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Mediation of Gene Flow in Tropical Trees of Sub-Saharan Africa

Oghenekome U. Onokpise[1] and Adejoke O. Akinyele[2,*]

[1]*College of Agriculture and Food Sciences, Florida A&M University, Tallahassee, Florida 32307, USA*
[2]*Department of Forest Resources Management, University of Ibadan, Oyo, Nigeria*

Abstract

Tropical forests whether fragmented or undisturbed or be they equatorial or deciduous, remain the storehouse of biodiversity for hundreds of thousands of plant and animal species. This unique characteristic continues to attract a wide range of scientists and international organizations to study and attempt to understand tropical forest ecosystems. Gene flow is mediated by pollen, seed and seedling dispersal, and factors affecting this gene flow include phenology, spatial distribution, population structures, seed predation, sexual and mating systems as well as physical and biological barriers to gene flow. Two methods are used in measuring gene flow: direct method that relies on the actual observation of seed and pollen dispersal, whereas indirect methods involve the use of genetic markers such as allozymes and DNA techniques. Political strife, extreme natural and artificial disasters, the lack of a comprehensive forestry research vision, coupled with difficult socio-economic conditions in Africa have made the environment quite difficult for sustained research activities on the part of those undertaking or wishing to undertake such studies. Gene flow studies in this region are few and far between. This review elaborates on the mechanisms of gene flow mediation in Sub-Saharan Africa.

Key Words: mechanism for gene flow, mediators, population ecology

Introduction

Gene flow is classically defined as the exchange of genes between two populations brought about by the dispersal of gametes or the migration of individuals (Klug and Cummings 2000). For plants, especially flowering plants, the definition of gene flow is often one of pollen and seed movement as well as the movement of seedlings (for viviparous species) and clonal materials (for easy to root tree species in tropical moist forests). According to Hattemer and Melchior (1993), Wang (2001), Finkeldey and Hattemer (2007), a gene flow system involves all elements of a genetic system that participate in the transport of genetic information. This implies that there has to be a mechanism for such transportation with its attendant barriers.

It is this transfer of genetic information whether between wild species and their domesticated relatives or vice versa (Ellstrand et al. 1999; Finkeldey and Hattemer 2007; White et al. 2007), that makes gene flow critical to diversity and genetic variation in plant populations. A small amount of gene flow is capable of concentrating other evolutionary forces of mutation, genetic drift and selection in natural populations (Ellstrand et al. 1999). Emphasis is on populations including Mendelian populations, for, only populations are capable of evolutionary change, that is, changes in gene frequencies over generations (Slatkin 1987; Hattemer and Melchior 1993). Gregorius et al. (1995), define a population as a group of sexual organisms, every pair

of which is capable of producing one or more offsprings over generations.

Characteristics of the Tropical forests

In tropical forests with sub-Saharan Africa as an example, as one moves inland from the equator to higher latitudes (north and south), there is a gradual transition from mangrove swamps to derived savannah or wood lands. The most important families of the mangrove swamps are Rhizophoraceae, Aviceniaceae, Combretaceae, Plumaginaceae and Sonnetiaceae (Chapman 1976). The mangrove forests are typified by their very long aerating roots and viviparous seedlings. The habitat is essentially one of low coastal plains characterized by lagoons, creeks, estuaries and river deltas. It is also possible to find freshwater mangrove swamps along river banks. Immediately following the mangrove swamps is the equatorial rain forest. This region contains most of the important commercial timber families (Meliacese, Sterulaceae, Verbanaceae, etc.) and it is the region that has received the greatest attention from biogeographers, conservationists, sociologists, evolutionists and taxonomists (Linder 2001), mostly because of its high deforestation propensity. The breeding systems of many members of these families vary from species to species and so play a major role in gene dispersal. The climate of this region is essentially one of high humidity with rainfall averaging 2,500 mm or more in the Benin forest region (Jones 1956) and being as heavy as 4,000 mm or more in certain parts of Malaysia (Ashton 1969).

The deciduous forest region which borders the equatorial rain forests has trees arranged in three distinct stories but the upper stories are less dense and their average height is perhaps lower than that of the evergreen equatorial rain forests. The floristic composition of the forests tends to be different as more light loving species such as *Triplochiton spp.* and *Lophira spp.*, become the dominant species. This region also borders the derived savannah area with a drier climate and subsequently, reduction in the number of tree species due to the environment, especially the incidence of the fire. There is a great contrast in floristic composition, structure and physiognomy between deciduous and wooded (derived) savannah lands (Linder 2001). For example, *Khaya senegalenssis* replaces *K. ivorensis*, *K. anthoteca*, and *K.*

grandifolia of the evergreen equatorial and deciduous forests respectively. Similarly, *Lophira alata* replaces the tall *L. procera* of the wet evergreen forests. Although it is species rich, most tropical forest species occur in low population densities and sparse species distribution especially among the overstory species (Connell and Lowman 1989). Increasingly, population structure and spatial distribution are being studied from the standpoint of fragmented patches of tropical forests ecosystems rather than the classical presentation just described. This is because large scale deforestation often leads to the reduction of effective population sizes and the genetic isolation of fragmented populations (Boshier et al. 1995; Aldrich and Hammrick 1998; Hamilton 1999).

Mechanisms for Gene Flow

Gene flow is mediated by pollen, seed, seedling and vegetative propagule dispersal. Each one of these is dependent on movement by animals (zoochorous gene flow), wind (anemochorous gene flow) or water (hydrochorous gene flow). Other modes of gene flow could also be utilized (MacDonald and Copeland 1997).

Pollen flow or pollen dispersal

In relatively close communities such as the tropical rain forests, pollination is mainly zoochorous (Baker 1970; Nason and Hamrick 1997; Aldrich and Hamrick 1998). This contrasts with temperate forests where pollination is mostly anemochorous (Clark and Clark 1986; Buckley et al. 1988; Finkeldey 2001; Finkeldey and Hattemer 2007; White et al. 2007). The flowers, when conspicuous are brightly colored, and when inconspicuous, produce animal attracting scents. These coupled with high levels of nectar production (pollination reward), as well as a characteristic sticky pollen, make animal pollination very significant. In the more open derived savannah regions and some understory tree species, anemochory may be quite significant (Bawa and Crisp 1980). Pollen flow in itself is not only dependent on the breeding system of the plant *per se* but also on the foraging habit and pollination behaviors of pollinators themselves. Thus, butterflies that are responsible for a lot of pollen dispersal in the tropics occupy mature communities with limited food resources and tend to maintain small sedentary populations (Webb and Bawa 1983).

Others indicate that there are also seasonal migratory patterns for these butterflies, suggesting that the movement of pollen by these pollinators may be more dependent on their behavioral response to forest fragmentation than to their physical capacity for pollen dispersal (Nason and Hamrick 1997). This is also true of several species of bees, hawkmoths, and mirids (Janzen 1971; Heithus and Flemming 1975; Frankie et al. 1976; Haber and Frankie 1989).

The commonality of extensive amounts of beehives in tropical forests may also attest to these sedentarism of these pollination agents (Appanah and Chan 1981; Chan 1981; Frankie et al. 1983). But for many species of humming birds and bats which exploit habitats rich in foodstuffs, there is high tendency to be more mobile. For such species, their own movement within and between forest ecosystems whether continuous or fragmented will be fairly high. Although species populations may be sparsely distributed, the plant density per unit area is extremely high in tropical forests, both at understory and overstory levels (Connell and Lowman 1989). Therefore, in the much more dense jungle-like tropical rain forests and mangrove swamps, the probability that a pollinator will forage fewer numbers of plants is quite high (Webb and Bawa 1983; Elmqvist et al. 1992; Mori and Okada 2001). Hence, gene flow becomes fairly restricted and only the presence of self incompatibility systems will help to avoid inbreeding and its effects. Such restricted gene flow can be important in species differentiation in response to environmental heterogeneity (Slatkin 1987; Nason and Hamrick 1997). Similar results have been obtained when indirect estimators such as the proportion of total genetic diversity distributions among populations at the Barro Colorado Island study site (Hamrick and Loveless 1989; Boshier et al. 1995).

Mechanisms such as "mass flowering" have been developed by species like *Pterocarpus robrii*, *Andira inermis* and *Piscidia carthogenesis*, to ensure adequate pollinator visits and so enhance outcrossing among plants. However, foraging habits such as "interference competition" between humming birds, lepidopterans and hymenopterans for example would actually restrict pollinators to a given number of inflorescences. This kind of competition sometimes results in "mistake pollination" and so ensures outcrossing as has been found in some members of the Caricaceae. Apart from humming birds, bees, butterflies, and bats, other agents of zoochorous pollen flow include midges, mosquitoes, thrips and syrphid flies. Studies from Central and South America have revealed differential behavior in pollen migration for these and many other species (Boshier et al. 1995; Nason and Hamrick 1997).

In species rich tropical communities where counter-specific individuals are usually widespread, anemochorous pollen flow is considered rare or non-existent (Janzen and Vasquez-Yanes 1991). Wind dispersal is in fact, likely to be very inefficient in such high density plant populations (Connell and Lowman 1989). Pollen dispersal by wind is dependent on wind velocity, air turbulence, pollen size and weight, and very many extraneous factors for which an open area such as the savannah or temperate regions would be more conducive. These factors notwithstanding, anemochorous pollen dispersal has been reported for *Soroces sprucei* (Moraceae) in Costa Rica (Bawa and Crisp 1980) and in Thailand, (Finkeldey and Hattemer 2007). It is important to note that virtually all these species belong to the Moraceae family which is found mainly in the understory occupying the areas of "light windows" or "light gaps." Anemochory in these species may be related to competition for pollinators, energetic limits, and other attractants. It could be that these species migrated from an area where environmental conditions allowed anemochory and the system persisted in the "new" habitat. This is reflected in theories related to peripatric and allopatric speciation (Slatkin 1987).

Hydrochorous pollen flow in tropical forests has received virtually no attention as no literature, both conventional and electronic, was found by the authors relating to this topic. Yet, it is possible that in the mangrove swamps and river deltas, hydrochory could be important. Ordinarily, pollination could take place below the water surface, in which case pollen is not apt to be hydrophobic. But for above water pollination, hydrophobicity may become necessary if pollen is to be effective in ensuring pollination. Hydrochory in itself does not preclude autogamy (Levin and Kester 1974).

Although studies on plant diversity and species endemism have been documented for the tropical forests of sub-Saharan Africa (Hamilton 1982; Linder 2001), yet specific studies on pollen flow by zoochory, anemochory and hydrochory are generally unknown or not reported. However,

studies from the neotropics and Southeast Asia may apply especially, in areas where there have been little disturbance to the ecosystem as in the Cameroon Korup National Forests, and the high forests of Congo and Gabon where zoochory should dominate pollen flow. In logged-over forests and Forests Reserves of Cote d'Ivoire, Ghana and Nigeria, while zoochory will still be significant, anemochory could become important because of "light windows" or gaps, and the replacement species in the secondary forests and many deciduous forest ecosystems.

Seed dispersal or seed flow

Tropical forest trees have high iteroparity just like their temperate and subtropical counterparts, which provides for high levels of heterozygosity especially among mature and older trees compared to juvenile ones (Hattemer and Melchoir 1993; Finkeldey and Hattemer 2007). It is the dispersal of these seeds in tropical forests that makes for the distinctive gene flow patterns mediated by seeds. Finkeldey (2001) has suggested that future research on gene flow in the tropical forests should take into consideration the importance of gene flow through seeds. Many studies reported for gene flow in tropical forests have tended to overemphasize pollen flow. Yet, seed flow is perhaps the most effective means of gene flow in tropical forests. There is usually a very good correlation between seed size and high dispersability (Harper et al. 1970). And because gene flow through seeds is responsible for two-thirds of the total genetic neighborhood size, it is essential for estimates of tropical tree breeding populations (Hamilton 1999). Herbs commonly display hairs and barbs which facilitate animal dispersal, shrubs often display conspicuous fleshly fruits which will attract vectors, and trees commonly produce large seeds whose dispersal is accomplished by animals which collect and store seed crops.

Generally, seeds of most rain forest trees are dispersed by fruit eating vertebrates like birds, bats, and terrestrial and arboreal mammals (Leighton and Leighton 1983; Pannell and Koziol 1987). In the *Aglia* genera belonging to the mahogany family, seeds are dispersed by hornbills, magpies, nymphs, broadbills, barbets, and bulbuls as well as orangutans, siamang and white-handed gibbons (Pannell and Koziol 1987; Pannell 1989). It should be noted that some troical forest tree species (*Funtumia elastica*, *Khaya senegal-*

ensis, and *Entandrophragma angolensis*) produce winged fruits and seeds to facilitate seed dispersal. Other relationships include larger seed size and air cavities in water dispersed seeds compared to wind and animal dispersal seeds (Harper et al. 1970), and more elaborate chemical and physical defenses in tropical seeds compared to temperate seeds (Janzen 1971).

Although zoochory may be predominant in tropical forests, the mode of dispersal may be dependent on the successional type. For example, approximately 46% of the species of the emergent story in a southern Nigerian rain forest had seeds or fruits that were wind dispersed, while 46% were obviously adapted for animal dispersal. In the lower storeys, on the other hand, the values were 6-8% and 70-80% for wind and animal dispersal respectively. Tree species, such as *Funtunia elasica* (Apocynaceae) and *Alstonia bornei* (Apocynaceae) as well as their related genera, possess seeds with long hairs to facilitate dispersal by wind. It is also possible for violent tropical storms to move seeds beyond their expected distances of dispersal. Branches and leaf interception of falling seeds restrict the distances to which a wind dispersed seed can travel. Wind mediated seed flow is similar to that described for pollen flow, but with a steeper decline in numbers at greater distances (that is, more highly leptokurtic). The implication is that most seedlings growing around a particular tree are the seedling offspring of that same tree.

Some tropical tree species have fruits and seeds adapted for dispersal in water. A typical example is the coconut tree (*Cocus nocifera*) which has a fibrous fruit and long seed dormancy and so it is able to be dispersed by water. This enables it to effectively colonize new ecological niches, especially along river banks. Hydrochorous seed dispersal, unlike long insect or bird flights, often results in significant genetic variation in what is considered the river hypothesis of speciation (Gascon et al. 1996; Mori and Okada 2001). This may be due to a more efficient interchange of genetic material between sparsely populated plant communities along river banks, estuaries, creeks, etc. Moreover, species that exhibit hydrochory tend to be zoochorous, thereby giving them more gene flow prospects, particularly in the transitional zones between wet lowland forests and wet upland forests.

Many of the detailed studies on seed dispersal over the

past three decades have come from Central and South America-the so called Neotropics (Janzen 1983; Reis and Guillaumet 1983; Howe 1986, 1990; Buckley et al. 1988; Mendellin and Gaona 1991; Boshier et al. 1995; Aldrich and Hamrick 1998; Hamilton 1999), along with others from Southeast Asia and Australia (Stocker 1981; Stocker and Irvine 1983; Finkeldey 1999, 2001; Finkeldey and Hattemer 2007). These references are by no means exhaustive as to the level of study into seed dispersal in the neotropics, South Asia and Australia. It is heartening to note that unlike pollen flow, some studies on seed flow dispersal have been reported for the tropical forests of sub-Saharan Africa (Liberman et al. 1979; Foster and Sork 1997).

Seedling and Vegetative Propagule Flow or Dispersal

Most mangrove species, apart from showing zygotic hydrochory, also exhibit sporophytic hydrochory which results from vivipary; a phenomenon described by Gill and Tomlinson (1969) as "--- the continuous development of the embryo without a dormant period. In the usual sense, there is therefore no true seed." Hence the dispersal unit is a "small tree." Because of the very moist and humid environments of the tropical mangrove swamps, to avoid excessive seed decay, these plant species may have evolved an alternative adaptive strategy to aid in their colonization of new ecological niches in an almost landless environment. In studies involving six mangrove species in Panama, Rabinowitz (1978), found that the dispersal properties of mangrove propagules (or seedlings) was correlated with spatial distribution of adults within the swamp. Genera whose adults were found on higher ground, on the landward edge of the interdal zone, had small propagules that required a period of freedom from tidal inundation of approximately five days in order to establish firmly in the substrate, while genera whose adults were found on the seaward edge of the swamp, in deeper water, had large heavy propagules and so could readily establish. There are no studies on seedling flow reported for the mangroves of sub-Saharan Africa despite an abundance of these mangrove ecosystems.

Conclusions

Pollen, seed, seedling and propagule dispersal as mediators of gene flow reveals that most tropical forests are mixes of animal, wind and water dispersed seeds and seedlings. Thus, according to Janzen and Vasquez-Yanes (1991), as perturbation increases or as forests invade open areas, these processes are differentially affected. For example, in a forest where vertebrates responsible for seed dispersal are removed by hunting or through selective logging and other means, the animal dispersed species not only decline in numbers and changes in relative abundance, the wind-dispersed species do the opposite (Pannell 1989). Oil pollution of mangrove ecosystems not only eliminates establishment substrates for propagules, it also hinders necessary species colonization of new intertidal zones.

Acknowledgements

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