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THE NATURE AND LIMITS OF CANOPY BIOLOGY

MARK W. MOFFETT

Museum of Vertebrate Zoology, University of California, 3101 Valley Life Sciences,
Berkeley, CA 94720, USA.
E-mail: moffett@uclink4.berkeley.edu

ABSTRACT. The way ecologists studying forests choose to define canopy biology could lead them to overlook other communities of spatially fixed organisms that may have properties usefully compared to or contrasted with forest canopies. This paper represents a series of reviews on the possible nature and limits of canopy biology and introduces the prospect for a general comparative science of biological canopies.

- Five rationales for the common practice of limiting discussions of canopy biology to terrestrial forests are considered: if people have unique interactions with or concerns about forest canopies; if a substantive basis exists for treating trees as a distinct category of plants; if a substantive basis exists for treating trees as a distinct category within forests; if a substantive basis exists for treating forests as a distinct category of terrestrial community; or if attributes of tree crown residents or ground-rooted plants in a forest prove distinct. In no case is there unequivocal evidence for the usefulness of separating the study of forest canopies from the study of the aerial parts of other terrestrial plant communities.
- Instead of restricting the sphere of canopy biology to plants in terrestrial systems, "canopy" can be defined in terms of any sessile organisms and the structural products derived from them. This opens the field to a range of communities that could share many properties with forest (or plant) canopies. A brief review is made of the canopy literature on kelp forests, algal turfs, periphyton, biofilms, and coral reefs. The word "canopy" has already been applied to each of these ecosystems, and biofilms in particular have great potential as model systems for studying assembly rules for canopy physical structure.
- In mainstream ecology the organisms of a community are typically studied in two dimensions, or as points on the earth. Canopy biology can in large part be distinguished as the science of treating plants (or other sessile hosts) as three dimensional, although the discipline encompasses all aspects of scientific study of the portion of a community that project into a medium.
- In many studies involving canopy species, the organisms' relationship to the canopy is treated as incidental. "Putting the canopy into canopy biology," that is, contributing fundamentally to canopy biology as an independent discipline, requires that aspects of biology specific to the canopy form an integral part of the research. Six approaches are proposed for putting the canopy into canopy biology: issues of community ecospace; properties emerging from a community in aggregate, such as stratification of microclimate; host distributions; host architectures; properties of a canopy's structural elements; and characteristics of the open spaces within a community.
- Much of the language and thinking of terrestrial canopy biology has been predicated on notions of plants as supports for other organisms. Structural support between individuals occurs as well in the rhizosphere, reminding us that distinctions between aboveground and belowground plant parts can be arbitrary. For example, in many ways it would be logical to define words such as "epiphyte" so that they apply to a plant in its entirety. For many research concerns, this idea suggests the validity of transcending canopy biology to fashion a more comprehensive science of plant associates, referred to here as "structural ecology," congruent with the approach used in animal parasitology or marine epibiosis.

Key words: algal turf, biofilm, biodiversity, biomechanics, canopy, community, coral reef, ecology, ecosystem, epiphyte, forest, kelp, periphyton, rhizosphere, stratification, structural support, tree

INTRODUCTION

Words compartmentalize information, and that has many repercussions (Lakoff 1987). This is true for how we identify subjects for academic study as well (Bates 1960, Hull 1988). The word "canopy" has been applied to vegetation in varied ways (Moffett 2000), leading to varied interpretations of the domain of canopy biology. To pick one example, if by "canopy" we mean the highest plant surfaces in a forest, as many authors do (e.g., Kritcher 1997; the "outer canopy"), it is likely that, out of habit, we as canopy biologists will develop a search image effective at picking out information on that subject. Our knowledge of parallel and potentially useful studies on shrubs and herbs, whether in forests or in other systems, or studies on the lower parts of forest trees, is likely to be marginalized. Philosopher W.T. Jones (in Bateson 1972) describes this as the "topography of ignorance." This intellectual fragmentation is borne out by the literature. For example, citations on stratification in herbaceous communities such as Monteith (1975, 1976) tend to be scarce in forest canopy publications. A consequence of this can be independent discoveries along parallel research tracks by different academics, such as those working in agriculture, economic entomology, or landscape ecology, needlessly wasting time and effort.

How then to define the boundaries for a discipline? While any "conceptual framing" can be arbitrary and subjective (Bohr 1955), criteria most likely to be compelling are those of general import to practitioners across a field for which relatively abrupt or unambiguous shifts occur in content or perspective. This is the case for the shift from mind to community that distinguishes psychology from sociology or the shift from molecules to structural integration that distinguishes biochemistry from cell biology. In this respect, it makes little sense to grant canopy biology an independent status as a discipline if by "canopy" we specifically mean "outer canopy," given that most aspects of the biology of that part of the forest grade in a continuous way with those found among the plant organs lying beneath the topmost foliage. This is not to deny, however, that some biologists will need to concentrate on the outer canopy because of its relatively pronounced features, such as the disproportionate significance of the upper leaves to forest productivity.

Is there any basis then for a preference on how we delineate canopy biology as a discipline? I will pursue the possibility that trees or forests are distinct from other terrestrial vegetation. Then I consider modifications of the definition of "canopy" that would encourage canopy biologists to compare environments previously ignored by forest-working ecologists, such as coral reefs and bacterial films. Following this I present unifying themes for an expanded canopy biology. To conclude I address the ramifications of conceptions about structural support and physical intimacy that can underlie many of our views about canopy residents.

SEEING THE FOREST FOR THE HERBS

Whereas often the word "canopy" is applied to the upper parts of forest ecosystems, I previously argued for approaching canopy biology broadly, so as to incorporate the literature on all aerial parts of any terrestrial plant community. We should adhere to this approach except when dealing with "concepts or situations necessarily restricted to trees"(Moffett 2000). In fact, no one to date has specified any rationale for the common practice of restricting the scope of canopy discussions to trees or to forests, as in the useful distinction made between "tree canopies" and "forest canopies" by Shaw (1996). Consider five criteria by which forest canopies could merit this kind of separate attention:

1. Humans have unique interactions with or concerns about forest canopies. There are grave concerns about extinction of canopy species, and there is great interest in the value of canopy products to societies past, present, and future. Because conserving the top of a forest is not possible without conserving its bottom, however, conservation issues are sensibly considered not specifically as canopy biology, but under the general rubric of ecology, which encompasses aspects of economics, ethnography, and conservation.

2. There is a substantive basis for treating trees as a distinct category. The diverse suite of characteristics associated with trees serves "as an example of the molding of the entire phenotype by selection pressures" that has come about convergently in numerous lineages (Niklas 1997). The ecological impetus discussed most often in reference to plant height is competition, especially for light (Tilman 1988, Givnish 1995, Leigh 1999), but the basic question of "treeness" per se may be primarily biomechanical (Niklas & Kerchner 1984). Any self-supporting terrestrial plant growing beyond a certain height appears to be channeled into evolving a main vertical trunk built of the stiffest available structural elements (especially around its perimeter), surmounted by a branched crown. In short, it becomes a tree. The transformation seems to occur in a similar way under diverse environmental conditions, and is a result of shifts from small herbaceous structural designs to one that allows large upright plants to cope with bending or torsion (Niklas 2000). If there is a critical point in this transformation at which many of these changes occur synchronously during the evolution of increasing mass or stature, e.g., 3–5 m in height (Givnish 1983), then the tree bauplan could be sufficiently distinct to treat the study of the canopies in tree-dominated ecosystems (forests) as an independent research discipline. Although this issue appears central to our very conception of "tree," it remains unresolved (Givnish 1984). Consider that trees allocate a large portion of their photosynthate to supportive tissues, and they pay a high price in aerodynamic drag, friction during fluid transport, and increased potential for structural failure if they have high crowns (see Vogel 1996). Given the character of woodiness and apparently also treeness has been labile in plant evolution (Judd et al. 1994, Dodd et al. 1999), because of the costs we would expect that plants would readily lose the tree bauplan where doing so would increase fitness. This would be true even if this growth form was once adaptive, for example by being the heritage of a forest-dwelling past. Nevertheless, trees in deserts, savannas, and other open ecosystems grow extremely tall even though they occur widely separated from neighbors and so by ecological criteria seem conspicuously overbuilt. Trees in these situations may be large because they store water in their trunks (Holbrook 1995); depend on height to avoid herbivory, as arborescent cacti do from tortoises (Dawson 1966) and acacias do from giraffes (Brooks & Owen-Smith 1994); are maximizing reproductive dispersal (Richards 1986); are avoiding damage from fast-moving ground fires (Givnish 1995); or are shading out grasses that compete with them for water (Walter 1973). Yet such factors appear neither pervasive nor severe enough to explain the almost ubiquitous occurrence of dispersed trees that are radically taller than other plants in their communities. For example, giraffes always forage below 5 m, whereas savanna acacia trees often exceed 20 m in height (T. Young pers. comm.). Plant evolutionary mechanics could hold the key to this apparent mystery, and further investigations in this area might thereby shed light on the nature of "treeness" itself.

3. There is a substantive basis for treating trees as a distinct category within forests. Although adult trees are usually assigned to separate strata from other plants in a forest, the question of whether they are distinct as a group or are part of a continuum with other, smaller forest plants has not been clearly resolved, in part because of inconsistencies among the research approaches to stratification (Parker & Brown 2000). In a frequency distribution of the size of mature vascular plant individuals in a forest, is there a distinct peak corresponding with trees? Size-frequency distributions are common in studies of animal diversity but apparently are absent for plant communities, presumably because modular construction and indeterminate growth can make plant size difficult to assess.

4. There is a substantive basis for treating forests as a distinct category. Forests could be considered a distinct category if by some parameter of community physiognomy they can be separated out nonarbitrarily from other terrestrial ecosystems. For example, I have the impression (perhaps it is merely the observational bias of a human-size species) that when scarce height extremes are excluded (recent treefall gaps in mature forests or trees in savannas), most communities are either much shorter or much taller than human height. Suppose we graph some measure of overall community height, say, the modal height reached by the vegetation averaged over randomly chosen points on the ground for each major community type in a classification of ecosystems. Suppose the distribution indeed turns out to be bimodal, such that forest systems represent a distinct peak. This would suggest that forests are more than an arbitrary construct that humans have split off from a continuum of natural communities. Perhaps forest canopies can be distinguished as a separate research discipline on that basis, but in fact no information seems to exist on patterns of overall height across communities. A practical difficulty to such an effort would be if available classifications are biased with respect to height (for example, if ecosystem taxonomists have been "splitters" with respect to forest communities), or if community categories are largely artificial, at best representing opportunistic associations of species (Brown 1995).

5. Attributes of tree crown residents or of ground-rooted plants in a forest prove distinct. If future studies of scaling effects on canopy residents demonstrate that trees harbor communities distinct in some fundamental and reasonably abrupt way from those dwelling in progressively shorter kinds of vegetation, that might be taken as evidence for distinguishing forest canopies as a distinct kind of biological entity. This seems unlikely, however, given that most resident canopy organisms respond not to height but to environmental factors that happen to correlate with height (Moffett 2000). Thus epiphytes seemingly associated with high forest canopy situations occur closer to the ground where conditions allow (McCune 1993, Benzing 2000). Biodiversity in forest canopies can be extreme, but given that most inventories of biodiversity to date have been made in tree crowns (e.g., Stork et al. 1997), the relation between species diversity and community scaling is likewise open to question. For any given latitude, how much of the high diversity of forest-canopy-dwelling species can be attributed to these canopies offering a relatively large overall mass, surface area, productivity, or microhabitat richness? There is also little basis to date for asserting that the organizational principles manifested by ground-rooted plants in forests (such as in the way the trees distribute horizontally or vertically) could be distinct from those operating in other communities, beyond matters of scaling that might be expected to vary in a reasonably continuous manner with successively shorter vegetative types (Moffett 2000).

In summary, no unequivocal basis is apparent for the common practice of treating forest canopies independently from the study of the canopies of other terrestrial plant communities, although further investigations of the nature of trees and forests may prove me wrong.

MORE TO POND SCUM THAN MEETS THE EYE

The essence of knowledge is generalization.
(Reichenbach 1951)

Incorporating into canopy science all studies of all aboveground (aerial) plant organs and their occupants within any community, natural and agricultural (Moffett 2000), is taken as a given in this article, and represents only a first step in the development of a truly comparative discipline. Indeed, widely unappreciated by terrestrial "macrobiologists," the word "canopy" is used extensively by aquatic and microbial scientists to describe ecosystems that share many properties with terrestrial plant canopies. Below is a preliminary synopsis of the canopy studies on several of these systems, especially those pertaining to the community-level physical structure of the sessile hosts, which, in contrast to hosts in terrestrial systems, are typically algal species and zooxanthellae-bearing animals rather than vascular plants (for an exception, see the review of seagrass communities, including issues bearing on canopy structure, by Williams & Heck 2001).

To encompass these kinds of hosts, "canopy" can be redefined from Moffett (2000) as the parts of any community of sessile organisms that emerge from a substrate. Canopy biology (or canopy science) is by this criterion the study of that portion of the community, including the organs of the sessile individuals and any affixed products of those organisms, and anything in, on, or between those organs and products. The affixed "products" can be dead organisms (such as tree snags), the skeletons of living corals, and algal mucilage.

In this article, "sessile" describes an organism that emerges from or adheres to a substrate at positions fixed over a large part of its life history. "Substrate" refers to any surface or structural matrix that provides points of attachment for a sessile species, fixing the location of individuals or colonies. The substrate thereby establishes the spatial relations between sessile individuals, including to some degree the organs that project into the fluid medium (the "canopy structure"); in turn, the sessile communities variously transform and stabilize the substrate (e.g., Stevenson 1996). (Many authors have applied "structure" and "architecture" to communities less literally than I have here, for example to nonphysical attributes of organization, such as to niche spaces and tropic hierarchies: e.g., Connell 1975). The substrate typically is a solid, but the air-water interface may give some level of stability to the relative position of organisms, such as in floating algal mats (metaphyton). I exclude from the canopy communities or portions of communities distributed entirely within the substrate matrix, as in the terrestrial soil community or its aquatic equivalent, the epipelic or bottom sediment community (consider for example the microphytobenthos: MacIntyre et al. 1996). I also exclude organisms located outside the canopy in the medium, namely most plankton or aerial plankton. As discussed in a later section, for many purposes these distinctions can be arbitrary. For example the same morphological adaptations of algae for attachment to substrates may be used for attachment to other algae to produce colonies in suspension (Stevenson 1996).

In some situations, the canopies of "different" ecosystems may be studied as one. In the shade of a forest, stream-dwelling algae may show some of the same physiological adaptations as understory terrestrial plants (Robinson & Minshall 1986, Hill 1996).

Kelp Canopies

Describing kelp communities off South America, Darwin (1839) wrote, "I can only compare those great aquatic forests of the southern hemisphere with the terrestrial ones in the inter-tropical regions." The term "kelp forest" has been common in the literature ever since. Application of the term "canopy" to kelp began with Jack Kitching, who, using a milk can with a window made from an old glass cookie box, was the first scientist to successfully dive into this ecosystem (Kitching et al. 1934). The human-biased perspective of experiencing a matrix of sessile organisms from within may be significant in the choice to apply the word canopy to systems such as forests or kelp (Moffett 2000).

In these and other algal communities, there is a relationship between canopy height and algal growth form (Neushul 1972, Hay 1986, Steneck & Dethier 1994). All kelp forests convergently accommodate guilds of species that fall into five distinct "canopies," or strata (including coralline crust as a stratum: Dayton 1985) (FIGURE 1). The largest and most complex canopies occur in shallow, productive sites (Vadas & Steneck 1988), however, as might be predicted given that water attenuates light sharply as compared to air in terrestrial communities. Indeed, illumination declines logarithmically as it passes through water, as it can passing through either aquatic or terrestrial vegetation as a result of shading, but of course in the former case attenuation occurs over a much larger scale.

Many findings from kelp forests parallel those for terrestrial communities, such as the following: light attenuation through strata in relation to frond coverage (Gerard 1984), which at the benthos beneath kelp communities often declines to ca. 1% of surface light, as is common in tropical rain forests (Richards 1996); the importance to succession of disturbance and gaps (Neushul 1971, Foster 1975, Dayton 1975a, Hurby 1976, Pearse & Hines 1979, Reed & Foster 1984, Dayton et al. 1999); the importance of sun flecks to understory growth and survivorship (Wing et al. 1993); differential survivorship resulting from the shading of benthic plants (Kastendiek 1982, Santelices & Ojeda 1984, Dean et al. 1989) and phytoplankton (Borchers & Field 1981); and other diverse competitive effects leading to specialized shade-tolerant (understory) communities (Dayton 1975b, Dayton et al. 1999). Unless predation is severe, sessile animals may outcompete kelp in low-light conditions in deeper parts of the benthos (Foster 1975), a pattern that holds to some extent in understory shade in shallower waters, though low-light adapted algae also occur there. Dayton (1971) distinguishes competition for space on the substrate ("primary space") from competition within the volume above that surface, that is, within the canopy ("secondary space"), a concept worthy of widespread application. Because of their flexible tissues, kelp and other (Carpenter 1986) algal communities could in some ways be more ecologically comparable to grassland than to terrestrial forest (but see Holbrook et al. 1991), even though kelp can rise 50 m or more in height. Because of their reliance on the opportunities for flotation offered by water, the capacity for upward growth in kelp is of course greatly enhanced over nonwoody terrestrial plants.

There have been general studies on the relation between canopy residents and kelp forest structure. Many fish stratify in kelp forests, although this generally becomes less pronounced as the fish mature (Anderson 1994). Manipulations of physical structure are common in the study of kelp communities, showing for example that simplifying canopy structure can increase fish mortality by removing refuges (Anderson 2001). Predators can be so efficient at feasting on prey passing through kelp canopies that recruitment to ecosystems closer to shore is strikingly reduced (Gaines & Roughgarden 1987). Shading by the kelp overstory can reduce algal growth rates in lower strata, thereby altering the abundance of some fish relative to canopy gaps (Carr 1989, Schmitt & Holbrook 1990, Jones 1992). In algal mats on boulders and within tide pools, canopy-resident diversity relates to algal architectural complexity (Dean & Connell 1987, Hacker & Steneck 1990). For a successional study of this kind of ecosystem, see Sousa (1979). Williams & Seed (1992) review the positive and negative effects of epiphytic animals on large algae.

Periphyton and Algal Turf Canopies

Periphyton (aufwuchs) constitute a "complex community of microbiota (algae, bacteria, fungi, animals, inorganic and organic detritus) that is attached to substrata" (Wetzel 1979, 1983). They are the microbial equivalent of an epiphyte mat. Indeed, periphyton can be epiphytic (Ruinen 1961, 1975, Morris et al. 1997, Claflin 1968). For the rhizosphere equivalent, see Pearce et al. (1995). "Periphyton" also applies, however, to growth on nonliving or deceased substrates, such as submerged leaf litter and carcasses that teem with predictable successions of microorganisms. Periphyton "have extensive vertical development on a small scale, and cells within the community matrix are tightly packed" (Boston & Hill 1991). They show a repeatable pattern of succession (Lowe et al. 1996). This pattern can be disrupted by a high disturbance regime as occurs with communities on the surface of sand grains (Miller et al. 1987) except when algal mucilage binds the grains together, allowing further community development (Hoagland et al. 1982). Succession proceeds from a monolayer community to a stratification of species and chemistry within a matrix of cells and their secretions (Jørgensen & Revsbech 1983, Jørgensen et al. 1979, Kuenen et al. 1986, Lassen et al. 1994, Johnson et al. 1997) (FIGURE 2). Stalked microalgae can contribute to the greater depth of late-successional communities, resulting in "an upperstory of growth perhaps functionally analogous to the canopies characteristic of terrestrial forests" (Hoagland et al. 1982). The upper stratum provides attachment points for diatoms that are specialized as epiphytes (Roos 1979, Roemer et al. 1983), described as "dependent organisms" or pseudoperiphyton, and treated as part of the same community as their hosts (Sládecková 1962). While some sessile algae cannot adhere to other algae and so require a direct connection with the substrate, other species may preferentially attach to algae in the layer below and thereby epiphytically form a canopy stratum of their own (FIGURE 2A). This strategy is unknown for terrestrial canopies. Vines positioning their foliage uniformly above that of their hosts (Putz 1995) may approach it; although, being rooted to the ground, these canopy plants are of course not epiphytes.

Canopy complexity of periphyton may be greater at sites with higher light intensities (Hudon & Bourget 1983). Furthermore, the internal physiognomy depends on local flow regime, in part because, for example, greater turbulence increases the penetration of nutrients and light (Peterson 1996). Wetzel (1993) argues in contrast that such penetration is rare, and that the high productivity of periphyton is a result of efficient recycling of nutrients within their canopies. Growth of the outer layer can shade the strata below (Johnson et al. 1997, Dodds et al. 1999) and block nutrient inputs to the understory (McCormick & Stevenson 1991, Peterson & Grimm 1992). Shading can lead to understory deterioration (Stock & Ward 1991) in time causing a community to slough from its substratum (Meulemans & Roos 1985). Substrates are colonized both by these detached communities (detrital microcosms: Korte & Blinn 1983) and by isolated cells in suspension (Stevenson 1983). Sloughing can be reduced where understory algae species can produce more photopigments or become increasingly heterotropic in dim conditions (Tuchman 1996, Peterson 1996), in which case the periphyton can last longer and achieve higher biomasses. Because of the cycle of growth, death, and sloughing, the community that establishes after a site is scoured by herbivores may depend on the prior successional status at the site (Peterson 1996), among other factors (Tuchman & Stevenson 1991).

Turfs are filamentous periphyton communities, typically a few millimeters high (FIGURE 3) that occur widely on coral reef surfaces and produce the bulk of reef primary productivity (Adey & Steneck 1985). Disturbances (say, by herbivores) reduce turf height and increase light penetration and turbulence through their canopy (Carpenter 1986, Williams & Carpenter 1990, Carpenter & Williams 1993, Cheroske et al. 2000). Stratification can occur within turfs but is limited (Hackney et al. 1989, R.C. Carpenter pers. comm.).

Bacterial Films

Until the 1980s, bacteria were studied only by traditional sampling and culture methods. Extrapolations from monospecies laboratory cultures led to serious misunderstandings about bacterial ecosystems (Costerton et al. 1995). In fact, almost all bacteria live packed within surfacebound multispecies communities (Molin et al. 2000, Watnick & Kolter 2000) called biofilms. When the bacteria and their accumulated remains form thick accretions, biofilms are called microbial mats or "stromatolites," which can include eukaryotes (Stal 2000). Indeed, biofilms often intergrade with eukaryote-dominated periphyton, and increasingly the term has been used broadly to include periphyton and even fungi (Reynolds & Fink 2001). In the algal dominated systems discussed in the previous section, for example, bacteria colonize early in succession (Hoagland et al. 1982), and, in combination with certain diatoms and fungi, "precondition" the substrate for adherence of algae (Korte & Blinn 1983, Burkholder & Wetzel 1989). In a developed periphyton community, the bacteria can be nutritionally dependent on excreted algal products (Haack & McFeters 1982, Sobczak 1996). The remainder of this section will focus on communities dominated by bacteria.

FIGURE 1. Kelp forests. **1A.** A forest at Naples reefs, near Santa Barbara, California. The understory strata at the bottom of the image are represented by articulated coralline algae and (above that) by a single individual of *Pterygophora californica.* Photograph by Dan Reed. **1B.** The upper (outer) canopy of a Channel Islands (California) kelp forest. Photograph by Flip Niklin (Minden Pictures).

For macroscopic canopies, interest typically falls into two arenas: studies of the substrate-bound species themselves (the hosts), and studies on species that live within the canopy generated by the hosts (canopy residents). This distinction is apparently of limited utility for bacterial biofilms and mats, which are formed of cells en masse (FIGURE 4). The internal organi-

FIGURE 1. Continued.

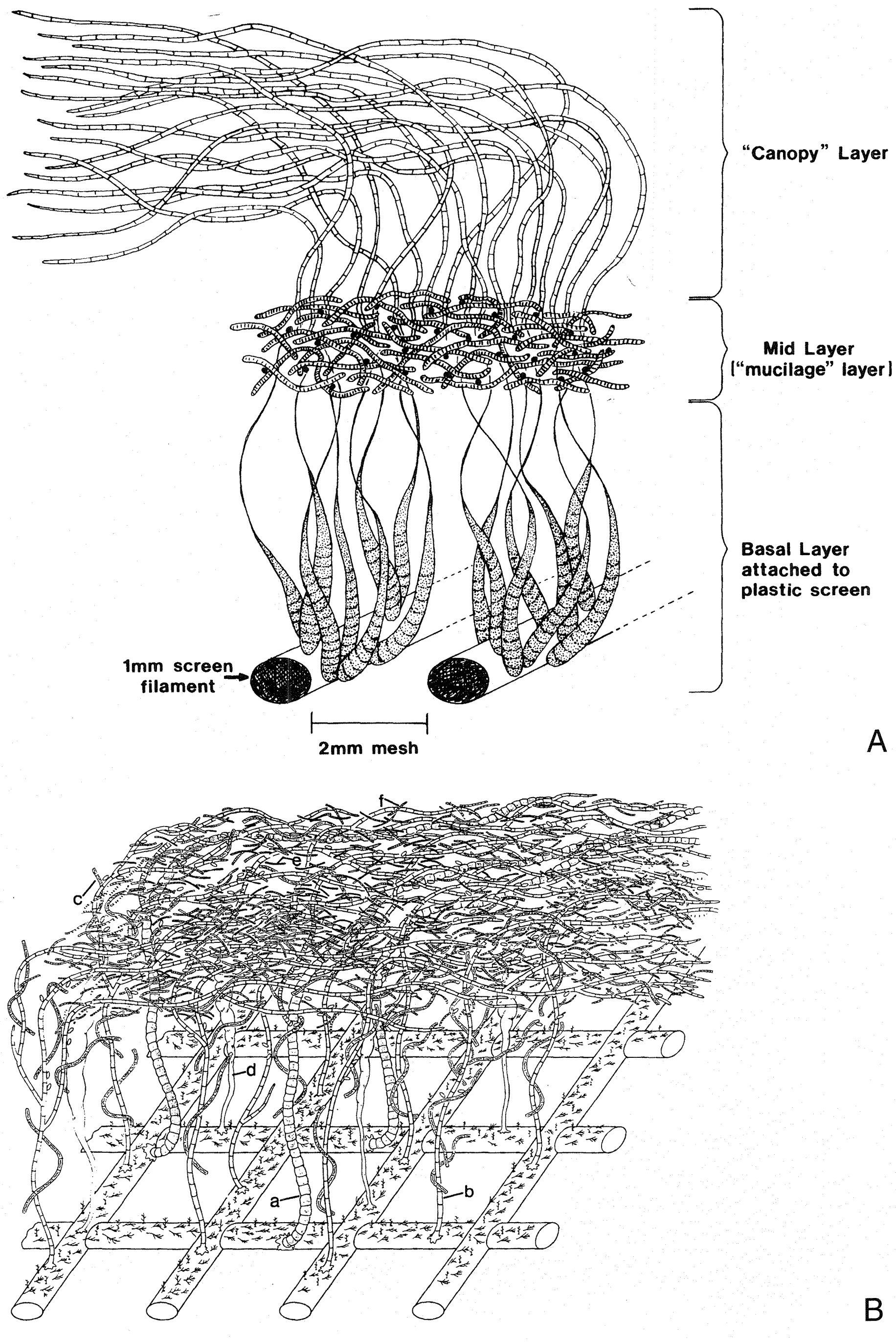

FIGURE 2. Multilayered periphyton attached to a screen in a marine aquarium (2A. from Adey & Loveland 1998) and to a screen in freshwater (2B. from Adey et al. 1993). Typically the layer directly attached to the screen (the hard rock or carbonate substrate in the wild) is dominated by either blue green (cyanobacteria), a diminutive green (*Stigeoclonium*) or red (*Herposiphonia*) algae (W. Adey pers. comm.). **2A.** Upper layers are attached to the layer below them and not the substrate, and so these entire strata are epiphytic on the lower strata. The middle layer consists of diatoms and small filamentous algae suspended in mucilage generated by the community. **2B.** The overstory layer is made up of large, typically branched filaments also attached to the substrate, along with the blue-green or small green and red "understory" algae. Much like vines (e.g., nomads; Moffett 2000), the *Spirogyra* and *Dichotomosiphon* spiral around their supporting hosts, perhaps moving along

FIGURE 3. Algal turf from St. Croix dominated by *Herposiphonia.* Width of the image is about 1 mm. SEM photography by Robert S. Steneck, reproduced with permission.

zation of films and mats include stratification, with anaerobic or anoxic species often occupying the depths of a film (Jørgensen et al. 1986, Sagan & Margulis 1988, Ramsing et al. 1993). Such structure is revealed by microscopic techniques (Molin et al. 2000) and other methods (Wimpenny 1992, Lewandowski et al. 1993, Kühl et al. 1994). Light penetration and chemical gradients are critical to the structuring of these communities (Jørgensen & Revsbech 1983, Revsbech et al. 1983, Wimpenny & Kinniment 1995, Stal 2000). While most biofilm residents are sessile or at least relatively immobile within the cell matrix (Costerton et al. 1995) the integrity of biofilms may be as much a product of a secreted matrix of polymers as of the fixed location of organisms. Thus motile species can shift position within the film, for example, moving to different "microzones" (strata), in response to light or chemical cycles (Doemel & Brock 1977, Garcia-Pichel et al. 1994, Stal 2000). This is also true of some periphyton-dwelling diatoms (Johnson et al. 1997). Biofilm residents are phenotypically distinct from conspecific planktonic forms, which are often physiologically dormant and function as a dispersal stage. The sloughing of bacteria from films, adhesion of the colonists to a surface or within the matrix, and other aspects of establishment and development of films have been documented or modeled in three dimensions (Bryers 2000), as has the succession of residents through time

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them by rotation and circumnutation *sensu* Darwin (Yeh & Gibor 1970). In monoculture, the *Spirogyra* will even coil around one another like plant tendrils with no alternative place to go. (2A. copyright Academic Press, reprinted with permission; 2B. copyright Society for Ecological Restoration, reprinted with the permission of Blackwell Science, Inc.).

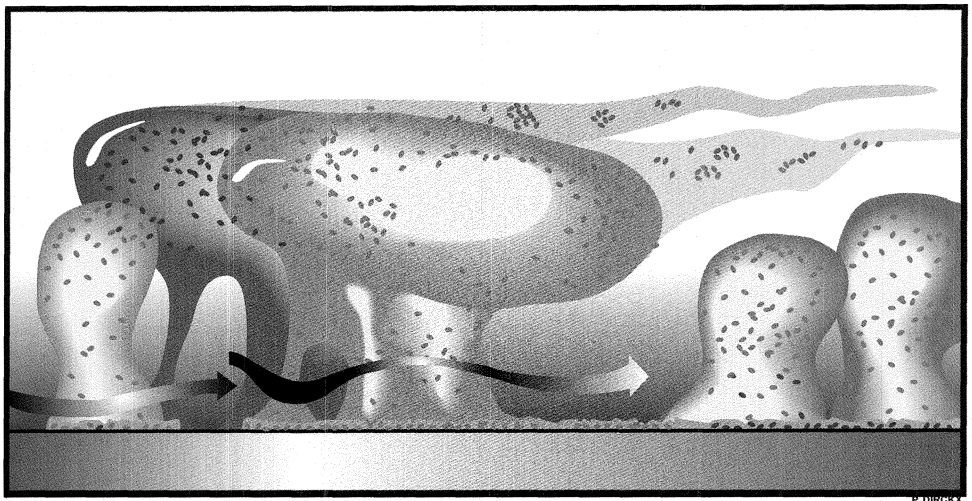

FIGURE 4. Schematic drawing of a generalized biofilm structure, showing microcolonies separated by channels. Arrow indicates waterflow in the film. Drawing by Peg Dirckx.

(Paerl 1985, Lawrence et al. 1995, Korber et al. 1995, Jackson et al. 2001).

The matrix of bacteria in a biofilm is typically described as developing channels or pores through which nutrients enter and wastes leave the community (Costerton et al. 1994, Massol-Deyá et al. 1995, Stoodley et al. 1999a). The structure of many biofilms is so fragmented by these "waterways" that on close inspection they do not resemble a "film" at all but rather a landscape of coneshaped and mushroomshaped bodies called "microcolonies" distributed intriguingly like trees in a forest (FIGURE 4). When mature the microcolonies may grow into contact, but they do not fuse so that they wave past each other when shear forces operate (J.W. Costerton pers. comm.). Although not universal (Wimpenny & Colasanti 1997), microcolony formation is widespread in natural and artificial systems, both for monocultures and for mixed-species communities, and is presumed to result from nutrient limitation and niche exploitation (Costerton et al. 1995). The distribution of microcolonies (including both the cells and the exopolymeric materials they secrete) and the channels and other spaces between them is referred to as biofilm "architecture" (Lawrence et al. 1991). Both the species composition and the nature of the substrate effect this architecture (Costerton et al. 1995, Wimpenny & Colasanti 1997). So does water flow around biofilms, which may cause entire microcolonies to drift across a surface (Stoodley et al. 1999b), straining the definitions of "sessile" and "canopy."

The advantages of living in biofilms include the proximity to nutrients associated with surfaces, buffering from external chemistry, and modulation of physical conditions within a film, as well as resistance to drying, to predation by protozoa, to infection by bacteriophages, and to antibiotic therapy and other chemical treatments (Allison et al. 2000). Microbiologists describe biofilms as coordinated communities with "primitive homeostasis, a primitive circulatory system and metabolic cooperativity" that can "resemble the tissues formed by eukaryotic cells" (Costerton et al. 1995, Costerton & Lappin-Scott 1995) perhaps as a result of rapid evolution through gene transfer within the films (Hausner & Wuertz 1999). There appears to be a stronger interdependency between different species in a biofilm than there is between most plants in a forest, such that certain bacteria depend on the metabolic products of other microbes (Kühl et al. 1996, Molin et al. 2000, Paerl et al. 2000) and show other forms of cooperation (Crespi 2001). In addition to these mutualistic "consortia," biofilms and microbial mats are home to diverse competitive and predator-prey interactions (Lawrence et al. 1995, Allison et al. 2000). A question wide open for investigation is how selective forces operating in the establishment and development of biofilms lead in time to cohesive systems that appear stable, functionally integrated, and structurally convergent.

Stolzenbach (1989) applied the word "canopy" to biofilms. Indeed, microbial communities could be easily manipulated for studies of canopy structure: various combinations of microbial species or strains could be mixed, centrifuged, and allowed to form biofilms to investigate assembly rules for canopies under specified nutrient or substrate regimes.

Coral Reefs as Canopies

Dahl (1973) writes of coral reefs that "organisms often occur in many layers and the substratum itself is organism generated." Because of the abundance of sessile animals throughout these layers, marine scientists are less concerned than plant-focused terrestrial canopy researchers with the phyla of the substrate organisms. It is not surprising, then, that overarching corals have been described as producing a "canopy" overtopping an "understory" community (Baird & Hughes 2000). While the supportive structure of coral is not living, it is an immediate by-product of living things and therefore can be treated as a part of a canopy in much the same way as snags are treated as part of a terrestrial canopy. Actually, there is a veneer of living tissue on live coral, much as there is a small zone of living phloem surrounding the mostly "dead" xylem of trees, so that in fact in both ecosystems a large part of the structural foundation of the canopy is dead.

Somewhat like trees (Horn 1971), the architectures of photosynthetic corals change with light regime (Porter 1976). Death or suppression of the growth of corals from shading by other corals results in an understory that can include shade-tolerant phototropic species (Stimson 1985) and that incorporates abundant sessile heterotrophs (Karlson 1999, Baird & Hughes 2000). Other shade-tolerant (or, in the case of sessile animals, shade-indifferent) species can densely occupy the undersurfaces of the corals themselves (Jackson et al. 1971, Maida et al. 1994). Colonization of these habitats can depend on active larval choice for "cryptic" (shaded) microsites (Maida et al. 1994, Mundy & Babcock 1998). The change of species composition with shading can parallel community changes resulting from light falloff with depth in the water column, such that understory shade permits certain deep-water species to extend their distribution into shallow water. In general, however, these understory corals are distinct from reef-building corals, as the latter, when adapted to dim conditions, tend to specialize on deeper or more turbid water. Other species prosper in the gaps formed by the death of overstory coral colonies, yielding a habitat mosaic (Stimson 1985). The coral reef community includes algae (among them the turfs discussed previously) that show a complex pattern of competition depending on their heights and interfrond densities (Steneck 1997). The structural complexity of coral reefs provides for a high abundance and diversity of canopy-dwelling organisms, such as fish (Dahl 1973) and zooplankton (Porter 1974).

Other Canopies

Various other sessile animals form dense aggregations that could be studied as canopies including both clonal organisms (e.g., anenomes, bryozoans, ascidians) and nonclonal species such as mussels and barnacles (Paine & Suchanek 1983). Further, if we allow that communities of these organisms have canopies we can apply the idea of an extended phenotype (that is, extending the definition of phenotype to include nonliving products of an organism such as nests or retreats: Dawkins 1982, Turner 2000) to enlarge the concept of canopy almost indefinitely, depending on our interests. Least controversial would be static structures like coral skeletons whose architectures and spatial relations are produced directly by living things. Tubes of polychaetes (Bell & Coen 1982) and stream fly larvae (Pringle 1985) attract assemblages of plants and animals. These structures recolonize rapidly after defaunation, forming communities organized around tube architecture (Bell & Coen 1982). On land, patches of earthworm castings (Maraun et al. 1999) or of fungal fruiting bodies (O'Connell & Bolger 1997) are possible analogs of plant canopies.

Systems that are not canopies by any definition could be useful models for examining canopy life. Suspended bacteria can stratify under conditions of low turbulence (Guerrero & Mas 1989). Studies of the planktonic cells show that "increased productivity produces a physical scaffold to support biological heterogeneity (as, for example, in the spatial complexity of forest canopies) on which other species can build" (Morin 2000).

Mineral Acquisition

In terrestrial communities, the capture of atmospheric nutrients by canopies may be significant to mineral budgets (Lindberg et al. 1986). Regardless, the possibility that productivity in these communities can be limited by atmospheric minerals remains to be proved, and clearly most habitats depend almost entirely on the substrate for mineral nutrition (for an exception, see Art et al. 1974). The situation is reversed in most aquatic and microbial communities, which absorb nutrients from water, a medium with a higher capacity to deliver nutrients than air (Lobban & Harrison 1997). These communities show complex patterns of cycling of the nutrients within their canopies (Burkholder 1996). Indeed, internal cycling may become increasingly important with increasing canopy complexity during succession, reducing loss of resources from the system (Sand-Jensen 1983, Paul & Duthie 1989, Peterson & Grimm 1992). On the other hand, algal holdfasts are believed to be just that: organs specialized at holding on to substrates. Although the complete absence of nutrient absorption from these organs is a commonplace assumption, holdfasts are localized structures without any rootlike proliferation of surface area presumably necessary to efficiently exploit substrates for nutrients. Further, most algal communities grow on rock, sand, and other relatively nutrient-poor substrates. In these situations, nutrient inputs are likely to be greatest in the upper (outer) canopy rather than at the substrate level, and therefore traits adaptive for light and nutrient procurement ideally will function in synchrony (McCormick 1996).

Seagrass ecosystems are an exception, in that these marine angiosperms receive most of their nutrition from the rich sediments into which they root (Williams & Heck 2001) and a few algae in the same communities produce rootlike rhizoids that absorb substrate nutrients as well (Williams 1984). Biofilms and some periphyton (Pringle 1990) are a second exception: those on organic matter clearly receive the preponderance of their nutrition from the substrate. Actually, this can also be true on inert surfaces like plastic or metal, at least in the initial growth phase of a bacterial community. Through surface charges and other effects, these substrates tend to concentrate mineral ions and organic matter from solution, encouraging biofilm establishment (Bryers 2000). Otherwise, the dependence of aquatic systems on minerals in solution and the direct relation between the rate at which nutrients are encountered in a medium and the flow of the medium means that the growth of affixed aquatic systems can be limited by the availability of waterborne nutrients (Atkinson 1988, Stevenson & Glover 1993, Carpenter & Williams 1993, Lobban & Harrison 1997, Sebens 1997, Hurd 2000). With sufficient water flow, even seagrass beds absorb a significant portion of their nutrient requirements through their canopies (S.L. Williams pers. comm.).

GEOMETRY OF CANOPY BIOLOGY

If we expand our definition of "canopy" beyond what I have suggested in Moffett (2000) to encompass all the parts of any community of sessile organisms that project into a medium, on what basis might canopy biology rest on firmer ground as a discipline?

Ecologists have traditionally dealt with plants (or other sessile organisms) in two dimensions, or as points on the earth. While orientation in canopy ants, the conservation of orchids, and foliage uptake of pollutants bear on canopy biology, much of the research on these topics falls squarely within this tradition. For example, most studies of orientation in canopy ants ignore spatial issues bearing on plant topographies, as well as other issues unique to canopy substrates, such as properties of pheromone diffusion from bark versus from leaves. In a typical experiment, ants are entirely removed from their canopy environment, as when a species normally found on foliage is studied on a flat laboratory surface. While we can learn a great deal about canopy organisms with this kind of approach, none of it has to do specifically with their origins in the canopy.

In contrast, the core of canopy biology as an independent discipline can be characterized in large part as the science of treating communities of plants (or other sessile organisms) as three dimensional. Expressed another way, creating a robust science focused on, for example, aerial plant organs requires us to "put the canopy into canopy biology" through research that contributes directly to understanding the distinctive aspects of life associated with plants. Typically this can be achieved by introducing the "z" axis or other canopy-specific attributes (see studies on ant orientation by Jander & Voss 1963, Beugnon & Fourcassie 1988, Fourcassie & Beugnon 1988, Jander 1990, Klotz & Reid 1992, Wohlgemuth et al. 2001). For example, Diekmann et al. (2000) conform to the 2D "mainstream tradition" except for some material on three dimensional gap structure, which by my criterion is the only part of their coverage of ecological geometry that represents canopy research *sensu stricto.* The same philosophy can apply to aquatic systems, which offer unique experimental opportunities: consider the value of artificial reefs of varied structure to understanding productivity and diversity of canopy residents (Bohnsack 1989, Hixon & Beets 1993, Carr & Hixon 1997).

I have outlined six approaches to "putting the canopy into canopy biology," calling these the core issues of the subject (Moffett 1999). By framing questions in regard to one or more of these issues, researchers can contribute fundamentally to canopy biology as a discipline. I review these issues below. To keep my treatment brief, I've chosen examples from the forest literature, although there is information on each issue available for other kinds of canopies. While I find that most scientific results can be partitioned along these lines, the issues clearly are not independent, and of course many studies make important contributions in two or more of them. I believe that in time a large part of canopy science may ultimately codify according to how these issues have contributed over ecological and evolutionary time to the diversity of both the host organisms and their occupants.

1. Community ecospace. For any canopy, the quantity and quality of space available to canopy dwellers depends on host structure. How much so is a matter of conjecture. Any small nimble bird or agile climbing animal like a gibbon seems to experience canopies as a volume, although even here not all points in the volume may be accessible, such as vegetation too dense to be navigated by a bird (Cuthill & Guilford 1990) or spaces too wide for primates to cross (Cant 1992, Cannon & Leighton 1994). At the other extreme, small flightless arthropods such as mites or earthworms are unlikely to register community ecospace as a volume. Ants, for example, are restricted to within millimeters of every surface within their territory. Because of this, and in spite of models to the contrary (Hölldobler & Lumsden 1980), ants experience canopies as something between a 2D and 3D space (Moffett 1994). In essence, a canopy represents for them a highly warped surface. Like a science fiction ship using a wormhole to bridge points normally experienced as distant from each other, *Oecophylla* (weaver ants) create shortcuts through this space by linking bodies into chains to access new branches (Hölldobler & Wilson 1977), and thereby can bridge whole tree crowns that otherwise could only be reached by way of a long march to and from the ground.

2. Aggregate structural properties of the community. Here I include the nonuniform vertical distribution of canopy structures and the concomitant stratification of other elements of a canopy environment, such as microclimate. Parker and Brown (2000) criticize studies of stratification for their lack of reproducibility, inconsistent terminology, and other weaknesses. Regardless of the difficulties, understanding stratification is at the core of much of canopy science (Moffett 2000). Whereas many studies of terrestrial nutrient interception treat the canopy as a single "black box" with overall inputs and outputs (lc. Coxson & Nadkarni 1995), some researchers have uncovered a complex internal pattern within canopies, which act as atmospheric filters (Wiman et al. 1985, Meyers et al. 1989, Lovett & Lindberg 1992) and nutrient transfer systems (Pike 1978, Reiners & Olson 1984, Coxson et al. 1992). Defining strata or gradients requires broad spatial averaging, while explaining any patterns that emerge necessitates research at a finer spatial scale. For example, bark pH can vary with height in trees (Hyvärinen et al. 1992). If the height distribution of an epiphyte corresponds to that of bark pH, we could propose that the plants prefer a particular pH. Testing this hypothesis requires determining the detailed distribution of bark pH at the actual locations occupied by the plants (e.g., Gauslaa 1995) followed by manipulations of pH in the field or laboratory (e.g., Hallingbäck 1990).

3. Host distribution. In all canopies, the substrate changes from place to place, for example from one host to the next. The likelihood that many canopy residents are specialists on one or a few plant taxa (e.g., Erwin 1982) suggests the usefulness of considering hosts as islands over evolutionary time (Janzen 1968, 1973), both in explaining levels of resident diversity, and potentially even in modeling processes occurring within and between plants that generate such bounty. But rather than treating hosts as islands in a uniform ocean to conform to the perspective of MacArthur and Wilson (1967), "patchwork" biogeography models could treat communities as a continuum of host islands of varied acceptability as sources of food, retreats, or transit routes to each canopy-dwelling species. In addition, diversity is organized at scales both smaller and larger than that of a host. Any stable canopy element that qualifies as an island *sensu* Haila (1990) could harbor a distinct community, such as a flower, phytotelmatum, and leaf (to a microbe) (Seifert 1975, Andrews et al. 1987, Jenkins & Kitching 1990, Richardson 1999), and potentially also certain microclimatic features (Herwitz & Slye 1992). Even ant territories could form habitat islands for residents within tropical canopies (Moffett 1994). Territories of different ant species exist as mosaics that overlay, but are partially independent of, the mosaic of the trees themselves (e.g., Dejean et al. 1999). Ants scour their territories to drive off intruders and kill prey while promoting survival of species-specific assemblages of associates (Hölldobler & Wilson 1990). Like other island-like canopy features, then, ants may add to the potential for species to pack into vegetable space.

4. Host architecture. All canopies from redwood forests to biofilms (Lawrence et al. 1991) have varied architectural parts. In forest ecology, there is a burgeoning literature on this topic, that is, the size, angles, distributions, development, and spatial relations of aerial plant parts. Classically, architecture is described for trees by the models of Hallé et al. (1978). The "Hallé-Oldeman architectural model" classification has been described by one key practitioner to be "comparable to the development of the binary system of nomenclature by Linnaeus" (Tomlinson 1983). Nonetheless, the system has been little used by nonmorphologists, arguably due in part to an overall neglect of the potential importance of substrate architecture on canopy organisms (but see Hallé 1990). There are studies of the effects of simple architectural attributes, especially branch angle and width, on the growth of epiphytes (e.g., Rasmussen 1975, Ingram & Nadkarni 1993, Moe & Botnen 1997) and on animal locomotion, particularly in reptiles (Plummer 1981, Irschick & Losos 1999, Beuttell & Losos 1999) and primates (Demes et al. 1995, Povinelli & Cant 1995, Warren 1997, Dagosto & Yamashita 1998, Hamrick 1998, McGraw 1998, Garber & Rehg 1999, just to mention recent citations on positional behavior). Yet there have been no broadly scaled studies of how plant architecture influences canopy life. Consider that many tropical canopies have well-beaten vertebrate highways which in some cases can be detected by the epiphytes that spread to each side of a branch like hair from a part (Perry 1978, Sillett et al. 1995). Perry (1978) found evidence of multispecies use and active pruning, but as yet no one has mapped such a trail in relation to the tree architectures available locally, or documented how the trail originates, how long it lasts, and how its usage shifts with changes in canopy physical structure and resource availability.

5. Open space. Not even biofilms are a continuous matrix of organisms; all canopies consist of a framework occupying a dynamic fluid matrix that has open communication and exchange with the adjacent atmosphere or hydrosphere. Open space (air or water) within canopies merits special consideration because of its potential effects on microclimate and on the locomotion or dispersal of organisms, and because many aspects of the subject remain virtually ignored. Space within or between forest trees is commonly distinguished into two categories, with "gaps" being the result of plant death and shyness-related space often being the result of plant growth and reconfiguration, that is, plant foraging (Hutchings & de Kroon 1994); this distinction is somewhat of a simplification because physical abrasion can also be involved in shyness patterns (Franco 1986). Gaps are the most commonly studied spaces because of their role in forest succession and species diversity patterns (Lieberman et al. 1989). Spaces represent barriers to some species and pathways ("flyways") to others (Brady et al. 1989, Aluja et al. 1989, Cuthill & Guilford 1990, Cannon & Leighton 1994, Brigham et al. 1997, Aylor 1999), but little information exists on how open space might be involved in structuring the population and species distributions of residents within canopies. There is a tendency to think in terms of canopy structures such as trunks and branches when the space between structures could be the resource used, as might be the case among gliding animals (Moffett 2000). Within the open spaces, boundary layers (the regions of lowered fluid velocity that exist around any surface in a flowing medium) are a general feature of attached communities. Their presence partially isolates canopies from the surrounding medium, and thereby can increase community reliance on efficient and potentially autogenically controlled internal (within-canopy) nutrient cycling. This isolation may be particularly important in flowing water (Mulholland 1996), where canopy physiognomy can substantially ameliorate the downstream displacement of chemicals or of any organisms that are moving within a canopy or that have a poorly developed capacity to attach to a substrate.

6. Properties of structural elements. In all canopies, the sessile hosts present associated species with a variety of surfaces, both between host individuals or species and within each host (such as wood versus leaves in a tree). These structural elements vary in their physical and chemical properties, such as the capacity for insulation or water absorption, tendency to leach nutrients, efficiency at transmitting vibration, and their texture, stability, density, hardness, compliance, stiffness, strength, pH, and so on. How do such variables affect life on or in a host? One of the oldest areas of canopy investigation in terrestrial biology is the question of substrate choice by epiphytes, especially cryptogams (e.g., Barkman 1958). Another area of intensive study has been herbivory as it relates to secondary compounds, nutrient content, and the mechanical difficulties of feeding (Schowalter 2000). Outside these research focal points, the literature is widely scattered, with many potential research avenues of enormous prospects.

GETTING TO THE ROOT OF THE MATTER

Both in the application of words and as a subject of study, much of terrestrial canopy biology has been based on our conception of sessile species as physical supports for other organisms. Because most substrates in a canopy are the parts of living organisms, a particular concern is the "social" (often interspecific) aspects of support, such as trees as supports for vines or vines as supports for trees. Consider that by interlinking a canopy, vines could prop up weak trees or pull down neighboring trees when a tree does topple (Smith 1973, Putz & Mooney 1991). The word epiphyte can similarly imply a support function for a host or at least direct physical association with a host, as this term is widely defined by terrestrial scientists as a plant growing on another plant. "On" signifies intimate and superficial, that is nonendophytic, contact, without reference to gravity: thus, moss growing on the underside of a branch is "on" the tree.*

The idea of "a plant growing on another plant" can be found as well in the rhizosphere literature, however. Roots of a plant can be said to grow on those of another in the sense that a tree's underground root mass may grow "on" bedrock. Still, in contrast to the aerial-plant literature, almost no data exists on the role of physical support between plant individuals in the rhizosphere. Studies to date on support functions of roots have treated each plant in isolation (e.g., Ennos 2000). But despite confounding effects from competition for space and nutrients (e.g., Atkinson et al. 1976, Mahall & Callaway 1992, Burgess et al. 1998), root systems in nature are seldom isolated. Consider the drawings in Weaver and Clements (1929) of herb and grass communities. The distribution of tree roots is not known to this detail, but see Chilvers (1972), Lyford (1975), and the figures in Külla and Lõhmus (1999). Coutts (1986) writes that the "interlocking of thicker roots between adjacent trees can have a substantial effect" on anchorage. He notes that if one Sitka spruce is uprooted, neighbor trees with interlocking roots are likely to topple with it (Coutts 1983). Vogel (1996) ascribes a supportive function to the "diagonal guying" by tangled bamboo roots, while Keeley (1988) and Basnet et al. (1993) ascribe a likely supportive role to natural root grafting, which is common in trees. Only the roots within a few meters of the base of a large tree are significant to anchorage (Ennos 2000), meaning such interactive effects may have to occur inside that radius. Yet in spite of the obvious role of the soil itself in plant support, there is no reason to assume the role of physical support between plant individuals is any less significant belowground than aboveground, at least for certain substrates and communities. Even for herbs, it is the commonplace observation of gardeners, but apparently not the subject of study as yet, that pulling up one plant can cause full or partial dislodging of neighboring plants. This suggests structural support exists between forbs, insomuch as that the presence of neighbors may add to the force required (say, by a herbivore) to extract a given plant. Incidentally, physical support between individuals within the substrate is likely to be absent for most if not all aquatic and microbial communities of affixed organisms, given that taxa such as algae and corals lack elaborate belowground organs.

For terrestrial systems, I explicitly identify "epiphyte" with residents of aboveground plant organs, that is, the canopy (Moffett 2000), conforming with the word's use in practice. Giving the literature on roots due consideration, however, commonplace definitions such as Barkman (1958) phrased in terms of "plants on other plants" are not at all clear on that score. This ambiguity may be unintentional. Still, based purely on the word's derivation (*epi* = on, *phyte* = plant) and the scarcity of clear definitions to the contrary, we may conclude that if one organism grows in physical intimacy with (on the surface of) a larger one (its host), and that larger one is a plant, the smaller individual could be called an epiphyte even if it occurs within the rhizosphere; after all, the term in general currency today is epiphyte, not air plant. Because such usage would break with convention among terrestrial ecologists, a more satisfactory choice to denote "a plant growing on another plant" would be "epibiont," a term common in marine biology (Wahl 1997). For example, definitions of epiphytes as "plants on plants" apply equally to any canopy plant (be it vine, mature hemiepiphyte or nomad), as confirmed by wordings found throughout the literature to indicate the position of these plants with respect to the host (e.g., Putz & Mooney 1991, Ray 1992, Lawton & Williams-Linera 1996).

Admittedly, beyond microbes such as mycorrhizae, root parasites, hemiparasites such as certain Scrophulariaceae, and plantlets growing from root buds, it remains problematic which subterranean associates might be considered epibiontic (or "epiphytic") on this basis. Whether or not the idea of epiphytism could (or should) ever be applied to the subterranean realm, my point is that the traditional split between rhizo-

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*An epiphyte mat (canopy plants and associated suspended soils in aggregate) unambiguously lies on a tree. Formally, however, an epiphyte growing in the suspended soil or in an ant carton nest is not necessarily "on" the tree, any more than the tree is "on" the earth's core, though these epiphytes are commonly included in the set of plants "on" a tree, apparently by loose application of the "canopy plants and soil in aggregate" perspective. Exclusion of animals that live and grow on plants from the epiphyte category may be attributed in part to the restriction of "epiphyte" to sessile residents, which is often how the word is used in marine biology. At least in terms of mobility on an appreciable scale relative to the host-plant size, epiphytes include most plants, fungi, and microbes. Nomadic vines (Moffett 2000) and insect scales, however, may render adherence to a strictly taxonomic interpretation problematic, if not archaic.

sphere and canopy can be arbitrary, which has fragmented of our understanding of life on or in plant bodies.

Does this apply as well to our understanding the plants themselves? Roots evolved from shoots prior to the evolution of leaves (Barlow 1994), and have remained developmentally distinct from leaves, without intermediates except in extraordinary cases (e.g., Von Teichman und Logischen & Robbertse 1977). In allorhizic species (dicots and most monocots), the difference begins to be expressed within the embryo, whereas in homorhizic plants (some monocots and all pteridophytes) it is not. Furthermore, homorhizic species lack a root "system," in that all roots originate adventitously from within the shoot system (Groff & Kaplan 1988); in both groups, roots can also arise from shoots and shoots from roots. In separating canopy from rhizosphere, however, it is especially significant that roots and shoots are not necessarily distinguishable in either function or location relative to the ground surface. Shoots can absorb nutrients and water (Parker 1983, Schaefer & Reiners 1989) and can occur belowground, where they are referred to as rhizomes; whereas roots can occur aboveground, where they are often photosynthetic (Benzing 1991) or have ventilation and aeration functions, as in mangroves. As is the case for canopy biologists, then, the distinction made by botanists between belowground and aboveground (and often between root and shoot) have been largely methodological, for example a matter of choice between using a climbing rope or a shovel. The resulting academic fragmentation can be transcended, as in the architectural research by Kohyama and Grubb (1994) and Van der Putten et al. (2001).

It is true that ecology took a long time to enter the treetops (Moffett & Lowman 1995). Yet given its inaccessibility, barring in most cases wholesale destructive intrusion (Smit et al. 2000) and its complexity (compare Beare et al. 1995 with Freiberg 1997), in many ways it is not the aerial world but the subterranean one that remains most alien to us today. The rhizosphere along with the soil associated with the roots therefore could merit equal consideration to the rainforest canopy as the last, though assuredly not the highest, biotic frontier (André et al. 1994); for example, compared to their crown architecture, the architecture of tree root systems is relatively poorly known (but see Jenik 1978, Atger & Edelin 1993). Detailed 3D studies of roots that extend beyond simple depth measurements of the kind reviewed by Jackson et al. (1996) are scarce (Mullins & Diggle 1995, Tsegaye et al. 1995, Lynch et al. 1997, Ge et al. 2000, Pages 2000, Pages et al. 2000). Most examples have been conducted at the level of a single plant rather than for a community (but see Caldwell & Richards 1986).

How would parasitology stand as a coherent discipline if its practitioners chose to look at the head of their subject while ignoring what its feet were doing? By amalgamating the findings from canopy biology with those from soil sciences, terrestrial biologists could fashion a comprehensive science of plant associates, roughly congruent with marine epibiosis. It could be helpful to use a different term, such as "structural ecology," to designate the discipline that takes the principles of canopy biology and applies them at the level of whole sessile organisms within any affixed community.

CONCLUSIONS

There are species from every Kingdom of life that attach to or grow from substrates, and, when aggregated, these organisms form three-dimensionally structured communities whose parts that emerge from the substrate in aggregate can be (and often have been) described as "canopies." Terrestrial studies appear to be categorized as "canopy biology" either on the basis of inaccessibility, as when specialized gear is required to access trees (Moffett & Lowman 1995), or on the basis of the communities' coverlike properties. In the latter case, "canopy" is treated as synonymous with "overstory" or used more broadly as any stratum with sessile host organs distributed so as to appreciably shade the layers below, as the word can be used in marine science (Dayton 1975a, Baird & Hughes 2000). Because such criteria are arbitrary and of limited utility, I appliy "canopy" to all above-substrate parts of sessile communities (plant communities in Moffett 2000). The common feature distinguishing studies as canopy biology is the treatment of sessile communities in three spatial dimensions, along with other attributes that may be unique to life within this "canopy space."

By projecting into a volume of fluid media, canopies can augment productivity through increasing the biotic mass and the live surface area available to capture and process nutrients and energy, and can enhance α diversity through transforming the climatic and chemical properties of the space they occupy in a heterogeneous way, potentially multiplying the niches associated with a given area of substrate (DeVries et al. 1999, Morin 2000, Moffett 2000), as well as by providing retreats from predators, competitors, or adverse conditions, and additional surface area that can to either attract or accumulate new species and the nutrients required to support a rich community (Dean & Connell 1987, Lovett

& Lindberg 1992, Jones et al. 1997). A challenge for the science of comparative canopy biology is to determine the rules by which ecosystems, including both the sessile species and the residents of those species, assemble in three dimensions and thereby create opportunities for increased production and diversity.

We also must explain the differences and even more intriguing similarities in physical structure and dynamics of canopies that develop in air as contrasted with water, and across orders of magnitude in host size. For example, compare Edred Corner's views on trees with Timothy Allen's on microalgae (Corner 1967, Allen 1977). Surely these size extremes are of special fascination: that may be the primary reason many of us climb trees for our studies (beyond fulfilling our sense of adventure). Will scaling functions prove sufficiently linear to permit straightforward extrapolations between the extremes? Of course, our understanding of many aspects of canopy biology is in its infancy, and generalizations can be of limited value without detailed information. But even at this early stage, I am confident that ideas developed for a particular type of canopy could prove useful to researchers working with other types of canopy. Ultimately, however, our knowledge of canopies must be integrated into a coherent structural ecology of sessile communities as a whole, that is by taking full account of the role of within-substrate organs such as roots and holdfasts.

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