes in conditions of uncertain funding. In addressing the challenge, the overall profitability of the crop is crucial, as increasing revenues will help ensure continued interest of national institutions and the farmers themselves. In the case of peach palm, as the current generation of orchards enters production, ICRAF and INIEA will assist farmers' groups in locating domestic and international markets for seed and fruits.

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