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On the definition of ecological species groups in tropical rain forests

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Abstract

The species richness of tropical rain forests creates difficulties for ecological analysis. It may usefully be simplified by defining ecological species groups whose members share characteristics of importance for determining forest structure and composition. Many such classifications have been published, but few are properly explained. The terminology is confused from lack of precise definitions. We propose a simple division of tree species into two groups or guilds, pioneer and non-pioneer (or climax), based on seed germination and seedling establishment. Within each guild there is continuous variation and we recommend arbitrary subdivision by height at maturity. We believe this classification to be applicable in all tropical rain forests.

Abbreviations: TRF = tropical rain forest(s); LHW = light hardwood species; HHW = heavy hardwood species

Nomenclature: either follows Hall & Swaine (1981), Whitmore (1972, 1973) and Ng (1978) or authorities are cited.

Introduction

There is now a generally accepted model of tropical rain forest (TRF) dynamics. Gaps develop in a closed forest, new trees grow up in them, and a mature canopy is eventually attained. We may recognise a forest growth cycle of gap, building and mature phases (Watt 1947; Cousens 1974; Whitmore 1975, 1982). Gaps are a crucial phase because what grows up determines the floristic composition of the whole cycle (Hartshorn 1978; Oldeman 1974, 1978; Whitmore 1978). The most active area of TRF research over the past decade has been on 'gap-phase replacement' to elucidate processes of establishment and growth, see for example recent reviews by Brokaw (1985) and Denslow (1987). Gap size is of fundamental importance. The bigger the gap the greater the solar radiation at the forest floor and the greater the changes in other facets of microclimate above and below ground from conditions beneath closed canopy. Tree species differ in their response to gaps. At one extreme, some species can germinate below a canopy and their seedlings establish and grow. Others need some increase in solar radiation for growth. All these species have the ability to regenerate *in situ* below a canopy. At the other extreme is a group or guild of species whose seedlings are not found below a canopy but which appear after gap creation. They do not regenerate *in situ*. This last group of species are often called 'pioneers' or 'secondary' species, the others 'climax' or 'primary' species. It has long been known to temperate zone foresters that tree species differ in the shade tolerance of their seedlings. In North America, for example,

foresters recognise up to five '(shade) tolerance classes' (Baker 1950; Graham 1954). The strong recent interest in TRF dynamics has led to a similar recognition and a very confused nomenclature has developed with a lack of precise definitions. No one doubts the phenomenon, only how to name and classify it. We believe that further progress in the analysis and understanding of TRF dynamics, and especially the currently developing area of ecophysiology (e.g. Bazzaz & Pickett 1980) is hampered by this confusion.

Ecological species groups

The purpose of classification of species into relatively homogeneous groups is to help people communicate and make generalizations. In the study of TRF such a classification is particularly necessary because many species are represented by only a few individuals in any study area. To classify species into groups or guilds imposes a degree of simplification which reduces information content, but reveals general patterns and facilitates predictions about forest processes. Taxonomic groups by genus or family are not suitable because of the poor correlation in plants between taxonomy and ecology.

The two main species groups

We believe that there are two qualitatively distinct groups of tree species in TRF with a simple observable difference between them. We call these *pioneer* and *climax* or *non-pioneer* species respectively.

Pioneers are species whose seeds can only germinate in gaps in the forest canopy open to the sky and in which full sunlight impinges at ground level for at least part of the day.

Non-pioneer or climax species are those whose seeds can germinate under forest shade (very rarely in full sun as well). The seedlings can establish in forest shade and survive there (though in a few species not for long). Young plants are thus commonly found below a canopy, but may also be seen in open environments.

The trigger for germination for all TRF pioneers so far studied is either the change in light quality (an increase in red light following canopy removal), or the strongly fluctuating temperature of soil exposed for part of the day to full sunlight. Other triggers found in the temperate zone, e.g. a flush of nutrient nitrogen, fluctuating soil-moisture content, or a wavelength – independent increase in radiation (the high irradiance reaction), have not yet been discovered in TRF. The important point is that these are all triggers provided by gap creation (see reviews by Whitmore 1983; Vazquez-Yanes & Orozco-Segovia 1984). All pioneers also require full sunlight for seedling establishment and growth. As a consequence seedlings and young plants are found in openings in the forest (tree-fall gaps, roadsides, landslips, felled areas, etc.) and are never found under a closed forest canopy, including their own.

These two groups have been widely recognised, though rarely precisely defined. Numerous pairs of names have been applied. Table 1 sets these out and shows our objections to most of them. We hope our preferred terms will now be adopted but realise this may not happen. More important than the names are the definitions of the groups. Loosely applied terminology has helped cause the present confusion. All too often, published work does not offer clear definitions, but it is evident that species are sometimes classed as pioneers simply because they are commonly found in regrowth after a major disturbance, e.g. on abandoned farms. This is an inadequate test as many non-pioneers often colonize cleared land along with true pioneers by any definition (e.g. Swaine & Hall 1983) or may regrow from stumps or root suckers.

Pioneer species possess a whole syndrome of characters in addition to the vital ones we have used to define them. These are listed in Table 2. Collectively these characters give a selective advantage for success in the pioneer ecological niche. For example, copious, well-dispersed seed improves the chance of reaching a new forest gap (van Steenis 1958). Rapid height growth enhanced the chance to fill the gap. However not all pioneers possess all these additional characters.

Table 1. Name pairs given to the two major ecological groups of tree species in tropical rain forests. Preferred terms are given in bold type.

Pioneer/Non-pioneer: Although a word in common English usage, pioneer is unlikely to be misunderstood in this context.

Colonizing/**Climax species:** The use of 'climax' may be taken to imply acceptance of Clementsian views on succession, and assumes an acceptable definition of climax vegetation.

Secondary/Primary species: Widely used, but easily confused with secondary and primary succession in vegetation.

Shade-bearers/Light-demanders (shade tolerant/intolerant): Applies to seedlings, not seeds, so that not all 'intolerants' (light demanders) are strict pioneers in the sense used here.

Non-equilibrium/Equilibrium species: Not much used, and rather cryptic; liable to confusion with application of these terms to vegetation.

r-selected/K-selected species (r-strategists/K-strategists): Assumes a knowledge of how the species evolved. Of zoological origin (MacArthur & Wilson 1967).

Weeds/species of closed vegetation: Weeds are associated with agriculture and horticulture and the term is not much used of forests.

Ephemerals/Persistents: Ephemeral is usually applied to plants with a life-span of less than one year; large tree pioneers could reasonably be called persistent.

Nomad/Dryad (van Steenis 1958): Nomad refers to continual movement across the forest at each generation; dryads are wood nymphs, true denizens of the forest. Dryad has scarcely been used since its introduction in this sense.

Table 2. Character syndrome of pioneer tree species in tropical rain forest. Not all pioneers possess all the characters iii-xvi.

i	Seeds only germinate in canopy gaps open to the sky and which receive some full sunlight.
ii	Plants cannot survive in shade – young plants never found under a closed forest canopy.
iii	Seeds small and produced copiously and more-or-less continuously.
iv	Seeds produced from early in life.
v	Seeds dispersed by animals or wind.
vi	Dormant seeds usually abundant in forest soil (especially fleshly-fruited species). Seeds orthodox (no recalcitrant species known) (1).
vii	Seedling carbon-fixation rate high; compensation point high (2).
viii	Height growth rapid.
ix	Growth indeterminate with no resting buds (*viz* syllleptic) (3).
x	Branching relatively sparse (4).
xi	Leaves short-lived (2).
xii	Rooting superficial (5).
xiii	Wood usually pale, low density, not siliceous.
xiv	Leaves susceptible to herbivory; sometimes with little chemical defence (6).
xv	Wide ecological range (7); phenotypically plastic (8).
xvi	Often short-lived.

(1) Terminology of Roberts (1973), includes capacity for dormancy, Whitmore (1983).
(2) Koyama (1978), Oberbauer & Strain (1984).
(3) Boojh & Ramakrishnan (1986).
(4) Whitney (1976).
(5) Shukla & Ramakrishnan (1986).
(6) Coley (1983).
(7) Hall & Swaine (1980).
(8) Baker (1964).

Subdivision of the groups

Much confusion also arises from attempts at subdivision of the two groups. We think that this is because within them variation is continuous. It is quantitative rather than qualitative and there are not sharp boundaries. Nevertheless, it is useful for many purposes to recognise subgroups. These are acceptable, so long as it is realised that they are arbitrary segments of a continuum.

We may plausibly advance many diverse factors as criteria for the definition of subgroups, but we are strongly constrained by what is known and practical. Differences between species in their demands for mineral nutrients, for water, or for photosynthetically active radiation may well be controlling influences in forest ecology, but our knowledge is at present inadequate. Any classification must be based on characters which we can reasonably expect to be known for all species. We do not have a strong preference for any particular scheme of subdivision. Some measure of height achievable at maturity is one possibility (cf. Hall & Swaine 1981). For this the scheme of Raunkiaer (1934) is suitable. In this scheme species are allocated to nano-, micro-, meso- and megaphanerophyte classes, defined by the height above

the ground of their perennating buds, which approximates to their absolute height at maturity. (The English words pygmy, small, medium and large may serve as alternatives). The classification can be extended without confusion to include shrubs, and large and small herbs. Amongst pioneer tree species, longevity increases with stature, but we do not know if large pioneers are generally shorter lived than large non-pioneers, so life span must only be used within each group.

In Table 3 we present examples from all three TRF regions of the pioneer and climax species groups and subgroups defined on height. The megaphanerophytes include 'emergents', which is another term difficult to define with precision. There is a similar vagueness about terms such as 'canopy-top', 'mid-canopy', 'understorey' which however are often used, and for some purposes may be sufficiently precise. It may be noted that some species differ infraspecifically at the subgroup level. For example *Discoglypremna coloneura*, a West African pioneer, reaches only 20 m in Ghana but 50 m in Nigeria (MDS pers. obs.).

Climax species response to solar radiation

Within the climax species groups there is variation in the amount of solar radiation needed for seedling growth ('release'). At one extreme there are species which need much solar radiation and then grow fast. These tend to have seedlings with rapid mortality be-

Table 3. Examples of the pioneer and climax tree species groups from Africa (AF), the Eastern Tropics (ET) and tropical America (AM) subdivided into height class subgroups.

Tree stature	Pioneers (germinate in full sun and require full sun for survival and growth)	Climax (germinate in shade, or rarely in full sun, and seedlings can survive and grow in shade)
Pygmy (Nanophanerophytes) <2 m tall	probably none, class occupied by shrubs eg *Solanum* spp. (pantropical)	*Pycnocoma macrophylla* (AF) many arecoid palms *Coussarea* spp. (AM) *Psychotria deflexa* DC. (AM)
Small (Microphanerophytes) 2 – 7.9 m tall	*Rauvolfia vomitoria* (AF) most *Trema* (pantropical) many *Macaranga* spp. (AF, ET) *Pipturus* (ET) Some *Piper* spp. (AM)	*Microdesmis puberula* (AF) most Melastomataceae (ET, AM) *Drypetes ivorensis* (AF) *Diospyros buxifolia* (ET)
Medium (Mesophanerophytes) 8 – 29 m tall	*Musanga cecropioides* (AF) *Anthocephalus* (ET) *Macaranga hypoleuca* (ET) *Cecropia* spp. (AM) most *Sloanea* spp. (AM)	*Turreanthus africanus* (AF) a few Dipterocarpaceae (ET) Fagaceae (ET) most Myristicaceae (ET, AM) *Minquartia guianensis* Aubl. (AM)
Large (Megaphanerophytes) ≥30 m tall	*Chlorophora excelsa* (AF) *Terminalia ivorensis* (AF) *Terminalia superba* (AF) *Lophira alata* (AF) *Pericopsis elata* (AF) *Paraserianthes falcataria* (ET) *Eucalyptus deglupta* (ET) *Goupia glabra* Aubl. (AM) *Laetia procera* Eichl. (AM) *Cedrela odorata* L. (AM) *Swietenia mahagoni* (L.) Jacq. (AM)	*Khaya ivorensis* (AF) *Entandrophragma* spp. (AF) *Funtumia elastica* (AF) *Aningeria robusta* (AF) nearly all Dipterocarpaceae (ET) *Virola surinamensis* Warb. (AM) *Pentaclethra macroloba* (Willd.) Kuntze (AM) *Couratari* spp. (AM) *Vochysia maxima* Ducke (AM) *Eschweilera* spp. (AM)

low canopy shade, not persisting for long. In Malaysia these are called Light Hardwoods (LHW) and include the Light Red Meranti *Shorea* spp. (Dipterocarpaceae). *Entandrophragma* spp. (Meliaceae) are West African examples. These species are important today for two reasons. Silviculturally, their regeneration is favoured by the massive canopy disturbance caused by modern high-volume timber extraction. Commercially, they have relatively pale and low density timber. Apart from the essential character of germination and seedling establishment below a leafy canopy, LHW species resemble pioneers. At the opposite extreme, via a continuum of response, are other climax species which require very little or no increase in solar radiation for release. These grow more slowly. They have dark, heavy, often siliceous timber and in Malaysia are called Heavy Hardwoods (HHW). They are less likely to regenerate following contemporary high-intensity logging. Their timber is less widely useful. *Neobalanocarpus heimii*, another dipterocarp, and *Cynometra alexandri* (Caesalpiniaceae) are Malaysian and African examples.

Late secondary species

Some authors have recognised a group they call late seral or late secondary species. These are ill-defined terms which we believe should be abandoned. Sometimes they refer to species which are dominant in late secondary forest, later than pioneers but before climax species become dominant (Budowski 1955). We believe that in this usage late secondary species are large pioneers which live longer than small ones (e.g. *Cedrela* spp. and *Swietenia* spp. in the neotropics). No one has demonstrated the existence of a third germination/establishment niche different from the pioneer/climax niches as defined in this paper. We do not believe there is a class of species which germinates and establishes below a pioneer canopy but not a climax one.

Another usage of 'late seral' is to refer to a more light-demanding, faster growing climax species, the LHW discussed above. In a forest which is now experiencing smaller gaps than previously, HHW will tend to replace LHW. This was the situation for which Jones (1955/56) used the term for the Okomu forest, Nigeria where *Entandrophragma* and other Meliaceae were regenerating poorly *in situ*, and at Sungai Menyala, Malaysia LHW megaphanerophyte dipterocarps have HHW dipterocarps coming up underneath (Whitmore 1975).

Conclusions

Universal adoption of the definitions we have made here will be of great value in communication between research workers in different continents, and should help in comparative studies of TRF dynamics and the search for general principles. If exceptions exist, and we know of none, they will only be revealed if authors (including ourselves) are quite explicit in the definition of the terms they use.

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