Different Respones to Gaps Among Shade-Tollerant Tree Species

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DIFFERENT RESPONSES TO GAPS AMONG SHADE-TOLERANT TREE SPECIES

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Most species of trees in the Eastern deciduous forests of North America can be considered shade tolerant (sensu Whitmore 1975, 1982, Swaine and Whitmore 1988) in that germination and seedling establishment can occur beneath a closed canopy. I propose that the ability to tolerate shade allows a range of responses to disturbances that are qualitatively different from those of intolerant species. Furthermore, quantitative differences exist among shade-tolerant species in their responses to gaps. Differentiation of the responses of shade-tolerant species to gaps has significant implications for general models of forest dynamics.

THE ROLE OF SHADE TOLERANCE IN CANOPY RECRUITMENT

The two extremes of shade tolerance are endpoints of a gradient in the degree to which shade-tolerant species respond to pulses of light created by openings in the canopy. At one extreme, juveniles grow slowly and consistently beneath a closed canopy, but do not respond greatly to periodic openings. Such growth beneath a closed canopy may fill an opening that forms overhead before it is closed by neighboring canopy trees or saplings of faster growing, shade-intolerant species. Eastern hemlock (*Tsuga canadensis* (L.) Carr.) may be the best example of this life history in the northeastern Unites States (Barden 1979, Hibbs 1982, Kelty 1986). However, this gradual form of tree-by-tree replacement appears to be rare in species of this region. At the other extreme, juveniles persist in the understory, but appreciable net growth occurs only following the formation of a gap and increased light in the vicinity. Sugar maple (*Acer saccharum* Marsh.) provides an example of this growth pattern in the northeastern United States (Canham 1985, 1988a).

Differentiation of the responses of shade-tolerant species extends the concept of the partitioning of gap microenvironments (Denslow 1980a, 1987) to include both shade-tolerant and intolerant species. The magnitude of response to gaps appears to be accompanied by a reverse gradient in the duration of periods of suppression that can be tolerated by different species (Poulson and Platt 1989). Hence, no single species appears capable of monopolizing all gaps that occur in forests.

At both ends of the gradient in shade tolerance there appear to be mechanical and physiological constraints on canopy recruitment in the absence of gaps. For species with slow but persistent growth, abrasion of the terminal shoots of understory saplings against lower branches of canopy trees may prevent growth into the canopy (e.g., Wierman and Oliver 1979, Kelty 1986). In addition, the ability to tolerate shade may decline as an individual grows if ratios of photosynthetic to nonphotosynthetic tissues decline as height and crown size increase. For both extremes of the gradient, prolonged suppression or slow growth with a marginal net carbon balance should increase the chances that saplings will succumb to pathogens, defoliation, or episodic drought (Waring 1987) and may also increase the lag time in the response to a future gap (Poulson and Platt 1988).

RESPONSES OF SHADE-TOLERANT SPECIES TO GAP LIGHT REGIMES

Measurements and simulations of gap light regimes demonstrate that enhanced understory light levels can cover a much larger area than the projected outline of a gap on the forest floor (Canham 1988b). For instance, beneath a hypothetical 5 m radius gap (78.5 m^2) in a 25 m tall canopy at 44° N latitude, an area >500 m^2 can potentially receive at least 1% of full sun through the gap over the course of a growing season (Canham 1988b). Since light levels beneath closed canopies are often as low as 1–2% of full sun, the additional light entering through such a gap will increase understory radiation in the vicinity by twofold or more. Such effects will blur the distinction between gaps and non-gaps (also see Lieberman et al. 1989b).

While an additional 1–2% of full sunlight entering through a gap may not trigger responses by shade-intolerant species, it is sufficient to trigger a strong release of understory saplings of shade-tolerant species such as sugar maple and beech (*Fagus grandifolia* Ehrh.) (Canham 1988a). Similar responses occur in juvenile oaks and hickories in southern hardwood forests (Platt

and Hermann 1986). As a result, rates of gap formation calculated from vertically-projected gap sizes will significantly underestimate the frequency of release of shade-tolerant species by gaps (Canham 1985). Thus, even if there were no physiological, morphological, or physical limitations on the ability of shade-tolerant species to reach canopy size in the absence of gaps, most saplings would, at some point, still encounter enhanced light levels from one or more gaps.

The dependence of shade-intolerant species on relatively large gaps is a consequence of their need for both relatively high illumination and openings large enough that a gap does not close laterally before a sapling reaches canopy height. Because of this, gap size has been viewed as a principal axis of differentiation among species (e.g., Denslow 1980a, Hibbs 1982). However, shade-tolerant species may respond to even slight increases in understory light levels produced by the penetration of diffuse radiation through small openings anywhere in the canopy (e.g., Canham 1988a). Coupled with the ability to withstand periods of suppression when no gaps are present nearby, this allows shade-tolerant species to exploit disturbances that create numerous ephemeral, small gaps (e.g., hurricanes; Platt 1987). Thus, in contrast to intolerant species, the fate of individual saplings of shade-tolerant species may depend on the frequency of disturbance and the duration of periods of release vs. suppression more strongly than on gap sizes or light levels per se.

MORPHOLOGICAL VS. PHYSIOLOGICAL RESPONSES TO GAPS

The competitive advantages of rapid growth rates in gaps have been discussed frequently (e.g., Hibbs 1982), and in principle the advantages should apply to both shade-tolerant and intolerant species. However, physiological traits that maximize responses of seedlings or saplings to increased light levels in gaps differ markedly from the traits associated with the ability to tolerate shade (Bazzaz 1979).

Bazzaz (1979) and Bazzaz and Carlson (1982) have suggested that the strongest selection for physiological plasticity should occur in species of open environments, because such plants encounter wider fluctuations in environmental conditions than do plants beneath a forest canopy. In fact, the few shade-tolerant tree species that have been examined do show more limited physiological plasticity than herbaceous and woody species of open environments (e.g., Logan and Krotkov 1969, Bazzaz and Carlson 1982). Nonetheless, limited physiological plasticity in shade-tolerant trees cannot be attributed to a limited range of fluctuation in understory light levels. Sunflecks and the more prolonged pulses of high illumination produced by gaps create pronounced temporal variation in light intensity above that imposed on an open environment by cloud cover and sun position. This suggests that there may be constraints on physiological plasticity in shade-tolerant species, rather than a lack of selection for plasticity in these species. Penning de Vries (1975) has suggested that a high turnover rate for leaf enzymes is a major factor in the ability of plants to acclimate physiologically to variation in light levels. However, a high protein turnover rate often leads to a high respiration rate (Penning de Vries 1975). Consequently, the low levels of physiological acclimation observed in shade-tolerant species may result from a trade-off between acclimation responses and low maintenance respiration rates necessary for shade tolerance in woody plants. This trade-off may be an important component of the differentiation of species along the shade-tolerance gradient described above.

The potential metabolic costs of physiological plasticity do not necessarily extend to plasticity in growth form and canopy architecture, which can often be achieved through fairly simple developmental processes. Both sugar maple and beech grow significantly faster in even very small gaps than they do beneath a closed canopy (Canham 1988a). However, beech has higher growth rates than sugar maple beneath closed canopies, while sugar maple growth rates are twice as high as beech in even small gaps. In even small gaps, sugar maple exhibits a significant increase in sapling leaf area, which results from production of numerous short lateral branches (Canham 1988a). In contrast, the canopy architecture of beech changes very little in gaps. Certainly, changes in canopy architecture incur metabolic costs through the investment in new shoots and foliage. Still, the architectural plasticity observed in sugar maple detracts little from its ability to persist beneath a closed canopy, because those costs are not incurred until the investment is made in response to increased understory light levels.

While morphological plasticity of the sort described for sugar maple may be an important component of the ability of shade-tolerant species to respond to small canopy openings, morphological plasticity by itself may be of limited value in responding to larger gaps when it is not accompanied by physiological acclimation to high light levels. As gap size increases, there is a corresponding increase in the duration of periods of full sunlight in the understory. Many shade-tolerant species are capable of responding to full sunlight with much higher leaf area (e.g., Horn 1971, Canham 1988a). Saplings of these species can experience high average illumination over a large total leaf area as a result of a columnar crown with large leaf and branch angles from a horizontal plane (e.g., McMillen and McClendon 1975), particularly when direct sunlight can be received from many directions. However, in those gaps where

direct sunlight is limited to a short period at a given time of day (and a limited range of incident angles), this architecture may produce much higher self-shading and lower net carbon gain from individual leaves, unless the leaves are capable of relatively high photosynthetic rates during short periods of high illumination. Such rates seem unlikely in the absence of an acclimation response, given the characteristically low, light-saturated photosynthetic rates of shade-tolerant species (Bazzaz 1979).

IMPLICATIONS FOR CANOPY DYNAMICS

The ability of shade-tolerant species to withstand periods of suppression between formation of gaps within localized areas of forests allows a much more complex pattern of canopy dynamics than the simple pattern of gap formation, colonization, and filling that characterizes shade-intolerant species (Whitmore 1975, 1982). In particular, the relative success of shade-tolerant species differentiated along the gradient described above is likely to depend strongly on the frequency and spatial pattern of gaps formed during a period of recruitment into the canopy that may last > 100 yr (Canham 1985, Poulson and Platt 1988).

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

FORESTS ARE NOT JUST SWISS CHEESE: CANOPY STEREOGEOMETRY OF NON-GAPS IN TROPICAL FORESTS

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Widespread interest in the role of gaps in the dynamics of tropical forests was stimulated by the insightful papers of Hartshorn (1978) and Whitmore (1978). Disturbances caused by the death of trees are conspicuous and often dramatic. Gap dynamics remains a leitmotif of research in both temperate and tropical forests. We focus upon a set of stimulating questions raised over a decade ago that have seldom been tested with objectivity and rigor. Differences of opinion still exist regarding the nature, significance, and even the definition of gaps (e.g., Barden 1989). We see two interrelated impediments to progress, one philosophical and the other methodological, and propose solutions based upon our studies of forest dynamics in lowland tropical forest at La Selva Biological Station in Costa Rica (details of the sites are presented in Hartshorn 1983, Lieberman et al. 1985a, b, c, Lieberman and Lieberman, 1989).

The gap paradigm is formulated as a gap vs. non-gap dichotomy of forests. This framework results in a similar orientation for most gap studies: gaps are selected in the field, boundaries delimited, and comparisons of some sort made between the gaps and adjacent non-gap areas. Such comparisons typically, and not surprisingly, show that conspicuous aspects of the physical environment (light, for example) are different in openings and beneath trees. It is also not uncommon to characterize a gap flora by simply determining which species are commonly found in gaps, a procedure by which a species could occur preferentially in the shade and still be viewed as a gap specialist. As a result of the approach, gap studies are often marred by circular reasoning: as Greig-Smith (1983) cogently observed, we cannot test the efficiency of a classification by asking whether results confirm our preconceptions.

Implicit in designs of most studies of gaps is the notion that the non-gap is a standard against which gaps can be evaluated. Notwithstanding the conceptual appeal, considering forests as a Swiss cheese of gaps and non-gaps does not even begin to do justice to the daunting complexity of real forests. In fact, non-gaps are as heterogeneous as gaps. Canopies vary in com-