Readings in FOREST ECOLOGY

Essays in Honour of Professor Saka Obafemi Bada

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Woody Plant Population, Dynamics and Regeneration in Tropical Dry Forest Formations

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Introduction

Tropical lowland rainforest formations are characterised with large numbers of woody plant species but few individuals. Woody plant association and composition within dry forest formations occur for various reasons making their distinctiveness significant and description difficult. A lot is known of the structure of tropical dry forest but there is little information on its formations and plant distribution mechanisms.

The evolutionary position of tropical dry forest has created diverse micro-habitats, plant species and life forms. These micro-habitats produce stable formations; but dynamic succession stages while speciation and competition provide opportunities for colonization of old and new species, with diverse life forms. Its dynamic succession is evaluated through eigen-value of plant population projection matrix which indicates the level of population stability.

Plant seeds size and seed predation have been implicated in plant colonisation and diversity. Also, forest formations and dynamics are influenced by plant seed size and seed predation (Wang and Smith, 2002). Forest life form and species diversity indicate forest community structure while forest community structure and physiognomy influence plant formation in tropical dry forest. Furthermore, density, frequency, and size-dependent mechanisms determine the forest physiognomy and population structure. All these mechanisms are not mutually exclusive to one another and this is what makes tropical dry forest formations complex ecosystems.

Tropical dry forest has been described extensively based on its structure, plant species diversity and its diverse phenological characteristics but little information is available on the factors that control its forest formations and plant distribution mechanisms. Tropical dry forest formation has high tree density and covers a large area and therefore develops a set of local climatic and ecological conditions that are different from adjacent formations (Baker, 1950). The tropical dry forest formations may be described based on their climax plant communities and are recognised by three or more distinct layers: upper canopy layer, understories and ground cover. The understories facilitate the replacement of the upper canopy trees. It is a complex and self-sustained ecological system. Tropical dry forest formation is described based on structure and physiognomy of its component plants. The structural properties of tropical dry forest include the height of the trees, canopy layers and the presence of different kinds of climbers and epiphytes. The knowledge of forest structure and regeneration is necessary for the study of forest dynamics while an understanding of forest dynamics gives insight into the succession stage of forest formation which is very useful in natural forest management. Therefore, this review focuses on the brief description of the factors that control the forest formations and plants spatial distribution in tropical dry forest.

Classification of tropical dry forest formations

Tropical dry forest formations harbour the greatest number of species and their destruction would have the most extensive global effects (Myers, 1990 and Oyama, 1993). The challenge of tropical lowland rain forest conservation lies mainly in the high diversity and low population densities or rarity of most tree species even in protected forests (Hubbel and Foster, 1983; 1992 cited by Falade, 2015). Tropical lowland rain forests have 30-90 tree species, 10-40m of canopy height and 17-40m^2/ha of basal area (which represents 50% of wet forests), although these varied between sites (Vieira and Scariot, 2006 cited by Falade, 2015). Tropical dry forests have 50-75% net primary productivity of wet forests (Murphy and Lugo, 1995), because their growth declines during the dry season.

The rainforest accounts for over 80% of the timber produced in Nigeria both for export and internal consumption (Kio, 1978; Osho, 1988 cited by Falade, 2015). Thus, the Nigerian rainforests are of great importance for the welfare of the nation. According to Osho (1996), the paucity of information on patterns of forest dynamics of tropical forest has seriously limited the proper management of this vital resource. The fear of extinction of some of the most valuable tree species from the forest is now real. It is obvious that the tropical dry forest is very easy to destroy but very difficult to regenerate, because its mechanisms of succession are still poorly understood.

Sahu *et al.* (2008) pointed out that stem density could predict the number of species in a forest. This situation is also reported for some other dry forests of India, where high number of individuals reflects greater number of species (Sagar and Singh, 2006). Schnitzer and Carson (2001) reported a positive correlation between tree density and diversity in some dry and moist tropical forests. However, data from a study of four tropical forests of the Abertine rift valley western Uganda, showed that tree density was independent of the number of species and indices of species diversity (Eilu *et al.*, 2004).

Postulated theories of plant species of tropical dry forest formations

In Southeast Asia, more than 100 species per hectare were found while Africa has less than 100 woody species per hectare (Longman and Jenik, 1974). However, African lowland rainforest has higher plant species diversity than American and Indo-Asia lowland rainforests. There is no single reason for high diversity of species in tropical lowland forests. One can ascribe the high diversity of species to more variable climate and soil because variable environment would tend to produce variable vegetations. The variable climate and soil create a wide range of microhabitats and consequently produce heterogeneous structure of the tropical lowland forest. Another reason for the diverse flora is that great part of the tropical forest region had small-scale paleo-climate fluctuation (Longman and Jenik, 1974). Thirdly, the species diversity of tropical forest is dependent of chance of interchange of different characteristics and factors from neighbouring formations. These factors or characteristics include: direction of wind and sea current, the orientation of river valley and mountain range, migration route of bird and herds of mammals (Longman and Jenik, 1974).

The diverse micro-habitats of tropical dry forests have created a suitable niche within its structure for migrant species and life forms. Tropical forest is dynamic because of the severe competition among its flora components (Longman and Jenik, 1974). Furthermore, classic ecological theory states that species can only co-exist if the levels of interspecific competition remain low enough to prevent competition exclusion of some members of the community (Turner, 2004). There are many mechanisms in tropical lowland dry forest ecosystem by which niches are created for more than hundreds of tree species to co-exist on small areas. These include light gradient from forest floor to canopy top, within the canopy gaps and soil physical and chemical properties cause variation required for provision of niches (Turner, 2004).

Seed Predation and Dispersal Dynamics in Tropical Dry Forests

A differential influence of seed predators on specific tree species may have important implications for entire forest communities. Specialist seed and seedling predators or pathogenic diseases may control the distribution of adult population density within the forest. Herbivores that preferentially consume a common species can alter the relative abundance of plants, and thus allow rare species to persist within a community (Jones *et al.*, 2008). Also, predators can change the competitive interactions among the species they feed on and thus, facilitate the growth of competitively inferior ones (Jones *et al.*, 2008). Seed predation by animals can be a major factor inhibiting seed dispersal which is a complex succession process. It links the end of the reproductive cycle of the adult plants with the establishment of their seedlings.

The application of new techniques, such as stable isotope analysis and molecular genetic markers, now make it possible to analyse the distributive pattern of dispersed seeds and seedlings with parent plants (Wang and Smith, 2002). Simmel *et al.* (2014) found that genetic variation within sub-canopy species was positively correlated with the size of their respective canopy tree. Genetic variation was low among but high within sub-canopy population. Therefore, they concluded that the low genetic variation among sub-canopy species is due to effective and directed dispersal by frugivorous dispersal agents. Seed dispersal dynamics influence processes ranging from colonization of new habitats to the maintenance of diversity, with implications for succession, regeneration and conservation (Wang and Smith, 2002).

Frugivores are important dispersal vectors for canopy and sub-canopy plants by feeding and defecating at the resting and nest sites in and around the canopy. Small and fleshy fruits are dispersed by birds and small mammals (Simmel *et al.*, 2014). In tropical forests, more than 66% of the canopy tree species have seeds which are dispersed by animals while North America had less than 33% of the forest trees with seeds dispersed by animals (Wunderle Jr., 1997). Often, wind is the predominant form of dispersal in temperate forests. However, a large proportion of understory plant species have animal-dispersed seeds (48-90% of shrub and vines in North America and 44 - 62% in Southern Spain) (Wunderle Jr., 1997). Plants with wind - or ant - dispersed seeds tend to be more prevalent in dry habitats while vertebrate - dispersed seeds are common in wet habitats.

Stephens *et al.* (2012) assessed the impact of post-dispersal seed predation on plant population in natural and degraded habitats and found that species with large seeds were removed more frequently by vertebrates while species with small seeds were removed by invertebrates. Therefore, restoration success requires a careful assessment of potential seed predators and habitat conditions that enhance germination and establishment of target plant species. In contrast, Moles and Drake (1999) found no relationship between seed removal, and seed size and mass. Also, plant pathogens affect establishment, reproduction and growth of their host and consequently, cause major changes in forest composition, development and structure (Godfree *et al.*, 2003).

The habitat, microsite and seed characteristics affect seed predation and consequently, its recruitment. Therefore, knowledge of factors affecting the local behaviour, food and habitat preference of seed predators will help to predict seed persistence and seedling establishment (Stephens *et al.*, 2012).

This information will be useful in planning seed collection and early seedling management.

Plant Regeneration and Seedling Survival in Tropical Dry Forests

Soil seed banks are an important component of many plant populations in tropical forests (Garwood, 1989). The knowledge of the emergence rate of the different species from soil seed bank can be used in sustainable forest management. Over short distances, degraded areas are easily colonized by wind-dispersed than vertebrate-dispersed plants. Soil seed banks are essential to the regeneration of disturbed communities and ecosystems. Seed banks may play important roles in conservation of genetic diversity and natural restoration, to recover endangered plant species.

The transition from seed to established seedling is one of the most vulnerable stages of a plant's life cycle. This is critical to plant population dynamics (Voysey *et al.*, 1999). Understanding of tree seedling ecology can provide basic information on forest development through improvement in recruitment, establishment and growth of the desired species. Therefore, plant regeneration studies have significant implications on the management, conservation and restoration of degraded natural forests (Tesfaye *et al.*, 2010). According to Khurana *et al.* (2006), small-seeded species, which were generally wind-dispersed, were more widely distributed compared to the large-seeded species in northern India. However, the structure of the tropical dry forest in northern India was determined by the medium and large seeded species. Thus, different seed sizes permit the occupation of the variety of niches available in the dry forest with respect to gradients of light, moisture and temperature, contributing to the maintenance of overall species diversity.

Density-dependent mechanism function in forest succession

Individuals in different life-cycle stages within a population differ in size and shape, and thus in their ability to acquire resources and in their response to environmental conditions. These lead to stage-specific differences in survivorship, growth and fertility. Therefore, density-dependent processes are likely to affect different transitions (vital rate) between stages (Silvertown, 1982). The density-dependent phenomena not only change population growth rate, but at various life-stage distribution (John *et al.*, 2002) and their fluctuation. At equilibrium, the population size will be equal to the carrying capacity and the value of λ will be equal to 1. A small increase in the value of one of the vital rates will produce a change in the population structure but density-dependent effects mean that λ remains at 1, so all sensitivities would be equal to zero (Grant, 1997). Apart from long-lived trees, asymmetric competition is known to be a dominant cause of plant mortality.

In dry forests, species diversity among seedlings, saplings and tree communities may increase, decrease or remain unchanged, depending on the ecological mechanism involved (Gonzalez *et al.*, 2010). If tree species comprise a large number of cohorts and their recruitment is successful for a time without disturbance, both species richness and eveness should increase from sapling to mature tree stages by frequency-dependent mechanism (Warner and Chesson, 1985). However, frequency-dependent mechanism may be barely detectable in species richness if many saplings are long-lived. A comparable pattern of increasing species evenness and unchanged species richness during the sapling-to-mature tree transition is also expected under negative density-dependent processes that favour rare species over abundant ones (Gonzalez *et al.*, 2010). Frequency-dependent mechanisms could increase species diversity of plants through time, whereas resource availability and interspecific competition could reduce species diversity of plants. Thus, solely assessing changes of species diversity across size classes is not enough to distinguish among the different mechanisms, which can shape community assembly (Gonzalez *et al.*, 2010). Tree regeneration information and density of soil seed bank can help to distinguish among the mechanisms that shape community structure.

The potential for population sustainability and stability has been assessed using life-table data and transition matrix model. However, an important problem with applying life-table analysis to populations, even if based on ontogeny, is that germination and seedling survival rates can vary greatly at many spatial scales with changing conditions such as management, perturbation, basal area, and stand age (Hett and Loucks, 1968). Hence, forest diameter class distribution can be used as a substitute for life-table information in many instances. The study of population dynamics is an important aspect of plant ecology and various methods have been used. Density-dependence model is being used to explain the regulation of tree population and the maintenance of plant diversity (John *et al.*, 2002). The Markov model produces sequence of results called the Markov chain. It could be used to predict the future diameter distribution and mortality rates from periodically collected data. Thus, the periodically collected data is used to examine mortality, recruitment and intrinsic rate of population increase.

Tree population dynamics in tropical lowland dry forest formations

The global forest area is estimated at 4 billion hectares, 16 percent of which is found in Africa (Kelatwang and Garzuglia, 2006 cited by Falade, 2015). African forest area is estimated at 635 million hectares, equivalent to 21 percent of the total land area. It ranges from the undisturbed primary forests (an estimated 9 percent) to the modified natural forests (87 percent), semi-natural forests (1 percent) and forest plantations (3 percent) (Kelatwang and Garzuglia, 2006 cited by Falade, 2015). According to the Holdridge System of life zone classification, dry tropical and subtropical forests and woodlands occur in frost-free areas where the mean annual temperature is higher than 17°C, annual rainfall is 250-2000mm, and the annual ratio of potential evapotranspiration (PET) to precipitation exceeds unity (Murphy and Lugo, 1986). Authors reiterated that tropical dry forests represented 42% of the tropical vegetation.

Enright (1978) reported that plant population suffers mortality losses overtime and such losses are often replaced through natural regeneration. The mortality and regeneration cause plant population to be dynamic in nature. Reddy and Pattanaik (2009) opined that knowledge of forest structure and regeneration is necessary for the study of forest dynamics. Two types of stability are described in forest dynamics; firstly, the population size is stable when the population size remains numerically unchanged, and secondly, when the populations of the various species remain unchanged. Several authors concluded that the single most important parameter in the determination of population size stability is the dominant eigenvalue (λ), which is associated with the population projection matrix. In population dynamics, λ is often referred to as the finite rate of increase (Osho, 1996) or dominant latent root (Enright, 1978 and Bada, 1984).

An eigen (λ) value of 1 implies a stable population structure while $\lambda < 1$ would imply a declining population size and $\lambda > 1$ would indicate an increasing population size. The dominant eigenvalue for the population projection matrix of a tropical lowland rainforest of Southwestern Nigeria (Idanre Forest Reserve) in 1988 was $\lambda = 0.97$ (Osho, 1991). He concluded that it is possible for the tree population of Idanre Forest Reserve to decline at sampled plot level but not on a large scale and therefore the plant population could be described to be stable. Forest stability studies have been reduced to the determination of the eigen-value or dominant latent root. The eigen-value of interest is usually the dominant eigen-value. Bada (1984) obtained a dominant latent root of $\lambda=1.927$ with a positive eigen vector of 0.383. Similarly, λ values >1 were obtained for the individual species in natural forests in southwestern Nigeria. The λ values for the individual species varied from 1.921 (for *Pausinystalia johimbe*) to 2.834 (for *Annonidium mannii*), though the species with the highest eigen-value (latent root) did not have the highest eigen-vector. Lack of equilibrium in rain forest species composition is mainly caused by temporal or spatial variations between the species abundance in the canopy and undergrowth. In some areas, species abundant in the canopy were absent in the undergrowth, whereas other areas were invaded by seedlings and young plants of large tree species which were virtually absent in the upper layers of the forest (Poorter *et al.*, 1996).

Conclusion

The lowland tropical dry forest is described by its structure and physiognomic characteristics. Plant population studies use population projection matrices to describe change in population size. Thus, eigen-value could indicate the stability status and population growth rate of plant formation. The density dependent limiting factors affect population size and its distribution. The high diversity of its species is ascribed to its wide range of micro-habitat and immigration of plant life forms and species. This produces diverse types of structure in tropical lowland dry forest. Also, forest formations and dynamics are influenced by plant seed size and seed predation.

Forest community structure and physiognomy indicate the plant formation while forest life form and species diversity indicate forest community structure in tropical dry forest. Furthermore, density-, frequency, and size- dependent mechanisms indicate the forest physiognomy and population size. Also, frequency-dependent mechanism, resources availability, competition and seed size influence community structure. Disturbance and environmental variation and consequently, competition were implicated in the patterns of variation and distribution of plants. Knowledge of the factors and availability of data on them would help sustainable natural forest management practices in tropical dry forest ecosystems.

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