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LANDSCAPE MOSAICS CREATED BY CANOPY GAPS, FOREST EDGES AND BUSHLAND GLADES

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ABSTRACT. The effects of canopy gaps on forest understory communities are well documented. However, there has been almost no documentation of the effects of gaps on the canopies themselves. Recent research has shown that portions of crowns adjacent to gaps undergo rapid growth, implying an increase in available carbohydrate (due to increased sunlight). It is reasonable to hypothesize that this would also lead to increases in flowering, fruiting, and epiphytic growth in these same crown portions. Limited data from a temperate forest presented here suggest that this is true. If so, gap-edge tree crowns could be hot spots of resource availability for folivores, floral visitors, frugivores, epiphytes, and associates of these species. As yet we have no documentation of these hot spots or how deeply their effects penetrate into the adjacent parts of the canopy. Because of limited access, canopy biology has concentrated on the vertical dimension, but studies in the horizontal dimension are equally important. Using examples from 'gaps' (glades) in an acacia bushland in East Africa and terrestrial temperate forest edges, I show how similar landscape mosaics have highly variable effects on the community, depending on the traits considered. I then consider parallels with forest canopy gaps, and possibilities for future research.

INTRODUCTION

Research in forest canopies has exploded in recent years, fueled by myriad new techniques offering increased access to the treetops (reviewed in Lowman & Moffett 1993). This research has understandably concentrated on the ecology of individual small-scale sites where such access is available. Studies of within-canopy variation have concentrated on the vertical dimension, usually along the axis of canopy access. Although they have a long history, studies in the horizontal dimension have not been part of this recent explosion of research. One area of research in the horizontal dimension is the study of edge effects on the landscape scale. There are good reasons to believe that canopy edges may provide rich heterogeneity on the landscape scale that can strongly influence community structure.

Forest edges are increasingly the subject of ecological study (Ranney *et al.* 1981, Alverson *et al.* 1994, Murcia 1995). It has been of particular interest to document how deeply the effects of non-forest edges penetrate into 'intact' forests. As forests are increasingly fragmented, there is the risk of producing forest fragments that are 'all edge' (Alverson *et al.* 1988). The effects of non-forest habitats penetrate into the forest to varying degrees (Alverson *et al.* 1994). Such effects include changes in seed predation, egg predation (Burkey 1993, Rudnicky & Hunter 1993, Paton 1994), microclimate (Williams-Linera 1990, Matlack 1993), community composition (Fraver 1994), and vegetation structure (Chen 1992). Most of this research has been restricted to the terrestrial effects of forest edge, and have not included the canopy.

Canopy gaps have long been known to strongly influence understory environment (Denslow 1987). When gaps occur, there is a sudden increase in the available light, often a nutrient pulse, and changes in soil temperature and moisture. These conditions provide opportunities for a flush of vegetative growth. Many of these gap species are fast growing and palatable (and near the ground). Canopy gaps are, in this sense, terrestrial hot spots of resource availability for a variety of plants and animals. However, canopy gaps may provide arboreal hot spots as well.

Tree branches on the edges of canopy gaps grow faster and are larger (Trimble & Tryon 1966, Ranney *et al.* 1981, Runkle & Yetter 1987, van der Meer 1994) than branches in the same crown that face away from the adjacent gaps. This produces asymmetrical crowns (Rogers 1989, Young & Hubbell 1991), and may lead to local increases in resource availability, most likely through increased light levels.

Horticultural scientists have long known that variation in light within and among tree crowns is correlated with variation in vegetative growth and reproductive output (Jackson & Palmer 1977a,b, Doud & Ferree 1980). For example, in cultivated walnuts (*Juglans regia*), unshaded shoots produced more flowers and more fruits than shaded shoots (Klein *et al.* 1989), and this was related to increased nitrogen flux (Weinbaum *et al.* 1991) as well as to apparently increased photosynthesis. However, there is little evidence that variation in reproduction within crowns of non-agricultural species is associated with differences in available light. Bertin (1982) found that shaded inflorescences had fewer female flowers (compared to less costly male flowers) than unshaded inflorescences within plants in buckeye (*Aesculus pavia*).

The relative independence of different branches on plants has been called autonomy, or sectoriality (Watson & Casper 1984). There is considerable evidence that plant modules (i.e., ramets, branches, inflorescences, or infructescences) are semi-autonomous, and that increased resource availability for a given part of the plant may be mostly used locally, rather than shared among all modules equally. It is therefore likely that local (within-crown) differences in resource availability will be expressed not only in greater growth, but in greater reproductive output. Here I present evidence from a temperate deciduous forest that this is the case.

This paper is not intended as a detailed empirical description of forest canopy edges. Instead, I use preliminary data and patterns recently documented in a semi-arid ecosystem in East Africa to illustrate my ideas about the landscape ecology of forest canopies, and I compare terrestrial forest edges, canopy edges, and glade edges in savannas. I not only propose an approach to canopy studies that is more horizontal, but also a canopy science that is less driven by techniques of canopy access, and more driven by conceptual issues.

METHODS

I surveyed five woody species in the vicinity of the Louis Calder Center of Fordham University in Armonk NY in October 1994. The Center contains over 100 acres of secondary deciduous forest and a small lake. The forest is 50–100 years old, and is dominated by oaks (*Quercus* spp.), maples (*Acer* spp.), black birch (*Betula lenta*), and beech (*Fagus grandifolia*). Numerous artificial forest edges are provided by roads, mown lawns, and parking areas.

I counted the fruits or inflorescences of five to ten branches on each of one to three individuals of five woody species growing at artificial forest edges. I sampled branches growing away from the forest, growing lateral to the forest edge, and growing into the forest. I measured the diameter of each branch. The reproductive output of each branch was weighted by its size to control for size differences among branches.

From October 1993 to April 1995, I carried out four experiments to document seed and egg predation relative to forest edges at the Louis Calder Center. Three different forest edges were used. In each experiment, piles of seeds (three or four walnuts) or three or four quail eggs were placed at forest edges and at ten meter intervals into the forest. These eggs or seeds were visited every two to four days thereafter, until at least half of the food items were taken. Previous studies showed that human scent did not effect egg predation rates (Hoi & Winkler 1994).

RESULTS

For all species surveyed, branches growing away from the canopy had significantly greater reproductive output than branches growing toward the forest interior ($p < 0.05$ for each species; Figure 1). Lateral branches were sometimes intermediate in reproductive outputs, and sometimes had reproductive outputs more similar to either gap branches or forest interior branches, depending on species.

Patterns of seed and egg predation were consistent across all four experiments (Figure 2). Eggs were more likely to be taken near edges, and seeds were more likely to be taken toward the interior of the forest.

DISCUSSION

The canopy reproduction results described here represent a small sample of trees in one disturbed ecosystem. But they parallel results obtained in horticultural systems (Jackson & Palmer 1977a,b, Doud & Ferree 1980, Klein *et al.* 1989). It appears that canopy edges represent areas rich in carbon and nutrients, and that this richness produces branches with more young leaves, more flowers, and more fruits.

If branches growing into canopy gaps have greater reproduction and support more epiphytes and animals, this would exacerbate crown asymmetry. Not only would crowns be larger on the gap-edge sides of trees, they would be relatively heavier. Trees with asymmetrical crowns have been demonstrated to have increased tendency to fall (Young & Perkocha 1994) and a tendency to fall in the direction of asymmetry (Young & Hubbell 1991, Young & Perkocha 1994). The added burdens of increased flowers, fruits and epiphytes should reinforce these patterns in addition to what might be expected from difference in crown shape alone.

Of interest at the community level are the consequences for those species that visit flowers, eat fruits, are epiphytes, or otherwise rely on these hosts. If canopy edges are arboreal hot spots for vegetative and reproductive growth, then they should also be hot spots for all those species dependent on those resources.

The results of the seed and egg predation experiments are consistent with other research. In a wide variety of studies, predation rates on artificial nests were greatest near forest edges (Paton 1994). In the only other study of forest edges

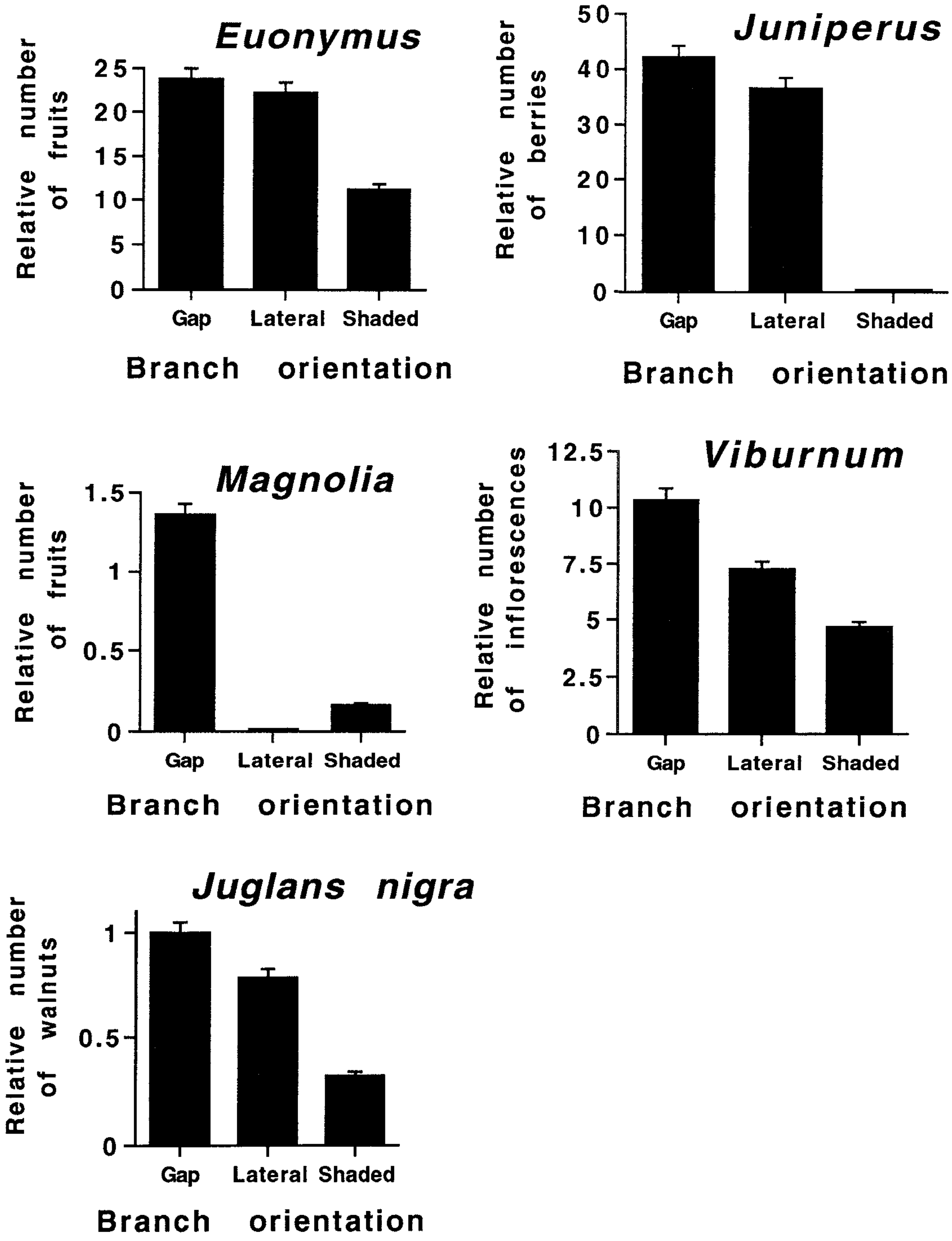


FIGURE 1. Relative reproductive outputs of branches facing gaps, lateral to gaps, and facing away from gaps, for five woody species in the vicinity of the Louis Calder Center of Fordham University, Armonk, NY. Values have been weighted by branch size. The gaps surveyed were forest edges maintained by humans. Bars represent one standard error.

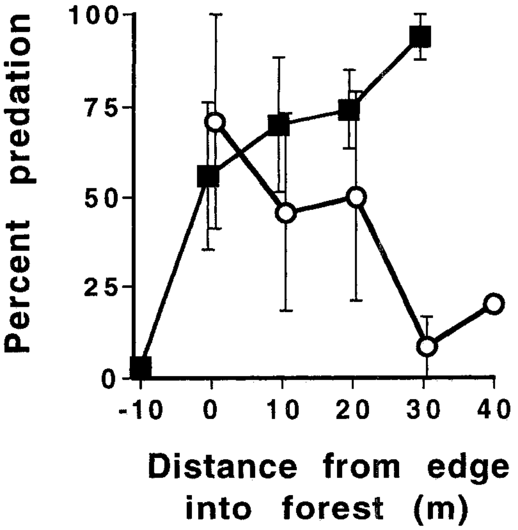


FIGURE 2. Rates of predation of artificial nests and seed piles placed on the ground at differing distances from forest edges in Armonk, New York. Open circles are quail eggs, and solid squares are English walnuts. Points are the means and standard errors of result from four field seasons from October 1993 to April 1995.

to examine at seed predation as well as egg predation (to my knowledge), Burkey (1993) similarly demonstrated greater egg loss near a forest edge and greater seed predation toward the forest interior, in a Panamanian rain forest. Several carnivore species prefer forest edges (Alverson *et al.* 1994). Seed predators may avoid edges either because of these carnivores, or because forest edge plants are less likely to produce large seeds. Do these patterns of seed and egg predation relative to edge also occur in the forest canopy? No one has looked.

Edge effects at the landscape scale

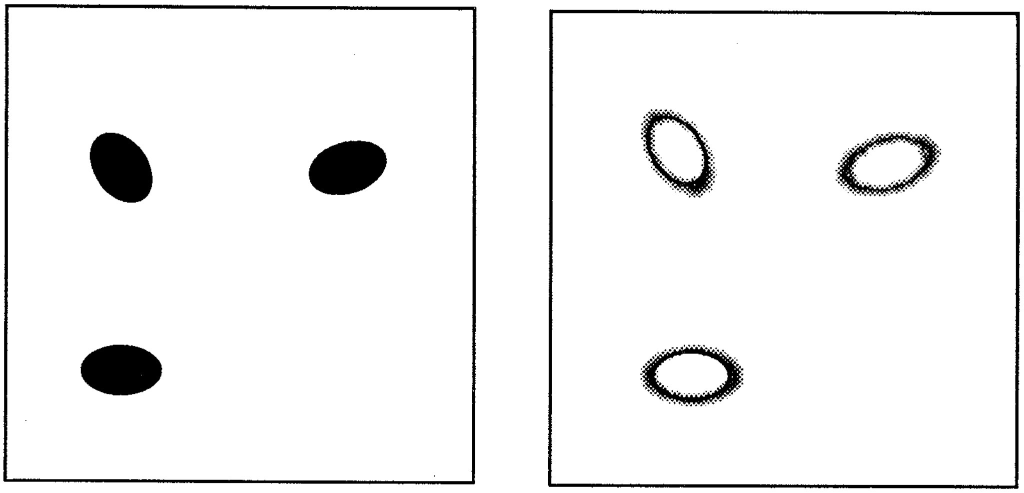
Traditionally, most studies of community edges have asked how these edges (often called 'ecotones') are different from their adjoining communities. Recently, there has been increased emphasis on the question of how deeply the effects of one community penetrate into another along their mutual boundaries. This literature indicates that different species respond in different ways to the edges in landscape mosaics (Alverson *et al.* 1994). I have documented the range of this variation in a landscape mosaic that is superficially very different from forest canopy edges, but which suggests the kinds of patterns one might expect to find in any mosaic landscape. I offer this comparison as a small step in the direction of a synthesis of edge effects in disparate systems.

ACACIA BUSHLAND. Throughout the Laikipia plateau in central Kenya, there occur isolated glades embedded in a landscape dominated by acacia bushlands and woodlands. In terms of vegetation and soils, these glades are distinctly different from the surrounding bushland, including open areas between individual trees and shrubs. These glades are characterized by a lack of woody vegetation, and by low herbaceous cover of prostrate grasses and forbs; they are often surrounded by a dense ring of tall grass. These glades are preferred grazing sites for a wide variety of large mammals. They appear to be the sites of cattle enclosures of pastoralists who left this area over 70 years ago (Young *et al.* 1995).

The glade edges are superficially abrupt, but many of their effects penetrate into the surrounding acacia bushland. I carried out a detailed survey of this landscape mosaic (Young *et al.* 1995). By running transects from each of several glades 200 m into the surrounding bushland, as well as through the bushland ('background'), I measured understory and overstory vegetation, density of large mammal dung, and soil chemistry.

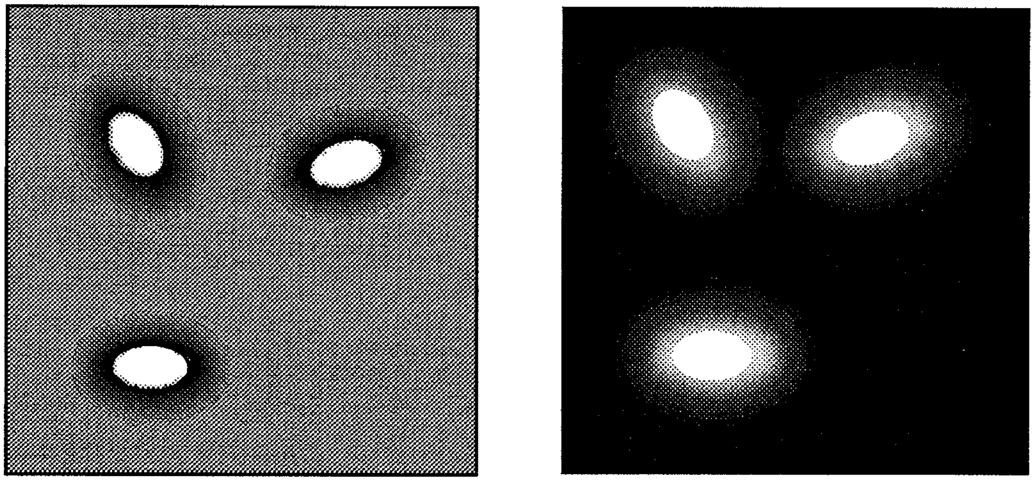
Each of these traits responded to glade edges in different ways, some positively and some negatively, some abruptly and some gradually, some near glade edges and some at great distances from glade edges (Young *et al.* 1995). For example, some plant species were restricted to glades, whereas others were found everywhere except glades. Of those not found in glades, some reached background densities very near glade edges, and some only gradually at 50–100 m from glade edges. The shrub *Croton dichogamous* was absent from within 200m of glade edges, then abruptly reached background densities. The dung of most large herbivores was most common inside the glades, gradually decreasing with distance from glade edges. However, the distribution of zebra dung paralleled that of the tall grass *Pennisetum stramineum,* with both being most common at glade edges. Some herbivores (hares and guinea fowl) seem to be glade specialists, foraging almost exclusively inside glades. The net result of these individual plant and animal responses is a landscape mosaic that takes on many different appearances, depending on the trait or species considered.

FOREST AND CANOPY EDGES. Similar patterns are to be expected in forests with canopy gaps. Based on the patterns in Figure 1, we may consider the forest canopy to be a mosaic consisting of background regions of general resource availability, and rings of high resource availability around canopy edges (Figure 3c). This is paralleled by a similar mosaic on the ground, which differs in



a. *Gap specialists*

b. *Gap edge specialists*



c. *Species that favor canopy edges*

d. *Species suppressed near gaps or gap edges*

FIGURE 3. A mosaic landscape from the perspective of different species or resources: a) understory gap specialists; b) understory or overstory gap edge specialists; c) overstory species using resources more available at gap edges; d) understory or overstory species suppressed by gap specialists, gap edge specialists, or other aspects of gap environments. Adapted from Young *et al.* (1995). Dark coloration represents areas of high abundance or desirability, and white coloration areas of low abundance or desirability. Shades of gray represent more or less gradual transitions between areas of high and low abundance.

part by having high resource levels inside the gaps as well as at their edges.

However, each species experiences this landscape mosaic in a different way. Here I highlight four possible classes of patterns. First, for understory gap specialists, the landscape is a sea of inhospitable habitat with isolated favorable sites (Figure 3a). Examples include heliophilic plant species and the animals that eat them, such as pygmy antelope (*Neotragus batesi*) in African forests (J. and T. Hart, personal communication).

Second, for understory or overstory gap edge specialists, the landscape is restricted to narrow rings around gap edges (Figure 3b). For overstory species using resources more available at gap edges, the landscape is generally available, but especially so at gap edges (Figure 3c). An example may be the *Anolis* lizards that feed on the flying insects blown out of canopy gaps (Dial 1994), or any species that specializes in new leaves, flowers or fruits. If we accept egg predation results as a bioassay of egg-predator abundance, egg-predators are apparently more abundant near terrestrial forest edges (Figure 2). In both temperate (Figure 2, Paton 1994) and tropical (Burkey 1994) forests, experimental seed piles on the ground near forest edges are more likely to escape predation, potentially making these edges hospitable sites.

Finally, for understory or overstory species suppressed by gap specialists or gap edge specialists, the landscape is a sea of hospitable habitat punctuated by islands of inhospitable habitat of varying sizes, depending on the depth of the edge effect (Figure 3d). Okapi (*Okapia johnstoni*) apparently reduce the abundance of some plant species in the vicinity of gaps (J. Hart and T. Hart, personal communication). Similarly, *Anolis* lizards may reduce the abundance of secondary prey species in parts of the canopy where they are most abundant, such as gap edge canopies (Dial 1994). Egg predation is higher in the vicinity of forest edges (Rudnicky & Hunter 1993, Burkey 1993, Paton 1994, Figure 2), making forest edges inhospitable places for ground nesting birds. Similarly, lower seed predation near forest edges (Figure 2, Burkey 1994) implies that seed predators avoid these sites. In addition, there may be species that do not fare well in the high light (low moisture?) environment of canopy gap edges. We are only beginning to gather the information that will allow us to recognize broad landscape patterns in the canopy, and we will undoubtedly find many more examples of the importance of forest edge for canopy community structure.

Although I have described these edge patterns in two horizontal dimensions, it is clear that there can be vertical dimensions as well, especially at canopy gaps. In the words of a perceptive reviewer, the distribution of gap edge specialists 'is not a circle, nor a halo, but more like a cylinder'. This third dimension should be more evident at forest canopy edges than at the 'vertically challenged' edges that have been the subject of terrestrial studies.

Clearly, many of these underlying patterns apply to human-created forest edges as well as to natural treefall gaps. Artificial edges may differ from natural edges in at least two ways. First, they are likely to be more permanent. Even if treefall gaps tend to recur repeatedly at the same sites (Young & Hubbell 1991), they should still be more transient overall than artificial forest edges formed by roads or agricultural clearing. The vertical component of canopy edges is likely to be particularly well-developed where edges are long-term, as illustrated by the 'jungle effect' of river edge forests. Second, the negative microclimatic effects of large-scale permanent forest edges may be greater than in natural treefall gaps, especially in the form of increased desiccation (Williams-Linera 1990, Matlack 1993).

A SYNTHETIC VIEW OF EDGES IN LANDSCAPE MOSAICS. Common to all of these edges (canopy edges, terrestrial forest edges, savanna glade edges) are three quantifiable observations: 1) Species differ in having either positive or negative (or neutral) responses to the proximity of edges. 2) The effects of communities do penetrate beyond their superficial 'boundaries', sometimes deeply. 3) Species differ in the 'depth' of these effects, and in whether their response to edges is gradual or abrupt.

There is likely to be a finite set of classes of edge responses, which can be fully described. A subset of this complete set is shown in Figure 3, and a fuller subset in Young *et al.* (1995). The description of a complete set, and an agreement on terminology, will go a long way toward unifying edge studies at the landscape scale into a useful synthesis.

THE FUTURE OF CANOPY RESEARCH. In its current incarnation, 'canopy biology' has been dominated by two characteristics that limit its scope and generality. The emphasis on techniques of close access to the canopy has come at the expense of a science more driven by concepts, and has also resulted in an over-emphasis on measurements in the vertical dimension—the 'axis of access'.

Most canopy research has studied patterns in the vertical dimension. There are two reasons for this. First, one of the key questions has been, 'How does the canopy differ from the understory?' This is largely a natural history question, and thus far most canopy research has been descriptive rather than manipulative, and data-driven rather than concept-driven. Second, techniques of access to the canopy have been better suited for asking vertical questions than for asking horizontal questions. However, the canopy is a sea, not a well, and if we are to understand it, we must also study it in the horizontal dimension.

At least three kinds of canopy research are active in this horizontal dimension. 1) The use of fogging allows the sampling of canopy insects over a broad range of sites (Erwin 1994, Longino 1994). 2) Primate ecologists study animals that move broadly in the horizontal dimension, and they have detailed information on forest canopies—phenology, herbivory, seed predation and dispersal, and the ranging and foraging behaviors of one of the canopy's most important mammalian guilds (e.g., see Struhsaker 1975, Milton 1980, Isbell 1983, Yeager 1989, Strier 1992). 3) Studies of canopy architecture, structure, and development have a long history (Trimble & Tryon 1966, Runkel & Yetter 1987, Young & Hubbell 1991, Herwitz & Slye 1992, van der Meer 1994, Vester 1994).

All these types of research share a common trait: they are done from the ground (or air). Although this limits close access to individual leaves, flowers, insects, and herps, it does allow greater mobility, at least in the horizontal dimension. Ecologists studying canopy birds and mammals will need to have 'access' to the canopy over a wide horizontal range, and this will probably mean that they will continue to work from the ground. The landscape approach described in this paper will likely be pursued both from accessible canopies (for fine-scale questions of canopy edges) and from the ground (for broad-scale patterns). We need to develop not only techniques for close access to the canopy, but also techniques that make canopies more 'accessible' for researchers who need to work from the ground (Ungar *et al.* 1995). Fogging is one such technique. Explorations of the use of global positioning systems (Wilkie 1989) and radio-tracking (Campbell & Sussman 1992) in forest environments are also valuable.

Not all canopy research will be done from ropes, cranes and balloons. It has been said that molecular biology is not a science, but a set of techniques. We must be careful that the same is not said for canopy biology. We must not only ask the question, 'Now that we have access, what can we study?', but also, 'What do we need to know about the canopy (and the biological world in general), and what techniques do we need to use to find this out?' I propose that canopy science be less driven by techniques, and more driven by theory (broadly defined), more experimental, and of course, more horizontal.

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