

Genetic Variation in Tropical Tree Species and Plantations: A Review

Tomiwa Victor Oluwajuwon^{1*}, Racheal Attafuah¹, Chinedu Joevita Offiah², Doris Krabel³

¹Institute of International Forestry and Forest Products, Technische Universität Dresden, Tharandt, Germany

²Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany

³Institute of Forest Botany and Forest Zoology, Technische Universität Dresden, Tharandt, Germany

Email: *tomiwaoluwajuwon@gmail.com

How to cite this paper: Oluwajuwon, T. V., Attafuah, R., Offiah, C. J., & Krabel, D. (2022). Genetic Variation in Tropical Tree Species and Plantations: A Review. *Open Journal of Forestry*, 12, 350-366.
<https://doi.org/10.4236/ojf.2022.123019>

Received: May 21, 2022

Accepted: July 11, 2022

Published: July 14, 2022

Copyright © 2022 by author(s) and Scientific Research Publishing Inc. This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

Abstract

The global efforts to restore tropical forests and their productive and ecological functions through plantation forestry largely depend on the available genetic variation in the tree species used to establish the plantations. However, there is limited information on the levels and trends of the genetic variation and variability of different plantation tree species in the tropics. Therefore, this study reviews several marker-based studies that have investigated genetic variation. Most of the top economic species like *Eucalyptus tereticornis* and *Mansonia altissima* are attributed to low levels of genetic diversity, while others like *Pinus caribaea* and *Swietenia macrophylla* still exhibit high expected heterozygosity across different populations. However, the levels of genetic diversity assessed may depend on the markers used. Microsatellites, i.e., simple sequence repeats (SSRs), mostly give higher estimates when compared to other polymerase chain reaction-based markers. Other factors that typically contribute to the directional pattern of genetic variation in tropical tree species and populations include their distribution, density, seed dispersal, succession, and reproduction. Also, anthropogenic impacts like logging and fragmentation have contributed to the vast genetic base reduction of many tropical species and populations. Having adequate genetic variation within the plantation populations is significant in improving their fitness, resilience, fecundity, productivity, and other ecological functions. It also provides a basis for tree improvement and breeding in plantation forests. Although clonal forestry is becoming widespread and considered highly productive, it is attributed to specific economic, technical, and ecological risks, such as the increased spread of pests and diseases. Therefore, further discussions and recommendations to maximise genetic diversity in tropical (clonal) plantations are provided.

Keywords

Genetic Diversity, Genetic Variation, Tropical Plantations, Tropical Tree

1. Introduction

Forest trees are an essential genetic subject as they are mostly undomesticated and long-lived, enabling them to “naturally” demonstrate genetic variation over a period of time (Ingvarsson & Dahlerg, 2019). However, over time, there have been subtle human impacts on forest ecosystems, more severely in the tropics through the increasing trends of deforestation and forest degradation, directly affecting their diverse genetic resources and associated functions (Finkeldey & Hattemer, 2007). A few examples of these effects include loss of rare but significant alleles, reproductive alteration and isolation among different tree populations (White et al., 2007). Therefore, more attention has been drawn to massive tropical forest landscape restoration, particularly through plantation forestry and agroforestry systems (ITTO, 2020). However, the increasing intensity and dynamics of climatic and environmental changes still limit the success of these plantation interventions, such as increasing their susceptibility to pests and diseases and affecting their productivity.

Nevertheless, some tree populations and species tend to exhibit more resilience and adaptation to those debilitating impacts while maintaining productivity, relative to others. This capacity is largely influenced and determined by the higher levels of diversity in their genetic composition, i.e., genetic variation (Koskela et al., 2007). Genetic variation in trees is expressed in different traits, which are essential to developing plantation forests in the tropics that are substantially resilient to varying environmental stresses and are also more productive in economic, social, and ecological dimensions. These important traits include, but are not limited to, growth rate, stem form, vigour, resilience to drought and pests (Finkeldey & Hattemer, 2007).

Despite the significance of genetic variation in forest sustainability and management, there has been limited information about its patterns and importance regarding tropical species and plantations (Finkeldey & Hattemer, 2007). Although different tree species or populations may naturally have different levels of genetic variability, specific silvicultural interventions can help maintain or improve the genetic diversity in plantation stands. These interventions may range from carefully selecting appropriate (or mixtures of) reproductive materials and provenances to engaging more technical tree breeding strategies in the plantation establishment efforts (Finkeldey & Hattemer, 2007; Ivetić & Devetaković, 2017). Therefore, it is essential to provide more information on the contexts, patterns, and importance of genetic variation in tropical tree species and, ultimately, plantations, to make suitable recommendations for improving it towards the establishment and management of more productive and resilient plantations to meet the critical forest restoration needs and demands for timber products and

other services. This review aimed to highlight the levels of genetic variation in common tropical tree species, identify why genetic diversity is essential in the species and their populations, and reveal ways whereby most tropical plantations miss adequate genetic variation and how it can be improved in the plantation forests.

2. What Is Genetic Variation?

Genetic variation defines the genetic differences in individuals within a population or among populations. It is the “mechanism” whereby individuals of the same population or species exhibit different genotypes (alleles) at each gene locus (Ewens, 2013), while genetic variability describes the population’s potential to produce individuals with different genotypes (Hattemer, 1995). The amounts, nature and patterns of genetic diversity vary across different plant species, of which trees have been generally found to have significantly more variations than other plant forms (Hamrick, 1979). Genetic variation explains the evolutionary change or adaptive potential and dictates the phenotypic variation of any tree population or species, expressed across their morphological or physiological traits. It provides raw materials for the variety of growth forms, yields and wood qualities for production, leafing and fruiting patterns, and adaptability to environmental changes and stresses, expressed differently by different tree species (Hamrick, 1979; Finkeldey & Hattemer, 2007).

Genetic diversity can significantly vary between tree populations, species or taxa as a result of differences in both internal attributes like genome structure & size and reproductive system, or external attributes like distribution, density and age, as well as location or environmental factors like human impacts (Hamrick et al., 1992; Akinagbe et al., 2019).

2.1. Forms and Measures of Genetic Variation

Genetic variation can be intraspecific, which refers to the range of genetic information available among all individuals or populations of one species, or interspecific, across different species. Of the two, the intraspecific genetic variation is more regarded, which is further described as either within or among populations (Finkeldey & Hattemer, 2007).

Genetic variation within populations often dominates the variability of most species, amounting to about 89% in tree species, and it is characterised by:

- Genetic multiplicity, which considers the occurrence or number of the genetic types, alleles or genotypes. It is estimated by the proportion of polymorphic loci (PPL), i.e., the number of polymorphic gene loci (PL) divided by the number of all loci investigated, or by the number of alleles at each locus in the population which is termed “allelic richness”.
- Genetic diversity, which additionally considers the (relative) frequency of the genetic types. It is variably measured by allelic diversity (i.e., the inverse of expected homozygosity), expected heterozygosity (i.e., one minus expected

homozygosity), or observed heterozygosity (i.e., the proportion of all heterozygotes from all trees investigated in a population). Expected homozygosity is the summation of all alleles. In population genetics, genetic diversity and expected heterozygosity are the commonest attribute and measure for assessing genetic variation within populations, respectively.

Genetic variation among tree populations can be characterised and measured by genetic distance and genetic differentiation. While the first quantifies the genetic differences between two populations, genetic differentiation measures the differences between an arbitrary number of populations (Finkeldey & Hattemer, 2007).

2.2. Sources of Genetic Variation

Genetic variation is a result of four evolutionary factors: mutation, random genetic drift, selection, and gene flow or migration (White et al., 2007; Ingvarsson & Dahlerg, 2019; Nonić & Šijačić-Nikolić, 2021). Mutations are heritable changes in the genetic structure of individuals, which are not attributed to recombination or gene interaction. They cause genetic variation in populations by creating entirely new alleles. Genetic drift defines the random fluctuations of genetic structures, strongly in small populations, often due to limited population size. It mostly leads to a loss of genetic diversity within populations. Gene flow or migration refers to the movement of alleles from one population to another through fruit, seed or pollen dispersal. For instance, gene flow both by pollen and seeds was significantly the source of maintaining the genetic diversity within populations of a pioneer tree species, *Croton floribundus*, in some Brazilian successional forests (Silvestrini et al., 2015). It could lead to either an increased intrapopulation genetic variability or, in the long-term, a decreased interpopulation genetic divergence. Lastly, selection describes a process whereby a population's genetic composition changes due to the greater reproductive contribution of individuals better suited to the environmental conditions. Unlike natural forest conditions, selection is done artificially in plantations based on several economically relevant factors like growth and resistance. This process thereby tends to reduce the genetic variability of man-made plantation forests (Nonić & Šijačić-Nikolić, 2021).

2.3. Assessment of Genetic Variation

Genetic variation within or among tree populations is assessed using gene markers. A gene marker, also known as gene locus or marker locus, is typically an environmentally stable trait whose variation is determined only by genetic factors. Different types of gene markers have been applied in genetic inventories of tropical forest trees. These include morphological or phenotypic, biochemical, and molecular markers (Finkeldey & Hattemer, 2007) and cytogenetic markers (Chesnokov et al., 2020). Further descriptions of the markers are provided in **Table 1** below.

Table 1. Common genetic markers and their features.

Feature	Markers			
	Phenotypic	Biochemical	Molecular	Cytogenetic
Description	Visual morphological indicators	Biochemical molecules, like proteins (e.g., isoenzymes), metabolites (e.g., carbohydrates)	DNA fragments of known locations on the chromosome	Chromosome structure —visible by microscopy
Examples	Colour, shape and size of flowers, seeds, or leaves	Isoenzyme gene loci	SNP, SSR or microsatellites, RAPD, AFLP	FISH, GISH
Genomic coverage	Low	Low	High	Average
Specialized equipment requirement	No	Yes	Yes	Yes
Cost-intensiveness	Low	Average	High	High

SNP single nucleotide polymorphism; SSR simple sequence repeats; RAPD random amplified polymorphic DNA; AFLP amplified fragment length polymorphism; FISH/GISH fluorescence/genomic in situ hybridization (adapted from (Chesnokov et al., 2020)).

3. Genetic Variation in Tropical Forest Tree Species

Several marker-based studies have investigated genetic variation in different tree species across the tropics. Finkeldey & Hattemer (2007) provided the last broad review of these studies. Therefore, this paper updates the review with more recent examples of genetic variation patterns in tropical tree species, as presented in Table 2.

Overall, tropical tree species differently possess varying levels of genetic variation within populations (HE): low, intermediate and high. In contrast, some top economic species have a low genetic variation (e.g., *Eucalyptus tereticornis*, *Mansonina altissima*), others like *Pinus caribaea* and *Swietenia macrophylla* exhibit high diversity. However, the levels and extents of genetic diversity vary with species, populations, provenances and the genetic markers used. The same tropical tree species could possess wide-ranging genetic diversity levels across different populations and with different markers. *Acacia mangium* earlier recorded as low as 0.01 within-population expected heterozygosity across tropical forest populations in Australia despite its indigeneity to the range (Butcher et al., 1998). Yuskianti & Isoda (2012) conversely found the species to have a high genetic diversity (0.623) in its other natural range/population in Indonesia. Similar findings have also been reported in species like *Prunus africana* even in same tropical Kenya, 0.137 (Dawson & Powell, 1999) against 0.830 (Farwig et al., 2008) and *Pinus merkusii* in Thailand (0.058) and Indonesian (0.559) populations (Changtragoon & Finkeldey, 1995; Nurtjahjaningsih et al., 2007).

The variation in genetic diversity has also been attributed to the markers used. This partly contributed to the differences in the genetic variations recorded in similar Malaysian populations of *Shorea leprosula* by Lee et al. (2000) and Ang et al. (2016) at isozyme and microsatellite gene loci, respectively. Furthermore, Fofana et al. (2013) compared the performance of SSRs and AFLPs in assessing

Table 2. Examples of tropical tree species and their levels of genetic variation within populations.

Species	Country/region	Marker type	H_e	References
Low variation				
<i>Acacia mangium</i>	Australia, New Guinea, Moluccas	RFLP	0.010 - 0.211	Butcher et al. (1998)
<i>Mansonia altissima</i>	Nigeria	AFLP	0.045	Akinagbe et al. (2019)
<i>Acer skutchii</i>	Mexico	SSR	0.112	Lara-Gomez et al. (2005)
<i>Prunus africana</i>	Ethiopia, Kenya, Cameroon, Madagascar, Uganda	RAPD	0.020 - 0.137	Dawson & Powell (1999)
<i>Moringa oleifera</i>	India	SSR	0.180	Ganesan et al. (2014)
<i>Eucalyptus tereticornis</i>	India	ISSR	0.130	Chezian et al. (2010)
<i>Pinus merkusii</i>	Thailand	Isozyme	0.058	Changtragoon & Finkeldey (1995)
High variation				
<i>Acacia albida</i>	West Africa	Isozyme	0.442	Joly et al. (1992)
<i>Acacia mangium</i>	Indonesia	SSR	0.623	Yuskianti & Isoda (2012)
<i>Celtis zenkeri</i>	Nigeria	AFLP	0.780	Olamidayo et al. (2021)
<i>Koompassia malaccensis</i>	Singapore	SSR	0.850	Noreen & Webb (2013)
<i>Triplochiton scleroxylon</i>	Nigeria	AFLP	0.267	Akinagbe et al. (2019)
<i>Prunus africana</i>	Kenya	SSR	0.730 - 0.830	Farwig et al. (2008)
<i>Tectona grandis</i>	Myanmar	SSR	0.586	Minn et al. (2014)
<i>Pinus merkusii</i>	Indonesia	SSR	0.559	Nurtjahjaningsih et al. (2007)
<i>Pinus caribaea</i>	Bahamas	SSR	0.555	Sanchez et al. (2014)
<i>Shorea leprosula</i>	Malaysia	Isozyme	0.406	Lee et al. (2000)
<i>Shorea leprosula</i>	Malaysia	SSR	0.762	Ang et al. (2016)
<i>Swietenia macrophylla</i>	Mexico	SSR	0.780	Alcalá et al. (2014)

H_e : average expected heterozygosity within populations.

genetic variation in *Tectona grandis* and found the estimates of variability acquired using SSRs to be higher than the latter. The report with *Acacia mangium* and *Prunus africana* substantiates the differential estimations due to markers, where microsatellites assessed higher diversity than their counterpart markers (Table 2). However, this is inconsistent with other studies where no significant distinction is found between/among the several polymerase chain reaction (PCR) markers, such as on *Jatropha curcas* (Gupta et al., 2008).

3.1. Some Factors Influencing Genetic Variation in Tropical Tree Species and Populations

Different factors typically contribute to the directional pattern of genetic variation among tropical tree species and populations (Figure 1). Following the hypotheses that species distribution and population density/size influence genetic

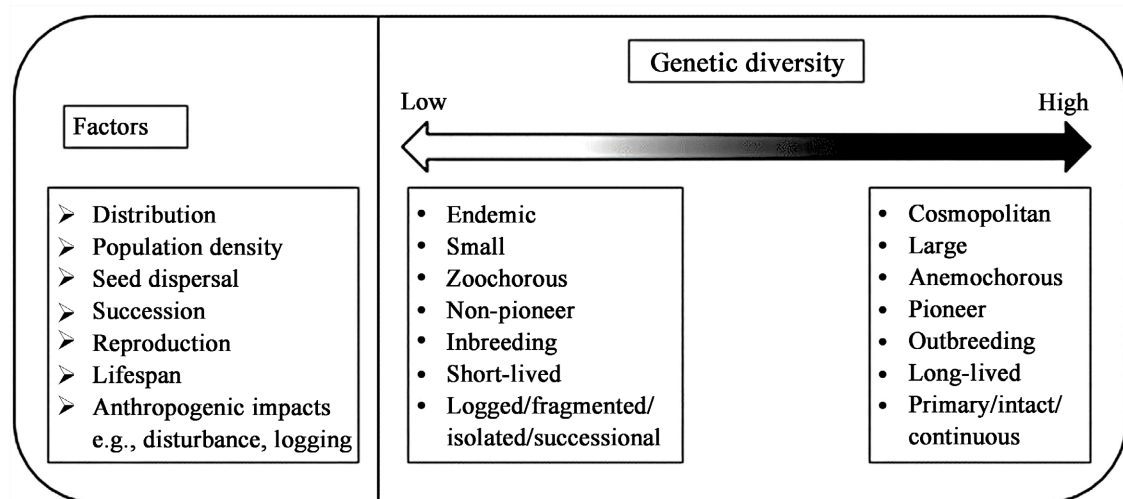


Figure 1. Directional factors influencing genetic diversity in tropical trees.

variability, this is also observed amongst tropical trees, where those that are endemic and with low density in the forests are attributed to lower genetic diversity, partly due to higher inbreeding. Thus, the smaller the population, the higher the chance of genetic drift, i.e., bottleneck effect, owing to the correspondingly small reproductive ability (Hamrick et al., 1992; Butcher et al., 1998). Seed dispersal also tends to influence genetic variation among tropical tree species, as anemochorous (wind-pollinated) tree species are likely to sustain higher genetic variability than the zoochorous (animal-pollinated) due to a better gene flow from longer-distance pollen dispersal (Finkeldey & Hattemer, 2007; Bittencourt & Sebbenn, 2007).

Similarly, anthropogenic impacts like fragmentation and logging on forest trees as well as their regeneration or succession status potentially affect their genetic diversity in the tropics. In this case, non-pioneer species and fragmented, isolated or logged populations are more prone to genetic erosion and diversity loss than the pioneers and continuous or primary tree populations (Pither et al., 2003; Akinagbe et al., 2019). The genetic variation in several tropical tree species has been critically reduced by human disturbance, such as *Prunus africana* in Kenya (Dawson & Powell, 1999), *Araucaria augustifolia* in Brazil (Bittencourt & Sebbenn, 2007), and *Shorea leprosula* in Malaysia (Ang et al., 2016). However, these directional trends of influence on tropical trees' genetic variation are not entirely always constant (Minn et al., 2014; Akinagbe et al., 2019). For instance, Noreen & Webb (2013) found high genetic diversity in *Koompassia malaccensis* populations across Singapore despite the high habitat loss. Silvestrini et al. (2015) reported similar levels of genetic diversity of *Croton floribundus* within some Brazilian primary and successional forests. Also, Wang et al. (2012) found no significant variance in genetic diversity between pre- and post-fragmentation cohorts of a wind-pollinated tree's populations (*Castanopsis sclerophylla*); rather, an enhanced gene flow due to the removal of genetic barrier by fragmentation.

By implication, genetic diversity (pattern) varies with individual trees, popula-

tions, provenances, species, markers and several ecological and anthropogenic factors. Hence, there is a need for suitable genetic inventories and, more importantly, establishing plantations populations with adequately selected plant materials of certain species and provenances with high levels of genetic variation.

4. Importance of Genetic Variation in Tropical Plantations

4.1. Genetic Variation Reduces Inbreeding Depression & Accumulation of Harmful Alleles and Improves Fitness and Fecundity of Plantation Trees

Inbreeding depression is the process whereby the offspring exhibit homozygosity, removal of heterozygote superiority, and an increased possibility of risky mutations resulting from mating genetically closely related parents, i.e., “inbreeding” (Reed & Frankham, 2003). Therefore, this tends to reduce the genetic base within the particular species or accumulate harmful alleles, which can directly impact the fitness, survival and fertility of the individual offspring trees/populations (Nonić & Šijačić-Nikolić, 2021). It can result in the loss of certain desired traits of plantation forest trees, such as vigour and growth form. Also, there are increased chances of tree population size reduction or even species extinction, owing to the resultant continual drop in their reproductive rate due to effects like embryo abortion, impaired fruit set, decreased overall seed yield and reduced germination of remnant seeds (Reed & Frankham, 2003; Nonić & Šijačić-Nikolić, 2021). Hence, it is essential to maintain genetic variation to avert the issue of wide fecundity among the tree species or populations whereby only a very few tree individuals in the forest are able to produce sufficiently vital genetic materials for subsequent sustainable rotations and productivity.

4.2. Genetic Variation Increases Forest Productivity

In plantation forests, there is often a positive relationship between the level of genetic variation and productivity (Nonić & Šijačić-Nikolić, 2021). An example is the varying high tree stem qualities, which potentially increase the economic versatility and productivity of the plantation products. In a provenance mixing experiment, genetic diversity from using different provenances of one tree species had a positive effect on tree growth and stand productivity (Pretzsch, 2021). That is, an increase in genetic variation within the stand through provenance mixtures/richness yielded proportionate increases in its incremental volume and stem diameter notwithstanding the stand densities.

The interspecific variation from species-mixtures could also enhance productivity, e.g., by facilitating products diversification from the plantations under several rotation periods (Forrester et al., 2006; Liu et al., 2018). Agroforestry systems are an essential component of plantation forestry in tropical forest landscape reforestation. Maintaining genetic variation in such systems is also of great significance while integrating trees into livelihood systems whereby the mixed

species create the opportunities to obtain a variety of attributes of desired products, thus enhancing local livelihoods. An example is the varieties of fruits obtained from a fruit tree species, which ripen at varying times to meet market demands over an extended period (Dawson et al., 2009).

4.3. Genetic Diversity Reduces Competition in Forest Stands

Genetic diversity brings about variation in structure in a forest stand, which tends to create differences in the use and competition for resources like space or light in the crown layer or water and nutrients in the soil. Different morphological/phenotypical traits are expressed by various genetically different provenances and plant materials. These varied expressions result in biomass partitioning, as well as diversification or asynchrony in sprouting, light assimilation, leaf shedding, and water uptake, all of which could decrease overlapping niches, increase resource use complementarity and site use efficiency, and reduce competition (Chmura & Rozkowski, 2002; Pretzsch, 2021). Such reduced competition also influences both productivity of the plantation site and stand. Furthermore, the genetic variation from combining species that have complementary traits like light-demanding with shade tolerant, fast with slow-growing, and shallow with deep rooting may limit competition within the plantations (Liu et al., 2018).

4.4. Genetic Diversity Drives Ecological Diversity and Ecosystem Functions

The importance of diversity cannot be overemphasized in maintaining the structure and functions of any forest ecosystem. Meanwhile, genetic diversity constitutes the basis of biodiversity (Nonić & Šijačić-Nikolić, 2021). Buttressing further, Zytynska (2011) found within-species genetic variation in a tropical forest of *Brosimum alicastrum* to influence the communities of epiphytes and invertebrates (including spiders, ants, crickets) around the tree trunks and leaf litter. The genetic distance between species populations, assessed using the AFLP marker, correlated positively with the community differences of the associated epiphytic plants and invertebrates. This could thus imply that the more genetically different tree populations or species are, the more ecologically diverse or relevant they are. Among other essential ecosystem functions provided by tropical forests (plantations) are carbon sequestration and storage, contributing significantly to the global carbon cycle. However, their potential to accumulate aboveground biomass or soil carbon can be affected by genetic variation in the species considered (Chmura et al., 2021; Mora-Orozco et al., 2022). Nevertheless, it is noteworthy that such relationships between genetic variation and ecological diversity or function may not always be strong, positive, or significant. For instance, in a tropical subdeciduous forest in Mexico, Cruz-Salazar et al. (2021) found both a significant relationship and a negative association between different indices of genetic diversity and tree species diversity.

4.5. Genetic Diversity Enhances Resilience against Changing Environment and Reduces Risks of Pests and Pathogens in Plantations

Forest trees are exposed to global and environmental changes due to their long gestation and largely non-domestication. The dynamic impacts of increased intensity and distribution of forest pests and diseases, temperature rise, rainfall pattern changes, drought, frost, and growing seasonal changes are evident in forest tree growth, productivity, and survival. However, enhancing genetic variation among tree populations and species can significantly improve their resilience and adaptability, that is, adaptive traits (Finkeldey & Hattemer, 2007; Nonić & Šijačić-Nikolić, 2021). White et al. (2007) consider it a major condition for the evolutionary adaptability of forest trees. Several other authors have also affirmed that considering tree species with high levels of genetic variation and ensuring such are maintained when establishing plantations will facilitate their adaptability to the changing environments and help them tolerate stress factors in the sites (Aitken et al., 2008; Dawson et al., 2009).

High genetic variability is needed in any species and plant materials considered for plantation forestry to cope with the outbreaks of (new) pests and diseases. This is particularly important because of the often low interspecific diversity in most plantation forests, even in the tropics, resulting from their usual mono-species/monoculture composition (Liu et al., 2018). For instance, when *Leucaena* tree species was first introduced to Asia and Africa in the 80's - 90's, its plantations were severely attacked and damaged by psyllid (*Heteropsylla cubana*). This event was significantly attributed to the narrow genetic base of the species introduced; that is, the variation in the genetic material and provenance required to adapt to the new region outside its natural range was low (Rao et al., 2000). Therefore, to maximise the survival and resilience of plantations in the tropics, it is essential to select and utilise plant stock and provenances with adequate levels of genetic diversity. Adaptability, and not just adaptedness to current environmental conditions, facilitates the long-term survival of tree populations (Nonić & Šijačić-Nikolić, 2021).

4.6. Genetic Variation Forms the Basis of Tree Improvement and Breeding

The genetic variation of populations or species in plantations is assessed and harnessed in breeding projects to modify the expressions of their economically and ecologically important traits, including growth and yield, stem form, vigour, wood quality, resilience to drought and pests, etc. This process involves selecting individuals, provenances and progeny families of tree species commercially suitable for plantation establishment (i.e., provenance-progeny trials). Besides the deployment of improved seeds from seed orchards, clonal forestry is widely and increasingly considered the best approach to deliver the greatest genetic gain through the use of well-tested clones in plantations, which is significantly based on genetic variation and its assessment. Cloning typically involves genotypic duplication

through vegetative means, preserving the original genetic composition and individual traits, unlike the seed propagation method (Monteuuis, 2021).

Among the several tropical tree species whose genetic variations in certain traits have been assessed, breeding programs have mostly been on *Eucalyptus* and *Pinus* species (Finkeldey & Hattemer, 2007), as well as others like *Acacia* (Harwood et al., 2015) and teak (Monteuuis, 2021). Taking acacia for instance, selected clones of *A. auriculiformis* and hybrid of *A. mangium* and *A. auriculiformis* have been successfully deployed, e.g., in Vietnam. Prospects for genetic improvement in wood qualities and form have also been established for the species, among other growth traits (Harwood et al., 2015). Similarly, teak clonal plantations have extensively developed over the last decades in many tropical countries, including Brazil, India, Côte d'Ivoire, Indonesia, etc., owing to their great possibility to produce enormous yields of best quality timber with high commercial value. This advancement largely hinges on the considerable provenance (genetic) variation exhibited in the species for the economically important traits, as well as the ease of assessment using genetic markers (Kollert & Kleine, 2017; Monteuuis, 2021).

5. Missing Genetic Variation in (Tropical) Plantation Forestry and Recommendations for Improvement

Plantations are mostly monocultures established through artificial selection of plant materials for uniformity, easy management, and increased yield, thus, potentially limiting their genetic variability (Liu et al., 2018). This, therefore, places great significance on choosing well-adapted and well-adaptable plant stock. The use of clones in monocultures has generally proven more successful in producing considerable yields over seedlings, together with other advantages like improved uniformity, the capture of favourable genetic gains and specific adaptations, independence of seed limitations, etc. (Libby & Rauter, 1984; Monteuuis, 2021). All these have contributed to the increasingly widespread adoption of clonal plantations globally. Finkeldey & Hattemer (2007) asserted that many of the world's most productive tree plantations use clones. They facilitate high-profit maximisation on plantation investments within the shortest time possible when outstanding genotypes and appropriate sites are considered (Monteuuis, 2021).

However, this practice is attributed to some economic, technical and ethical concerns and risks, especially in large-scale monoclonal plantations (Kleinschmit et al., 1993; Monteuuis, 2021). The deployment of a large number of individuals of one or a few clones, which are completely homogenous, increases the risks of the spread of pests and diseases, climate change impacts, as well as causes vitality and productivity losses due to the missing genetic diversity (Kleinschmit et al., 1993; Burdon & Aimers-Halliday, 2006). To avert these risks of plantation failure, deploying an appropriate maximum number of clones is essential. Also, a considerable emphasis must be placed on ensuring that the clones are of rela-

tively equal proportions to maximise genetic differentiation within the plantations (Roberds & Bishir, 1997). Different forest geneticists have proceeded to provide suitable recommendations in these regards. While Libby (1982) earlier recommended mixtures of between 7 - 25 genetically distinct and equally represented clones, Roberds & Bishir (1997) reported planting up to 30 - 40 unrelated clones in clonal plantation mixtures is a more sufficient and better strategy to provide resistance against risks of failure.

It is equally important to consider selecting an adequate deployment method to establish the plantations. Clones are deployed mainly in two forms: intimate multi-clonal mixtures or mosaics of small monoclonal blocks (or rows) (Kleinschmit et al., 1993; Roberds & Bishir, 1997; Burdon & Aimers-Halliday, 2006). While multi-clonal mixtures may be more effective in averting the risks of plantation failure or pest and disease damages than monoclonal mosaics, such strategy has been conversely attributed to possible undesirable heterogeneity in stem growth, asymmetry in competitive interactions, and incompatibility in silvicultural interventions among the clones (Burdon & Aimers-Halliday, 2006; Donnelly et al., 2017). Although it is said not to significantly affect plantation stand productivity (Donnelly et al., 2017), the monoclonal mosaics/blocks pattern is mostly adopted in large-scale industrial clonal plantations of teak and eucalypts, for instance (Zobel & Talbert, 1984; Monteuuis, 2021). The size of the monoclonal mosaics is typically dependent on some factors: “the total number of clones deployed, their genetic relatedness, their individual phenotypic characteristics, the rotation length and the total area to be planted” (Monteuuis, 2021). Therefore, it is crucial to provide adequate information about the genetic origins and features of the different clones to establish the clonal plantations, whether in mixtures or mosaics, to optimise the complementary benefits of their genetic diversity. Furthermore, shortening the economic rotation lengths of the clonal plantations is a viable approach to reducing environmental risks. In this way, the trees are harvested or harvestable before the pests and pathogens get well-adapted to the plantations (Kleinschmit et al., 1993).

Lastly, there has been a growing interest in mixed-species plantation systems, which can maintain (interspecific) genetic variation. Establishing plantations with more diverse and complex mixtures of tree species that express complementarity in structural and functional traits like growth rate, shade tolerance, rooting depth, and crown structure can help maximise their resource use, productivity and resistance to catastrophes. However, species mixtures can reduce soil fertility, tree growth and productivity in some cases and can be complex to select, combine and manage multiple species effectively. Hence, they require adequate and careful design and appropriate management (Liu et al., 2018).

6. Conclusion

Genetic variation is highly significant in tropical tree species and plantations by enhancing fecundity, vitality, productivity, and resilience. Although tropical tree

species are of varying levels of genetic variation from low to high, their plantations are mostly monocultures, established mainly for yield increment but usually with low/missing genetic diversity. The risks of genetic base reduction and failure become more prominent with the growing use of clonal plantations due to the absolute genetic homogeneity of such plant materials. Therefore, deploying multiple clones with equal proportions in mixtures managed under shortened rotations and gradual transition to mixed-species systems are vital to increasing genetic variation in tropical plantations, thus improving their resilience against climatic, biological, and environmental risks.

Acknowledgements

Our sincere appreciation goes to the anonymous reviewer who provided constructive remarks and edits that significantly shaped the paper.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

- Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T., & Curtis-McLane, S. (2008). Adaptation, Migration or Extirpation: Climate Change Outcomes for Tree Populations. *Evolutionary applications*, *1*, 95-111. <https://doi.org/10.1111/j.1752-4571.2007.00013.x>
- Akinagbe, A., Gailing, O., Finkeldey, R., & Lawal, A. (2019). 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. *Tropical Conservation Science*, *12*, 1-9. <https://doi.org/10.1177/1940082919864267>
- Alcalá, R. E., Salazar, H., Guitérrez-Granados, G., & Snook, L. K. (2014). Genetic Structure and Genetic Diversity of *Swietenia macrophylla* (Meliaceae): Implications for Sustainable Forest Management in Mexico. *Journal of Tropical Forest Science*, *26*, 142-152. <https://doi.org/10.1080/17550874.2016.1270363>
- Ang, C. C., O'Brien, M. J., Ng, K. K. S., Lee, P. C., Hector, A., Schmid, B., & Shimizu, K. K. (2016). Genetic Diversity of Two Tropical Tree Species of the Dipterocarpaceae Following Logging and Restoration in Borneo: High Genetic Diversity in Plots with High Species Diversity. *Plant Ecology & Diversity*, *9*, 459-469.
- Bittencourt, J., & Sebbenn, A. M. (2007). Patterns of Pollen and Seed Dispersal in a Small, Fragmented Population of the Wind-Pollinated Tree *Araucaria angustifolia* in Southern Brazil. *Heredity*, *99*, 580-591. <https://doi.org/10.1038/sj.hdy.6801019>
- Burdon, R. D., & Aimers-Halliday, J. (2006). Managing Risk in Clonal Forestry. *CAB Reviews*, *1*, 1-9. <https://doi.org/10.1079/PAVSNNR20061035>
- Butcher, P. A., Moran, G. F., & Perkins, H. D. (1998). RFLP Diversity in the Nuclear Genome of *Acacia Mangium*. *Heredity*, *81*, 205-213. <https://doi.org/10.1046/j.1365-2540.1998.00392.x>
- Changtragoon, S., & Finkeldey, R. (1995). Patterns of Genetic Variation and Characterization of the Mating System of *Pinus merkusii* in Thailand. *Forest Genetics*, *2*, 87-97.
- Chesnokov, Y. V., Kosolapov, V. M., & Savchenko, I. V. (2020). Morphological Genetic Markers in Plants. *Russian Journal of Genetics*, *56*, 1406-1415. <https://doi.org/10.1134/S1022795420120042>

- Chezian, P., Yasodha, R., & Ghosh, M. (2010). Genetic Diversity Analysis in a Seed Orchard of *Eucalyptus tereticornis*. *New Forests*, *40*, 85-99. <https://doi.org/10.1007/s11056-009-9184-1>
- Chmura, D. J., & Rozkowski, R. (2002). Variability of Beech Provenances in Spring and Autumn Phenology. *Silvae Genetica*, *51*, 123-127.
- Chmura, D. J., Guzicka, M., & Rozkowski, R. (2021). Accumulation of Standing Above-ground Biomass Carbon in Scots Pine and Norway Spruce Stands Affected by Genetic Variation. *Forest Ecology and Management*, *496*, Article ID: 119476. <https://doi.org/10.1016/j.foreco.2021.119476>
- Cruz-Salazar, B., Ruiz-Montoya, L., Ramírez-Marcial, N., & García-Bautista, M. (2021). Relationship between Genetic Variation and Diversity of Tree Species in Tropical Forests in the El Ocote Biosphere Reserve, Chiapas, Mexico. *Tropical Conservation Science*, *14*, Article ID: 1940082920978143. <https://doi.org/10.1177/1940082920978143>
- Dawson, I. K., & Powell, W. (1999). Genetic Variation in the Afromontane Tree *Prunus africana*, an Endangered Medicinal Species. *Molecular Ecology*, *8*, 151-156. <https://doi.org/10.1046/j.1365-294X.1999.00518.x>
- Dawson, I. K., Lengkeek, A., Weber, J. C., & Jamnadass, R. (2009). Managing Genetic Variation in Tropical Trees: Linking Knowledge with Action in Agroforestry Ecosystems for Improved Conservation and Enhanced Livelihoods. *Biodiversity and Conservation*, *18*, Article No. 969. <https://doi.org/10.1007/s10531-008-9516-z>
- Donnelly, L., Grant, O., & O'Reilly, C. (2017). Effect of Deployment-Type on Stem Growth, Biomass Partitioning and Crown Characteristics of Juvenile Sitka Spruce Clones. *Silva Fennica*, *51*, Article ID: 1714. <https://doi.org/10.14214/sf.1714>
- Ewens, W. J. (2013). *Population Genetics*. Springer Science & Business Media.
- Farwig, N., Braun, C., & Böhning-Gaese, K. (2008). Human Disturbance Reduces Genetic Diversity of an Endangered Tropical Tree, *Prunus africana* (Rosaceae). *Conservation genetics*, *9*, Article No. 317. <https://doi.org/10.1007/s10592-007-9343-x>
- Finkeldey, R., & Hattemer, H. H. (2007). *Tropical Forest Genetics* (p. 315). Springer. <https://doi.org/10.1007/978-3-540-37398-8>
- Fofana, I. J., Silue, S., Diarrassouba, N., Kadio, A. A., & Sangare, A. (2013). Comparative Analyses of Amplified Fragment Length Polymorphism (AFLP) and Simple Sequence Repeat (SSR) in Genetic Diversity of Teak (*Tectona grandis* Lf). *International Journal of Advance Agricultural Research*, *1*, 114-23.
- Forrester, D. I., Bauhus, J., Cowie, A. L., & Vanclay, J. K. (2006). Mixed-Species Plantations of Eucalyptus with Nitrogen-Fixing Trees: A Review. *Forest Ecology and Management*, *233*, 211-230. <https://doi.org/10.1016/j.foreco.2006.05.012>
- Ganesan, S., Singh, R., Choudhury, D. R., Bharadwaj, J., Gupta, V., & Singode, A. (2014). Genetic Diversity and Population Structure Study of Drumstick (*Moringa oleifera* Lam.) Using Morphological and SSR Markers. *Industrial Crops and Products*, *60*, 316-325. <https://doi.org/10.1016/j.indcrop.2014.06.033>
- Gupta, S., Srivastava, M., Mishra, G. P., Naik, P. K., Chauhan, R. S., Tiwari, S. K. et al. (2008). Analogy of ISSR and RAPD Markers for Comparative Analysis of Genetic Diversity among Different *Jatropha curcas* Genotypes. *African Journal of biotechnology*, *7*, 4230-4243. https://doi.org/10.1007/978-1-349-04627-0_5
- Hamrick, J. L. (1979). Genetic Variation and Longevity. In O. T. Solbrig (Eds.), *Topics in Plant Population Biology* (pp. 84-113). Columbia University Press.
- Hamrick, J. L., Godt, M. J. W., & Sherman-Broyles, S. L. (1992). Factors Influencing Levels of Genetic Diversity in Woody Plant Species. In W. T. Adams (Eds.), *Population*

- Genetics of Forest Trees* (pp. 95-124). Springer.
https://doi.org/10.1007/978-94-011-2815-5_7
- Harwood, C. E., Hardiyanto, E. B., & Yong, W. C. (2015). Genetic Improvement of Tropical Acacias: Achievements and Challenges. *Southern Forests: A Journal of Forest Science*, 77, 11-18. <https://doi.org/10.2989/20702620.2014.999302>
- Hattermer, H. H. (1995). Concepts and Requirements in the Conservation of Forest Genetic Resources. *International Journal of Forest Genetics*, 2, 125-134.
- Ingvarsson, P. K., & Dahlberg, H. (2019). The Effects of Clonal Forestry on Genetic Diversity in Wild and Domesticated Stands of Forest Trees. *Scandinavian Journal of Forest Research*, 34, 370-379. <https://doi.org/10.1080/02827581.2018.1469665>
- ITTO (International Tropical Timber Organization) (2020). *Guidelines for Forest Landscape Restoration in the Tropics* (Policy Development Series No. 24). International Tropical Timber Organization.
- Ivetić, V., & Devetaković, J. (2017). Concerns and Evidence on Genetic Diversity in Planted Forests. *Reforesta*, No. 3, 196-207. <https://doi.org/10.21750/REFOR.3.15.39>
- Joly, H. I., Zeh-Nlo, M., Danthu, P., & Aygalent, C. (1992). Population Genetics of an African Acacia, *Acacia albida*. I. Genetic diversity of populations from West Africa. *Australian Journal of Botany*, 40, 59-73. <https://doi.org/10.1071/BT9920059>
- Kleinschmit, J., Khurana, D. K., Gerhold, H. D., & Libby, W. J. (1993). Past, present, and Anticipated Applications of Clonal Forestry. In M. Ahuja, & W. J. Libby (Eds.), *Clonal Forestry II* (pp. 9-41). Springer. https://doi.org/10.1007/978-3-642-84813-1_2
- Kollert, W., & Kleine, M. (2017). *Global Teak Study: Analysis, Evaluation and Future Potential of Teak Resources*. International Union of Forest Research Organizations (IUFRO).
- Koskela, J., Buck, A., & du Cros, E. T. (2007). *EUFORGEN Climate Change and Forest Genetic Diversity*. Biodiversity International.
- Lara-Gomez, G., Gailing, O., & Finkeldey, R. (2005). Genetic Variation in Isolated Mexican Populations of the Endemic Maple *Acer skutchii* Rehd. *Allgemeine Forst und Jagdzeitung*, 176, 97-103.
- Lee, S. L., Wickneswari, R., Mahani, M. C., & Zakri, A. H. (2000). Genetic Diversity of a Tropical Tree Species, *Shorea leprosula* Miq. (Dipterocarpaceae), in Malaysia: Implications for Conservation of Genetic Resources and Tree Improvement. *Biotropica*, 32, 213-224. <https://doi.org/10.1111/j.1744-7429.2000.tb00464.x>
- Libby, W. J. (1982). What Is a Safe Number of Clones Per Plantation. In H. M. Heybroek, B. R. Stephan, & K. von Weissenberg (Eds.), *Resistance to Diseases and Pests in Forest Trees* (pp. 324-360). Centre for Agricultural Publishing and Documentation.
- Libby, W. J., & Rauter, R. M. (1984). Advantages of Clonal Forestry. *The Forestry Chronicle*, 60, 145-149. <https://doi.org/10.5558/tfc60145-3>
- Liu, C. L. C., Kuchma, O., & Krutovsky, K. V. (2018). Mixed-Species versus Monocultures in Plantation Forestry: Development, Benefits, Ecosystem Services and Perspectives for the Future. *Global Ecology and Conservation*, 15, Article ID: e00419. <https://doi.org/10.1016/j.gecco.2018.e00419>
- Minn, Y., Prinz, K., & Finkeldey, R. (2014). Genetic Variation of Teak (*Tectona grandis* Linn. f.) in Myanmar Revealed by Microsatellites. *Tree Genetics & Genomes*, 10, 1435-1449. <https://doi.org/10.1007/s11295-014-0772-7>
- Monteuuis, O. (2021). Clonal Teak. In Y. Ramasamy (Eds.), *The Teak Genome* (pp. 155-169). Springer. https://doi.org/10.1007/978-3-030-79311-1_10

- Mora-Orozco, C., Garnica, J. G. F., Acuña, I. J. G., Solorio, J. D. D. B., Martínez, C. S. M., & Valencia, L. I. P. (2022). Soil Carbon Storage in Experimental Forest Plantations with Tropical Species. *Open Journal of Forestry*, *12*, 1-18. <https://doi.org/10.4236/ojf.2022.121001>
- Nonić, M., & Šijačić-Nikolić, M. (2021). Genetic Diversity: Sources, Threats, and Conservation. In W. Leal Filho, A. M. Azul, L. Brandli, A. Lange Salvia, & T. Wall (Eds.), *Life on Land* (pp. 421-435). Springer. https://doi.org/10.1007/978-3-319-95981-8_53
- Noreen, A. M., & Webb, E. L. (2013). High Genetic Diversity in a Potentially Vulnerable Tropical Tree Species Despite Extreme Habitat Loss. *PLOS ONE*, *8*, Article ID: e82632. <https://doi.org/10.1371/journal.pone.0082632>
- Nurtjahjaningsih, I. L. G., Saito, Y., Tsuda, Y., & Ide, Y. (2007). Genetic Diversity of Parental and Offspring Populations in a *Pinus merkusii* Seedling Seed Orchard Detected by Microsatellite Markers. *Bulletin-Tokyo University Forests*, *118*, 1-14.
- Olamidayo, F., Amadu, L., & Victor, A. (2021). Impact of Anthropogenic Activities on Genetic Diversity of *Celtis zenkeri* Engl in South-West Nigeria. *International Journal of Genetics and Genomics*, *9*, 31-35. <https://doi.org/10.11648/j.ijgg.20210902.11>
- Pither, R., Shore, J. S., & Kellman, M. (2003). Genetic Diversity of the Tropical Tree *Terminalia amazonia* (Combretaceae) in Naturally Fragmented Populations. *Heredity*, *91*, 307-313. <https://doi.org/10.1038/sj.hdy.6800299>
- Pretzsch, H. (2021). Genetic Diversity Reduces Competition and Increases Tree Growth on a Norway Spruce (*Picea abies* [L.] KARST.) Provenance Mixing Experiment. *Forest Ecology and Management*, *497*, Article ID: 119498. <https://doi.org/10.1016/j.foreco.2021.119498>
- Rao, M. R., Singh, M. P., & Day, R. (2000). Insect Pest Problems in Tropical Agroforestry Systems: Contributory Factors and Strategies for Management. *Agroforestry Systems*, *50*, 243-277. <https://doi.org/10.1023/A:1006421701772>
- Reed, D. H., & Frankham, R. (2003). Correlation between Fitness and Genetic Diversity. *Conservation Biology*, *17*, 230-237. <https://doi.org/10.1046/j.1523-1739.2003.01236.x>
- Roberds, J. H., & Bishir, J. W. (1997). Risk Analyses in Clonal Forestry. *Canadian Journal of Forest Research*, *27*, 425-432. <https://doi.org/10.1139/x96-202>
- Sanchez, M., Ingrouille, M. J., Cowan, R. S., Hamilton, M. A., & Fay, M. F. (2014). Spatial Structure and Genetic Diversity of Natural Populations of the Caribbean Pine, *Pinus caribaea* var. *bahamensis* (Pinaceae), in the Bahaman Archipelago. *Botanical Journal of the Linnean Society*, *174*, 359-383. <https://doi.org/10.1111/boj.12146>
- Silvestrini, M., McCauley, D. E., Zucchi, M. I., & dos Santos, F. A. M. (2015). How Do Gap Dynamics and Colonization of a Human Disturbed Area Affect Genetic Diversity and Structure of a Pioneer Tropical Tree Species? *Forest Ecology and Management*, *344*, 38-52. <https://doi.org/10.1016/j.foreco.2015.01.026>
- Wang, R., Compton, S. G., Shi, Y. S., & Chen, X. Y. (2012). Fragmentation Reduces Regional-Scale Spatial Genetic Structure in a Wind-Pollinated Tree Because Genetic Barriers Are Removed. *Ecology and Evolution*, *2*, 2250-2261. <https://doi.org/10.1002/ece3.344>
- White, T. L., Adams, W. T., & Neale, D. B. (Eds.). (2007). *Forest Genetics*. Centre for Agriculture and Bioscience International. <https://doi.org/10.1079/9781845932855.0000>
- Yuskianti, V., & Isoda, K. (2012). Genetic Diversity of Acacia Mangium Seed Orchard in Wonogiri Indonesia Using Microsatellite Markers. *HAYATI Journal of Biosciences*, *19*, 141-144. <https://doi.org/10.4308/hjb.19.3.141>

- Zobel, B., & Talbert, J. (1984). *Applied Forest Tree Improvement* (No. 04; SD399. 5, Z6.). Wiley.
- Zytynska, S. E., Fay, M. F., Penney, D., & Preziosi, R. F. (2011). Genetic Variation in a Tropical Tree Species Influences the Associated Epiphytic Plant and Invertebrate Communities in a Complex Forest Ecosystem. *Philosophical Transactions of the Royal Society: Biological Sciences*, *366*, 1329-1336. <https://doi.org/10.1098/rstb.2010.0183>