

Managing genetic variation in tropical trees: linking knowledge with action in agroforestry ecosystems for improved conservation and enhanced livelihoods

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Abstract Tree species in agroforestry ecosystems contribute to the livelihoods of rural communities and play an important role in the conservation of biodiversity. Unless agroforestry landscapes are productive, however, farmers will not maintain or enhance the range and quality of tree species in them, and both income opportunities and biodiversity will be lost. Productivity depends on both tree species diversity and genetic (intra-specific) variation, but research on the latter has until recently not received the recognition it deserves. Worse, when knowledge on tree genetic variation in agroforestry systems has become available, it has not generally been linked in any systematic way with management, indicating a disjunction between research and field-level practice. In this essay, we attempt to bridge this gap by considering three questions: why is genetic diversity important in tree species? What is our current state of knowledge about intra-specific variation in trees in agroforestry systems? And, finally, what practical interventions are possible to support the conservation of this diversity in agricultural landscapes, while enhancing farmers' livelihoods? A wide genetic base in agroforestry trees is essential to prevent inbreeding depression and allow adaptation to changing environmental conditions and to altering markets for tree products. Recent evidence shows, however, that many species are subject to poor germplasm collection practice, occur at low densities in farmland, and are found in highly aggregated distributions, all of which observations raise concerns about productivity and sustainability. A range of germplasm-access based interventions is necessary to improve current management, including the enhancement of community seed- and seedling-exchange networks, and the development of locally based tree domestication activities. Equally necessary, but more difficult to address, is

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the development of markets that support genetic diversity in tropical tree species; we discuss approaches by which this may be undertaken.

Keywords Agroforestry ecosystems · Biodiversity management · Genetic variation · Tropical trees

Introduction

As the tropical forests of Africa, Asia and the America's contract, agriculture-based approaches for conserving the biodiversity they contain are required (Garrity 2004; McNeely 2004; FAO 2006; Leakey 2007). Agroforestry—the practice of integrating trees with crop production and other farm activities in order to provide products and services previously obtained from wild resources—provides an important means for conserving biodiversity, as when an active tree planting culture exists hundreds of indigenous tree species can be found in tree-crop ecosystems (Schroth and da Mota 2004; Acharya 2006; Tata and van Noordwijk 2008). Indeed, Simons et al. (2000) predict that human activity will have such a negative impact on many currently forested regions in the tropics that in the future it will only be possible to conserve many important trees species if they are managed *circa situ* in farmland. This is because *ex situ* conservation methods for tropical trees—in which species are stored as seed or living plants in gene banks—are generally not practical, because of the sheer number of taxa involved, frequent seed recalcitrance, specific associations with micro-organisms that must be maintained for proper growth, the prohibitive expense of maintaining live gene banks for taxa with large growth forms, and the time required to regenerate species with long generation intervals, among other factors (Kindt and Lengkeek 1999).

Although the potential for agroforestry is clear, unless function is maximised in agricultural landscapes farmers will not engage in tree cultivation and silviculture, they will not maintain or enhance the range and quality of tree species that are found on farms, and valuable contributions for livelihoods and conservation will be lost (Atta-Krah et al. 2004). As the value of agroforestry ecosystems for conserving biodiversity has become more widely recognised, research on tree species diversity in these landscapes and how it relates to productivity has received greater attention (Kindt 2002; Steffan-Dewenter et al. 2007; Kirschenmann 2007). Research suggests that there is a positive relationship between species diversity and ecosystem function in farmland, which is conditional on the growth characteristics of trees, the spatial scale of intervention and the level of environmental heterogeneity. Trees are able to provide the structural diversity to sustain associated fauna in agricultural landscapes, which are needed for critical functions such as crop pollination, the economic value of which equates to billions of US Dollars annually (McNeely and Scherr 2001). Although tree species diversification in farmland can increase the mean and reduce the variance of farmers' incomes from agroforestry practices, this depends on how different production activities complement each other (Kindt et al. 2006b). Interventions that support biodiversity whilst improving livelihoods should therefore be more concerned with maximising functional diversity than with increasing the number of tree species found in landscapes *per se*.

While the role of tree species diversity in maximising the productivity of agroforestry systems is now better recognised, until recently the relationship between genetic (intra-specific) variation and productivity (at a species and ecosystem level) has received less attention, and where knowledge is available on genetic structure it has not generally resulted in more

suitable field management practices that support farmers. In this essay, we address this issue by first considering why genetic diversity is important within tree species, and then relating what our current state of knowledge on genetic variation within tree taxa in agroforestry systems is. Finally, we discuss the practical interventions that are possible to support the conservation of this diversity in farm landscapes, at the same time as enhancing farmers' livelihoods. Through the use of examples, including case studies in which the authors have participated, our intention is to set out a structure for further discussion, research and intervention on this important topic.

The importance of genetic variation in tree species

High levels of genetic variation within tree species—in discrete populations and in a taxon overall—are important for two main reasons. First, whereas most agricultural crops have undergone long processes of local and/or commercial breeding to select out deleterious, recessive alleles from populations, this is not the case for many tree species found on farms in the tropics, which are out-crossing 'incipient' or 'semi-' domesticates (Jamnadass et al. 2008). As a result, unless a wide genetic base within species is maintained, trees are vulnerable to inbreeding depression, the process by which self- or related-matings lead to homozygosity, the loss of heterozygote superiority and the 'exposure' of deleterious mutations (Boshier 2000; Lowe et al. 2005). Inbreeding depression reduces individual fitness and raises the possibilities of population and/or species extinction (Charlesworth and Charlesworth 1987; Hansson and Westerberg 2002; Reed and Frankham 2003); indeed, the negative effects of inbreeding in trees are well documented and include embryo abortion, limited fruit set, reduced overall seed yield and lower germination rates for remaining seed. Furthermore, selfed or inbred progeny can suffer from lower seedling vigour and poor growth form, and end up being less productive when they reach maturity (Hardner and Potts 1997; Gigord et al. 1998; Wu et al. 1998a, b; Koelewijn et al. 1999; Stacy 2001).

Inbreeding depression is worsened by the large variations in fecundity often observed in tree species (El-Kassaby et al. 1989; El-Kassaby and Cook 1994). This phenomenon, in which a small number of trees contribute disproportionately to the seed crop, can result in the effective population size of a tree stand (N_e)—the size of an 'idealised' population that would have the same genetic properties as that observed for a real population—being much lower than the census size, and lower than that required to maintain heterozygosity and productivity (Wright 1931; Lengkeek et al. 2005b). N_e is also lowered if the reproductive connectivity between trees in a landscape is weak. Connectivity depends on the density and evenness of distribution of sexually mature individuals in the landscape and, if a species relies on animal pollinators and/or seed dispersers, on the presence of these agents to facilitate gene flow (Nason and Hamrick 1997).

Second, high levels of genetic variation are important because they provide the ability for tree species to adjust to new environments, such as the shifting climate and more variable weather conditions caused by elevated CO₂ levels and global warming, allowing local adaptation and the migration of better-suited provenances along ecological gradients (Bawa and Dayanandan 1998; Atta-Krah et al. 2004; Williams et al. 2007; Aitken et al. 2008). Variation is also crucial to respond to new pests and diseases: taking temperate forestry as an example, low genetic variation in cultivated stands appears to have been partly responsible for Dutch elm disease, which decimated elm populations in the twentieth century (Gil et al. 2004), and in larch for larch canker (Geburek 2005).

In the context of agricultural systems, selection pressures are not only a function of ecology, but depend on the changing requirements of the markets that producers serve. Genetic variation that is already present in the farm landscape allows farmers to more easily respond to new markets that are looking for different characteristics in tree products (Lengkeek 2003). Genetic variation in agricultural landscapes also helps farmers to manage their inputs in more efficient ways. For example, a range of varieties of a fruit tree species that ripen at different times may be beneficial for farmers, because this allows the more efficient use of labour and capital, and prevents the gluts (with depressed prices and waste) that occur when perishable products are brought to market over a short period of time (Dawson et al. 2007).

The current state of knowledge for agroforestry systems

Until recently, studies on the genetic structure of tree species in agroforestry systems have been limited because of practical and conceptual limitations in undertaking research (Atta-Krah et al. 2004; Geburek and Konrad 2008), among which the following four issues appear paramount:

- (1) *Lack of recognition of the nature of the problem* Since trees can persist in landscapes even when they are no longer reproductively viable (Janzen 1986), problems related to inbreeding, lack of seed set and regeneration may not be immediately evident. By the time that problems do become clear, the landscape may have been modified to such an extent that it may already be too late to devise practical interventions to do anything about the situation.
- (2) *An inability to assemble appropriate teams to undertake effective research* The institutional frameworks within which researchers work rarely support the team-based, multidisciplinary approaches that are needed to properly assess genetic variation and then apply this knowledge through appropriately devised management interventions. For agroforestry, the situation is acute, as ‘forestry’ and ‘agriculture’ are traditionally considered as discrete schools of research that should be treated separately, whereas aspects from both must be combined together if effective action is to be realised.
- (3) *Difficulties in recognising and quantifying variation* Due to the low level of formal domestication of most tree species, genetic variation may be difficult for farmers to measure in agricultural landscapes, as they are not able to recognise important ‘varietal’ differences in trees in the same way as they can for traditional agricultural crops (Brodie et al. 1997; Edwards and Schreckenber 1997). Important variation may sometimes be ‘cryptic’ to users (i.e., not evident to the naked eye; Atta-Krah et al. 2004) and ‘surrogate’ measures of genetic variation have not been widely explored (Jennings et al. 2001).
- (4) *The large number of species involved* A very large number of tree species are found in agroforestry systems, and comprehensive analysis of genetic variation in all taxa is impractical. Some researchers have questioned whether studies on a subset of species within a particular context can provide useful information for other taxa and wider ecosystems: is the concept of ‘model’ species—targets for research from which general recommendations for intervention can be devised—relevant or not (Scott 1998; Atta-Krah et al. 2004)?

Although not all of these issues have yet been addressed, new tools such as molecular markers have become available to characterise diversity, and conceptual advances in more

traditional approaches to research have been made. The development of these methods has been supported by a wider understanding of the ‘systems-oriented’ approach that is required in such research, as evidenced by recent studies that demonstrate the role of genetic variation in determining not only the performance of particular species but of entire ecosystems (Reusch et al. 2005; Crutsinger et al. 2006; Whitham et al. 2006; Hajjar et al. 2008). This has resulted in the availability of a number of technologies that, either directly or indirectly, can provide insights into tree genetic structures and effective population sizes in agroforestry landscapes. In the following sections, we describe recent interesting case studies using some of these methodologies, with a view to promoting similar approaches by others. Where relevant, we give illustrations from our own research on agroforestry systems in Africa and Latin America, before providing a summary of the current state of knowledge on the topic.

Direct measures of genetic variation: using morphological and molecular markers

Despite difficulties in characterising morphological variation in tree species (see above; Brodie et al. 1997; Edwards and Schreckenberg 1997), a number of interesting recent studies have been undertaken on taxa of high value. Of particular relevance for an understanding of the history of existing farmland populations are studies that have directly compared cultivated trees with wild stands of the same species. For example, phenotypic variation has been characterised extensively in farmers’ fields and natural forest for a number of commercially and historically important fruit trees in west Africa, including bush mango (*Irvingia gabonensis*) and safou (*Dacryodes edulis*) (Leakey et al. 2004, 2005). In this research, farmers’ perceptions of fruit diversity, as well as scientific measurements, were studied. In both species, morphological variation in fruit traits was higher in planted than natural stands in certain locations (*I. gabonensis* in Nigeria, *D. edulis* in Cameroon), but not elsewhere. Where variation was greater in farmland, this suggested ‘semi-domestication’ through selective seed collection and planting by farmers for specific traits over many years, leading to a mixture of selected and unselected phenotypes being present in the agricultural landscape (Leakey et al. 2004). Related research on sheanut (*Vitellaria paradoxa*) fruit in the northern sub-Sahara (Maranz and Wiesman 2003) has also provided some evidence for human selection of particular phenotypes in the species. The ways by which ‘informal’ selection operates on these and other fruit trees are likely to be complex, however, and depend on how produce is used: e.g., if humans collect and eat the best seed from fruits then only the worst genotypes may remain to propagate (dysgenic selection), whereas if seed is a ‘by-product’ of fruit collection that is subsequently planted, then positive selection can occur if farmers harvest only the best produce (Weber et al. 2001; Leakey et al. 2004).

Agroforestry timber trees have recently been the subjects of increased participatory field trials in Latin America. Research has focused on practical questions such as assessing the risks of mal-adaptation due to transfer of seed across ecological zones in the context of climate change, and the correlations between tree growth and wood properties. Studies show that genetic variation in commercially important traits can be identified at a relatively early age in farmers’ fields, reducing the time and expense required for evaluation (Hodge et al. 2002; Boivin-Chabot et al. 2004; Rochon et al. 2007). On-farm studies in Peru have indicated that, while provenances of local origin for a given species may be better adapted than introduced material, this is not always the case (see Weber and Sotelo-Montes 2008; Sotelo-Montes et al. 2003, respectively, for bolaina [*Guazuma crinita*] and capirona [*Calycophyllum spruceanum*]). The correlation between tree growth and wood properties

varied among provenances, species and planting environments (Weber and Sotelo-Montes 2005, 2008; Sotelo-Montes et al. 2006).

Little morphological data is available on the impacts of possible dysgenic selection on timber trees in agroforestry systems, but the phenomenon is known to be significant occasionally in natural populations, where the best trees are intensively logged and inferior individuals are left to seed and establish subsequent generations (Gentry and Vasquez 1988; Rodan et al. 1992; Rowe and Cronk 1995; O'Neill et al. 2001; Sokol et al. 2004). Farm landscapes may be more environmentally uniform than natural forest, which means that selection may be more 'genetically efficient' when felling trees in agricultural land (a greater proportion of the morphological variation observed among individuals is heritable); this may lead to more intense dysgenic selection in farmland.

Morphological measurements can only describe a small portion of the underlying genetic diversity present in taxa, are subject to environmental variation, and are not readily understandable in the context of the biological processes involved in shaping genetic structure. In the last 15 years, molecular approaches based on directly determining polymorphism in DNA have become available and these can assess genetic variation in much more detail (Jamnadass et al. 2005, 2008). Such techniques reveal markers that are both highly polymorphic and have the capacity to measure heterozygosity, a variable that relates to fitness in populations by preventing inbreeding depression (see above). Molecular markers can provide information on how diversity is structured within and among natural, managed and cultivated stands, and can measure the extent that individuals and populations are connected to each other. In addition, they can be used to determine the breeding systems of trees, measure relationships among different taxa, assess hybridisation and other interactions between species, and evaluate human impacts on tree stands through population fragmentation, selection, cultivation, etc. (Hamrick et al. 1992; Jamnadass et al. 2008).

Although molecular marker studies on tree populations in agroforestry systems have to date been limited, efforts have commenced to rectify this deficiency. Of most interest is the small number of studies that have assessed geographically matched wild, managed and cultivated populations of tree species. For example, recent molecular studies in Africa have involved comparing genetic variation in 'unmanaged' natural stands of sheanut (*Vitellaria paradoxa*) with geographically matched (neighbouring) agroforestry populations of the same species in Mali (Kelly et al. 2004). Similarly, Lengkeek et al. (2006) directly compared natural forest and proximate remnant/planted farm stands of the timber tree Meru oak (*Vitex fischeri*, synonym *Vitex keniensis*) in central Kenya. In both cases, levels of genetic variation were similar across stand categories, and little differentiation between unmanaged and managed stands was observed.

In contrast, matched farm-forest comparisons for the indigenous fruit trees inga (*Inga edulis*) and jocote (*Spondias purpurea*) in Latin America have shown clear genetic differences between stand categories. In inga, genetic bottlenecks were evident in planted agroforestry stands in the Peruvian Amazon, suggesting limited sampling during introduction of the species into cultivation in the region (Hollingsworth et al. 2005). However, molecular genetic variation in farmland stands was still 70–80% of that in forest, suggesting that planted populations could still be useful resources for conservation. Further analysis indicated that farmland populations of inga were differentiated from local wild material and were derived from multiple sources (Dawson et al. 2008b), meaning that a strategy in which inga seed collected from natural forest is planted in neighbouring farmland may not be appropriate for conservation, due to the potential risks of outbreeding depression (dilution of locally adapted alleles and/or the breakdown of co-adapted gene complexes, Ledig 1992). In jocote, Miller and Schaal (2005, 2006) found that molecular variation in cultivated stands in

Mesoamerica was significantly less than in wild populations, and, similar to the situation observed for inga, data suggested multiple sources of cultivated germplasm. The reason why differences are observed for inga and jocote but not for sheanut and Meru oak may reflect the greater sustained intensity of human planting and management of the first two species, and possibly factors such as relative longevities, generation intervals and generation overlaps (Hollingsworth et al. 2005).

Although molecular studies can reveal great detail about genetic variation in trees, the application of results to improve management practices—in forests, plantations or farmers' fields—has to date been very limited (FAO 2004). One restricting factor is that molecular approaches generally reveal 'neutral' markers that cannot provide information directly about traits of social, ecological or economic value. To address this, combined morphological and molecular research has begun on the same material in some species (e.g., in African fruit trees, Sanou et al. 2005 and Bouvet et al. 2008 in sheanut, *Vitellaria paradoxa*; Assogbadjo et al. 2006 in baobab, *Adansonia digitata*; Akinnifesi et al. 2006 in marula, *Sclerocarya birrea*). However, more fundamental 'systemic' problems are also evident in the application of molecular markers: in particular, laboratory practitioners tend to work in isolation from other disciplines, and need to adopt a more 'systems-oriented' mindset (see above; Dawson et al. 2008a).

Indirect measures of genetic variation: using germplasm source surveys and on-farm tree inventories

Morphological and molecular markers provide a direct handle on genetic variation, but are costly and time consuming and are generally applied to one species at a time. As an alternative, survey techniques are available that can be more easily used on many species simultaneously, although these methods give less precise information and require extrapolation. Here, we explain the utility and consider the results of two of these methods, one based on germplasm source surveys and the second involving on-farm tree inventories. Germplasm source surveys consult all the stakeholders involved in supplying planting material to farmers—including farmers themselves, tree nursery managers, seed businesses, national tree seed programmes and non-governmental organisations—and ask them about the origins of seed and seedlings and the practices adopted for collecting them. Source surveys have recently been undertaken in agroforestry systems across the tropics, although there has been an emphasis on Africa and Latin America (Lengkeek 2003). For example, in the most extensive study conducted to date, which involved interviewing private tree nurseries serving smallholder farm clients in Kenya, Tanzania and Uganda (Lengkeek et al. 2005a), considerable variation was observed between nurseries and tree species in: (1) the number of trees sampled for seed to establish nursery lots, (2) the quantity of seedlings raised in a nursery lot; and (3) the projected number of clients purchasing seedlings of a species.

In the 143 cases analysed by Lengkeek et al. (2005a), seed collected to establish nursery lots came from a mean of only 6.4 trees, while each sampled tree produced sufficient progeny to provide all the seedlings received by a typical nursery client. In 22% of cases, seed to establish nursery populations was sampled from only a single tree. Results clearly identified current seed collection practice as an obvious bottleneck in delivering genetically diverse germplasm to farmers, and indicated that not mixing progeny from different trees of the same species in nurseries could also significantly reduce genetic variation in planted populations, conclusions supported by similar research elsewhere (e.g., Weber et al. 1997; Holding and Omondi 1998; Kindt 2002). Furthermore, surveys in East Africa have shown that much germplasm is vegetatively propagated for on-farm planting, a practice which

may rely on only a few genotypes, and that once farmers have established trees on their farms, they tend to rely on these trees as sources for future generations of planting rather than returning to external sources, as this is more convenient and cheaper (Lengkeek et al. 2005b). These factors appear to be particular concerns for trees that produce large fruit that are perishable and have recalcitrant seed (Brodie et al. 1997; Weber et al. 1997; Lengkeek et al. 2005b). Both of these practices are eventually likely to further reduce genetic diversity in planted populations, though the time taken to do so will depend on the longevity of species and interactions between overlapping generations in farmland.

Through consulting farmers and mapping their holdings, on-farm tree inventories are used to: (1) characterise the diversity of tree species found in farms, (2) assign variation to functional use groups, particular planting niches, different silvicultural practices, and various markets; and (3) partition variation geographically within the wider agricultural landscape (Kindt et al. 2006b, c). From a genetic perspective, the relevance of on-farm tree inventories lies in the information they reveal on the density and the level of aggregation of tree species in farmland, and the insights they can therefore provide into effective population sizes in agricultural landscapes, which are related to connectivity, levels of outcrossing and possible inbreeding depression. Recent inventories have shown that many tree species have extremely low densities in tropical farms, to a greater extent than observed for natural stands of the same taxa (for Africa, see Kindt 2002; van Oijen 2002; Lengkeek et al. 2005b). For example, Lengkeek et al. (2005b) found densities of less than one mature tree per hectare for approximately 75% of the species observed on surveyed farms in central Kenya. Furthermore, more than half of the species observed in the same study (primarily indigenous ones) had a density of less than 0.25 mature trees per hectare. According to Lengkeek et al. (2005b), the low density of most taxa reflected the large number of different tree species found in agroforestry systems in the surveyed area (around 300 taxa across 35 farms), and the limited space farmers could therefore allocate to any one taxon. Furthermore, a few exotic or (more rarely) indigenous tree species were often observed to dominate farming landscapes, perhaps because germplasm of these species was most readily available, leaving little room for all other taxa (Kindt 2002; Lengkeek 2003).

In addition to low tree densities, farm inventories have shown that many tree species exhibit extremely aggregated distributions in agroforestry landscapes. For example, in a survey of villages in Cameroon, Kenya and Uganda, Kindt et al. (2006b) observed that much variation in species presence was structured at the ‘between-village’ level, suggesting that there is greater sharing of tree germplasm within than among villages. Aggregated distributions appeared also to reflect patchily distributed natural forest fragments that can seed farmland. Kindt (2002) and Lengkeek (2003) indicated that, in the systems they had studied, aggregation appeared to be an important factor in limiting farmer access to tree germplasm, an issue we return to later in this essay. Whatever the cause, both low tree densities and aggregated distributions are likely to reduce N_e for tree stands in farm landscapes.

Indirect measures of genetic variation: information from other managed ecosystems

Although not considering agroforestry systems specifically, a number of recent reviews based on other managed tree ecosystems provide information that is highly relevant for understanding genetic variation in agricultural landscapes. Of most relevance are two reviews on neo-tropical forests by Lowe et al. (2005) and Ward et al. (2005). Lowe et al. (2005) reviewed the impacts of anthropogenic habitat degradation, especially due to logging, on the genetic resources of disturbed natural stands of tree species, while Ward et al. (2005) reviewed mating systems and pollen dispersal in both natural and fragmented populations of

trees. Based on 31 case studies, Lowe et al. (2005) indicated that human impacts did not appear generally to produce significant immediate effects on the genetic diversity of tree stands in neo-tropical forests. However, significant anthropic effects were observed in several studies that assessed progeny inbreeding, reproductive output and fitness, including in remnant trees that had become isolated in farmland, where trees exhibited lower fruit production, and progeny showed reduced seed germination rates and lower seedling vigour. In the context of agroforestry development, the demonstrated loss of performance in the progeny of remnant trees in farm landscapes may be a serious issue, as these are the trees from which farmers are likely to collect seed for planting. According to Lowe et al. (2005), these observations correspond with theoretical considerations of forest fragmentation, which indicate that genetic diversity in remnant trees may be slow to decay over time, e.g., due to long generation intervals, whereas inbreeding effects may be observed immediately after disturbance.

Based on 36 case studies, Ward et al. (2005) indicated that, as expected, self-fertilisation rates in neo-tropical trees generally varied inversely with population density, although lower stand density did not always lead to lower outcrossing. Direct measures of pollen flow, using genetic markers, indicated that reproductive connectivity and N_e are generally lower in fragmented populations, although this was not always the case and longer pollen dispersal distances were sometimes observed in fragmented landscapes than in natural forest. One factor increasing dispersal in fragmented landscapes appears to be increased wind exposure, allowing pollinators to drift along air currents. Long distance dispersal suggests that apparently isolated individuals and small groups of trees in farmland may not be the 'living dead' (no longer able to mate and produce seed; Janzen 1986) that they were once assumed to be, but despite possible reduced seeding and lower progeny vigour (Lowe et al. 2005) may still be able to regenerate in farmland. In addition, where remaining natural forest is conserved in a landscape mosaic with agricultural land, farm trees may contribute to the maintenance of wild populations through genetic exchange with forest fragments, and by providing 'stepping-stones' for animal pollinators and seed dispersers (Boshier 2004).

Summary of current knowledge

Based on studies such as those described above, it is evident that genetic variation can be structured in complex ways in tree species in agroforestry systems. When species are managed intensively, evidence points to losses of molecular genetic variation and increases in phenotypic variation, e.g., in fruit trees. Effects may however take considerable time to become evident (e.g., fruit trees have been managed by humans over several millennia; Miller and Nair 2006; Jamnadass et al. 2008) and limited research has considered the correlation between molecular and morphological variation in these cases. Although there appears to be a paradox between lower molecular variation and higher morphological diversity in cultivated stands, this is consistent with the domestication process for annual crops, where although a multitude of phenotypically distinct varieties is selected and maintained, there is an overall narrowing of the genetic base of planted germplasm (Harlan 1975). This results in 'tradeoffs' between productivity and sustainability in these crops: higher short-term yields are often coupled with a need for greater farm inputs (fertiliser, irrigation, tilling, etc.) and an increased vulnerability to changing environments conditions and altering market demands. In order to maintain the productivity of annual crops in the longer-term, this requires that the genetic resources that are needed to respond to change be maintained as a 'public good' in genebanks outside farmers' fields (see Dawson et al. 2007 for further discussion). As *ex situ* conservation methods are not suitable for many trees, it

follows that greater onus needs to be placed on maintaining genetic diversity *circa situ* in agricultural landscapes than for annual crops (Cornelius et al. 2006).

Poor collection practice and the ‘one-off’ nature of many germplasm introductions mean that the genetic base of many tropical trees in cultivated landscapes is likely to be decreasing, although these effects take time to become evident when remnants are present in farmland to cross with new introductions, and because of the longevity of many species. ‘One-off’ introductions are of particular concern if they are already of low genetic base, and/or represent low quality or mal-adapted material. Many tropical trees in farm landscapes also demonstrate both extremely low densities and highly aggregated distributions, which—even if long distance pollen transfer is sometime possible—will reduce effective population sizes and promote inbreeding. In extreme conditions, some trees will exist only as the ‘living dead’ in farmland, unable to reproduce and persisting only until the current generation dies. With planted trees, the relative distance between human settlements compared to pollen and seed dispersal distances may be an important factor in determining N_e , as villages can be an important unit of population aggregation.

Options for intervention: linking knowledge with practical action

It is evident that in order for tropical agroforests to efficiently support livelihood and conservation functions in the future, germplasm-access based interventions to broaden the genetic base of tree populations and improve the connectivity between trees in farmland are required (Kindt 2002; Lengkeek 2003; Lengkeek et al. 2005b). These interventions must be placed clearly within a framework of the livelihood opportunities and the other services that they provide to local people, and must be developed in a participatory manner that builds on current farm practice, as communities will not otherwise invest in them (Edwards and Schreckenber 1997; Scott 1998; Friis-Hansen and Sthapit 2000; Lengkeek 2003; Lengkeek and Carsan 2004). Furthermore, required are measures that preferentially improve access to currently under-represented and threatened indigenous taxa or varieties, since these are the most important for conservation and are the most vulnerable to the consequences of low genetic variation. Intervention will clearly be most successful when current differences in tree abundance do not relate to differences in farmer preferences, but to particular bottlenecks in accessing rare taxa (Kindt et al. 2006d). Of course, planting of currently rare species should not be stressed to the degree that these become the new dominants in farm landscapes, thereby raising new management problems for once more common trees (Lengkeek et al. 2005b). In the below, we consider some specific germplasm-access based measures that are relevant for intervention.

Enhancing germplasm-exchange networks

Developing and strengthening networks that exchange tree seed and seedlings should facilitate the distribution of genetic diversity in farm landscapes (Kindt 2002; Lengkeek 2003). Training is needed to promote better germplasm collection methods for all actors involved in networks—farmers, non-governmental organisations, national tree seed centres, small businesses, etc.—as current practices are inadequate for sampling variation and for providing seed of good genetic and physiological quality (Lengkeek et al. 2005a; Kindt et al. 2006a; Graudal and Lillesø 2007). Emphasis needs to be placed on sampling more parents for seed, and returning to natural stands rather than remnants where this is possible (in order to minimise potential inbreeding effects associated with the latter; Lowe et al. 2005).

Furthermore, training is required in how to establish community seed banks in which germplasm can be pooled, stored and redistributed (Friis-Hansen and Sthapit 2000), and in farm management approaches that elevate the effective population sizes of tree stands, such as bee keeping, which promotes pollination and provides an additional revenue stream for farmers (honey production; Vaughan and Hoffman Black 2006).

Training of small commercial seed and seedling enterprises is particularly important, as these businesses are more sustainable and are able to reach more farmers than other germplasm supply actors, and governments in many tropical countries are increasingly relying on them for the provision of tree seed nationally (Graudal and Lillesø 2007). These businesses need training not only in the ‘technical’ aspects of supply (collection and handling approaches), but also in small enterprise development, so that they can operate efficiently and profitably in the market, and can work together with other partners (Nathan et al. 2005). These suppliers also need policy support, e.g., measures are needed to encourage non-governmental organisations to stop their common current practice of providing free tree seed and seedlings to farmers, as this represents unfair, donor-subsidised competition to commercial enterprises (Graudal and Lillesø 2007).

During the development of germplasm networks, proper consideration must be given to geographic scale. As significant variation in tree species availability is observed between communities (Kindt et al. 2006b), developing village-to-village linkages is important. Significant mal-adaptation and/or outbreeding depression are however possible if germplasm exchange occurs over too large a geographic area (Ledig 1992). In semi-arid regions like the West African Sahel, even relatively short-distance transfer of germplasm—if from more humid to drier zones—may result in significant mal-adaptation (Weber et al. 2008). The prospects for both mal-adaptation and outbreeding depression clearly depend on the historical use and past human exchange of individual species, so ‘recommendation domains’ for distribution may be required for specific taxa (Kindt et al. 2006a).

In developing networks, it is especially important that ‘nodal’ farmers and nurseries, that play a particular role in maintaining and distributing a wide range of tree species and varieties, are considered (Lengkeek 2003). For species in high demand, communities and commercial suppliers may also need to establish dedicated germplasm multiplication stands (Dawson and Were 1998). The founder material of such stands should be well collected, and populations should be established at locations where common access can be ensured, e.g., in the grounds of schools, hospitals or government offices. Different villages may agree with each other to establish multiplication stands of different tree species, with the view of exchanging the seed produced through networks.

Improving access through ‘diversity fairs’

An extension of the network approach for improving access to germplasm is the use of ‘diversity fairs’ (van der Steeg et al. 2004). This approach, which has been employed in recent years to enhance diversity in traditional agriculture crops in smallholders’ farms, involves organising social events to which farmers are encouraged to bring local varieties of crops, and to exchange germplasm and associated knowledge. Prizes are often awarded for the most unusual or interesting cultivars exhibited (Friis-Hansen and Sthapit 2000). Although widely applied for annual crops, fairs have rarely been considered to date for managing tree genetic variation in farm landscapes. This is because fairs work best when the most important qualities of a particular variety are clear from the propagule of the species, e.g., when it is the seed or fruit itself that is the product for which a crop is grown. A direct relationship between use and propagule is clearly not evident if it is the timber,

leaves, or bark of a tree that are important, in which case other means of quality verification are required, such as displays of wood or bark samples. A pragmatic starting point in the use of diversity fairs is to encourage the increased inclusion of fruit trees—where use and propagule are clearly related—in events designed primarily for the promotion of other crops; this approach is currently being undertaken to manage genetic diversity in fruit trees in the West African Sahel (J. C. Weber, personal observations).

Encouraging participatory tree domestication

Participatory domestication is about empowering local communities to consciously carry out crop breeding activities for themselves (Weber et al. 2001). Participatory approaches involve ensuring that local people are trained in a range of germplasm collection, selection, propagation, management, harvesting and processing techniques, and then encouraging communities to apply these skills to the semi- or previously un-domesticated taxa that they find in the landscapes around them. Such approaches have been adopted in circumstances where a very large range of species may be subject to promotion, a situation where application of these methods can make an important contribution to the genetic management of a range of different taxa all at the same time (Dawson et al. 2007).

The participatory domestication of tropical trees is most relevant when high genetic diversity is still available in the local landscapes that farmers occupy, e.g., when agricultural land borders still wild or relatively unmanaged forest habitat, as occurs in the humid tropics of West Africa and the Amazon (Weber et al. 2001; Leakey et al. 2003, 2005, 2007). To assure germplasm availability under these conditions, policy interventions may be required to allow communities access to local forest, especially if trees occur within protected areas that are managed by government authorities. Allowing farmers to have ‘official’ access to protected areas has the additional advantage of providing an incentive for their involvement in participatory forest management strategies, approaches that many countries in the tropics have recently attempted to promote (Wily 2003).

Final considerations

Although available data provide a strong case for action to improve the management of tree genetic variation in tropical agroforestry ecosystems, interventions will only be successful at a significant scale if they support the livelihoods of local communities. As well as devising supply-side interventions based on germplasm access, therefore, it is also essential to consider the development of market structures that support genetic diversity (Degrande et al. 2006; Leakey et al. 2007). Incorporating farmers into markets may seem counterproductive for conservation, as higher market access is often coupled with intensification and greater emphasis on short-term productivity, resulting in losses in species diversity (a tendency to monoculture) and reduced genetic variation in farming systems (Donald 2004; Dawson et al. 2007). Tools are available, however, to align conservation and market goals in better ways than are practised presently (Hellin and Hignan 2005; Nill and Böhnert 2006) and markets can effectively support genetic diversity if attention is given to the development of appropriate cultivar ‘ideotypes’ and niche markets that support a range of variation within a species (Smale et al. 2002; Leakey and Page 2006). ‘Denomination of origin’ (DO) and similar approaches, which associate particular varieties with specific geographic territories and with particular communities and their traditional practices, carry potential if they can be applied beyond coffee and cocoa to a wider range of tree species and

products (Dawson et al. 2007). In order to allow wider application of the DO approach, brand recognition of different sources of tree products is required, which appears most relevant currently for fruit tree varieties.

Clearly, both germplasm-access and market-based interventions are required to manage tree genetic variation better in agroforestry systems. Based on more than 40 years of Danish development experience on this topic, Graudal and Lillesø (2007) developed a model for the design and implementation of support programs in which tree seed and seedling supply, and product (fruit, timber, medicine, etc.) sale, are considered as parts of one value chain. In this model, the actors that procure and distribute germplasm sources, that plant and manage trees, and that trade and purchase tree products, are all seen as part of a single system. For effective livelihood development and environmental protection, the linkages between these actors must function properly, and these connections should be the subject of future research.

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