New Perspectives on Tropical Rain Forest Vegetation Ecology in West Africa:

Typology, Gradients and Disturbance Regime

Renaat Van Rompaey*

1 Introduction

The ecology of tropical forests in Africa has been dealt with in a number of standard works (e.g. Aubréville 1938; Dawkins 1958; Richards 1964). Since these works many ecological studies have taken place in all parts of the tropics, and these have changed and nuanced many of the insights of these earlier studies (e.g. Hall and Swaine 1981; Whitmore 1975; Hawthorne 1996). In recent times, many global change studies have again added much further information about these ecosystems at other scale levels, including through the use of predictive modelling (e.g. Maley 1996; Alcamo *et al.* 1998; Jolly *et al.* 1998; Elenga *et al.* 2000).

Some of the new perspectives forwarded in these more recent generations of ecological study are highly relevant both for understanding the ongoing interactions between people and forests in West Africa, and for the development of conservation policies in rain forest areas. In this article I will highlight three topics that are crucial to understanding change in the forests of West Africa. In each case, it becomes important to differentiate more finely than has often been done in the past between the kinds of forest where different dynamics occur.

First I will deal with terminology, as much confusion surrounds the terms used for vegetation types and biomes in West Africa. In particular, it is important to compare terms between French and English, the two languages that, since colonial times, have dominated science and administration in the region. After defining the forest zone and reading from satellite imagery the extent of current forest cover, I will demonstrate the important variation in species composition that exists among currently forested areas, mainly related to the climate gradient. I will then expand on the dynamics of these forests and how well adapted some of their tree species are to severe disturbance, be it of climatic or anthropogenic origin. The article argues that the highly dynamic semi-deciduous forests recover well from it, in contrast to the evergreen forests, which are rich in rare and endemic species and much more vulnerable to disturbance.

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2 Advances in vegetation typology and terminology

When studying the vegetation of West Africa, one comes across significant differences between French and English terminology for vegetation types. Direct translation between these frequently leads to confusion. Terms such as rain forest, high forest, moist forest, dry forest, woodland, shrub land, and savanna have different definitions in French and English. A term like *savane guinéenne* (Guillaumet and Adjanohoun 1971) corresponds to 'Sudanian transition woodland' in English literature (White 1983), and to *forêt claire* in the French translation of it (White 1986, French version). In French, *forêt classée* is also used to designate a gazetted reserve or *domaine vacante et sans maître, réservé pour l'Etat* ('an empty domain without master, reserved for the state'; Parren 1994), in Burkina Faso, for example, with very shrubby vegetation (Guéhi 1993).

Following White (1983) I distinguish the 'forest zone' as existing where tropical rain forest can grow as continuous vegetation cover. On NOAA (National Oceanic & Atmospheric Administration) satellite images, taken in the dry season (February), one can distinguish this zone from the 'savanna' zone north of it, even if the forests are replaced by fallow vegetation (see Figure 1) because the impact of fire is different in each zone.

North of the forest zone lies a more open vegetation belt, often referred to as 'savanna.' White (1983) concluded that the term savanna had been defined in so many different ways that he could no longer use it for precise classification. Thus he uses terms such as woodland, bushland, scrubland and (secondary, wooded) grassland. On better soils these areas have at times been covered with 'drier types of peripheral semi-evergreen rain forest', as an ecotone (or transitional zone) between forest and woodland. It seems preferable to name this biome after the woodland vegetation that it has sometimes carried, than after the savanna, which is frequently found there under current climatic and land use conditions.

French terms for these vegetation types are more elastic. There is *forêts denses sèches*, *forêts claires* (for woodland) and *formations herbeuses boisées* for wooded grassland (White 1983). In conclusion, the French term *forêt* is used for vegetation types that extend much further north than does the vegetation that the English call 'forest'. The Food and Agriculture Organisation (FAO) definition of forest, i.e. land with more than 10 per cent tree crown cover of trees more than 5 metres high (FAO 2001), seems to follow the French 'forêt' but is in no accordance to what Oxfordian botanists like White and AETFAT (*Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale*) and UNESCO term 'forest'. This leads to very confusing statistics: e.g., Côte d'Ivoire has about 7 million ha of forest according to FAO definitions, but only 2 million ha of high forest, as British terminology would define it, while 13 million ha of forest are said to exist in Mali (FAO 2001). In consequence, FAO's figures concerning deforestation relate in no way to changes in rain forest cover.

Figure 1 shows the forest zone as mapped by White (1983, black line) and as based on NOAA satellite images (Olesen 1994, light grey). The forest cover in 1992 based on the same images (Olesen 1994) is shown in dark grey. It is worth noting, in particular, the difference between the two forest zone boundaries in Sierra Leone. White restricted the zone to the existing continuous forest cover, and thus just covered the Gola forests of the extreme south-east of the country. In contrast, in the interpretation of the NOAA satellite image, the entire southern half of Sierra Leone is classified as forest zone fallow. Coastal savannas in Liberia are also more restricted according to the satellite imagery than as mapped by White. In eastern Côte d'Ivoire and Togo, White included areas within the Guineo-Congolian forest domain where the satellite can no longer detect any forest fallow. Southern Benin is classified as part of the forest zone, so the so-called 'Dahomey gap' of savanna there (according to earlier analyses) appears in reality more as a 'south-east Ghana-Togo gap'. Not all classifications of satellite imagery, whether using NOAA or SPOT (Satellite Pour l'Observation de la Terre) vegetation 1 km-resolution, show the forest zone as clearly as Olesen (1994), nor in the same places. Some precaution is therefore needed before using such images to alter definitively how the boundaries of the Guineo-Congolian forest domain, and its Upper Guinean epicentre, are drawn.

In Ghana, the current forest area corresponds well with the actual forest reserves and national parks.

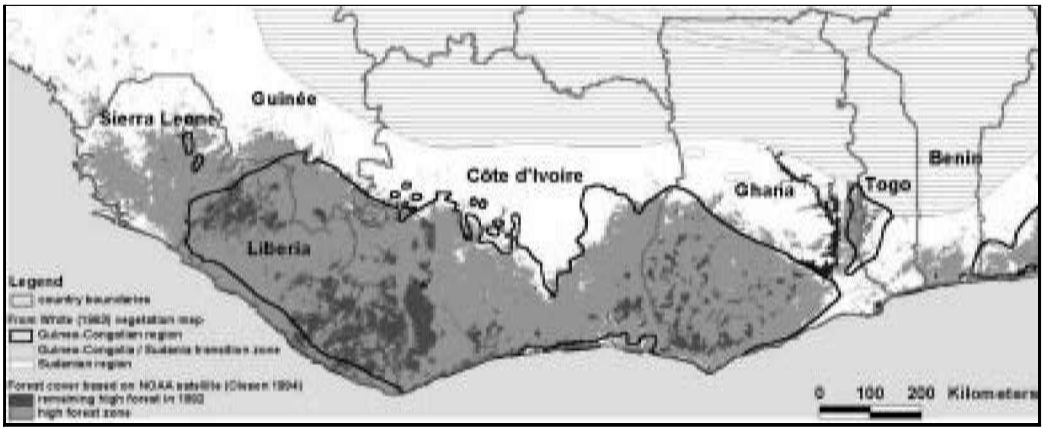

Figure 1: West Africa: Forest cover in 1992 and forest zone according to White's (1983) map of vegetation and NOAA satellite imagery (Olesen 1994)

Hawthorne and Abu-Juam (1995) assessed the condition of all 214 Ghanaian forest reserves with regard to farming, logging and fire impact. Six condition classes were defined, ranging from 'excellent' to 'no significant forest left' (although whether these areas carried forest cover at the time of their reservation is debatable, see Fairhead and Leach 1998). Except for the least forested classes, satellite imagery could not detect the differences in condition, so for sustainable forest and protected area management this important information has to be collected 'on the ground'.

3 The gradual nature of changes in species composition

Although vegetation maps may suggest that so-called 'climax' forest types are uniform over their range, the reality is much more complex. Furthermore, forest cover maps produced from satellite images (as in Figure 1) represent present forest cover in a uniform colour, while following Richards (1964) some people talk about 'the tropical rain forest'. After Oldeman (1990), however, I prefer always to use the plural form 'tropical rain forests' in recognition of the huge variation and many exceptions that exist in what is one of the most complex ecosystems in the world. Botanical studies (Hall and Swaine 1981; Van Rompaey 1993) now show that species composition changes continuously and gradually both locally in the landscape, and regionally along climatic gradients. Most of the species in West Africa's rain forests respond strongly to water availability, or inversely, to drought stress (Bongers *et al.* 1999), although climate interacts with other factors such as soil type. Thus badly distributed rainfall may result in drier forest types or savanna, such as occurs in parts of north-west Liberia through to Conakry on the coast of the Republic of Guinea. However, parent soil material such as the schists of eastern Côte d'Ivoire give clayey soils that allow wetter forest types to survive even when rainfall is less abundant. In the south of Taï National Park in Côte d'Ivoire, Van Rompaey (1993) found semi-deciduous forests on granite bedrock with many boulders at the surface, similar to the forests found in the north of the Park on gneissic bedrock. Some kilometres eastward across the geological fault truly evergreen forests existed on schist parent material. Such mosaic patterns exist at the meso-scale in many parts of the Upper Guinea region.

Figure 2 shows a new regional forest gradient map for West Africa (Van Rompaey 2001) prepared using national timber inventory data (more than 3 million measured trees). This was processed in a standardised way using ordination techniques, and spatially represented using a Geographical Information System (GIS).

In central Côte d'Ivoire, a V-shaped incursion of woodland and grassland exists within the forest zone, called the V-Baoulé, after the people living there. East of the V-Baoulé the majority of the forests are of the drier semi-deciduous type,

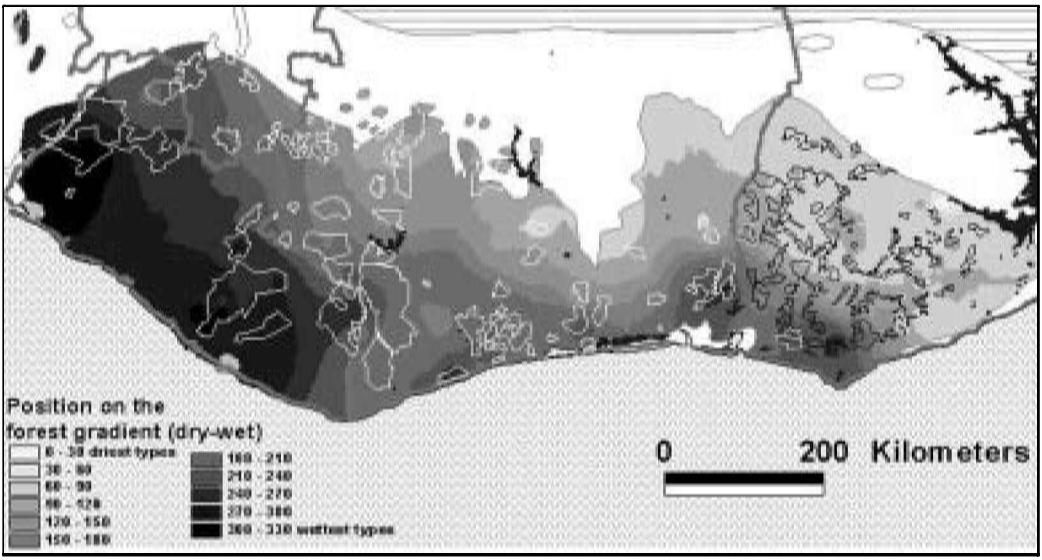

Figure 2: Forest vegetation gradient map based on species composition of timber trees, from national inventories (Van Rompaey 2001). Forest reserves and national parks are shown in white or black outline

whereas west of the V-Baoulé this type becomes rare. In coastal Liberia vast tracts of very humid evergreen forest exist of a type that is absent even from Ghana, and that is found only in south-east Nigeria and west Cameroon: the Biafran forests rich in *Caesalpinioideae* tree species.

Hall and Swaine (1981), Hawthorne (1995) and recent studies by the ECOSYN project (Universities of Wageningen, Cocody-Abidjan, Oxford) have shown that these wetter forest types have higher species diversity, are richer in rare and endemic species and can be considered as Pleistocene refugia, i.e. areas where forest species survived the colder and drier spells in the Quaternary past.

4 From the 'virgin forest concept' to 'perpetuity of disturbance' and the different response strategies of species

There was a time when vegetation ecologists tried to distinguish between primary and late secondary forests in West Africa. At the moment, the major distinction is between unlogged and logged forest, as traces of anthropogenic disturbance have been discovered in almost all African forest ecosystems (Schwartz 1992; Maley *infra*; White 2001).

In fact, in Ghana, Hawthorne (1996) recognised that in semi-deciduous forests, many canopy tree species are light-demanding or pioneer in character, suggesting that the forests have experienced a heavier disturbance regime than in wetter forests (Figure 3a). The disturbance in this zone in the past has mainly been climatic. Over the last million years, this part of the forest zone has experienced a dramatic oscillation of dry and wet spells, with dry phases being the most frequent (see Maley, *infra*). In this respect, the semi-deciduous forest is a recently installed forest, and this explains the abundance of pioneer and light-demanding species, and the quasi-absence of rare and endemic species. Hawthorne (1996) expressed this using a Genetic Heat Index, corresponding to the average rarity of the species in a forest (see Figure 3b). Anthropogenic disturbance from farming, tree felling and road construction, for example, are experienced by the tree species as the forest climate gets drier. At the same time, forest fires burn litter on the forest floor, which can improve conditions for seed germination and seedling installation, while fires sometimes induce mast fruiting of trees.

The regeneration strategy of these light-demanding species is one of discontinuous waves of highly successful seedlings. Thus they frequently lack the smooth exponential size class distribution which

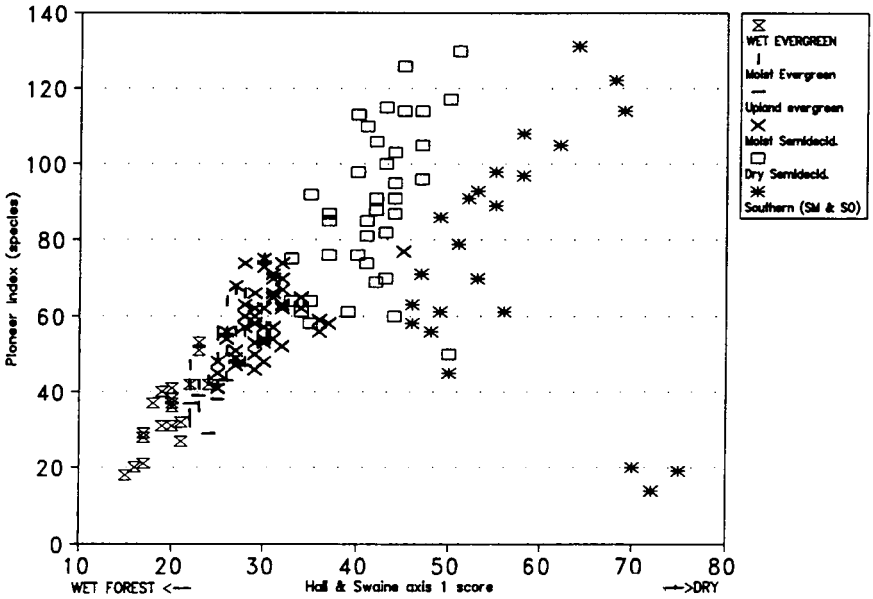

Figure 3(a) Positive correlation between percentage of species with a pioneer character (Pioneer index) and the position of the forest in question along the wet-dry gradient (Hall and Swaine 1981, axis 1 score) in Ghana (Hawthorne 1996)

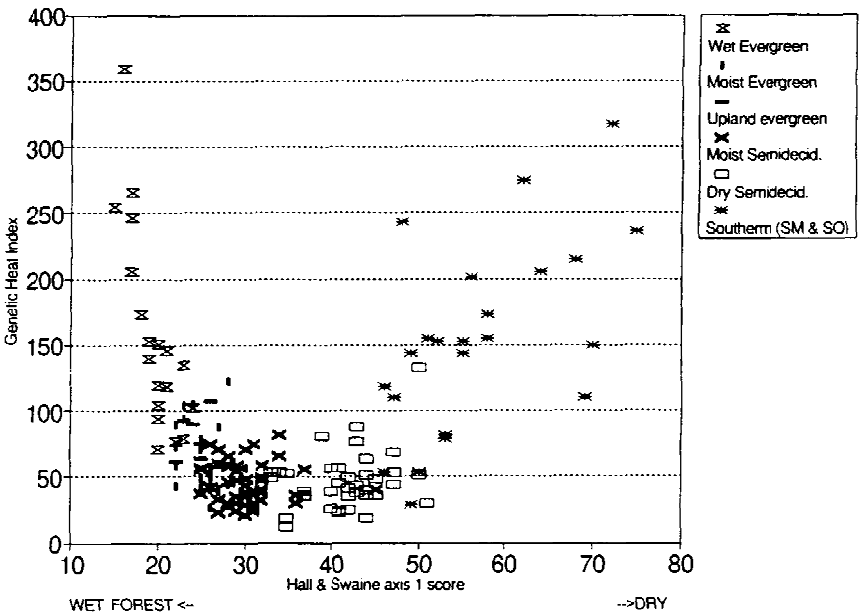

Figure 3(b) Negative correlation between average rarity of the species (Genetic Heat Index) and position of the forest on the wet-dry gradient. The very dry forests contain very few species, so the index values are more scattered

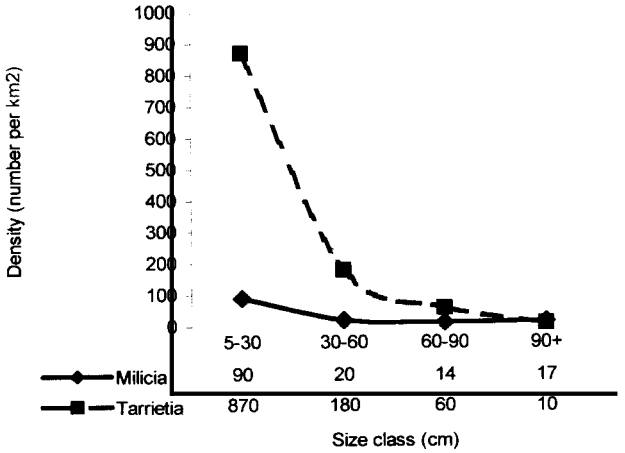

Figure 4: Size class distribution of the pioneer trees *Milicia spp.* in dry semi-deciduous forest and the shade-bearer *Tarrietia utilis* in wet evergreen forest (Ghana national timber inventory, Hawthorne 1995)

older analytics in forest ecology would have expected, comprising very many seedlings, many saplings and fewer larger trees. This makes their regeneration difficult to predict and their sustainable forest management hard to model. For example, one can compare the pioneer timber trees *Milicia regia* and *excelsa* (Figure 4) mainly found in drier forests with the shade-bearing tree *Tarrietia utilis*, synonymous with *Heritiera utilis* (Figure 4) from the wet forests. The light-demandingness of species like *Heritiera* shifts from shade-bearing in youth to growing in full light when mature. *Milicia* trees were always found growing in sunlit conditions in the Ghana timber inventory, regardless of age (Hawthorne 1995).

The light-demandingness of a species can also be read from the form of the size class distribution: steeply exponential for shade-bearers, to flatly exponential or irregular for pioneers (Figure 4). *Tarrietia* and *Milicia* have equal densities among the big trees of the respectively wet and dry forests where they occur, but in the small size class in wet evergreen forests *Tarrietia* is very abundant. *Milicia* saplings (5–30 cm diameter) and young trees (30–60 cm diameter) are ten times rarer in dry semi-deciduous forest, and moreover they grow in sunlit places, which are often more difficult to walk through. These densities seem to be sufficient for both species to survive in the forests where they live, although Alder (1990) was unable to model a stable population from the mortality and growth data from Ghana that he processed. An explanation may be that successful regeneration only occurs within a time frame of several decades, which is beyond the measuring period of the Ghana Forest Service.

5 Conclusion: no uniform rain forest zone, but two clearly different systems

The rain forest zone is clearly not a uniform cover of undisturbed forest. Rather, present-day species composition reflects both past disturbance regimes, and gradients of water availability as they interact with a complex of other factors including soil types and land use. While the outcomes of these interacting factors are highly variable over space and time, it is possible to identify two poles within the forest zone:

- Forests with continuous water availability thanks to a fairly constant climate and/or water retaining soils: *evergreen forests*, rich in rare and endemic species, because there has been little need for the species to migrate, and few extinction events.

- Forests with a long history of climatic disturbance, with irregular water availability and a climate with irregular dry spells: *semi-deciduous forests*, with few rare species and little endemism.

These distinctions have important implications for rain forest conservation and management. The

evergreen forests are of the highest conservation priority, and by fortuitous chance, also contain fewer timber species of high economic value. The semi-deciduous forests are of lower conservation priority for the sake of rare and endangered species, although the currently-undisturbed form of these forests has become very rare, and thus merits protection at a number of places. These forests have many timber species of high economic value, and are thus of greatest value from a timber productivity perspective.

5.1 Implications for conservation priority setting

From Figure 2 it appears that the protected areas and forest reserves within the Upper Guinea region are spread over the vegetation gradient in a rather uneven way. For example:

- Sapo National Park is the only representative of the very wet evergreen forests of Liberia
- The Nimba Reserves in southern Guinea, Liberia and Côte d'Ivoire are the only protected upland evergreen forests
- Taï, Azagny and Banco National Parks (Côte d'Ivoire) and Nini-Suhien National Park (Ghana) contain wet and transitional forest types, while Bia and Kakum National Parks in Ghana are transitional forests
- Marahoué National Park contains the driest semi-deciduous forest at its boundary to woodland and secondary grassland. This type is also found in forest patches in Comoé National Park in north-east Côte d'Ivoire.

This overview therefore suggests that if forest conservation strategies are to represent the region's forest types accurately, Liberia should give protected area status to more of its very wet forests, especially in the high rainfall zone (4,000 mm rain annually) in eastern Liberia extending some 100 km inland from the coast. Equally, more upland evergreen, or submontane, forests in Liberia, Guinea, Côte d'Ivoire (e.g. the Monts de Dan) and Ghana (e.g. the Atewa range, Hawthorne and Abu-Juam 1995) deserve protected area status. Furthermore the driest forests, especially in Ghana where they contain several local endemics, might be seen to merit more conservation attention, especially where they are under threat from fire, timber and firewood logging.

In short, recent perspectives and research in vegetation ecology make forests in West Africa harder to classify, and the classes harder to map than was thought before. Many tree species show survival strategies that allow them to deal with heavy disturbance, whether of climatic or anthropogenic origin. When deciding on conservation and sustainable management options for these forests, evergreen and semi-deciduous forests show highly contrasted opportunities, while both represent variable and dynamic ecosystems which challenge earlier management models based on ideas of stable populations and regeneration patterns.

Notes

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The author can be contacted on Renaat.Van.Rompaey@ULB.ac.be

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