

# Chapter 11

## The Response of Woody Plants to Disturbance: Patterns of Establishment and Growth

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I.	Introduction .....	198
II.	Natural Disturbances and Resource Availability .....	198
III.	Establishment of Woody Plants Following Disturbance .....	199
	A. Seed Production and Dispersal .....	199
	B. Seed Storage and Germination .....	201
	C. Seedling Establishment .....	203
IV.	Growth and Resource Use by Woody Plants Following Disturbance .....	205
	A. Rate versus Efficiency of Growth and Resource Use of Woody Plants .....	206
	B. Aboveground Growth Patterns and the Uptake and Use of Resources by Woody Plants after Disturbance .....	209
V.	Discussion .....	213
	Recommended Readings .....	216

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## I. INTRODUCTION

Hypotheses on the coexistence of plant species (Connell, 1978), niche differentiation (Grubb, 1977), and resource partitioning (Denslow, 1980a) in plant communities have relied heavily on the requirement for some form of disturbance during the life cycles of many plant species. In general, disturbances reduce the dominance of a site by established individuals and create openings for colonization and growth by new individuals. Where regrowth of vegetation following a disturbance is rapid, competition for those openings should be severe.

In this chapter, we examine traits that affect the ability of woody plants to respond to openings created by natural disturbances. Our approach is to consider traits that determine the types of disturbances in which a species is most likely to be successful in reaching reproductive size. We focus primarily on trees of closed forests, particularly the deciduous and mixed conifer-hardwood forests of eastern North America with which we are most familiar. However, many of the patterns we describe below are common to trees, shrubs, and lianas in any habitat that can support a closed forest canopy.

## II. NATURAL DISTURBANCES AND RESOURCE AVAILABILITY

One of the principal effects of natural disturbances is to alter the availability of resources for plant growth. There are at least two mechanisms by which disturbances can temporarily increase the availability of light, water, and soil nutrients. The first is simply the reduction in rates of uptake or use of resources due to the loss of biomass. This effect is most apparent in the enhancement of light levels in canopy openings (March and Skeen, 1976; Chazdon and Fetcher, 1984). A second mechanism is the decomposition and mineralization of nutrients held in organic matter. Increased insolation at the soil surface and reduced transpiration following large-scale windthrow, for example, may increase nutrient availability by increasing the rate of decomposition of soil organic matter (Bormann and Likens, 1979). Fires will often increase the availability of some nutrients despite losses via groundwater, smoke, and volatilization (Christensen and Muller, 1975a; Grier, 1975; Krebs, 1975; Sanchez, 1976; Stark, 1977; Chapin and Van Cleve, 1981). Severe disturbances may actually reduce the rate of supply of water and certain nutrients through physical degradation of the site (see, e.g., Nye and Greenland, 1964; Garwood *et al.*, 1979) or through disruption of nutrient cycling (Christensen, 1977; DeBano and Conrad, 1978). However, in closed forests, most forms of canopy disturbance produce a temporary increase in some of the resources necessary for the establishment of new individuals or the growth of understory plants.

In general, there is a positive relationship between disturbance size or intensity and the availability of resources for plant growth. An increase in the size of an opening in a closed forest, for example, will increase the amounts of both diffuse and direct radiation in the understory (see, e.g., Minckler *et al.*, 1973). The intensity of a disturbance (as measured by the reduction in biomass per unit area) should

also be directly related to the degree of reduction in rates of transpiration and interception of water and the uptake of nutrients. However, for a given size of disturbance, the magnitude and even direction of change in the availability of water and nutrients can be affected by changes in many factors, such as the amount of water lost in surface runoff and evaporation. The relationship between disturbance size and resource availability may be strongest for small-scale disturbances that primarily cause local reductions in the interception of light and the uptake of water and nutrients, without substantial physical disruption of the site.

An important feature of any increase in resource availability produced by a disturbance is its transient nature. As biomass is reestablished at a site, the relative availability of resources for future colonists will, in general, decline. Tilman (1982) has presented an analysis of plant competition for levels of resources available when the rate of uptake by an intact community has equilibrated with the rate of supply of a resource. The transient pulses of resources produced by many natural disturbances represent a distinctly different pattern to which plant species can respond. Traits traditionally associated with the response of woody plants to disturbance (e.g., rapid growth rates, small sizes, and early reproduction) appear to facilitate the exploitation of such pulses of resources.

### III. ESTABLISHMENT OF WOODY PLANTS FOLLOWING DISTURBANCE

In communities where there is rapid regrowth of vegetation following a disturbance, the availability of resources for colonization should reach a peak soon after a disturbance. Consequently, the first plants that become established after a disturbance should enjoy greater availability of resources than plants that become established later. Establishment of seedlings of many species of woody plants is often limited to a brief period following disturbance (c. 1–5 years), particularly when reestablishment of biomass is rapid (Oliver, 1981). The competitive advantages of early arrival time and large propagule size have been demonstrated for herbs (see, e.g., Black, 1957; Holt, 1972). Early arrival time should be particularly critical for species of woody plants that are intolerant of shade.

#### A. Seed Production and Dispersal

Patterns of seed production and dispersal vary widely among woody plants. One of the most conspicuous patterns of seed production and dispersal—early and copious production of light, wind-dispersed seeds—is generally correlated with the ability to respond to large disturbances (Baker, 1974). Many factors other than seed crop size and seed weight, of course, will influence the availability of seeds in a disturbance, and we can ask to what extent other aspects of seed production and dispersal lead to differentiation in the response of woody species to disturbances. The factors considered below are fluctuations in annual seed production and the mode, seasonal timing, and duration of seed dispersal.

Relative constancy in annual production of seeds should enhance the likelihood

that seeds are available for colonization of recent disturbances. However, there is substantial annual fluctuation in the size of seed crops within and between species. The frequency of annual seed crop failures or near failures in temperate trees appears to be higher in large-seeded trees (e.g., species of *Quercus*) than in small-seeded trees (e.g., species of *Populus*) (data of Godman and Mattson, 1976). In some cases, seed crop failures are the result of problems such as the adverse effects of weather on some aspect of reproduction (suggested by the data of Godman and Mattson, 1976), high energetic costs of repeated production of large crops of large seeds, or indirect effects of extreme weather or animal feeding that reduce or eliminate sexual reproduction by reducing overall plant productivity. In contrast, the synchronous production of large numbers of seeds at irregular intervals may satiate seed predators (Janzen, 1971).

The mode of seed dispersal should also influence the amounts, kinds, and distribution of seeds within disturbances. Following cutting and burning of mature terra firme forests of the Amazon basin, bird- and bat-dispersed seeds of *Cecropia* and other woody pioneers were clumped, presumably reflecting roosting site preferences (Uhl *et al.*, 1981; McDonnell and Stiles, 1983). In an early study, Watt (1925) described the tendency of seedlings of *Fraxinus excelsior* (wind dispersed) to be concentrated near the center of forest gaps, while seedlings of the heavier-seeded *Fagus sylvatica* (bird and mammal dispersed) were more common near the periphery of gaps. On the other hand, where dispersal distances are greater, plants with animal-dispersed seeds may achieve higher densities than plants with wind-dispersed seeds. For example, it is common to observe a greater density of bird-dispersed rather than wind-dispersed woody plants in the central parts of large abandoned agricultural fields in the northeastern United States (P. L. Marks, personal observation).

It seems reasonable to expect frugivorous birds that feed in open habitats to carry seeds of fleshy-fruited pioneer trees and shrubs from one large opening to another (see, e.g., Marks, 1974). However, in forests where regrowth following large disturbances is rapid, it is questionable whether the partnership between bird and plant works in the expected way; by the time a large blowdown (or its equivalent) contains plants producing fleshy fruits that would attract open-habitat, frugivorous birds, conditions at the soil surface may no longer be favorable for the establishment of pioneer plants. Moreover, the expected partnership assumes prompt germination of seeds following excretion or disgorgement by birds. Many of the fleshy-fruited invaders of temperate forest openings and fallow agricultural fields, however, have seeds that will not readily germinate when freshly collected (e.g., *Prunus pennsylvanica*, *Rhus typhina*, *Cornus racemosa*). Undoubtedly, passage through a bird facilitates germination of such seeds (Krefting and Roe, 1949). However, for bird-dispersed seeds that have poor germination when fresh, it remains to be shown whether seeds commonly arrive soon enough, and in suitable condition, to germinate and produce seedlings with a reasonable likelihood of growing to maturity in disturbances where subsequent regrowth is rapid. It may turn out that bird dispersal

of seeds functions more to maintain input to buried seed pools in closed forests (Uhl *et al.*, 1981).

A final aspect of dispersal—the seasonal timing and duration of seed dispersal—should also influence the availability of seeds in an opening. Seeds of a number of temperate floodplain trees (*Populus deltoides*, *Salix* spp., *Ulmus americana*) are dispersed in late spring. Seeds of another major floodplain tree, *Platanus occidentalis*, ripen in the fall but do not normally disperse until the following spring (Fowells, 1965). The combination of spring dispersal and rapid germination in these floodplain species should contribute to the establishment of seedlings on fresh alluvium deposited by spring floods.

The duration of seed dispersal from woody plants varies enormously, from species whose seeds are released relatively synchronously (within a week or so) to species some of whose seeds remain on the parent plant for the better part of a year. Examples of relatively synchronous release of seeds are those trees with extremely short-lived seeds (*Populus*, *Salix*) and at least some temperate zone fleshy-fruited species (Thompson and Willson, 1979) in which flowering and fruit ripening are relatively synchronous. Examples of temperate tree species with a prolonged duration of seed dispersal are *Liriodendron tulipifera*, species of *Fraxinus*, and species of *Betula*, all of which often release seeds from fall until spring, despite synchronous flowering. Release of seeds throughout much of the year is also accomplished by species, common in the tropics, that flower (on the same plant) through all or much of the year (Frankie *et al.*, 1974). *Magnolia grandiflora* is a warm temperate example. For wind-dispersed species, it seems likely that extended release of seeds from a given plant will result in greater variability in the distance and direction of seed dispersal because winds of different directions and velocities will be involved. A wider distribution of seeds around a parent plant should increase the probability that some of the seeds will find their way into an opening. In moist tropical forests in which canopy openings and seed germination can occur throughout much of the year, extended release of seeds from a given plant would also seem to have an advantage in placing fresh seed in a recent opening. On the other hand, plants that rely on animals as pollinators or dispersers may have greater reproductive success if flowering, fruiting, and seed dispersal are synchronous (Bazzaz and Pickett, 1980).

## B. Seed Storage and Germination

It is possible to recognize three general patterns of seed storage and germination.

1. No or minimal delay between dispersal and germination. The salient feature of this pattern is the lack of a persistent buried seed pool. As a result, colonization of a disturbance must come from either a pool of suppressed seedlings (if one exists), the sprouting of surviving roots or boles, or more or less continuous production and dispersal of seeds from beyond the disturbance area.

2. Extended delay between dispersal and germination, with germination being triggered by some aspect of disturbance. The salient feature of this pattern is the extended storage of seeds in the soil. A key question, for which there is currently inadequate information, concerns the extent to which repeated input of seeds is required to maintain the seed pool from one disturbance to the next.

3. Intermediate delay between dispersal and germination. Here innate seed dormancy is long enough to compensate for poor seed production in one to several years, but short enough (c. 5–7 years) so that frequent input of seeds is required to maintain a soil seed pool from one disturbance to another. The remainder of this section expands on the above patterns.

Species with little or no delay between dispersal and germination include shade-tolerant trees of the eastern United States, more than half of 180 rain forest species reported by Ng (1978) for Malaya, the floodplain trees of the northeastern United States, and some pioneer trees (e.g., *Populus*). In cases in which there is a delay between dispersal and germination, the delay is normally keyed to seasonal aspects of climate. The proximate cause of the delay is either an unfavorable environment at the time of dispersal or innate properties of the seed. For example, in a seasonal tropical forest, seeds dispersed either toward the end of the rainy season or in the dry season did not germinate until the next rainy season (Garwood, 1983). Most seeds of woody plants subsequently germinated within the first 2 months of the 8-month rainy season (Garwood, 1983).

In the northeastern United States, seeds of *Acer rubrum* are shed in spring not long after flowering. After dispersal, they are sensitive to the ratio of red/far red light, presumably due to the presence of phytochrome (Smith, 1972; Marquis, 1973; Bazzaz and Pickett, 1980; Cook, 1980). Plant canopies absorb much of the incident light in the red wavelengths (660 nm), which reduces the red/far red ratio at the soil surface and prevents germination beneath a full canopy. Thus, only the seeds that fall within canopy openings germinate during the season of dispersal. *Acer rubrum* seeds that do not germinate during their first growing season germinate the following spring before trees are in leaf and before the next year's crop of seeds has been shed (Marquis, 1973). Thus, unlike other species whose seeds do not remain alive for more than 1 year, *A. rubrum* has an extra growing season during which its seeds germinate only in response to disturbance.

The second pattern of seed storage and germination involves woody species that have a substantial delay between dispersal and germination; the seeds of such species remain alive in the soil for periods ranging from years to decades. Many pioneer trees fit this pattern. When combined with a germination response that is keyed to an effect of a disturbance, extended storage of seeds in soil can virtually ensure that seedlings will be present soon after the formation of a canopy opening (Bazzaz, 1979). In species in which germination of buried seeds is triggered by an opening, live seeds should tend to accumulate in the soil until a disturbance occurs, subject to losses from consumption, rot, or a low rate of germination in the absence of disturbance. In one study of buried seeds of the pioneer tree *Prunus pensylvanica*

in a 60-year-old forest in New Hampshire (Marks, 1974), contributions to the soil seed pool came in unknown proportions from plants that had previously grown on the site and from bird dispersal of seeds from other populations. Loss of seeds was high, particularly due to consumption by small mammals that consumed an average of c. 100 seeds per square meter over an estimated 3–5 decades since the last disturbance. Other losses of seeds from the buried seed pool included as many as 45 seeds per square meter that succumbed to either embryo abortion prior to dispersal or rot in the soil and 12–15 seeds per square meter that germinated in the shade over a period of several decades. Despite all of the losses, there were still about 40 viable *P. pensylvanica* seeds per square meter on average. Although some germination of *P. pensylvanica* occurs in the absence of disturbance, most of the seeds in the soil do not germinate until triggered by some aspect(s) of the environment of an opening. The specific germination trigger is still under investigation. Several studies (Cheke *et al.*, 1979; Hall and Swaine, 1980; Holthuijzen and Boerboom, 1982) indicate that many tropical pioneer trees have seed storage and germination characteristics similar to those just described. Phytochrome control of germination has been described in the tropical pioneer trees *Cecropia obtusifolia* and *Piper auritum*, whose seeds otherwise behave more or less like those of *P. pensylvanica* (Vázquez-Yanes and Smith, 1982).

The third pattern of seed storage and germination involves short-term storage in the soil (c. 3–7 years) followed by germination that is not necessarily cued to disturbance. *Prunus serotina* provides an example. Unlike those of *P. pensylvanica*, seeds of *P. serotina* remain alive in the forest floor for only 3–5 years (Wendel, 1972, 1977; Marquis, 1975a). Observations of germination of *P. serotina* seeds of known age under natural conditions (Wendel, 1972, 1977; Marquis, 1975a) showed that the vast majority of an initial cohort of seeds germinated after 3 years in the absence of a disturbance. Like *P. serotina*, at least some temperate zone gap trees (*Fraxinus americana*, *Liriodendron tulipifera*) have seeds capable of being stored for several years in the soil (Leak, 1963; Clark and Boyce, 1964; Marquis, 1975a). It would be interesting to know whether the seeds of these trees accumulate in the soil until a disturbance occurs, or whether some (variable) fraction of an initial cohort germinates each year without regard to disturbance, as suggested for *P. serotina* by the results of Marquis (1975a) and Wendel (1977). One major effect of this pattern of short-term storage in the soil and relatively continuous germination of seeds is a pool of buried seeds that provides a buffer against annual fluctuations in seed production and dispersal.

### C. Seedling Establishment

Since the work of Salisbury (1942), it has been known that there is a correlation between seed size and the ability of different species to establish seedlings under a closed forest canopy. Large-seeded plants are more likely to become established in closed forest than are small-seeded plants for at least two reasons. Because of access to seed reserves, seedlings of large-seeded plants are more independent of the

physical environment than are seedlings of small-seeded plants. It has been shown, for example, that the ability of small seedlings to grow in shade is closely related to seed size (Grime, 1966), and Ng (1978) has commented on the ability of first-year seedlings of large-seeded trees in Malaya to persist in closed forest for up to 6 months. The second influence concerns leaf litter and humus. In those forests in which there are matted leaves resting on a surface organic layer, small-seeded plants are unlikely to become established in large numbers, even under the favorable conditions following a disturbance, if the litter layer is intact. This is because matted leaves act as a physical barrier to initial establishment, and frequent desiccation of the surface organic layer, particularly in the warm, sunny environment of a large opening, causes high mortality of small seedlings (Marquis, 1965; Putz, 1983). However, virtually all disturbances involving fire and most large wind-caused disturbances will result in at least some exposed mineral soil conducive to the establishment of small-seeded plants. It is also worth noting that although small-seeded plants have a greatly reduced likelihood of becoming established as seedlings in the presence of thick litter and humus layers, the subsequent growth of seedlings is much greater in soil with the humus layer intact (Marquis *et al.*, 1964). Thus, for small-seeded plants in certain kinds of forests, conditions that promote establishment (i.e., exposed mineral soil) differ from those that promote subsequent rapid growth of seedlings (i.e., an intact humus layer).

In conclusion, we might ask: How precisely are the traits that govern seedling establishment coordinated with respect to particular types or intensities of disturbance? There are notable examples of mechanisms that tie the production, dispersal, storage, and especially the germination of seeds to disturbances that create conditions favorable for the growth and reproduction of a species. The cueing of germination of buried seeds to conditions associated with particular types or intensities of disturbance involves substantial specialization in the mode of establishment following a disturbance. At the same time, however, most woody plants seem to have at least some capacity to place seedlings in the favorable environments created by most disturbances, and that capacity does not necessarily involve close coupling of particular life history stages with the size, the kind, or even the occurrence of a disturbance. Consider the mode of seed dispersal. It is difficult to argue that a particular mode of dispersal is ideally suited to one kind or size of disturbance. Temperate woody pioneers, for example, include species with small, short-lived, wind-dispersed seeds (*Populus*) and others with large, long-lived, bird-dispersed seeds (*Prunus*). The release of seeds from serotinous cones provides an example of the cueing of seed dispersal by a disturbance, but the effect of serotiny is largely to allow the accumulation of a protected seed pool (in this case, stored in cones rather than in the soil) in advance of a fire. Thus, the colonizing ability of woody plants can result from many combinations of different traits. Many woody species depend on buried seed pools or advance regeneration to provide a pool of individuals present at a site in advance of a disturbance. Other species rely on annual production of widely dispersed but short-lived seeds, while still others compensate for fluctuations in annual seed crop size by maintaining a buried seed pool for a few years.



Interestingly, species of *Quercus* not only tend to have large year-to-year variation in seed production but also lack the ability to compensate by accumulating individuals as buried seeds. Thus, factors such as seasonality, seed predation, and the relative unpredictability of both seed dispersal and suitable disturbances appear to place constraints on the degree of specialization in the mode of establishment of woody plants following disturbance.

#### IV. GROWTH AND RESOURCE USE BY WOODY PLANTS FOLLOWING DISTURBANCE

In communities where there is rapid regrowth of vegetation following a disturbance, we would expect strong competition among plants that either sprout from roots (or boles) or become established from seeds. The number of plants present at a site soon after a disturbance will generally far exceed the number that can eventually reach reproductive size, and we would thus expect differential growth rates to be an important aspect of competition during the early stages of the recovery of biomass. A seedling with a higher rate of growth in a given microsite should prevail over a more slowly growing, neighboring seedling established at approximately the same time. This outcome is to a significant degree determined by the ability of the faster-growing seedling to increase its level of resource use, often at the expense of its neighbors (Harper, 1977).

A high relative growth rate in a particular disturbance is likely to be the product of a large number of physiological and morphological traits. Aspects of the physiology of plant response to natural disturbances have been reviewed by Bazzaz (1979) and Bazzaz and Pickett (1980). Much of the physiological research on plant carbon gain has focused on factors affecting the photosynthetic response of a unit area of leaf tissue to different environmental conditions. However, a similar pattern of photosynthetic response in two different species does not necessarily imply similar levels of whole plant carbon gain, since, for example, differences in the magnitude of respiration by shoots and roots will influence whole plant growth rates (Evans, 1975). In woody plants, in which the ratio of nonphotosynthetic to photosynthetic tissue can be relatively high, respiratory losses can be substantial (Yoda *et al.*, 1965; Whittaker and Woodwell, 1967; Kira, 1975). Moreover, there are often substantial differences between species in the patterns of allocation of net photosynthate to different structures within a woody plant (see, e.g., Logan and Krotkov, 1968; Cannell and Willett, 1976). Models of water use efficiency, for example, suggest that different sizes and shapes of leaves require differences in the amount of photosynthate that must be allocated to roots (Orians and Solbrig, 1977; Givnish, 1979). Thus, even when unit photosynthetic and respiration rates of different tissues are known, their net effect on whole plant growth rates will be mediated by differences among species in plant growth form. The extensive literature on plant growth analysis (Evans, 1972; Hunt, 1978), although primarily dealing with herbaceous and crop species, underscores the effect of plant growth form on net growth

rates. Even parameters such as unit leaf rate (the amount of biomass produced per unit of leaf area and time) are determined by a combination of physiological and morphological traits (Causton and Venus, 1981). In general, whole plant growth rates should be strongly influenced by the effects of plant growth form on such factors as the uptake of water and nutrients, the interception of light, and the allocation of carbon to the maintenance of roots and shoots.

### **A. Rate versus Efficiency of Growth and Resource Use of Woody Plants**

The response of woody plant growth rates to increasing size or intensity of disturbance is shown for four hypothetical species in Fig. 1A. The growth curves are defined by three features: first, the minimum size of disturbance required for net growth of seedlings and saplings; second, the growth rate of a species in large disturbances in which resources may be overabundant; and third, the shape of the curve describing growth rates for intermediate sizes of disturbances. Studies of the relationships between shade tolerance and the growth rates of trees in different light regimes suggest that there is generally a direct relationship between the growth rate of a tree species in large disturbances and the minimum size of disturbance required for net growth of seedlings (Grime, 1966; Grime and Hunt, 1975; Marks, 1975). Shade-intolerant tree species tend to have higher growth rates in the open than shade-tolerant species (Grime, 1966; Grime and Hunt, 1975; Marks, 1975). Studies of the response of tree seedlings to different light levels indicate that growth rates increase rapidly as light levels increase above the minimum required for net growth of seedlings (Logan, 1965, 1970; Strothman, 1967; Logan and Krotkov, 1968). However, particularly in the case of shade-tolerant species, growth rates may level off or even decline at light intensities well below that of full sunlight (Logan, 1965; Canham, 1984).

In general, competition between seedlings should act to restrict the success of a species to sites at which its seedlings have higher rates of growth than other seedlings. Because the growth rates of most species show a general increase over a wide range of disturbance sizes, the growth rate of a species in a disturbance should not necessarily be directly correlated with its competitive ability in a given disturbance. For example, although a shade-tolerant tree species may have a higher growth rate in a large blowdown than in a small canopy gap, it may have a much greater competitive ability in a small canopy gap. The hypothesis that a seedling with a higher growth rate should outcompete a more slowly growing seedling established at approximately the same time makes no predictions about the portions of a gradient in disturbance size or resource availability in which a species should be most successful in competition with a variety of other species.

In order to make such predictions about those disturbance sizes in which a species should compete most successfully with other species, we will use the concept of growth efficiency. The gradient of disturbance size in Fig. 1A corresponds to a gradient in resource availability, particularly in the case of light levels for different

sizes of openings in closed forests (see, e.g., Chazdon and Fetcher, 1984). The efficiency of growth for a species in a given disturbance can be defined as the quantity of biomass produced per unit of biomass and time relative to (divided by) the quantity of the most limiting resource available in the disturbance per unit area and time. If the gradient of disturbance sizes is scaled to correspond to an approximately linear gradient in resource availability, then the growth efficiencies for the four hypothetical species in Fig. 1A are shown in Fig. 1B. The curves for species A in both Fig. 1A and Fig. 1B are drawn to represent species that may be capable of responding to a disturbance in the absence of faster-growing species or if the establishment of faster-growing species is delayed.

The portions of the disturbance size gradient in Fig. 1A in which a species has higher growth rates than the other species are the portions where the species has its highest growth efficiency (Fig. 1B), rather than its maximum growth rate. This suggests the hypothesis that a species should be most successful in responding to disturbances for which it has its highest efficiency of growth, rather than its highest potential growth rate, simply because at its sites of highest efficiency it is more likely to have higher rates of growth than species whose maximum growth efficien-

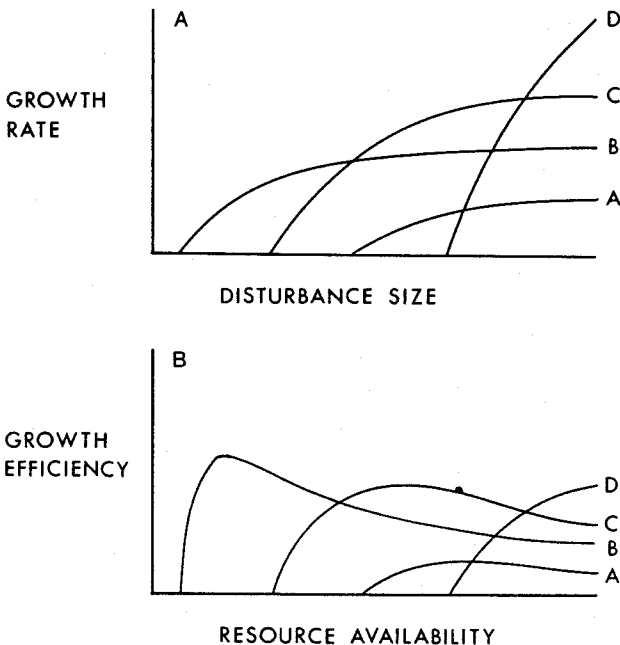


Fig. 1. (A) Generalized patterns of the relative growth rates of four hypothetical tree species with increasing size of disturbance. (B) The growth efficiencies of the four hypothetical species shown in (A) over a corresponding range of resource availability. Growth efficiency is defined as the growth rate divided by the level of the most limiting resource available at a site. If the gradient of disturbance size is scaled to represent a linear gradient of resource availability, then the growth efficiency at any point on one of the curves in (A) is equal to the slope of a line drawn through the origin and the point on the curve.

cies occur at higher or lower levels of resource availability. In more general terms, we are suggesting that the types or intensities of disturbances for which a species is most likely to have a higher rate of growth than other potential competitors are those in which the species is most efficient at exploiting the available resources.

The growth rates and efficiencies depicted in Fig. 1 are for the response of a species to the transient pool of resources available following different disturbances in a single environment. In general, the effect of a particular disturbance should vary at different sites. For example, the effect of a small canopy gap on understory light levels will be influenced by the slope, aspect, and latitude of the site. The degree of change in the availability of nutrients and soil water in and around a gap should also vary for different sites. There have been few studies that have explicitly considered the effects of differences in the quality of a site (as reflected in the levels of resources available to undisturbed portions of a community) on the response of woody plants to disturbance (see, e.g., Smith, 1983). It is likely that the growth rates and growth efficiencies of a species following a particular size or type of disturbance will vary in different environments.

The curves in Fig. 1 are clearly hypothetical and are intended to illustrate the relationships between disturbance size, growth rate, and growth efficiency in a relatively simple case. They are most applicable to sets of species and ranges of disturbance intensity in which a single resource such as light is limiting for all the species considered. Even when species are limited by different resources or combinations of resources in different disturbances, we would still expect a species to be most successful in responding to those disturbances for which it has its highest growth rate relative to resource availability (e.g., in the disturbances in which it has its highest growth efficiency). Note that by our definition of growth efficiency, a species with a higher efficiency of growth than other species at a particular site also has a higher growth rate for that site than do other species. Thus, the hypothesis that competition should act to restrict the success of species to sites at which they have their highest efficiency of growth is not in conflict with the postulated importance of growth rate per se. Rather, the hypothesis makes a prediction about the portion of a gradient of disturbance size or resource availability in which a species should be most successful in reaching reproductive size.

By focusing on the efficiency of growth and resource use by woody plants, it is possible to evaluate the effects of different growth forms on the potential growth rates of species in different environments. To this end, the overall efficiency of growth can be partitioned into two components: a resource uptake efficiency and an internal use efficiency, in which uptake efficiency is defined as the rate of uptake of a resource relative to the rate of supply of that resource at a site. Internal use efficiency is then the rate of biomass production relative to the rate of uptake of the resource. So,

$$\text{Growth efficiency} = \text{resource uptake efficiency} \times \text{internal use efficiency}$$

where

$$\text{Resource uptake efficiency} = \frac{\text{resource uptake}}{\text{resource availability}}$$

and

$$\text{Internal use efficiency} = \frac{\text{biomass production}}{\text{resource uptake}}$$

Warren Wilson (1981) has proposed a modification of the traditional growth analysis equations (Evans, 1972) to incorporate equivalent terms for the efficiency of utilization of light by crops. Overall growth efficiency will reflect compromises between the efficiency of uptake of resources and the efficiency of internal use of resources by different growth forms. For example, a growth form with a pattern of leaf display that allows a high rate of absorption of light at high light levels (and thus high uptake and growth efficiencies) can be expected to have a low growth efficiency at low light levels in part because of high metabolic costs of supporting excess leaves and branches (and thus a low efficiency of internal use of resources). Aspects of the morphology and physiology of plants that affect these efficiencies are likely to be important in understanding the differentiation of species along gradients of resource levels created by natural disturbances.

## **B. Aboveground Growth Patterns and the Uptake and Use of Resources by Woody Plants after Disturbance**

Allocation of carbon to nonphotosynthetic tissues in woody plants implies that the rate of increase in growth with increasing plant size is limited by the degree to which woody plants can increase their effective leaf display and light absorption. While the fraction of available light absorbed by a canopy is largely a function of leaf display, the quantity of biomass produced for each unit of light absorbed will be determined, in part, by the respiratory costs of maintaining roots and shoots. In the rest of this section, we review studies that suggest that differences in the efficiency of uptake of light and the internal use of photosynthate due to differences in branching and leaf display may have a significant influence on the competitive ability of woody plants following disturbances. We will concentrate on aboveground patterns because of the scarcity of information about roots.

Horn's (1971) monograph on the relationship between leaf display and the successional status of trees is perhaps the most widely cited work on the ecological significance of leaf display in woody plants. He argued that trees with sparsely packed leaves on many layers of branches should have higher rates of total canopy photosynthesis at high light levels than trees with uniformly packed leaves in one or a few layers (Horn, 1971). The converse should be true at low light levels. In general, late successional temperate trees show lower numbers of effective layers of leaves, whereas species characteristically found in high light regimes following large disturbances have higher numbers of layers of leaves.

The predictions of Horn's model are based largely on the efficiency of uptake and the use of light by different patterns of leaf display. Although a single layer of densely packed leaves could have an uptake efficiency equal to or greater than that of several layers of more sparsely packed leaves, the efficiency of the internal use of high light levels will be higher for the multilayer if individual leaves are light

saturated at considerably less than full sun and the overall interception of light is partitioned among a greater total leaf area. However, Horn's model does not consider the consequences of allocation of photosynthate to the roots and shoots required for the support of different patterns of leaf display. Subsequent studies have begun to consider the influence of different branching patterns on the efficiency of interception and use of light (see, e.g., Whitney, 1976; Honda and Fisher, 1978; Steingraeber *et al.*, 1979).

While Horn's work dealt largely with the display of leaves in whole crowns, there is an extensive literature on environmental influences on individual leaves (see, e.g., Parkhurst and Loucks, 1972; Taylor, 1975; Givnish and Vermeij, 1976; Givnish, 1979). Temperate tree species that grow rapidly in large disturbances and correspondingly high light levels tend to have more vertically oriented leaves than later successional species (McMillen and McClendon, 1979). Higher leaf angles in high light regimes should allow greater penetration of light to leaves deeper in the crown and should thus allow a greater effective area of leaves displayed per unit area of ground. Thus, high leaf angles in a crown with a high leaf area index should increase the overall efficiency of the use of high light levels for the same reasons that multilayered leaf displays have a high use efficiency at high light levels. High leaf angles can also reduce the heat load on leaves, and thereby potentially decrease water stress and the reduction of photosynthesis due to stomatal restriction of gas exchange (McMillen and McClendon, 1979). The correlation between leaf angle and light levels does not appear to be as strong in moist tropical forests, where a number of species that respond to large disturbances have large, nearly horizontal leaves (Whitmore, 1975).

Studies have also investigated the effects of branching patterns on the efficiency of interception of light by woody plants. Honda and Fisher (1978) and Fisher and Honda (1979) have modeled the effects of branch angle and length on the efficiency of leaf display in *Terminalia catappa*. Measured branch angles in trees of *T. catappa* were close to angles predicted by a branch simulation model for the maximization of effective leaf area (Honda and Fisher, 1978). A series of studies of branching patterns in forest shrubs (Pickett and Kempf, 1980; Kempf and Pickett, 1981; Veres and Pickett, 1982) indicate that different species can minimize leaf overlap through a variety of patterns of branching.

There have been a number of attempts to use stream-ordering techniques to describe the architecture of branching of woody plants (Leopold, 1971; Oohata and Shidei, 1971; Whitney, 1976; Steingraeber *et al.*, 1979; Pickett and Kempf, 1980; Steingraeber, 1980; Veres and Pickett, 1982). According to the stream-ordering system developed by Horton (1945) and modified by Strahler (1957), terminal leaf-bearing shoots are considered first-order branches. Whenever two branches of equal order meet, the resulting branch is assigned the next highest order. The resulting ordering of both physical and biological branching patterns reveals several fairly consistent patterns. The most often cited pattern is for the numbers of branches of successively higher orders to decrease geometrically. In addition, the mean diameter of branches of successively higher orders increases approximately geometrical-

ly. The average ratio between the number of branches of successive orders is termed a "bifurcation ratio."

The relationship between bifurcation ratios and the efficiency of leaf display by woody plants was first explored by Leopold (1971), who suggested that leaves could be displayed in a horizontal plane using the shortest total length of branches if the branch system had a low bifurcation ratio. The total length of branches required for the display of leaves in a vertical, cylindrical crown would be minimized by a branch system with a high bifurcation ratio (i.e., many short first-order branches off a few nearly vertical second-order branches). Whitney (1976) subsequently reported that for 16 woody species in the northeastern United States species characteristically found in open, high light regimes had higher bifurcation ratios than shade-tolerant species. He proposed that high bifurcation ratios were characteristic of the branching patterns of species with multilayered leaf display. Whitney (1976) and Oohata and Shidei (1971) also suggested that bifurcation ratios were species-specific constants. However, Steingraeber *et al.* (1979) and subsequent workers (Pickett and Kempf, 1980; Veres and Pickett, 1982) have shown that for a number of species individuals from different light regimes had systematic differences in bifurcation ratios.

The use of bifurcation ratios to describe branching patterns in trees has been criticized on the grounds that the ordering system does not reflect the actual process of development of the shoot systems in woody plants (Borchert and Slade, 1981; Honda *et al.*, 1981). However, the very features that led to these criticisms by developmental biologists provide the motivation for the recent interest of ecologists in bifurcation ratios. Both within and between species, bifurcation ratios of whole shoot systems and of separate branches within the crowns of various species have been shown to be correlated with both light intensity and growth vigor (Steingraeber *et al.*, 1979; Pickett and Kempf, 1980; Borchert and Slade, 1981; Veres and Pickett, 1982). Despite these results, the relationship between bifurcation ratios and the efficiency of the uptake or use of light is unclear. Dimensions of a branch system that are likely to affect both the pattern of leaf display and light interception (i.e., branch angles) and the metabolic costs of producing and maintaining branches (i.e., branch density, length, and surface area) cannot be currently predicted on the basis of bifurcation ratios.

The relationships between the uptake of light by the canopy of a woody plant and the costs of that uptake in terms of allocation of photosynthate to the production and maintenance of roots and branches are only poorly understood. However, there are a number of ways in which branching patterns can differ in the magnitude of allocation of photosynthate to the support of leaves. The costs of producing branches are reflected in both the synthesis of new shoot material and the maintenance respiration of existing branches (Penning de Vries, 1972, 1975). Studies of the respiration of the branches of woody plants indicate that maintenance respiration rates are correlated with the surface area or diameter of branches (Yoda *et al.*, 1965; Whittaker and Woodwell, 1967; Kinerson, 1975; Yoda, 1983). Denser wood should have higher costs of synthesis of a unit volume of tissue (Penning de Vries, 1972), but the higher

wood density may allow smaller diameter twigs to provide sufficient mechanical and hydraulic support for leaves with lower annual maintenance respiration due to the smaller average diameter of branches. King (1979) suggested that the stout but low-density twigs of some early successional trees may have low net costs over the relatively short lifetime of a branch (and thus a high internal use efficiency) because initial synthesis costs per unit volume of wood are low. Because the branches are rapidly self-pruned as the trees increase in height, the potentially high long-term maintenance costs of these branches are avoided (King, 1979). Dense, slender branches in many late successional species may have lower net costs than stouter twigs of the same weight if the slender branches are functional for longer periods of time before being self-pruned. Early successional tropical trees with horizontal layers of large, often compound leaves may represent an extreme example of this trend. Large leaf sizes and compound leaves allow some tropical pioneers to display large total leaf areas with a minimum of allocation to secondary branch growth (Givnish, 1978). Rapid height growth in these species would seem to favor minimizing allocation to lateral branches during juvenile stages.

The studies discussed in this section suggest that a high rate of growth following a given disturbance (and thus a high efficiency of growth for that disturbance) will often involve a pattern of branching and leaf display that is less efficient in exploiting other disturbances. Our hypothesis that interspecific competition should act to restrict species to disturbances in which they have their highest efficiency of growth is largely based on the apparent specialization of plant architecture and physiology to particular ranges of disturbance intensity. A woody plant with a maximum growth efficiency for a particular combination of resources may well have a higher rate of growth in a larger disturbance because of an increase in the availability of one or more of those resources. But if the overall growth efficiency is lower, there is a greater chance that there is another species with physiological and morphological traits that are more efficient in exploiting the increased concentration of resources in the larger disturbance.

Genotypic variability, phenotypic plasticity, and physiological and morphological acclimation should all act to expand the range of disturbances in which a species has both a high rate and a high efficiency of growth. A number of studies indicate that species that respond to large disturbances have a considerable ability to acclimate to changes in environmental conditions and resource availability (Bazzaz, 1979; Bazzaz and Carlson, 1982; Fetcher *et al.*, 1983). However, there are comparable examples of plasticity and acclimation in the morphology and physiology of species that respond to small disturbances (see, e.g., Logan and Krotkov, 1968; Steingraeber *et al.*, 1979).

Quantifying the effect of plant architecture on the growth of woody plants following disturbance will require considerable research on whole plant physiology and morphology under different levels of resource availability. There has been surprisingly little empirical work on the efficiency of the interception of light by different patterns of leaf display in woody plants. More research is also needed on variation in the respiration rates and metabolic costs of the branching systems of different



species. Although most empirical studies of the ecological significance of plant architecture deal solely with aboveground patterns, Orians and Solbrig (1977), Caldwell (1979), and Givnish (1979) have used cost/benefit models to explore the allocation of photosynthate to roots required for different patterns of leaf display. More research is needed on the effects of differences in the allocation of photosynthate to roots versus aboveground growth on the ability of woody plants to respond to disturbance.

There have been relatively few studies that have explicitly considered the effect of site differences on the response of woody plants to disturbance (see, e.g., Smith, 1983). Work on the effect of soil fertility on shade tolerance in an understory herb (Peace and Grubb, 1982) suggests that the effect of soil fertility on the response of tree species to canopy gaps should be investigated. The existence of interactions between site quality and gap response would provide an additional dimension for resource partitioning in gap phase species.

Of more general significance is a greater understanding of the effect of actual growth rates per se on the ability of woody plants to respond to disturbances. We have focused mainly on growth in terms of net aboveground carbon gain. However, differences in the allocation of carbon to specific aspects of growth (e.g., branch diameter growth, height growth, or lateral spread of the crown) should affect the competitive status of a plant (Grime, 1979). The crown form in densely grown trees of *Populus tremuloides* was close to that predicted from a biophysical model for maximizing height growth while maintaining a minimum of structural support (King, 1981). However, rapid height growth in these individuals appears to have been achieved at the expense of a higher susceptibility to windthrow than many later successional species (King, 1981). In contrast, saplings of both *Fagus grandifolia* and *Acer saccharum* show little increase in height growth rates as gap size increases in old-growth forests of northern New York (Canham, 1984). However, lateral growth of the crowns of both species increases continuously across a broad range of gap sizes. Rapid height growth in woody pioneers would seem to be of particular significance in habitats where herbaceous species are capable of establishing a dense layer that can persist long enough to eliminate subordinate individuals of shade-intolerant species. The significance of height growth may be more problematic in shade-tolerant species, in which canopy recruitment may depend on the response of saplings to repeated periods of both suppression and subsequent release in small gaps.

## V. DISCUSSION

In many forests, natural disturbances are a principal cause of mortality in woody plants (White, 1979). The variety of traits that reduce the susceptibility of woody plants to mortality by frequent and often severe disturbances suggests that differential mortality has been an important selective process in environments subject to recurrent disturbances. Even if the patterns of mortality following disturbances were

entirely nonselective, natural disturbances would still play a major role in the ecology and evolution of woody plants by providing a diverse set of conditions for seedling establishment and plant growth. It is well known that pioneer species require disturbances in order to complete their life cycle. But recent work suggests that even some climax species may depend on the pulses of resources produced by small-scale disturbances to complete their life cycles. In old-growth forests of the Adirondack Mountains of New York, the growth rates of saplings of *A. saccharum* and *F. grandifolia* were too slow for saplings to reach the canopy within the expected life span of either species (Canham, 1981, 1984). However, both species showed significant increases in growth rates in small canopy gaps (Canham, 1984). The significance of shade tolerance in these two species appears to be twofold. Understory saplings have a clear advantage over smaller seedlings in exploiting small canopy gaps before they are closed. However, particularly in the case of *F. grandifolia*, the relatively slow growth rates of saplings even in gaps suggest that many beech trees reach the canopy through multiple episodes of gap formation. The ability of understory saplings to persist for long periods under a closed canopy and subsequently to respond to new gaps is an important element of this mode of canopy recruitment.

Seeds of woody plants are dispersed, germinate, and become established in a much wider range of conditions than the range in which they can successfully reach reproductive size. There are well-known examples of mechanisms that tie the dispersal, germination, and establishment of seedlings to disturbances that create conditions favorable for growth and reproduction of a particular species. Pine trees with serotinous cones release many years of seed crops only after the heat from a fire allows the cone scales to open. Similarly, at least some chaparral shrubs (*Rhus laurina* and *R. ovata*) have dormant seeds that are stored in the soil until stimulated to germinate by the heat of a fire (Stone and Juhren, 1951). And in still other woody plants, germination of stored seeds is coordinated with the occurrence of a canopy opening by means of the light-sensitive pigment, phytochrome. Such examples of specialization, however, should not obscure the fact that many woody plants routinely become established following disturbances as a result of less specialized but perhaps more common traits that allow relatively continuous production, dissemination, and germination of seeds. For example, new plants may come from recently dispersed seeds (e.g., species of *Populus*), from pools of short-lived buried seeds (e.g., *Prunus serotina*), or from a layer of shade-tolerant seedlings (e.g., *A. saccharum*). In addition, most woody angiosperms and a few gymnosperms have the ability to produce sprouts and other kinds of vegetative responses to disturbances. Thus, following disturbance of many kinds of woody communities, a variety of mechanisms, only some of which show specialization with respect to the kind, size, or occurrence of a disturbance, allow the establishment of new individuals and the persistence of residual plants.

It is worthwhile to ask why examples of specialization in patterns of woody plant establishment following disturbance are not more frequent. The absolute frequency of cases of precise cueing of the germination of woody plants to disturbance is

unknown. However, even in known cases of phytochrome-induced germination, there appear to be limitations on the ability of seeds to limit germination to disturbances that are large enough to allow growth to reproductive size. While seeds of *Cecropia obtusifolia* germinate in response to canopy openings, many seeds apparently germinate in openings that are smaller than the minimum size required for growth to maturity (Vázquez-Yanes and Smith, 1982). The inability of seeds to sense an environment suitable for growth to reproductive size may be more common in woody plants, in which there is a greater disparity between the size of the immediate environment of a seedling and the eventual amount of space required by an adult than it is for smaller herbaceous species. Apart from the cases involving inducement of germination by the environment of a disturbance, the other major mode of specialization during establishment seems to be limited to habitats where disturbances occur at highly predictable times. Spring dispersal of seeds by temperate floodplain species should be particularly effective in the deposition of seeds on any fresh alluvium left by spring floods. However, many forms of disturbance are predictable only in their occurrence somewhere within a habitat in a given interval of time. To the degree that rapid colonization of a disturbance confers a subsequent competitive advantage, a relatively generalized pattern of dispersal and germination in which a habitat is flooded with seeds that germinate throughout climatically favorable seasons would seem to have advantages in habitats where there is considerable unpredictability in the precise timing and location of disturbances. Similarly, for shade-tolerant tree species, widespread establishment of seedlings in a forest understory prior to a disturbance should confer an advantage in initial height over seedlings that germinate after a small gap opens in the canopy.

It has been frequently noted that pioneer and early successional species have higher potential growth rates than species capable of responding to small disturbances (Grime, 1965; Grime and Hunt, 1975; Marks, 1975). Rapid growth rates are often cited as a basic correlate of *r*-selection in plants (Grime, 1979). We suggest that rapid growth rates should confer a selective advantage even in species that respond to minor disturbances, but that their growth rates are rapid only in proportion to the relative availability of resources in small disturbances. To the degree that a particular set of morphological and physiological traits will result in high growth rates for only a limited range of disturbance sizes or resource availability, the ability of a woody plant to respond to a disturbance should be more closely correlated with growth efficiency (i.e., growth rate relative to resource availability) than with growth rate per se.

In contrast to many of the combinations of traits involved in seedling establishment, the traits that determine woody plant growth appear to be more specialized in their response to disturbance. The studies discussed in Section IV suggest that a particular growth form will have a maximum growth efficiency in a fairly narrow range of disturbances or levels of resource availability. Factors such as patchiness in the patterns of seedling establishment, differences in the timing of establishment, and regrowth of surviving plants can act to reduce the importance of differential growth rates and efficiencies in the regrowth of vegetation following disturbance.

However, for disturbances that result in a pulse of seedling establishment, differences in the efficiencies of uptake and use of resources by different growth forms should be an important factor in the ability of a woody plant to reach reproductive size.

## ACKNOWLEDGMENTS

We thank R. E. Cook and D. S. Gill for helpful comments on the chapter.

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# The Ecology of Natural Disturbance and Patch Dynamics

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**ACADEMIC PRESS, INC.**

**Harcourt Brace Jovanovich, Publishers**

San Diego New York Berkeley Boston

London Sydney Tokyo Toronto

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**ACADEMIC PRESS, INC.**  
1250 Sixth Avenue, San Diego, California 92101

*United Kingdom Edition published by*  
**ACADEMIC PRESS INC. (LONDON) LTD.**  
24-28 Oval Road, London NW1 7DX

**Library of Congress Cataloging in Publication Data**  
Main entry under title:

**The Ecology of natural disturbance and patch dynamics.**

Bibliography: p.

Includes index.

1. Natural disasters—Environmental aspects.
  2. Biotic communities. I. Pickett, S. T. A.  
II. White, P. S. III. Title: Patch dynamics.
- QH545.N3E28 1985 574.5'22 84-18599  
ISBN 0-12-554520-7 (hardcover) (alk. paper)  
ISBN 0-12-554521-5 (paperback) (alk. paper)

**PRINTED IN THE UNITED STATES OF AMERICA**