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# Towards Conservation of Genetic Variation of Tropical Tree Species With Differing Successional Status: The Case of *Mansonia altissima* A. Chev and *Triplochiton scleroxylon* K. Schum

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**Abstract**

Two important West African timber tree species with differing successional status, *Mansonia altissima* A. Chev and *Triplochiton scleroxylon* K. Schum were investigated in this study. *Triplochiton scleroxylon* is a pioneer species found in open forests, whereas *Mansonia altissima* is a nonpioneer light-demanding tree species occurring in closed forests. Amplified fragment length polymorphism markers were used to compare the genetic diversities of these two timber species in stands with different degrees of human impact (isolated forest patch, logged forest, farmland, plantation, and primary forest). Contrasting effects of human impact on genetic diversity were detected for these two timber species. The results suggested severe effects of human impact on the genetic diversity of *Mansonia altissima*, a nonpioneer species. However, no adverse effect was recorded in *Triplochiton scleroxylon*, a pioneer species. These findings indicate that nonpioneer tree species could be more prone to genetic erosion than pioneer tree species as a result of adverse human impacts. Therefore, conservation of genetic diversity in both pioneer and nonpioneer tree species populations would likely necessitate different measures.

**Keywords**

*Mansonia altissima*, *Triplochiton scleroxylon*, human impact, genetic diversity, conservation, successional status

## Introduction

Finkeldey and Hattemer (2007) pointed out that deforestation in the tropics frequently involves conversion of continuous forest cover to fragmented landscapes with remnant forest patches set in an agrarian matrix. Previous studies on tree species such as *Prunus africana* (Hook.f.) Kalkman (Farwig, Braun, & Bohning-Gaese, 2008) and *Carapa guianensis* Aubl. (Dayanandan, Dole, Bawa, & Kesseli, 1999) have revealed that outcomes of these human activities are loss of rare alleles (White, Boshier, & Powell, 2002), modification of pollen movement and other reproductive functions among remnant trees (Finkeldey & Hattemer 2007; Rossetto, Gross, Jones, & Hunter, 2004), and reproductive isolation and inbreeding (Cascante, Quesada, Lobo, & Fuchs, 2002). However, other reports revealed that some tropical tree species are resilient even in the face of habitat disturbance due to a mandatory outcrossing mating system and efficient pollen dispersal (Aldrich & Hamrick, 1998; Chase, Moller, Kesseli, & Bawa, 1996; Dick, 2001).

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According to seed germination and seedling establishment, tropical trees can be grouped into pioneer and nonpioneer species (Swaine & Whitemore, 1988). In connection with germination of seeds, pioneer species germinate in gaps within forest canopies and open forest areas, while nonpioneer species mostly germinate under forest cover. Consequently, regeneration of pioneer tree species can be initiated by human disturbance, while, in contrast, removal of the forest canopy can hamper regeneration of nonpioneer species (Bazzaz, 1991). In view of the fact that human disturbances are likely to have contrasting effects on the regeneration capability of pioneer and nonpioneer species, different impacts on genetic diversity levels are likely. However, no studies have tested this hypothesis and analyzed genetic diversity in pioneer and nonpioneer tropical trees coexisting in the same natural ecosystem. Testing this hypothesis in tropical trees at different regimes of human impact will be of importance to forest conservationists. Information from such investigations can also play a crucial role in designing strategies and shaping policies to conserve genetic diversity in tropical tree species populations. *Mansonia altissima* A. Chev (Malvaceae) is a light-demanding nonpioneer tree species (Gyimah & Nakao, 2007; Veenendaal et al., 1996) which is naturally more abundant in primary forests, while *Triplochiton scleroxylon* K. Schum (Sterculiaceae) is a pioneer species found more frequently in secondary forests, woodlands, and farmlands (Forestry Research Institute of Nigeria [FRIN], 1977; Hall & Bada, 1979; Veenendaal et al., 1996). *M. altissima* seeds germinate under shade but their seedlings and wildlings require light for further growth (Veenendaal et al., 1996), while *T. scleroxylon* is adapted to colonizing secondary forests and degraded areas although its population does not decrease rapidly after forest vegetation has been established (Hall & Bada, 1979). With regard to flowering and fruiting, *M. altissima* flowers and fruits every year, while, in contrast, *T. scleroxylon* is noted for its erratic flowering and irregular fruiting (Nketiah, Newtonb, & Leakey, 1998).

Although the two species have differing morphological features (see Figure 1), they both are valuable timber species (Hawthorne, 1995). Both species also grow naturally in dry areas of lowland tropical rainforests of West Africa with a distribution stretching from Sierra Leone to the Republic of the Congo (only *T. scleroxylon*). These two species have been logged in the past for their valuable timber. Currently, the tree populations are affected by nonsustainable logging activities and by illegal encroachment for farming activities.

In this study, we tested the hypothesis that human impact has negative effects on the genetic diversity of *M. altissima* and *T. scleroxylon* species. In essence, we are testing this hypothesis to propose appropriate strategies for conserving the genetic diversity of tropical trees, even with differing successional status.

## Materials and Methods

### Plant Material

Fresh leaves of adult trees and saplings of *T. scleroxylon* and *M. altissima* were collected from the same plots in Akure Forest Reserve, Nigeria, namely, isolated forest area, logged forest, and a monumental forest, which represents primary forest. Young leaves were also collected from farmland plots for *T. scleroxylon* and from a *M. altissima* plantation. The isolated forest area (5.5 ha) is a portion of the old forest that was cut off from the rest of the forest by farming activities and the establishment of a teak forest about 33 years ago, while the logged forest represents an area in the forest reserve where selective logging has been carried out for six decades. A map of Nigeria with Akure Forest Reserve is presented in Figure 2(a) and (b).

The primary forest, which represents an undisturbed forest is a monumental forest of 23.52 ha, set apart for research on tropical forestry since 1934, before the period of increasing human impact on Nigerian forests (Akinnagbe, Gailing, & Finkeldey, 2010). The *M. altissima* plantation was 5-year-old established mainly by wildlings picked up within the forest reserve, while the farmland, where *T. scleroxylon* samples were collected, was made up of fallow lands experiencing succession and portions of land with ongoing mixed farming practices. Akure Forest Reserve was selected for this study because the entire Forest Reserve was previously a single unfragmented primary forest (Akinnagbe et al., 2010). However, within the last six decades, various forms of human disturbances depleting the forest were identified. The populations sampled in the study area are presented in Figure 2(b), while the geographical location, sample size, and density information of the two species in the sampled populations are shown in Table 1. For both species, complete enumeration was carried out in all plots (i.e., samples of all trees in the sampled area were taken), with the exception of *M. altissima*. Chev in the primary forest and plantation where sampling covered 2.8 ha and 0.25 ha, respectively, of the total area as a result of the high tree density in these populations.

### DNA Isolation

The total genomic DNA of both species was isolated from a small portion (circa 0.5 $cm^2$) of dried leaf tissue in accordance with a modified QIAGEN DNeasy® 96 Plant Kit protocol (QIAGEN GmbH, Hilden, Germany). The modifications are thus as follows:

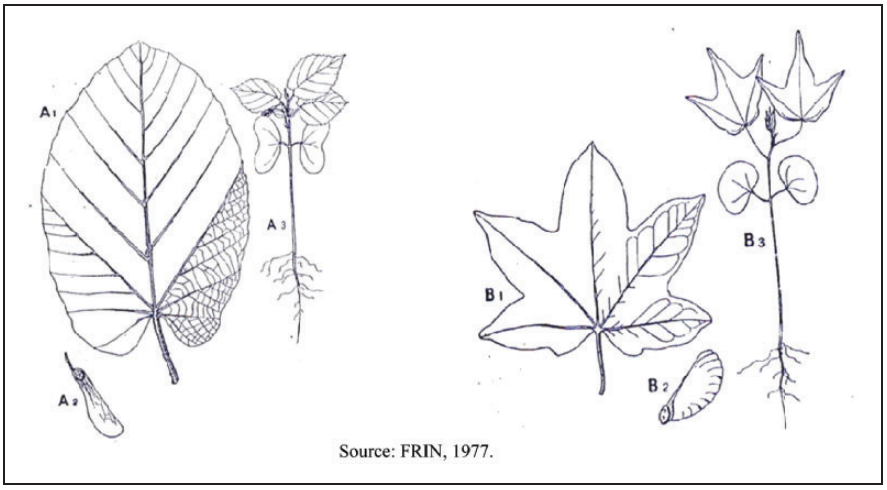


**Figure 1.** *Mansonia altissima* (A1 = leaf; A2 = fruit; A3 = seedling); *Triplochiton scleroxylon* (B1 = leaf; B2 = fruit; B3 = seedling). Source: FRIN (1977).

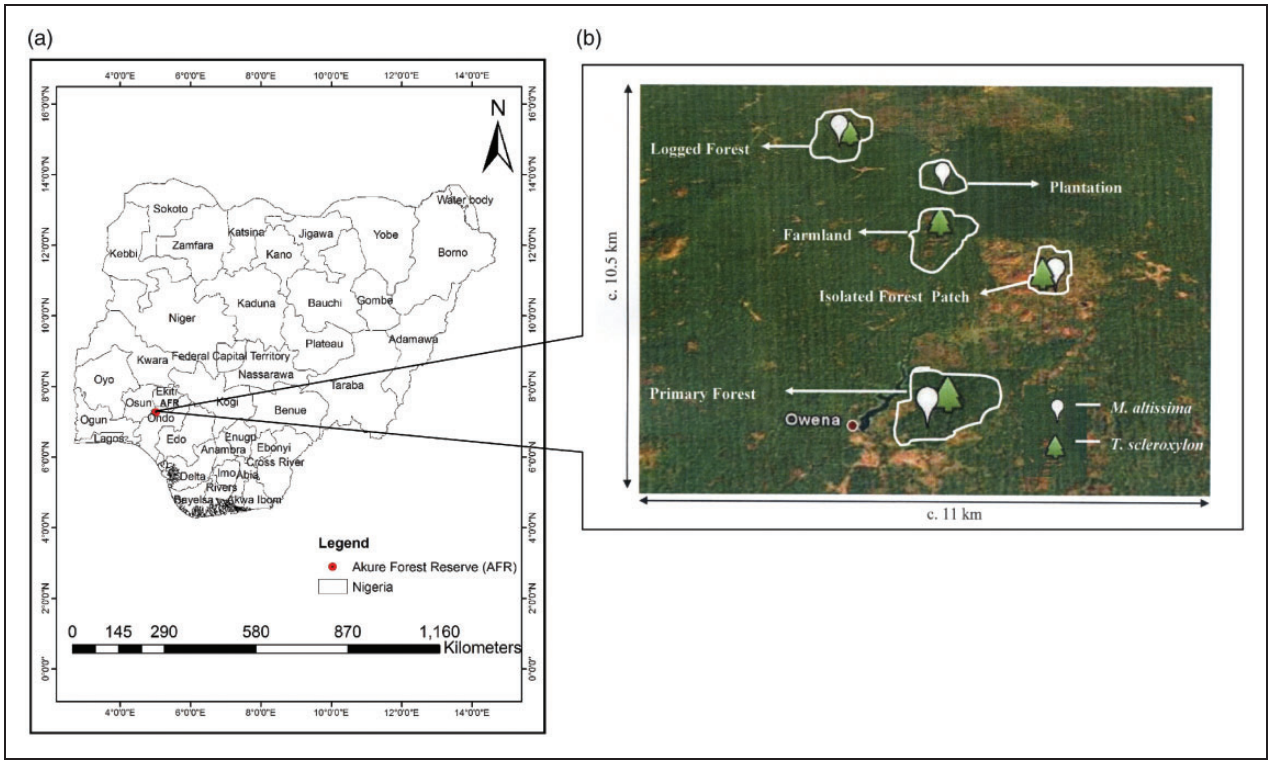


**Figure 2.** (a) Map of Nigeria with Akure Forest Reserve. (b) Satellite image of sampled plots in the study area. Source: Google Earth.

(a) Addition of polyvinylpyrrolidone (PVP) to the AP1 buffer, thereby forming a stock solution of 0.026 g/ml, such that each 100 ml of AP1 buffer contained 2.6 g PVP. (b) Incubation of a mixture of 100 ml AP1/PVP (for 2 × 96-plates) with 224 µl RNase and 224 µl DX at 65°C for 90 min in a water bath. After DNA extraction, the quality and quantity of DNA were checked with 0.8% agarose gels (100 V in Tris-acetate-ethylenediaminetetraacetic acid buffer), visualized by ethidium bromide staining, and photographed under ultraviolet light. Thereafter, storing of the DNA was done at −20°C.

**Table 1.** Geographic Location and Sample Size (No. of Individual [*n*]) of *M. altissima* and *T. scleroxylon* Populations.

| Species | Population | Sample size (*n*) | Latitude | Longitude | Altitude (m) | Plot size (tree/ha) | Density (trees/ha) |
|---|---|---|---|---|---|---|---|
| *M. altissima* | Primary forest | 44 | 7° 12′12N | 5° 01′40E | 282 | 2.8 | 18 |
| | Logged forest | 43 | 7° 16′27N | 5° 00′52E | 296 | 5 | 12 |
| | Plantation | 44 | 7° 12′15N | 5° 01′40E | 283 | 0.25 | 400 |
| | Isolated forest patch | 39 | 7° 13′47N | 5° 02′42E | 281 | 5.5 | 6 |
| Total | | 170 | | | | | |
| *T. scleroxylon* | Primary forest | 44 | 7° 15′42N | 5° 01′40E | 282 | 23.52 | 2 |
| | Logged forest | 45 | 7° 16′27N | 5° 00′52E | 296 | 5 | 10 |
| | Farmland | 22 | 7° 14′57N | 5° 02′13E | 288 | 50 | 2 |
| | Isolated forest patch | 27 | 7° 13′47N | 5° 02′42E | 281 | 5.5 | 4 |
| Total | | 138 | | | | | |

## *Amplified Fragment Length Polymorphism Analyses*

Amplified fragment length polymorphism (AFLP) analyses were based on the Vos et al. (1995) protocol. Two restriction enzymes, namely, *Eco*RI and *Mse*I, were used to digest the total genomic DNA of each sample and the *Eco*RI and *Mse*I double-stranded adaptors were joined (i.e., ligation) to the ends of the restriction fragments in order to produce the DNA template for polymerase chain reaction (PCR) amplification in two sequential steps, namely, preselective amplification and selective amplification. The E01/M03 primer combination was used for the preselective amplification in which the restricted DNA fragments were amplified with each using a single selective nucleotide, A and G. The sequence of AFLP adaptors and primers used in this study is presented in Table 2.

In the selective amplification phase, a very low number of polymorphic fragments were found for *M. altisima* during the initial screening. Therefore, in order to increase the information spectrum of the AFLP markers, four primer combinations were used (Bonin, Ehrich, & Manel, 2007; Meudt & Clarke, 2007), namely, E35/M73, E41/M63, E41/M64, and E41/M72. For *T. scleroxylon*, only one primer combination (E41/M63) was used for the selective amplification because there was an appreciably high level of polymorphism. The AFLP primers' nomenclature used in this study is based on the Keygene standard AFLP primers list (http:/wheat.pw.usda.gov/ggpages/keygeneAFLPs.html). All PCR reactions were performed using a Peltier thermal cycler (PTC-200 version 4.0, MJ Research), and for the purpose of electrophoresis in an ABI Genetic Analyzer, Primers E35 and E41 were labeled with the 6-FAM fluorescent dye. After PCR amplification, the amplified restriction products were resolved electrophoretically in an ABI Genetic Analyzer 3100 (Applied Biosystems) together with GeneScan 500 ROX (fluorescent dye ROX) from Applied Biosystems as internal size standard.

**Table 2.** Sequence of AFLP Adaptors and Primers Used in This Study.

| Name | Sequence (5′ to 3′) |
|---|---|
| *Eco*RI adaptor | CTCGTAGACTGCGTACC |
| | CATCTGACGCATGGTTAA |
| *Mse*I adaptor | GACGATGAGTCCTGAG |
| | TACTCAGGACTCAT |
| Primers | |
| Pre-selective amplification | |
| *Eco*RI + 1 (EO1) | GACTGCGTACCAATTCA |
| *Mse*I + 1 (MO3) | GATGAGTCCTGAGTAAG |
| Selective amplification | |
| *Eco*RI + 3 (E35) | GACTGCGTACCAATTCACA |
| *Eco*RI + 3 (E41) | GACTGCGTACCAATTCAGG |
| *Mse*I + 3 (M63) | GATGAGTCCTGAGTAAGAA |
| *Mse*I + 3 (M64) | GATGAGTCCTGAGTAAGAC |
| *Mse*I + 3 (M72) | GATGAGTCCTGAGTAAGGC |
| *Mse*I + 3 (M73) | GATGAGTCCTGAGTAAGGG |

GeneScan 3.7 and Genotyper 3.7 software packages (Applied Biosystems) were used to determine the size of the AFLP fragments. For the purpose of testing reproducibility, the AFLP reactions starting with ligation, preselective amplification, and selective PCR amplification phases were replicated for eight samples per species including two negative controls to test fragment reproducibility. In total, 504 fragments were analyzed for *M. altissima* and 134 for *T. scleroxylon*. For further analyses, fragments that had 100% reproducibility in the size range from 50 bp to 500 bp were considered.

## *Data Analyses*

AFLP fragments were adjudged as dominant markers, and each fragment was viewed as a locus with two alleles. Fragments of each species were scored as presence (1) or absence (0) markers. The resulting data matrix was used for further analysis. Allele frequencies were calculated

**Table 3.** Genetic Diversity Within Populations of *M. altissima* and *T. scleroxylon* in Akure Forest Reserve, Nigeria.

| | *M. altissima* | | | | | *T. scleroxylon* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Population | Sample size | PPL (%) | $B_r$ | $H_e$ | Ranking of $H_e$ | Sample size | PPL (%) | $B_r$ | $H_e$ | Ranking of $H_e$ |
| Primary forest | 44 | 21.00 | 1.204 | 0.062 | 4 | 44 | 59.7 | 1.211 | 0.249 | 1 |
| Logged forest | 43 | 17.00 | 1.165 | 0.044 | 3 | 45 | 60.4 | 1.323 | 0.269 | 2 |
| Plantation[a] | 44 | 20.00 | 1.190 | 0.042 | 2 | – | – | – | – | – |
| Farmland[b] | – | – | – | – | – | 22 | 64.9 | 1.641 | 0.276 | 3 |
| Isolated forest patch | 39 | 09.00 | 1.089 | 0.032 | 1 | 27 | 67.2 | 1.625 | 0.277 | 4 |
| Mean | 42.50 | 16.75 | 1.162 | 0.045 | | 34.5 | 63.05 | 1.450 | 0.267 | |

*Note.* PPL = percentage polymorphic loci; $B_r$ = band richness; $H_e$ = expected heterozygosity. The program AFLP-SURV v1.0 was used to estimate $H_e$, while PPL and $B_r$ were estimated using AFLPDIV ().

[a]*T. scleroxylon* plantation in the study area was destroyed by fire.

[b]*M. altissima* was not encountered on farmland.

using AFLP-SURV v.1.0 (Vekemans, Beauwens, Lemaire, & Roldan-Ruiz, 2002) based on the Bayesian approach with nonuniform prior distribution of allele frequencies (Krauss, 2000; Meudt & Clarke, 2007; Zhivotovsky, 1999). These allelic frequencies (Appendix 1 and 2) were used to estimate gene diversity ($H_e$) for each population in line with the method described by Lynch and Milligan (1994; i.e., removing all loci with allele frequencies below 0.05). The allelic frequencies from AFLP-SURV v.1.0 were used to compute the percentage of polymorphic loci and band richness ($B_r$) in AFLPDIV (Coart, Van Glabeke, Petit, Van Bockstaele, & Roldán-Ruiz, 2005) based on the rarefaction approach described by Petit, El Mousadik, and Pons (1998) and Coart et al. (2005).

## Results

Generally, *M. altissima* ($H_e = 0.045$; PPL = 16.75; $B_r = 1.162$) exhibited a much lower genetic diversity than *T. scleroxylon* ($H_e = 0.267$; PPL = 63.05; $B_r = 1.450$; Table 3). Contrasting results were found for the two species with respect to the outcome of human impact on genetic diversity. Highest diversity in terms of PPL, $B_r$, and $H_e$ was observed in the primary forest (PPL= 21.0, $B_r = 1.204$, $H_e = 0.062$) for *M. altissima*, while the lowest diversity was observed in the isolated forest patch (PPL = 9.0, $B_r = 1.089$, $H_e = 0.032$). Contrarily, the lowest diversity was observed in the primary forest for *T. scleroxylon*, and the highest diversity was found in the isolated forest patch. Interestingly, genetic diversity in the farmland population of *T. scleroxylon* ($H_e = 0.277$; PPL = 64.9; $B_r = 1.625$) was higher than the primary forest ($H_e = 0.249$; PPL = 59.7; $B_r = 1.211$). Specifically, genetic diversity ($H_e$) in *M. altisima* decreased with human impact or fragmentation (Table 3), while in the case of *T. schleroxylon*, genetic diversity increased slightly with increasing fragmentation suggesting that human impact may not necessarily reduce genetic diversity (Table 3).

## Discussion

The comparative genetic analysis for the two tropical tree species investigated in this study revealed that the genetic diversity was significantly lower in the nonpioneer species *M. altissima* than in the pioneer species *T. scleroxylon*. Wehenkel, Bergmann, and Gregorius (2006) asserted that pioneer tree species, unlike nonpioneer species, are early colonists, which need a high degree of resilience in order to adapt physiologically to diverse unpredictable environmental conditions during their lifetime (Stern & Roche, 1974). However, caution should be taken in establishing this as a theory using our data, because AFLP markers employed in this study are potentially neutral gene loci, and may not reflect adaptive genetic variation.

In comparing how the two species reacted to human impact, contrasting results were observed. While *M. altissima* showed relatively low genetic diversity in populations with human impact, the results show an opposite trend for *T. scleroxylon*. Negative effects of isolation on genetic diversity were observed in *M. altissima* but not in *T. scleroxylon*. The genetic diversity in the isolated forest area of *M. altissima* was considerably less than genetic diversity in the primary forest, probably due to the decline in population size (see Table 1) and restricted gene flow. Although there is no documentation specifically on the pollination biology of *M. altissima*, it is suspected to be pollinated by insects due to its fragrant flowers. Findings of Kantsa et al. (2017) further corroborated this in establishing that plants use their flowers' fragrance to attract pollinators. Since *M. altissim*'s closest flowering neighbors are located about 2 km away from the isolated forest patch, it is likely that their pollinators may be unable to connect spatially isolated populations, although in-depth research is still

needed in order to provide accurate information on the nature of its pollinators. For *T. scleroxylon*, the closest reproductive trees are found about 1 km away from the isolated forest patch. Similar reports of relatively high genetic diversity in populations isolated by some kilometers from the nearest neighboring population exist for other tropical species such as *Eucalyptus albens* (Prober & Brown, 1994), *Swietenia humilis* (White et al., 2002), *Spondias mombin* (Nason & Hamrick, 1997), and *Dizinia excelsa* (Dick, 2001). These results were elucidated by effective gene flow because their pollinators can connect isolated reproductive trees, which are hundreds of meters apart. The above cited tree species are mainly outcrossing and insect pollinated, which is similar to *T. scleroxylon*. *T. scleroxylon* has an outcrossing mating system and is insect pollinated (Hall & Bada, 1979). Thus, effective pollen transport by insects and mandatory outcrossing may explain high levels of genetic diversity in *T. scleroxylon*, even in isolated forests. It is then likely that a blend of mechanisms (i.e., self-incompatibility) that enhances outcrossing and probably pollen transfer from distant trees accounted for the high genetic diversity of *T. scleroxylon* in the isolated population.

In numerous studies, logging has shown adverse effects on genetic diversity (Buchert, Rajora, Hood, & Dancik, 1997; Prober & Brown 1994; Wickneswari, Lee, Norwati, & Boyle, 1997), while in others, no distinct impact was observed (Lee, Wickneswari, Mahani, & Zakri, 2002; Zheng et al., 2005). There was no clear disparity between genetic diversity in logged forests and primary forests for the tree species investigated in this study. For both species, however, an opposing trend was observed. For instance, genetic diversity of *M. altissima* in the logged population was marginally lower than its diversity in the primary forest, while *T. scleroxylon*'s genetic diversity was somewhat higher in the logged population as compared with the primary forest. This result is consistent with findings of Akinnagbe et al. (2010). According to this study, the highest genetic diversity of *M. altissima* was observed in the primary forest ($H_e = 0.062$; PPL = 21.00%; $B_r = 1.204$), with the lowest genetic diversity in the isolated forest ($H_e = 0.032$; PPL = 9.00%; $B_r = 1.089$). The slight decrease in genetic diversity in the *M. altissima* population suggests that the impact of logging on the genetic diversity of the species was small. On the other hand, the slightly higher genetic diversity in the logged forests of *T. scleroxylon* than in the primary forests may be as a result of its higher ability to regenerate in open forests as pioneer species (FRIN, 1977). Successful forest regeneration is an important factor in conserving genetic diversity in species (Wickneswari et al., 1997).

Absence of *M. altissima* on the farmland, which used to be a continuous primary forest, is probably due to its very poor regeneration in an open landscape. In contrast, the farmland population of *T. scleroxylon* had a higher genetic diversity than the primary forest despite the lower sample size of *T. scleroxylon* on the farmland. Some of the *T. scleroxylon* trees of the farmland population were original relics from the old forests but regenerated, thus providing an appropriate comparison with the primary forest. Higher genetic diversity of *T. scleroxylon* could also be attributed to its orthodox seed storage behavior (Orwa, Mutua, Kindt, Jamnadass, & Anthony, 2009) which is characteristic for pioneer species (Swaine & Whitmore, 1988). Generally, regeneration from soil seed banks after disturbance is often dominated by pioneer species (Garwood, 1989). There is evidence for the stimulation of new seedling recruits in forests disturbed by logging operations especially in felling gaps (Swaine & Agyeman, 2008). This effect of gap microclimate is stronger in larger canopy openings because these conditions break dormancy of seeds in the soil seed bank (Duah-Gyamfi, Swaine, Adam, Pinard, & Swaine, 2014).

The relatively high genetic diversity observed in the farmland population and in the isolated patch is in contrast to the traditional concept of genetic erosion as a result of human impacts (Saunders, Hobbs, & Margules, 1991; Young, Boyle, & Brown, 1996). Contrarily, this study suggests that the farming practice in the study area has not imposed a genetic bottleneck in *T. scleroxylon*. *T. scleroxylon* even has higher genetic variation in the isolated forest area than in the primary forest, which can be associated to its preference for open forest colonization. Apart from *T. scleroxylon*, another tropical tree species known to maintain its diversity even on farmlands is *Vitellaria paradoxa* (Kelly et al., 2004). Both species, *Vitellaria paradoxa* and *T. scleroxylon*, have in common their ability to colonize open forests because they demand high irradiance for establishment and continued growth.

Artificial regeneration by establishment of man-made forests often leads to changes in genetic composition of target tree species (Finkeldey & Ziehe, 2004). In line with this, Rajora (1999) and Hollingsworth et al. (2005) observed lower genetic diversity in plantations of *Picea glauca* (White spruce) and *Inga edulis*, respectively, when compared with old natural stands. Likewise, the planted stands of *M. altissima* show slightly lower genetic diversity than the population from the primary forest. Indeed, the *M. altissima* plantation was established by seeds collected from parent trees in few clusters largely within the study area and partly from about 60 km away from the study area (D. Adeyelu, personal communication January 3rd, 2008). A high genetic diversity in the plantation is possible if there is admixture of seeds and propagules from different source populations (Comps, Gömöry, Letouzey, Thibaut, & Petit, 2001; Petit, Aguinagalde, Beaulieu, & Bittkau, 2003). The lower level of genetic diversity in the plantation as compared

with the primary forest may be accredited to the already low genetic diversity in the populations where the seeds were collected from, and to the collection of seeds from a limited number of parent trees. Our results are consistent with the conclusion of Finkeldey and Hattermer (2007), that plantations established from a small number of related founder individuals have reduced levels of genetic variation due to random loss of alleles.

Genetic diversity provides the basis for adaptation and evolution of species populations, and therefore, the conservation of genetic diversity in tree species is critical for their future sustainable use. We found that regimes of human impact in the study area do not have adverse effects on the genetic diversity of the pioneer species *T. scleroxylon* but of the nonpioneer tree *M. altissima*. This suggests that *T. scleroxylon* may be less susceptible to genetic erosion due to human impact than *M. altissima*. Unlike *M. altissima*, *T. scleroxylon* appears to have the ability to maintain its genetic diversity despite human impact due to its ability to colonize open forest areas (FRIN, 1977). However, from the perspective of genetics, some authors have revealed that colonization events usually lead to strong founder effects in plant species (Raybould, Goudet, Mogg, Gliddon, & Gray, 1996; Westerbergh & Saura, 1994). On the contrary, it is likely that *T. scleroxylon* possesses features that permit the colonization of disturbed forest areas without losing genetic diversity. One attribute of *T. scleroxylon* reported to prevent loss of genetic variation is delayed reproduction. *T. scleroxylon* is a tree with erratic flowering and fruiting (FRIN, 1977), and the period from juvenile to the first flowering of *T. scleroxylon* in the natural forest environment could be about 15 years (Leakey, Ferguson, & Longman, 1981). Austerlitz, Mariette, Machon, Gouyon, and Godelle (2000) expounded that many trees avoid founder effects due to delayed reproduction, which allows a large increase in the number of initial founders of a given population before reproduction begins. This process can be observed in a well-described example of a recent colonization event in *Prunus avium*. In a study on *P. avium*, Mariette et al. (1997) reported that a very young population showed almost the same level of diversity as a long-established neighboring population (~120 years old), and both populations were not differentiated from each other ($G_{ST} = 0.014$). The delay in reproduction allows build-up of founders in the young plantation, which enhances maintenance of genetic variation.

## Implications for Conservation

Genetic diversity is essential in order to ensure survival and continuous existence of important tree species under changing environmental conditions. Forest conservationists more accustomed to the traditional view of conserving tropical tree species only in strictly protected primary forests need to be conscious of the fact that genetic diversity of pioneer trees like *T. scleroxylon* may also be managed outside the primary forests, in an environment conducive for their regeneration. It is more likely that forest patches, farmlands, and secondary forests would serve as a safe haven for the conservation of genetic diversity in pioneer tree species as compared with nonpioneer tree species. Contrarily, lower genetic diversity in *M. altissima* populations with human impact as compared with the primary forest suggests that human impact in the study area could pose a serious threat to the future viability of the species if no conservation measures are taken. Thus, strict in-situ conservation of nonpioneer species like *M. altissima* in primary forests, where conditions favor their germination, may be the key to the successful conservation of their genetic diversity. Generally, our study implies that in-situ conservation of genetic diversity in pioneer species and nonpioneer species requires different strategies. Since effects of human impact on the investigated pioneer and nonpioneer tree species appear to differ, also approaches to conservation of genetic diversity in the two species should be different. To maintain genetic diversity of these important timber species in the face of exploitation, seed germplasm collection and replanting should be adopted as part of strategies for their gene conservation.

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### Supplemental Material

Supplemental material for this article is available online.

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