Chapter 12

Agroforestry Systems: Important Components in Conserving the Genetic Viability of Native Tropical Tree Species?

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In the tropics, human forest disturbance is omnipresent. The wide range of human uses of forests (e.g., timber, fuel, food, clearance for habitation, agriculture, grazing) vary in their impacts, depending on the type and intensity of use. However, increasing deforestation rates in recent decades have led to dramatic reductions in the area of forest (see Chapter 1, this volume) and its fragmentation into smaller patches of varying size and spatial isolation. For some tropical forest ecosystems, the remaining forests often are highly fragmented and below the size considered viable, such that the ideal of maintaining large, continuous reserves is impractical (Soulé 1987). The agricultural matrix in which many forest remnants now exist is in itself a complex mosaic of varying land use practices. They vary in their degree of tree cover from almost none (e.g., monocultures of crops such as sugarcane) to highly complex agroforests in which there is maintenance not only of a high degree of tree cover but also a variety of tree species (see Chapter 10, this volume). Therefore, in some cases conservation initiatives must consider approaches that depart from the traditional in situ conservation paradigm, involving protected wilderness areas, to ways in which managers can conserve the species of an already highly altered forest type by managing networks of small forest patches in such mosaics of land use types.

Deforestation and fragmentation may have obvious effects, such as the elimination of some species. However, there may also be less immediate effects on the longer-term viability of species through impacts on ecological and genetic processes. Managers must consider the reproductive and regenerative capacities of priority species and the perpetuation of management practices that allow natural or artificial regeneration to ensure that populations have a long-term future. The effects of fragmentation on remnant stands and trees, their gene pools, and consequent conservation value are the subject of debate (Saunders et al. 1991; Heywood and Stuart 1992; Young et al. 1996). At the pessimistic extreme are views characterizing remnant trees in agroecosystems as "living dead," of little conservation value because isolated from potential mating partners they may not produce offspring or offspring may fail to establish new generations (Janzen 1986). More optimistically, the possibility of extensive gene flow between isolated trees of many taxa, through pollen transport over long distances by animal or wind vectors, suggests that remnant forest patches and trees can be effective and important in conserving genetic diversity (Hamrick 1992).

This chapter examines the role that trees in agroforestry systems may play in conserving the genetic viability of native tropical tree species in protected areas, forest fragments, and the same agroforestry systems. Tree species found both in agroforestry systems and forest patches may contribute to both gene flow and the overall gene pool of those species. Species found only in agroforestry systems may still contribute to the conservation of forest tree species by providing habitat for pollinators and seed dispersers that facilitate gene flow in other tree species (Slocum and Horvitz 2000) or by creating an environment that favors seedling regeneration.

The chapter explores what is known about the level and nature of intraspecific genetic variation actively conserved in trees in agroforestry systems, the distance at which forest fragments become genetically isolated, the particular types of agroforestry systems that favor gene flow and the tree species most likely to profit from it, and the consequences of gene flow between managed and remnant natural populations. This discussion leads to consideration of tree planting and natural regeneration in agroforestry systems, biological corridor design that combines target species conservation and sustainable use compatibility, better targeting of resources to more critically threatened species, and research and education needs.

At the outset we need to consider what we want to conserve. Effective conservation entails clear definition of objectives, which may range from preservation of actual diversity to conservation of evolutionary potential (Eriksson et al. 1993). However, genetic variation and processes are dynamic and respond to changing conditions. A pragmatic objective is one that maintains options for future generations while satisfying present needs (WCED 1987), such that sufficient genetic variation is conserved for tree populations and species to continue to adapt in the future. Achieving both short- and long-term goals entails an understanding of the basic processes of tree reproductive biology (sexual systems, incompatibility mechanisms, flowering patterns, and pollination processes) and how they combine to produce observed patterns of gene flow and genetic variation. Identifying the potential for agroforestry systems to facilitate, critically alter, or endanger these processes is key. Reducing the possibility or impact of inbreeding and maintaining diversity in naturally outcrossing tree species is important, and maintenance of breeding system flexibility is a priority for species that naturally combine outcrossing and inbreeding.

Gene Flow and Mating Patterns in Tropical Tree Populations

Understanding of gene flow and mating patterns in tropical forest trees has progressed over the last 50 years from theories to direct estimates based on field studies and molecular markers (Young et al. 2000). Trees in tropical forests, with low to medium species densities, were once thought likely to be self-pollinated because large interplant distances and asynchronous flowering would reduce the chance of successful cross-pollination (Corner 1954; Federov 1966). Subsequent studies based primarily on hand pollination to determine self- and cross-compatibility and observations of pollinator behavior indicated strong barriers to selfing and led to the conclusion that tropical trees are predominantly outcrossed (Janzen 1971; Bawa 1974; Zapata and Arroyo 1978; Bawa et al. 1985). In fact, the extent and pattern of gene flow through pollen depend on a number of factors:

- *Sexual system:* Tropical trees have a diverse array of sexual systems (Bawa and Beach 1981; Loveless and Hamrick 1984; Bawa et al. 1985; Loveless 1992). In dioecious species male and female flowers occur on different trees, so these species are unable to self-pollinate, being obligate outcrossers. In hermaphroditic species (trees with both male and female function), individuals may have monoecious (single-sex) or hermaphrodite (both sexes) flowers, such that self-pollination may occur. In hermaphroditic species, however, self-pollination and self-fertilization may be reduced or prevented through a variety of mechanisms (e.g., differential maturation of female and male phases on the same tree).
- *Mating system:* Mating may be predominantly outcrossing in some hermaphroditic and monoecious species where incompatibility mechanisms (physiological or genetic barriers) prevent selfing (self-fertilization) despite self-pollination. However, the lack of such an incompatibility mechanism does not mean that a species will be obligately selfed. Some self-compatible tropical tree species show mixed mating (both selfing and outcrossing), such as *Cavanillesia platanifolia* (Murawski and Hamrick 1992a), *Ceiba pentandra* (Murawski and Hamrick 1992b; Gribel et al. 1999), and some *Shorea* spp. (Murawski et al. 1994).
- *Mechanism of pollen dispersal:* Depending on the type of vector (e.g., wind, bees, hummingbirds, or bats), pollen may be dispersed over different distances, while pollinator behavior such as traplining (preferential movement along corridors or between precociously flowering trees), as seen in some

bee, bat, and butterfly species (Frankie and Baker 1974; Gilbert 1975; Ackerman et al. 1982), has a significant effect on dispersal patterns.

- *Spatial distribution and density of trees:* The spatial distribution and density of mature trees (Murawski et al. 1990; Murawski and Hamrick 1991, 1992b) and flowering synchrony (Boshier et al. 1995b) may also influence pollen dispersal and hence the extent of outcrossing. Hamrick (1992) typified mating in neotropical tree populations as showing two contrasting trends: individual trees receive pollen from relatively few pollen donors, but the genetic composition of the pollen varies greatly from tree to tree; and although a high proportion of fertilization is affected by nearest neighbors, a significant proportion of pollen movement occurs over relatively long distances. Consequently, the effective breeding area of an individual tree of a common tropical tree species is large (25–50 ha; Hamrick and Murawski 1990).

Gene flow in trees also occurs through seed dispersal. Ashton (1969) argued that tropical trees would be genetically structured (i.e., neighboring trees would be more closely related—with more alleles in common—than more distant trees) as a consequence of limited seed dispersal from mother trees, a high degree of selfing and near neighbor pollinations, and selection for adaptation to the local environment. Recent studies show that some local genetic structure (over tens of meters) in tree populations is indeed typical (Boshier et al. 1995a; Hamrick et al. 1993), particularly for taxa with wind-dispersed seed, where most seed falls out within a short distance of the mother tree (Augspurger 1984). Where such local genetic structure occurs, the relative extent of pollen and seed dispersal influences the extent of related mating (inbreeding). If pollen and seed dispersal are similar, much mating will be between related individuals, whereas if pollen dispersal is much greater than that of seed, the amount of mating between closely related trees will decrease and outcrossing will predominate.

In natural populations of *Eucalyptus* spp. such family groups appear to lead consistently to a degree of inbreeding, with outcrossing rates averaging about 0.75 (Eldridge et al. 1993). Outcrossing rates (t_m) theoretically range from 0 (complete selfing) to 1.0 (outcrossed to a random sample of the population's pollen pool). Values significantly lower than 1.0 indicate a degree of inbreeding, which may result from selfing and mating between related individuals. In contrast to natural populations, in plantations the use of collected seed, which is normally mixed from a number of mother trees, breaks up such family structure, and mating there shows a corresponding increase in outcrossing (e.g., *E. regnans:* 0.74 for a natural stand, 0.91 for a plantation; Moran, Bell, et al. 1989a). However, molecular marker studies have found that pollen dispersal generally is much more extensive than any local genetic structure, so the majority of tropical tree species avoid such related mating (Stacy et al. 1996; Nason et al. 1997; Boshier 2000) and show high levels of outcrossing (Nason and Hamrick 1997; Lepsch-Cunha et al. 2001). However, if naturally outcrossing species are forced by human disturbance (e.g., from increased physical isolation) to inbreed (increased related mating and selfing), there may be associated risks of reduced fertility, growth, and environmental tolerance and greater susceptibility to pests and diseases (Sim 1984; Griffin 1990). Maintenance of genetic diversity is vital for the long-term viability and adaptability of populations of many tree species.

Intraspecific Genetic Variation Conserved in Agroforestry Systems

From both conservation and use viewpoints we need to know about the extent of genetic variation (allelic richness) within a species and the distribution of genetic variation (allelic evenness, i.e., whether populations have the same alleles or different ones). Tree taxa generally show high levels of genetic diversity (allelic richness) in comparison with nonwoody plants, with most alleles (typically 70–80 percent) common across most populations (Loveless 1992; Hamrick 1992; Hamrick et al. 1992; Moran 1992). However, levels of genetic diversity vary by mating system, with higher levels (high allelic richness) maintained in the predominantly outcrossing species because of high levels of mating between unrelated individuals. In contrast, inbred species show lower levels (low allelic richness) in inbreeding populations but greater interpopulation variation because of the more limited gene flow that occurs with inbreeding. Gene flow may also be limited by geographic separation (i.e., gaps in a species' natural distribution), such that species with disjunct distributions often show high genetic differentiation between the disjunct areas (e.g., *Acacia mangium;* Moran, Muona, et al. 1989). Widespread species with continuous distributions may be characterized by a hierarchy of population structure, such that whereas there is little differentiation between nearby populations, geographically distant populations diverge genetically. Thus a larger proportion of the total genetic variation within the species often is between physically distant regions, sometimes corresponding to geographic regions (e.g., Pacific and Caribbean watershed divide for *Cedrela odorata;* Gillies et al. 1997) rather than between populations within regions.

Although genetic differentiation between populations is low, it is often of major significance for adaptation or production. This is evident from provenance trials of many tropical tree species, where trees from different seed sources often show differential performance on a common trial site (Zobel and Talbert 1984; Eldridge et al. 1993). Significant interactions between genotype and environment generally occur only with large environmental site differences (e.g., dry and wet zones, alkaline and acidic soils; Boshier and Billingham 2000). Therefore, conservation of different populations is also important to tropical tree genetic resources. However, protected area design and management are determined mostly by political, social, and economic constraints, with reserves often located on slopes, on sites of lower fertility, and in stands of lesser economic value, which in turn biases their composition and limits their value for genetic resource conservation (Ledig 1988). Selective land clearance for agriculture has also decimated populations of many tree species on flat, fertile soils. Consequently, where there is genetic adaptation of populations to specific soil types, remnant trees and their offspring in agricultural fields, pastures, and agroforests may be the sole representatives and opportunity for conserving particular gene pools of some species. Therefore, the question is how adequate such tree populations might be for genetic conservation. The answer depends on the stage at which forest fragments and trees become genetically isolated, the extent of genetic adaptation to particular sites, and whether farmers' management practices, especially the conservation of remnant trees and their regeneration, maintain population gene pools and are therefore compatible with conservation objectives. Although few studies specifically address this scenario, there is plenty of relevant research that allows us to extrapolate some principles.

At What Distance Do Forest Fragments Become Genetically Isolated?

To attempt to answer this question we must look at a number of studies that have been conducted in recent years and show a range of results. The first study concerns *Swietenia humilis,* a mahogany species listed in Appendix II of the Convention on International Trade in Endangered Species (CITES), growing in secondary dry forest patches and as remnant trees in pastures that replaced the original dry forest on the Honduran Pacific coastal plains. Forest remnants were 1 to 4.5 km apart, varying in size from 10 to 150 ha (containing 8 to 44 *S. humilis* trees), while a continuous forest area was also studied as a control. *S. humilis* is self-incompatible, such that geographically isolated trees should be "living dead" unless there is pollen exchange with other trees. Molecular markers showed that at this degree of isolation, fragmentation did not impose a genetic barrier between remnants but increased levels of long-distance pollen flow into the smaller fragments, resulting in a network of pollen exchange over a 16-km^2 area (White and Boshier 2000). In both the continuous forest and fragments there was a predominance of near neighbor mating (within 300 m of the maternal tree). In the forest fragments, 53–62 percent of the pollen donors were from the same fragment, indicating that 38–47 percent of the pollen was imported by pollinators from other fragments. With such extensive pollen exchange, there was no evidence of increased inbreeding even in the smallest fragments. One tree, separated by 1.2 km of pasture from the nearest *S. humilis* trees, in accord with the species' self-incompatibility, showed 100 percent external pollen sources, with more than 70 percent from trees in a forest more than 4.5 km away. In addition, seed production was much higher and more reliable in pasture and other disturbed environments than in the closed forest (Boshier et al. 2003).

A study of *Dinizia excelsa,* a canopy-emergent tree, also showed an extensive network of pollen flow in Amazonian pastures and forest fragments with increased seed production, even in the absence of native pollinators (Dick 2001). African honeybees were the predominant floral visitors in fragmented habitats and replaced native insects in isolated pasture trees. Molecular markers showed that genetic diversity was maintained across habitats, with gene flow over as much as 3.2 km of pasture, although there was a slight increase in selfing in the pasture trees (t_m=0.85) as compared with trees in forest fragments and those in continuous forest (t_m=0.95).

Similar results were found in a study of pollen flow into continuous forest and five island populations (Lake Gatun, Panama Canal) of *Spondias mombin,* a self-incompatible, insect-pollinated tree (Nason and Hamrick 1997). The control forest showed pollen immigration rates of 45 percent from more than 100 m distance within the forest, whereas in the island populations 60–100 percent of the effective pollination was from at least 80-1,000 m away. However, the more isolated islands (1-km isolation) showed lower seed set and germination rates than the control forest, apparently because a lack of effective cross-pollination led to higher rates of self-fertilization. The inbred seed either abort or fail to germinate, and viable seed are predominantly those produced by long-distance pollen dispersal. Although this suggests that isolation reduces the species' ability to regenerate, it is likely that the same degree of fragmentation in a terrestrial land use mosaic would have less severe consequences because pollinator movement between fragments would probably be better than between true islands separated by water.

A negative effect on seed production as a result of reduced cross-pollination of isolated trees was also visible in the Southeast Asian timber tree *Shorea siamensis* (Table 12.1; Ghazoul et al. 1998). High-intensity logging resulted in much lower fruit set, although the number of flowers pollinated was similar. This resulted from the lower frequency of intertree movements by pollinators in the more open environment increasing the self-pollination frequency of this self-incompatible species.

In *Enterolobium cyclocarpum,* a self-incompatible, dominant tree of seasonally dry forests and associated pastures in Central America pollinated by bees and hawkmoths, there was no difference in the outcrossing rate between trees in continuous forest (t_m=1.00) and those in pasture (t_m=0.99; Rocha and Aguilar 2001a). There was extensive pollen flow into fragments separated by 250–500 m, while isolated pasture trees experienced more pollen donors than trees located in tree clumps (Apsit et al. 2001; Rocha and Aguilar 2001a). This contrasts with earlier predictions that spatially isolated trees are more likely to

Table 12.1. Fruiting in *Shorea siamensis* under disturbance resulting from different levels of timber extraction.

	Heavy	*Moderate*	*Undisturbed*
Tree density (trees/ha)	22.0	86.0	205.0
Flowering trees/ha			
1996	9.0	62.0	96.0
1997	5.0	59.0	76.0
Percentage fruit set			
1996	0.7	2.2	2.5
1997	1.5	5.5	5.5
Percentage stigmas with >5 pollen grains	62.0	59.0	79.0

Source: Ghazoul et al. (1998).

deviate from random mating and receive pollen from fewer donors (Murawski and Hamrick 1991). However, the isolated trees did show more year-to-year variation in their pollen donors than trees located in less disturbed habitats. Trees grouped in clumps showed less temporal variation, often because of within-clump mating (Hamrick 2002). Similar year-to-year variation was also found in *Hymenaea courbaril* (bat-pollinated) and *Spondias purpurea* (small insect-pollinated), although the magnitude varied between trees.

Cecropia obtusifolia, a dioecious, wind-pollinated pioneer tree, showed extensive pollen flow from natural forest (27 percent and 10 percent from 6 and 14 km, respectively) into a pristine forest reserve in Veracruz, Mexico, although there was apparently none from forest fallows at the same distances (Kaufman et al. 1998). The precise reason for the lack of pollen flow from this human-disturbed system, despite the high density of the species there, is uncertain. Trees are notably shorter and tree densities much higher in fallows than in tree fall gaps in natural forest, and it may be that the pollen is simply intercepted by the surrounding vegetation in the fallows. Apparently the dynamics of gene flow in such wind-pollinated species under disturbance may differ from those of animal-pollinated species.

Studies of how outcrossing rates vary with tree or flowering tree density in natural forest may also be informative because the range of tree densities in agroforestry systems varies. Differences between and annual variation in outcrossing rates for individual trees of several neotropical tree species have been reported to be consistent with changes in local flowering densities and the spatial patterns of flowering individuals (Murawski and Hamrick 1991). Species occurring at low densities appeared to combine significant levels of biparental mating (each maternal tree mates primarily with one other tree) with long-distance gene flow, whereas higher-density species showed more random mating, generally over shorter distances. In three neotropical tree species (*Calophyllum longifolium, Spondias mombin,* and *Turpinia occidentalis*) occurring naturally at low densities, mating patterns were strongly affected by the spatial distribution of reproductive trees, although they still showed high levels of outcrossing. Where trees were clumped, the majority of matings were with near neighbors, whereas with evenly spaced trees a large proportion of matings was over several hundred meters and well beyond the nearest reproductive neighbors (Stacy et al. 1996). The degree of flowering synchrony between neighbors may also increase the tendency toward inbreeding, such that in an outcrossing population of *Cordia alliodora* (self-incompatible) some trees, surrounded by a few trees of similar genotype with which flowering was highly synchronous, showed related mating, whereas other asynchronous flowerers in the same group were outcrossed (Boshier et al. 1995b). In the self-compatible species *Cavanillesia platanifolia,* outcrossing rates were lower where flowering levels were lower in different years (t_m=0.57 with 74 percent trees flowering, 0.35 with 49 percent, and 0.21 with 32 percent; Murawski et al. 1990; Murawski and Hamrick 1992b). In years of greater flowering, more floral rewards are available, such that there is a greater tendency for pollinators to move between trees, resulting in cross-pollination. However, when few trees are flowering there is a greater tendency for self-pollination.

The evidence to date clearly supports the idea that trees in agroforestry systems can be important in facilitating pollen flow between forest fragments. It is apparent that for some tree species under fragmentation, pollination occurs over much greater distances than are often considered and more in accord with distances previously identified by entomologists (Janzen 1971; Roubik and Aluja 1983), with the potential to maintain genetic variation. This contrasts with traditional views of the genetic effects of fragmenting populations, where increases in spatial isolation and population size reduction have been considered to reduce gene flow between fragments, leading to losses in genetic diversity (Saunders et al. 1991).

The potential to move between patches depends on the behavioral response of pollinators to the resultant mosaic of land use types. Some bat species move preferentially down forest tracks and pathways (Estrada et al. 1993). Many tree species are pollinated by bees, particularly social bees. It is likely that some cases of enhanced pollen flow in degraded tropical ecosystems result from domestic or African honeybees replacing native bees as principal pollinators (Dick 2001). However, bees typically live in habitats where nesting and floral resources are patchily distributed, such that all but perhaps the smallest bees normally move between resource patches isolated in an unrewarding matrix (Cane 2001). Bees of medium body size regularly fly 1–2 km from nest site to forage sites (Cane 2001), with some moving more than 4 km across agroecosystems between forest patches (Frankie et al. 1976; Raw 1989).

Changes in pollinator assemblages in fragmented landscapes may strongly affect patterns of gene flow and reproduction in remnant tree populations, such that considerations of pollinator management (e.g., provision of alternative food sources) may be as important as that of trees. Concerns that declines in pollinator populations in agroecosystems may eventually limit tree reproduction require monitoring of numbers and evidence of pollinator limitation (Allen-Wardell et al. 1998). Pollen flow dynamics in the many tree species that have a range of nonspecialist pollinators are probably far less susceptible to habitat disturbance than those with more specialist or limited-range pollinators (e.g., small beetles on *Virola* sp.). However, even *Ficus* spp., with species-specific wasp pollinators, were shown to form extensive metapopulations in fragmented landscapes (Nason et al. 1998).

However, there is obviously a distance beyond which genetic isolation will occur, with associated problems for population viability and adaptation (Young et al. 1996). Although determination is experimentally problematic, thresholds will vary between species depending on pollinator characteristics and availability, the specificity of the tree-pollinator relationship, and the presence and strength of any self-incompatibility mechanism. Whether greater physical isolation of trees results in increases in selfing appears to be controlled mainly by whether the species of interest has a self-incompatibility mechanism. Self-compatible species that normally show some level of outcrossing (Murawski and Hamrick 1992b) or are only weakly self-incompatible are likely to show higher levels of inbreeding at much shorter distances of separation (lower thresholds) than strongly self-incompatible species. The latter are more likely to show evidence of a threshold through reduced seed production.

Possible Consequences of Gene Flow between Managed and Remnant Natural Tree Populations

Although the studies reviewed earlier provide evidence that trees in agroforestry systems can be important mediators of pollen flow across fragmented agroecosystem landscapes, it is equally important to consider the possible consequences of this gene flow. What is the impact on the level and quality (genetic diversity and viability) of seed produced? A study of mating patterns and regeneration of the tree species *Symphonia globulifera* in fragmented and continuous forest in Costa Rica (Aldrich and Hamrick 1998) shows that the impacts may be more complex than might at first be apparent. This self-compatible species showed a predictable increase in selfing, as with *Cavanillesia platanifolia,* among remnant trees growing at low densities in pasture (t_m=0.74) as compared with trees in both continuous and forest fragments (t_m=0.9). The forest fragments were superficially healthy, showing much higher seedling densities than in the control forest (Table 12.2), with trees in the surrounding pasture playing an important role in pollination. However,

Table 12.2. Sources of *Symphonia globulifera* seedling production in fragmented forest.

	Continuous	*Fragmented*
Seedling densities	27.5 per ha	152.3 per ha
Origins of reproduction (%)		
Same plot or fragment	31.5	4.5
Other plot or fragment	15.0	15.0
External to assessed forest or fragment	53.5	12.5
Pasture	0.0	68.0

Source: Aldrich and Hamrick (1998).

52.5 percent of seedlings in the forest patches were fathered by two pasture "super adults." Such reproductive dominance by a few trees reduces effective population size, that is, the number of trees effectively contributing to reproduction, leading to losses of genetic diversity in following generations.

With reduced or no crown competition, many trees in agroforestry systems show greater crown size and exposure, with the potential for the formation of many more flower initials than in closed canopy forest. Higher seed production in pasture trees was also shown for *S. humilis* (in each year some 72 percent of pasture trees showed moderate to heavy seed production, compared with 12 percent of closed forest trees), but not for *Bombacopsis quinata* (Boshier et al. 2003). Trees of *Dinizia excelsa* in pasture and forest fragments produced more than three times as many pods per tree as trees from adjacent continuous forest populations, although there was no difference in fecundity between those in pasture and those in forest fragments (Dick 2001). In *Samanea saman,* the total number of seeds per fruit and the number of sound seeds were similar regardless of location in the landscape (i.e., isolated pasture trees or continuous forest; Cascante et al. 2002). In contrast, *Enterolobium cyclocarpum* flowers from trees in continuous forests were more likely to have pollen deposited on their stigmas than flowers from trees in pastures (52 and 32 percent, respectively), with trees from continuous forests almost six times more likely to set fruits and produce more seeds per fruit than trees in pastures (Rocha and Aguilar 2001a).

As well as potentially dominating the pollen pool by high flower production, such trees may also be a more attractive food source to pollinators, increasing the proportion of pollinations that originate from these trees. Thus, although trees in agroforestry systems may facilitate pollen flow between forest fragments, they may also reduce the effective population sizes of forest trees by dominating regeneration (where fragments are within seed dispersal range) and the pollen pool by producing more flowers or attracting a higher percentage of pollinators (where fragments are within pollen dispersal range).

In two studies (*Enterolobium cyclocarpum,* Rocha and Aguilar 2001a; *Cedrela odorata,* Navarro 2002), although the function of pasture trees in pollen movement between fragments has been recognized, seeds from pasture trees have shown less vigorous growth than those from trees of the same species found at higher densities, with the suggestion that the seeds are not appropriate for use in plantations. In *Enterolobium cyclocarpum,* the tendency for some fathers to be overrepresented in the seed crop (Rocha and Aguilar 2001b) and the greater yearly variation in pollen of pasture trees (Hamrick 2002) suggest a need for rigorous procedures when making seed collections for plantations, with broad sampling of each tree, a high number of trees, and avoidance of seed from poor-flowering years.

The genetic origin of trees in agroforestry systems also raises potential issues for genetic conservation and of gene flow from agroforestry systems to natural populations. Levels of genetic diversity are influenced by the means of tree establishment. Trees originating from natural regeneration may show some level of related mating caused by interactions between a number of factors rather than any particular factor (e.g., spatial and temporal genetic structure associated with incompatibility mechanisms, variation in flowering, and stand composition and density). Provided that seed production levels are not adversely affected, any abnormal, increased levels of inbreeding may be unimportant from an evolutionary viewpoint, with selfed individuals selected against at various stages of regeneration (seed production, seedling establishment, and growth). There is good evidence that genetic diversity is maintained in these on-farm populations (e.g., Chamberlain et al. 1996). However, increased levels of inbreeding may be critical in terms of the levels of diversity that are sampled for planting, ex situ conservation, or tree-breeding programs. Where trees are planted, the levels of genetic diversity maintained also depend on species and the seed collection process. Apart from the exceptions for self-compatible species already outlined, genetic diversity is likely to be maintained where normal seed collection protocols are followed (Schmidt 2001). However, in species that produce large quantities of seed per tree there is a tendency to make collections from a limited part of the crown and from a small number of trees, which leads to limited sampling of the gene pool (Boshier et al. 1995a). Consequently, through use of a reduced gene pool or future domination of the pollen pool (as in *S. globulifera*), some tree planting in agroforestry systems may be less beneficial, from a genetic conservation viewpoint, than might be expected.

Such considerations are not specific to any particular agroforestry system. Instead, the species characteristics, tree density, and origin (natural regeneration or planted) in any system are the most important factors influencing gene pools. However, the living fenceline is one agroforestry system in which the method of establishment can greatly influence the size of the breeding population and gene pool of native tree species. The use of living fencelines is common practice in many tropical countries (see Chapter 11, this volume; Kass et al. 1993). A wide range of species (e.g., *Bombacopsis quinata, Erythrina berteroana, Gliricidia sepium,* and *Spondias mombin*) and management practices are used, depending on local preferences. However, a constant factor is that the species used are vegetatively propagated from large stake cuttings. This feature has led to their characterization as lacking in genetic diversity and as sources of selfed seed, with possible adverse effects on the growth of subsequent trees. In some land use mosaics they may form a very high proportion of the tree component and therefore will dominate the pollen pool. Understanding how they influence tree gene pools (e.g., genetic variation, pollen flow, outcrossing rate) therefore is important in understanding the potential role of agroforestry for conservation.

An evaluation of genetic diversity in two living fencerows of *B. quinata* in Costa Rica found a smaller genetic base in comparison with material from a seed orchard (Table 12.3; Sandiford 1998). The first fencerow showed only 8 genotypes among the 42 trees sampled, with 57 percent of the trees represented by one genotype (clone). A second fencerow was more variable, with 20 different genotypes among the 42 trees sampled. However, both fencerows showed a high outcrossing rate (t_m=1.023, *SE*=0.060), comparable with those found for *B. quinata* in natural and fragmented populations (Sandiford et al. 2003) and with no evidence of selfing or inbreeding between related individuals. However, differences in allele frequencies between the pollen and ovule pools were evidence of a degree of nonrandom mating resulting from a combination of characteristics common to other fencerow species and particulars of the reproductive biology of *B. quinata* (maternal differences in fertility, nature of the self-incompatibility mechanism, and selection against homozygotes at seed maturation phase; Sandiford 1998). These characteristics are accentuated by the behavior of the pollinators (long-tongue bat, *Glossophaga soricina*) in terms of their preferential (nonrandom) visits to certain trees and their long-distance flights, which facilitate extensive pollen flow from outside the seed population.

Table 12.3. Number of maternal genotypes of *Bombacopsis quinata* for two living fencerows in Costa Rica and a seed orchard in Honduras.

Site	*Number of Trees*	*Number of Genotypes*	*Most Common Genotype*
Fencerow 1	42	8	57%
Fencerow 2	42	20	12%
Seed orchard	12	11	

Source: Sandiford (1998).

To what extent are such results typical of other species used in fencerows? By the nature of their establishment method, fencerow populations are not random populations, with the small and biased number of genotypes meaning there is little likelihood that they are in genetic (Hardy-Weinberg) equilibrium, with consequent heterozygote excesses or deficiencies. Seed collections obviously include mainly those trees with abundant fruiting, whereas those that fail to fruit are not represented or are represented only in the pollen pool. Under such conditions, only a relatively small number of genotypes may act as mothers, whereas a larger majority will act as fathers, unbalancing the allelic frequencies for pollen and ovules, as does the entry of pollen from outside the fence populations, unlike the mating patterns typical of natural forest. A low degree of flowering synchrony between trees also increases the probability of nonrandom mating. Although a species incompatibility mechanism may prevent selfing, in fencerows there may be many individuals of the same clone such that there are high levels of self-pollination with possible failures of fruit production (see the *Shorea siamensis* and *Spondias mombin* studies mentioned earlier) if there is insufficient cross-pollination.

Promotion of the planting and use (e.g., for faster growth) in agroforestry systems of exotic species or provenances at the expense of natural regeneration of local populations or species may have deleterious effects for genetic conservation. The replacement of native species (e.g., *Leucaena salvadorensis* by *Leucaena leucocephala;* Hughes 1998) may reduce population sizes or even eliminate particular populations of threatened species. Hybridization of introduced species with native species is particularly prevalent in certain genera (e.g., *Leucaena,* Hughes 1998; *Prosopis,* Carney et al. 2000) and has obvious implications for conservation of native gene pools (see also Chapter 15, this volume). Evidence to date of outbreeding depression (reduced growth or fertility from the breakup of co-adapted allelic complexes or dilution of adapted alleles; Ledig 1992) from crossing between different populations of the same tree species is inconclusive because of a lack of studies. Controlled crossing between populations of *B. quinata* saw outbreeding depression (reduced seed set) only when populations as genetically distinct as those from Honduras and Colombia were crossed. In contrast, there was no outbreeding depression in *S. humilis* when populations from a 500-km distance were crossed (Billingham 1999). For species of *Syzygium* and *Shorea* in southwestern Sri Lanka, there was a significantly lower fruit set in crosses with the most distant pollen donor (approximately 12 km; Stacy 1998). The author suggested the apparent outbreeding depression at a fairly small scale was more likely to result from spatial heterogeneity in the selective environment than from isolation by distance, with the geographic heterogeneity of the study area possibly of a finer scale than that of the majority of tropical forested landscapes.

Which Agroforestry Systems Favor Gene Flow, and What Types of Tree Species Are Favored by Gene Flow?

As the previous examples show, the assessment of the benefits of agroforestry systems for genetic conservation of tree species entails integration of genetic, ecological, and management information to reflect the complexities of the systems. Such complexity suggests that it may be very difficult to predict when and for what pairs of forest fragments connectivity will be a critical issue and to assess the connectivity of different systems. Conservation strategies to address the issues posed by fragmentation have generally been based on island biogeography theory, leading to the idea that fragments linked by a corridor of similar suitable habitat are likely to have greater conservation value than the same fragments if isolated (Diamond 1975; Wilson and Willis 1975). More recent developments recognize that forests do not exist as islands in a sea of completely hostile, biodiversity-poor environments but as a mosaic of modified land uses and habitats that vary in their ability to fulfill the original ecological functions and consequently vary in their value as corridors (see also Chapters 1 and 3, this volume).

Connectivity has two distinct but related components under broad headings of gene flow and migration related to home range. Some habitats are suitable for certain species to live in, others may not be but may not inhibit movement, some may allow movement only seasonally, while others may be totally inhospitable. Connectivity may be sought to reduce the susceptibility of small populations to a variety of impacts, including genetic stochasticity (e.g., genetic drift, inbreeding depression, and predator and competitor population fluctuations).

The integration of landscape models that use spatially explicit information on habitat type mosaics with metapopulation models that describe a set of connected populations within a landscape (see Chapters 2 and 3, this volume) offers a means to examine the influence of landscapes and habitats on genetic processes and structure of populations. Although metapopulation theory provides a conceptual model for understanding population dynamics in fragmented environments, there is currently limited evidence of its practical value in conservation management. There is limited knowledge of the scale of many animal species' movements, their habitat needs, disturbance tolerance, or the other impacts of fragmentation and hence limited information on the relative effectiveness of different systems to act as migration sources or sinks or as connectors between populations. Connecting genetic and demographic models at landscape scales entails adopting scales of study that are more relevant than those over which migration is currently measured and that are sensitive to recent changes in gene flow. Direct parentage analysis methods have generally been applied over relatively small spatial scales (less than 100 ha), whereas the studies reviewed here suggest that under fragmentation, pollen flow distances may increase by factors greater than 10 (kilometers rather than hundreds of meters). In addition, although pollen and seed movement may influence genetic structure differentially, from the perspective of demographic processes (i.e., colonization) in metapopulation and landscape models, seed dispersal data may be as important as pollen dispersal, requiring the use of a range of markers for direct comparisons between relative gene flow levels resulting from pollen and seed dispersal (Sork et al. 1998).

Against this background land managers are asked to select, design, and manage landscape links that will be effective in conserving biodiversity. The studies summarized here suggest reasons for optimism about the connectivity value of trees in agroforestry systems. They clearly support a broad vision of corridor design that embraces a range of land use mosaics rather than just continuous corridors of intact forest. The emphasis therefore should be on connectivity (for genes, species, and ecological processes) of landscape mosaics through maintenance and improvement of land use patterns that promote connectivity and conservation of biodiversity more generally. Corridor design, management, and monitoring should thus involve assessment of different land use types in terms of how well, individually and in combination, they meet the biological criteria of connectivity, amongst others, and how the balance of land use types may need modification to maintain or improve connectivity. This can be done, at least as a first approximation, in a simple way (Laurance et al. 1997; see also Chapter 3, this volume) by qualitatively scoring or ranking agroforestry practices and other land uses for their likely contribution to connectivity (capacity to allow movement and gene flow for species, or wildlife habitat provision), as well as other conservation and environmental amelioration values (e.g., protection from fires and exotic species, softened edge effects; see Chapter 2, this volume).

Any assessments are inevitably site specific given the variable connectivity, species, and sustainable land use aims of different areas and their differing degrees of resilience to disturbance. Such assessments can be summarized as matrices, specific to each area, in which land uses relevant to that area are ranked for each service of potential interest. They can help to identify priority agroforestry practices that show high connectivity and sustainable use compatibility and those that do not. In an area of high forest cover, agroforestry systems may be assessed principally for gene flow, whereas in much more highly deforested areas a fuller complement of benefits may be sought from particular systems, with their specific location in the corridor zone also being important. Thus, in the highly deforested dry forest zone of western Honduras the traditional Quezungual fallow system (Kass et al. 1993), in which farmers manage naturally regenerated shrubs, fruit trees, and timber trees among their crops, is likely to provide a variety of genetic conservation benefits for a range of native tree species (see also Chapter 8, this volume). Other complex systems, such as traditional shaded coffee or jungle rubber, may rate highly for all the possible genetic conservation benefits (see Chapters 9 and 10, this volume). In contrast, simpler agroforestry systems such as pasture trees and living fencerows offer fewer genetic conservation benefits and are unlikely to prove effective mediators of pollen flow for species without a self-incompatibility mechanism (see Chapter 11, this volume).

In most cases, however, assessments of the genetic conservation benefits of agroforestry systems are less likely to be system specific than species specific, taking account of the farming systems context of an area, the density of trees, and their origin (natural regeneration or planted). For example, maintaining native timber trees over large areas of coffee is likely to have beneficial genetic effects for gene flow, population numbers, and conservation of particular populations. In contrast, the same system in only a small area may lead to a reduced genetic base in seed production through related or biparental mating. Thus, the area or management unit should be measured in numbers of participating households or numbers of land units in which agroforestry land uses beneficial to target species conservation are practiced (Boshier et al. 2004). Given the speed with which land management practices may change in response to market prices, this measure in itself may require monitoring.

Identifying the factors that leave some species genetically susceptible to human disturbance requires extensive reproductive and regeneration ecology and genetic data. The lack of information, resource limitations, and the need for more immediate action in many situations necessitate pragmatic best-guess approaches to identify which species will be favored by gene flow between agroforestry areas and which will not. The ability to extrapolate from results from model species to make more general recommendations for species management groups (combining ecological guild, spatial distribution, and reproductive biology) depends on the existence of basic biological information (e.g., incompatibility and pollination mechanisms, dispersal, and seedling regeneration) that enables species to be classified (Jennings et al. 2001).

Consideration of available information suggests that the following species types are unlikely to show genetic conservation benefits from agroforestry systems: outcrossing species that are self-compatible, slow-growing species that reproduce only when they are large (extreme of monocarpic species, i.e., those that flower only once in their life), species with poor regeneration under human disturbance, species with highly specific pollinators or seed dispersers susceptible to disturbance, rare species with low population densities, and species with highly clumped distributions. Inevitably such generalizations will be qualified by the range of factors that have been shown to influence patterns of genetic variation in trees.

Conclusions

Evidence suggests that for many species, populations, and individuals of tropical trees, gene flow may be high across agroforestry landscapes with little apparent forest cover. The view of forest fragmentation as producing genetic isolation may be more a human perception than a true reflection of actual gene flow. It is therefore important to recognize the complementary role that maintenance of trees on farms is already playing to in situ conservation. Trees in a whole range of agroforestry practices may play an important but varied role in the long-term genetic viability of many native tree species, facilitating gene flow between existing reserves, conserving particular genotypes not found in reserves, maintaining minimum viable populations, and acting as intermediaries and alternative host habitat for pollinators and seed dispersers (Harvey and Haber 1999). Underestimating the capacity of many species to persist in large numbers in these agroecosystems under current practices could lead to the misdirection of limited conservation resources toward species not under threat (Boshier et al. 2004). Agroforestry tree populations may represent a considerable conservation resource, which if taken into consideration may show species to be thriving that are currently assumed to be threatened by habitat loss (Vandermeer and Perfecto 1997).

However, although they undoubtedly contribute to reproduction in remnant forests, the benefits and effects are more complex than at first might be predicted and vary from species to species. Uneven representation and overrepresentation in pollen pools and mating may lead to nonrandom mating, with reductions in genetic diversity in subsequent generations. Evidence of the quantity and quality of seed produced is variable and currently insufficient to draw more general conclusions, although of the range of agroforestry practices only living fencelines and very low-density trees in pastures are likely to cause problems.

However, we should not overestimate the extent to which agroforestry systems will benefit the genetic conservation of forest tree species. In addition to some of the complications raised in the studies reviewed here, it is evident that many of the tree species found in agroforestry areas already exist in adequate numbers in existing reserves. Similarly, some of the species threatened by low population numbers are not of the type that will easily persist in such systems. The greatest potential role of agroforestry will be in highly deforested areas where reserves are very small or nonexistent and where the trees maintained in agroforestry systems represent an important part of a particular population's or species' gene pool. In such circumstances, the fact that many tree species that live in such disturbed vegetation can be conserved through existing agroforestry practices can free resources for the conservation of more critically threatened species requiring more conventional, resource-intensive approaches.

A multidisciplinary vision is needed to establish the general potential for integrating conservation and development and, more specifically, which species are or could be sustainably conserved in such systems, from both biological and human management perspectives. Efforts to maintain genetic diversity and adaptive capacity are irrelevant if current management drastically alters population persistence.

We still don't know at what distance forest fragments become genetically isolated. Fragmentation thresholds for gene flow must be determined and the possible selection pressures exerted by farmers elucidated. The complementary benefits of different agroforestry practices for genetic conservation must be further evaluated, recognized, and promoted. There is a need to raise awareness among development professionals of the value of natural regeneration as both a conservation and a socioeconomic resource. Pushing of a limited range of species, often exotics, by development agencies may reduce the potential genetic benefits of such systems, besides creating potential problems of invasiveness (see Chapter 15, this volume). However, there is also a need for conservation planners, more accustomed to in situ methods, to consider the possibility that tree populations found outside protected areas have a role in biodiversity conservation (Boshier et al. 2004). This in turn necessitates the direct involvement of development organizations in biodiversity conservation and an effective interaction between them and traditional conservation organizations to ensure both conservation and development benefits.

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