

# WILEY

---

Canopy Gaps and the Two Major Groups of Forest Trees

Author(s): T. C. Whitmore

Source: *Ecology*, Vol. 70, No. 3 (Jun., 1989), pp. 536-538

Published by: Wiley

Stable URL: <http://www.jstor.org/stable/1940195>

Accessed: 08-02-2017 17:51 UTC

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://about.jstor.org/terms>



Wiley is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*

*Ecology*, 70(3), 1989, pp. 536–538  
 © 1989 by the Ecological Society of America

## CANOPY GAPS AND THE TWO MAJOR GROUPS OF FOREST TREES

T. C. WHITMORE

*Oxford Forestry Institute, Department of Plant Sciences,  
 University of Oxford, Oxford OX1 3RB England*

In all forests there is a cycle initiated by disturbance. We may arbitrarily recognize gap, building, and mature phases (Watt 1947, Cousens 1974, Whitmore 1975, 1978, 1982), thereby designating forests as spatial mosaics of structural phases which change over time as a result of dynamic processes. Gaps, openings in the forest canopy, drive the forest cycle. Very tiny gaps may be filled by lateral ingrowth of surrounding trees. Usually, though, trees grow up from seedlings to form an immature forest of saplings and poles which grow on and develop into mature trees. The mature phase may enter a fourth degenerate phase as trees become senile, but often is destroyed at a stroke by some external factor.

Differences in sizes of gaps result in differences in species composition of the next cycle. Present evidence suggests that, in all forests, tree species fall into one or other of two groups. In small gaps seedlings that became established in the shade of the closed forest are released (i.e., commence height growth). By contrast, a quite different group of species colonizes large gaps. Seeds of these species germinate only in the open, so seedlings occur only after formation of gaps. Swaine and Whitmore (1988), while recognizing that there are no universally accepted terms, propose that these groups be called climax (non-pioneer) and pioneer, respectively. Pioneer species only regenerate in large gaps. When a mature canopy of pioneers enters the degenerate phase, small gaps develop, and these are closed by growth of climax species that became established under them. The next cycle is composed of climax species that, unlike the pioneers, can regenerate in situ. The gap phase is thus the most important part of the growth cycle for the determination of floristic composition. Competition among tree species and their different light requirements at the building and mature phases play a lesser role.

Intensive study of forest dynamics since the early 1970s suggests this paradigm is applicable to many forests at all latitudes (Whitmore 1988). There are, however, numerous embellishments, as well as many alternatives, and these lead to the great diversity seen even within a single forest biome. A few examples

include: clonal spread occurs in some temperate forests; in some tropical rain forests big gaps may be invaded by woody climbers that arrest the next growth cycle; both pioneer and climax species differ in longevity (hence size) and in autecology (e.g., microsite preferences for seedling establishment).

### THE FOREST CYCLE

The phases (or stages) of the forest cycle are arbitrary but useful subdivisions of continuous changes occurring within the lives of trees that colonize a gap. These changes result in canopy reformation following disruption. Some authors have talked about "mature-phase species" but that confuses the forest growth cycle, which only concerns forest structure, with the species that comprise the cycle.

Gaps are heterogeneous. They may contain upturned root-plates that expose mineral soil and form mounds, as well as areas of fallen branches, twigs, and leaves. Continental European authors have introduced the medieval French term *chablis* to signify this heterogeneity and diversity, feeling that "gap" has too simple a connotation (Hallé et al. 1978). There are now several studies relating differences in species composition to location on different microsites within a gap (e.g., for tropical rain forests, Riera 1985, Brandani et al. 1988).

### ECOLOGICAL GROUPS OF SPECIES

Tree species differ from one another in numerous ways. In their autecology they fall into two (and two only) groups (classes or guilds) on a simple qualitative difference of profound ecological consequence (Swaine and Whitmore 1988).

The climax (non-pioneer) class contains species whose seeds can germinate under a forest canopy (though, in a few cases, also in the open), and whose seedlings are able to establish in forest shade. Juveniles of these species may survive in shade for some years. The pioneer class contains species whose seeds can germinate only in canopy gaps open to the sky in which full sunlight impinges at ground level for at least part of the day. Therefore, seedlings of pioneer species do not occur under canopy shade. The two species groups are

widely recognized, but have rarely been precisely defined. Swaine and Whitmore (1988) suggested this simple qualitative difference as the criterion for distinguishing the two groups and listed the numerous pairs of names that have been suggested. A whole syndrome of characters is associated with each group in addition to the vital ones, and these characters collectively confer selective advantage. For example, pioneer species commonly produce copious small, well-dispersed seeds, which enhance the chances of reaching a gap plus rapid height growth which increases the chance to fill the gap. Climax species often produce fewer, larger seeds which contain adequate food reserves for germination and establishment at low levels of solar radiation. These additional characters, listed by Swaine and Whitmore (1988), differ from the vital characters in that not all species possess them.

The recognition of just two major groups of tree species is based on a simple, qualitative difference, and this classification seems to result in a natural division of ecological importance. A species cannot be assigned to a group without knowledge of the ecology of its seeds and seedlings. Cases reported of species apparently not fitting this paradigm will, I believe, be resolved by close scrutiny of their seed germination and seedling establishment (however, see Martínez-Ramos et al. 1989, Schupp et al. 1989).

Among *climax (non-pioneer) species*, there is a gradation in responses to light (also see Canham 1989). At one extreme, there are species whose seedlings are very persistent in deep shade and are released, either with no or only small increases in light, such as occurs in a tiny canopy gap. These species grow slowly and typically have dark, dense, often siliceous timber (e.g., *Parinari* spp.). At the other extreme are species whose seedlings persist only under light shade, in some cases not for long, and are released by substantial increases in light (e.g., *Anisoptera thurifera*, *Entandrophragma* spp.). In a sufficiently large canopy gap seedlings of these latter species are capable of rapid growth. They typically produce pale, low-density timber. The least shade-tolerant climax species resemble pioneers except in the vital capacity for germination and establishment beneath the forest canopy.

There is no very good nomenclature for the different categories of climax species. In Malaysia they are known from their timber properties as "Heavy and Light Hardwoods." In North America, foresters have recognized tolerance classes of tree species. Four of these classes contain climax (non-pioneer) species with different degrees of seedling shade tolerance (Baker 1950); it is realized that these classes are convenient slices of a continuum and that responses vary somewhat depending upon site conditions (see Spies and Franklin 1989, Veblen 1989). Tropical rain forests also have various subgroups of species. For example, three

subgroups can be distinguished among the 10 common climax (non-pioneer) species of large trees on Kolombangara Island (Whitmore 1974).

The *pioneer class* of species ranges from very short-lived and small-statured species to long-lived and large-statured species, respectively. For many purposes it is useful to categorize subgroups, but we must remember these are arbitrary parts of a continuum. Thus, *Cecropia*, *Musanga*, and many *Macaranga*, the tropical pioneers par excellence of America, Africa, and the Orient, respectively, are relatively short-lived, small species. The long-lived, large pioneers include many useful timber trees, well known to modern foresters because of their suitability for plantations. Examples include *Cedrela* spp., *Goupia glabra*, *Laetia procera*, *Swietenia* spp., and most *Vochysia* spp. (America), *Chlorophora excelsa* (Africa), and *Eucalyptus deglupta* and *Paraserianthes* spp. (Asia).

A confusion has been introduced by those authors who talk about a distinct and separate class of "late secondary species" in tropical forests. I do not believe that any such group exists. Two things have been confused (Swaine and Whitmore 1988). So-called late secondary species are often those dominant in forests after small, short-lived pioneers have died and before climax (non-pioneer) species have become prominent in the canopy (Budowski 1965). Such species are long-lived pioneers (e.g., *Cedrela* and *Swietenia* in the neotropics). Also, but in a loose sense, the Light Hardwood subgroup of climax (non-pioneer) species have also been considered late secondary species (Whitmore 1982). For example, in West Africa *Entandrophragma* and *Khaya* commonly lack sapling and pole-size stems, and so are not regenerating in situ (Jones 1955, 1956). More complete study shows these two genera (among others such as *Triplochiton*, Aubréville 1938) are climax (non-pioneer) species that need substantial canopy opening for release of juveniles. Saplings and poles are not present where such openings have not occurred. In the forest Jones studied, these taxa were declining in the absence of sufficiently substantial canopy openings.

#### RELATIVE ABUNDANCES OF PIONEER AND CLIMAX (NON-PIONEER) SPECIES

Forests differ in the gap-forming processes to which they are prone. Papua New Guinea, for example, is a land of cyclones, earthquakes, volcanic eruptions, and periodic fires (Johns 1986), all of which cause catastrophic destruction of large swathes of forest. The mosaic of structural phases is coarse and forests dominated by shade-intolerant species are widespread (also see Spies and Franklin 1989). Borneo and Surinam, by contrast, have little catastrophic destruction; fine structural mosaics and shade-tolerant species are widespread.

It has been suggested that the most abundant class of tree species in a region will be the one adapted for gap sizes which are more common there (Denslow 1980*b*, 1984). However, the very species-rich tree floras of Papua New Guinea, Borneo, and Surinam are characterized by few pioneer species, and this is true of tropical rain forests in general. I suggest that the scarcity of pioneer species in such forests is linked to the biology of these species, notably copious well-dispersed seed (Whitmore 1984; also see Brokaw and Scheiner 1989).

#### SHIFTS IN FLORISTIC COMPOSITION

When large gaps are replaced at the next forest cycle by small ones, there is a shift from pioneer to climax species (i.e., relay floristics; Egler 1954). In forests in which only small gaps occur, successive forest cycles consist of climax (non-pioneer) species. In all but the most species-poor forest the next cycle may have different composition from the previous one on that site. We may refer to cyclic replacement (Miles 1979), sometimes loosely called cyclic succession.

Sometimes both pioneer and climax (non-pioneer) species grow up in a large gap, the latter growing either from juveniles persistent from the previous mature forest or from sucker shoots (also see Brokaw and Scheiner 1989, Poulson and Platt 1989). This simultaneous colonization (Egler 1954) of gaps produces more subtle shifts in species composition. The pioneer species grow more rapidly and so enter the overstory first, and these are subsequently progressively replaced by more slowly growing climax species. This was shown by Budowski (1965) for the tropical rain forests of Central America where small pioneers, large pioneers, and then

climax species successively attain dominance. I believe simultaneous colonization is likely to be common in forests recovering after a felling operation, with pioneers colonizing the most open sites, intermingled with those seedlings of climax species which have survived disturbance, and supplemented by sprouts from damaged stems and roots. Such succession has been described at Hubbard Brook and contrasted with succession by relay floristics, which occurs on nearby abandoned pastures (seedlings and sprouts of climax species are absent from the pastures; Bormann and Likens 1979).

Many forested landscapes are likely to contain patches with different floristic composition. This is what Bormann and Likens (1979) called the shifting mosaic steady state: overall the floristic composition of the landscape remains stable although patches change in species composition over time.

#### CONCLUSION

Ecologists are continually searching for generalizations. Attempts to formulate general rules are followed by applications and discoveries of exceptions. Paradigms are useful, nonetheless, if they stimulate enquiry and raise questions not previously considered.

I believe the existence of a forest cycle and the division of tree species into two groups as discussed here fits our present knowledge of forest dynamics. The test will come from more work focused on autecology, especially of germination, seedling establishment and growth, and survival of prereproductives, as well as the interaction of all these with gap size.

For reprints of this Special Feature, see footnote 1, page 535.

*Ecology*, 70(3), 1989, pp. 538–541  
© 1989 by the Ecological Society of America

## SPECIES COMPOSITION IN GAPS AND STRUCTURE OF A TROPICAL FOREST

NICHOLAS V. L. BROKAW

*Manomet Bird Observatory, P.O. Box 936, Manomet, Massachusetts 02345 USA*

AND

SAMUEL M. SCHEINER

*Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115 USA*

Forests are often hypothesized as consisting of patches in different stages of a forest cycle that includes open (gap), growth, and closed phases (see Whitmore 1989). Study of gap formation and closure, therefore, should provide insight into forest composition and structure.

A critical question is the extent to which gap dynamics contribute to the mosaic structure of the forest landscape (Christensen and Franklin 1987; also Lorimer 1989, Spies and Franklin 1989).

In this essay we examine how variation in gap size