What's "Up"? A Critical Look at the Basic Terms of Canopy Biology[1]

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ABSTRACT

The lack of recent critiques about terminology has led to the frequent misuse or confusingly varied use of the words that are more or less specific to the field of terrestrial canopy biology. I provide definitions for *ca* 170 terms and subterms, with translations into four languages. Rather than limit coverage to tree crowns, I define canopy biology as the study of life within any aboveground parts of all plant communities, temperate and tropical. This broadened perspective enables ecologists to consider the entire range of challenges faced by organisms living in aboveground plant life, from just above the rhizosphere to the outer limits of plant growth into the atmosphere. Further, this redefinition may reduce the potential for anthropocentric biases in interpreting life on trees or other plants; encourage the use of alternative ecosystems for hypotheses that may be difficult to address in treetops; and promote more general conceptual thinking about life on vegetation, most notably the importance of scaling in ecology. Among the salient points in terminology: the concept of "stratification" has been criticized in part because strata have been defined many ways, but a flexible application of the word is central to its utility; the source of nutrients is pivotal in distinguishing epiphytes from parasites, rather than the more general issue of an organism's effects on its host; "hemiepiphyte," as currently used, confounds two radically different life cycle strategies, suggesting a new term, "nomadic vine," to describe the strategy typical of many aroids; there is a confusion in the literature caused by varied applications of the word "climb;" locomotor terms may have to be modified as more becomes known about forces underlying limb kinematics; and studies of leaping and falling organisms tend to overemphasize arbitrary distinctions between gliding and parachuting to the detriment of the more critical issue of capacity for "controlled descent."

Key words: arboreal; architecture; canopy; climb; endophyte; epiphyll; epiphyte; glide; hemiepiphyte; locomotor behavior; parachute; parasite; positional behavior; stratification; vine.

THERE HAVE BEEN INCONSISTENCIES OVER THE PAST QUARTER CENTURY with the terminology specific to terrestrial canopy biology. My goal is to address those inconsistencies in the extended definitions below, with emphasis on terms in wide use with respect to the organisms that live on aboveground plant parts, and to a lesser extent, the host plants themselves. Some of these terms have been misused while others never have been defined to adequately reflect the variety of their widespread and legitimate usage in the literature (Box 1). Moreover, several words have a confusing history, and a number of alternative terms and subcategories have been suggested over time.

SOURCES OF TERMINOLOGICAL CONFUSION—Certain canopy terms can be used in various ways in relation to different attributes. "Vine" defines a *habit* that may or may not occur in a canopy (vines can scramble on the ground or on vegetation at ground level) and that may or may not be expressed by particular individuals of species with flexible developmental programs (certain species that often form vines also can grow as shrubs). Some terms can refer to a species' *growth program* as it bears on an individual's relation to the ground: epiphyte, climber, nomad ("secondary hemiepiphyte"), hemiepiphyte, or strangler. The same words also can be used to describe a particular *life cycle phase*: "hemiepiphytic species" (as defined by a growth program) begin life as epiphytes and transform into hemiepiphytes or stranglers: "secondary hemiepiphytes" start out as climbing plants, and by sometimes discarding all roots to earth, transform into epiphytes. Other terms can refer to a *spatial relation* (endophyte vs. epiphyte) or *physiological relation* (parasite vs. epiphyte) to a host (or again can be used to describe a life cycle phase). For example, a sessile canopy parasite should not be described as an epiphyte, a restriction that does not apply to other growth forms (and indeed there are parasites that grow as climbers, hemiepiphytes, nomads, or seemingly every combination of these strategies; Kuijt 1964, 1969). These subtle patterns of usage can be confusing but are an unavoidable part of a

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BOX 1. AN APPROACH TO DEFINITIONS.

How does one create a definition that adequately reflects usage? Knowledge of the literature is crucial, but few scientific papers define their terms; even when one does, the intent is seldom to provide an exhaustive statement of usage, but rather to guide the reader in a shorthand way. The same is true for academic dictionaries. Consider the word "epiphyte." Every definition of this term I have seen contains serious discrepancies with actual usage. Often there is no indication that an epiphyte must have no root connections to the ground (*e.g.*, not be a climbing plant) and that the term can be applied without controversy to fungi and microbes growing on plants. Also, many definitions state that for the word "epiphyte" to apply, an organism must not derive nutrients and water from its host. Yet sloughed bark and leached minerals from the host can be nutrient sources for epiphytes (Benzing 1990). An accurate definition reflects that an epiphyte is not a parasite; *i.e.*, it does not actively extract nutrients or water from the living host tissue. The meaning of parasite needs to be spelled out in the definition because epiphytes are sometimes described as "mechanical" parasites.

When such core points about word usage are resolved, the definition is complete, at least in some cases. To the best of my knowledge, "stemflow" can be defined in one straightforward sentence. No further qualifications are needed to interpret its full range of application in the literature. Not so for "epiphyte," however, a term laden with semantic issues. Consider two of many questions left unresolved by definitions to date. Should a plant on a snag be called an epiphyte? Is one in a hollow tree trunk an endophyte or an epiphyte (most terse definitions imply the latter)? Because the term is applied without comment in discussions of both subjects (Schimper 1898, Barkman 1958, Richards 1996) and because no criticism of either usage appears to have been made in decades (Oliver [1930] excludes snags), my phrasing reflects both usages as accurate. No citations are provided to support either point because the decisions are based on the accumulation of consistent information across sources rather than on reliance on a particular authority. Citations are given when they bear specifically on the usefulness of that term or the limits of its application.

All definitions are opinions at some level, as is most obvious in choosing at what point misuse begins. For example, there have been two divergent approaches in distinguishing "parasite" from "epiphyte," namely in terms of an organism's effect on the health or fitness of its host or in terms of its source of nutrients and water. Three of my most important criteria (word origin, history of usage by ecologists, and practicality of application) jointly establish the efficacy of the latter view. In a few cases, the issue of practicality has led me to remove from definitions criteria that others have considered central, such as the notion that in order for a plant to be called a strangler it must "cause" the death of its host (such decisions are explained in the text). Everywhere else I have tried to be conservative. Unless one or more authors clearly specify they are establishing a novel usage (*e.g.*, the definitions given under "branch"), I ignore atypical usages as errors. Such errors exist even for common terms, as when "arboreal" is applied to residents of shrubs or herbs. Rather than criticizing specific researchers, I focus throughout on refining definitions so that pitfalls are avoided.

language's "historical baggage." Clarity can be achieved only by context and clear writing.

A few terms with special canopy meanings are usually applied today only to plants, fungi, or protists, but could be used to describe animals as well. If the application of these words in parallel to their current meaning for other kingdoms is attempted, I suggest treating them as adjectives: epiphytic animals (*e.g.*, arboreal spiders), parasitic animals (*e.g.*, insect herbivores; Price 1977), and endophytic animals (*e.g.*, leaf miners).

It is surprising how little the obvious parallels between life on plants and life on animals have been discussed. Parasitology has a long history as an established discipline and a literature larger than that of canopy biology. Canopy researchers might take advantage of precise definitions developed by parasitologists for such common terms as habitat, locality, site, incidence, abundance, prevalence, colonization, and so on. For definitions of these kinds of general terms, I recommend Bush *et al.* (1997).

If pushed sufficiently hard, any definition outside those for mathematical terms and other abstractions will break down. Show me a car, and I might show you a pile of junk that once functioned as a car (and maybe in a mechanic's mind it still is). Show someone a star, and an astronomer points to a mass of convergent superheated dust. The hallmark of a good definition is not entirely that it tidily delimits a set of Xs, but that it also necessarily causes problems (breaks down) when things get conceptually interesting about X, as when the biological species concept presents difficulties for organisms undergoing the kinds of changes Mayr (1963) considered pivotal to the generation of new species, or when a parasitic plant starts to resemble a mutualist. By this criterion, "glide," "parachute," and many terms for climbing behaviors may need to be refined as locomotion studies progress (*e.g.*, Dickinson *et al.* 2000; for a linguist's perspective, see Lakoff 1987: 69–74).

THE SCOPE OF CANOPY BIOLOGY.—I propose one change in word usage that may seem fundamental: the meaning of "canopy" itself. Most ecologists working with trees limit canopy biology to the uppermost portions of forests, a viewpoint that may have more to do with the challenges of gaining access to trees than with science. As a result, our understanding of tree crowns has been seriously impeded as an independent intellectual endeavor by an obsession with arboreal access and study techniques and with dendrocentric viewpoints on processes that are attributes of all vegetation, not just treetops (*e.g.*, herbivory and other plant–animal interactions). Such biases are explained in part by the youthfulness of a field encumbered by physical and logistical challenges. One consequence has been a dearth of conceptual thought about what, if anything, makes forest canopies unique and therefore worthy of separate discussion. I believe it is more productive and ecologically meaningful to expand the scope of terrestrial canopy biology to include plant communities and heights in vegetation that happen to achieve scales less imposing to human-size arborists. In fact, there is already a tradition mostly among agricultural scientists of applying "canopy" in this broad sense (Monsi & Saeki 1953; Monteith 1965; Russian-language articles from the 1960s cited in Ross & Nilson 1975).

Our bias toward human-scale issues of height becomes obvious if one puts eye to ground and imagines the three-dimensional complexity of the "terrestrial" world for an ant. Overarching herbs form a canopy around us. Ignoring this perspective can lead to fundamental misinterpretations of canopy versus ground adaptations. Consider stump-tailed *Brookesia* chameleons of Madagascar, "ground" dwellers commonly depicted for the absurdity of having clear "arboreal" adaptations such as clasping feet. Actually, the animals spend most of their time clambering on plants or sticks within centimeters of the forest floor (C. J. Raxworthy, pers. comm.). From our perspective as biologists, who as humans belong in the minute fraction of animal species that stand more than a millimeter or two in height, pondering canopy life requires that the word "up" be defined to include the plants at our feet.

Broadening our perspective on canopies encourages us to pursue the reasonable hypothesis that most or all ecological processes scale up from a meadow to a redwood grove, so that problems considered intractable in the latter can be addressed by looking at shorter systems. Could we, for example, add to our understanding of tree-restricted organisms, such as arboreal vertebrates or epiphytes, through the examination of their miniature and more accessible counterparts in other communities? Consider the possibility that microbes on herbs could serve as a model system in understanding the distribution of large epiphytes. As with many microfungi (Stone *et al.* 1996), epiphylls (Olarinmoye 1974, Rogers 1995), and large vascular epiphytes (review in Benzing 1990) on trees, herb-dwelling microbes can stratify in vegetation and show complex distributions across host architectures (Kinkel 1997, Leuchtmann & Clay 1997). In each case, these patterns result from characteristics of colonization and survivorship across a three-dimensional plant matrix. Dispersal is difficult to measure in forests (Ackerman *et al.* 1996, Murren & Ellison 1998). Air currents and boundary layers are comparatively easily monitored and even controlled in smaller communities, allowing detailed studies of how particles such as microbes depart from or lodge upon surfaces (Aylor 1999). The growth and spread of microbes across different plant substrates and the competition among species for space also can be studied directly in a timely and relatively straightforward manner (Mmbaga *et al.* 1994, Jacques *et al.* 1995). In many cases, these processes can be only inferred for vascular epiphytes because of their slow growth (Benzing 1990). Are patterns of colonization and survivorship shared between microbes and plants at the two extremes in host size? How do the patterns change as canopy resident size is varied, or host size is varied? Some of the "big thinking" engendered by tropical trees (Corner 1967) has brought results (*e.g.*, Lowman & Nadkarni 1995); it is time to start thinking small again.

THE TERMS

Major terms are listed alphabetically within five categories: basic canopy terms, host plant-specific terms, canopy plant-specific terms, animal-specific terms, and airborne locomotor terms. In each case, the opening sentence represents the definition in brief; all else is commentary. A term defined within commentary on another term is indicated by *italics;* a term mentioned in a definition that has its own entry elsewhere in the text (*e.g.*, as a single noun) is indicated in **bold face**. The terms are indexed in the appendix.

BASIC CANOPY TERMS

AERIAL.—See **terrestrial**.

ARBOREAL.—A **canopy organism** living in trees at least half of the time during at least one stage of its life cycle (as compared to *semiarboreal,* which can be applied to an organism routinely found in trees but spending less than half of its time there). See Lillywhite and Henderson (1993). Also, relating to or found in trees. For **residents** of herbs and shrubs, see terms under "canopy organism."

CANOPY.—The aboveground plant organs within a community. *Canopy biology* is the study of those organs and anything in or between them, whether living (see **canopy organism**) or dead (*e.g.*, **snags, suspended soil,** or air spaces). A few authors have applied the word "canopy" to single herbaceous plants, apparently reflecting the lack of an alternative to the word **crown** in labeling **aerial** parts of such species. In general, the use of "canopy" to describe individuals should be avoided, although where plants are widely spaced, the distinction between single plants and plant communities may be less critical.

Previous applications of the term "canopy" to forests are varied and with little evident historical pattern. Similar definitions often arose independently (or at least without attribution). Divergent examples include "the uppermost layer of foliage" (Kritcher 1997; see **outer canopy**); "a more or less continuous layer of tree **crowns** forming the 'roof' of the forest" (Richards 1996; see **overstory**); "the combination of all leaves, twigs, and small branches in a stand" (Parker 1995); "the sum total of the **crowns** of the trees of all heights" (Grubb & Whitmore 1966; note that this definition and the previous one exclude **trunks**); "the whole vegetational ocean beyond easy reach of [human] ground dwellers" (Moffett 1994); and "the total plant community above the ground" (Whitmore 1984). As Richards (1996) has pointed out, the term sometimes has been used informally as a synonym for **stratum**, as in a "multi-canopy forest."

Most of these usages emphasize plant apices or **crowns**, or otherwise indicate aboveground delimitations between canopy and noncanopy realms. Not only are these delimitations arbitrary but also they are restrictive to our understanding of ecosystem processes with respect to the conditions that **aerial** plant organs create for life on their surfaces or in their tissues. Consider **epiphyte** communities, which extend from the uppermost foliage to just above the ground, or other canopy plants (**climbers** and mature **hemiepiphytes**), which can span this distance as individuals. By sharing with Whitmore (1984) the widest view imaginable of the vertical range encompassed by canopy biology, we unequivocally include in this discipline all **epiphytes** and all of the ascending or descending parts of other canopy plants, regardless of their specific height or location on a **host** (which is often what is done in practice anyway, notably in many ground-based canopy projects). Indeed, the only portions of **host** plants that are excluded from canopy study are the ground and **terrestrial** soil layers with their associated rhizosphere (roots and their environs).

Furthermore, I encourage the application of "canopy" to all flora, reserving the phrase "forest canopy" to concepts or situations necessarily limited to trees. This definition is not as radical as it may appear to many forest biologists. The word "canopy" has been used by agricultural scientists and other community ecologists to refer to the **aerial** portion of plant communities for more than four decades, and these communities have included both cultivated and natural forbs and grasses (Monteith 1975–1976, Campbell & Norman 1998). These publications and numerous others (*e.g.*, Roxburgh *et al.* 1993, Hirose & Werger 1995) have demonstrated that such communities show many of the attributes commonly attributed to forests, among them **gap** dynamics and the well-developed **stratification** of their ground-rooted plants, physical conditions, and canopy **residents**.

As defined here, canopy biology embraces several core areas of investigation (as outlined in Moffett 2000), among them issues of community ecospace, properties generated by the plants in aggregate (such as **stratification** of microclimate), plant species distributions, plant **architectures**, properties of structural elements such as bark and leaves, and the characteristics of the open (air) spaces contained within the vegetation.

Canopy organism (*e.g., canopy plant* and *canopy animal*).—A taxon or single organism in which all or some (*e.g.,* **climbers** and **hemiepiphytes**) of each individual's mass is located at least half of the time for at least one life cycle stage aboveground on or in canopy structures or residents. The phrase "canopy tree" is an exception, since it usually describes a ground-rooted tree with a **crown** extending to the **outer canopy**. **Arboreal** applies when the occupied plants are trees.

Canopy structure.—Defined by Campbell and Norman (1989) as "the spatial arrangement of the aboveground organs of plants in a plant community." Includes plant **architectures**, spatial relations (interconnections and distributions), and **physiognomy**, which can be determined largely by the species present. Primary vertical attributes are determined by **stratification**; horizontal attributes, by **crown shyness, gaps**, and vegetation *texture* (the combination of plant species diversity, densities, and distributions; Kareiva 1983). Temporal attributes of structure arise from disturbance regime, succession, competition, and plant life history patterns. Canopy structure has been analyzed many ways (Hallé *et al.* 1978, Russell *et al.* 1989, Sumida 1995, Van Pelt & North 1996, Parker 1997, Brokaw & Lent 1998, Bongers 2000). For a discussion of **canopy** "complexity," see **stratum**.

Cover.—The percentage of sky obscured by vegetation as seen from ground level, or the percentage of ground area obscured by vegetation as measured from above the plants, commonly for a single plant species (as in a monoculture). If **crowns** are relatively continuous, a forest is said to have a *closed canopy*, and if widely spaced, an *open canopy*.

Emergent.—An individual tree growing higher than all (or virtually all, if in a clump) others in its vicinity within a forest, so that its **crown** rises markedly above the adjacent **overstory**. Less commonly used also in describing an "emergent species" (a species in which mature individuals commonly match this description) and an "emergent stratum" (the **stratum** containing such mature trees, although more often, emergents are treated as part of the **overstory stratum**). Where trees of an emergent species are abundant, for example, they may locally form a new (higher) **overstory**. By the first and third definitions, such trees are no longer considered emergents; by the second (more problematic) definition, they still may be (*e.g.,* Ashton & Hall 1992).

Gap.—Commonly used in ecology to indicate a space in a **canopy** created by the partial or whole death of a plant (*e.g.,* a branchfall or treefall; *branchfall gap* or *treefall gap*). Brokaw (1982) envisioned more specific criteria for using the term treefall gap, but his views on shape (*i.e.,* vertical sides "extending through all levels") and position (*i.e.,* "down to an average height of 2 meters above ground") are not clearly relevant to either forest dynamics or **canopy** ecology. As I propose the word be used, gaps do not necessarily either extend to earth or begin at the topmost sunlit layer of vegetation (Connell *et al.* 1997, Salvador-Van Eysenrode *et al.* 1999), although those with the latter characteristic are most critical in altering **canopy** microclimate by creating a portal for radiation, water and wind, and by allowing ready access of airborne species to the interior. Treefall gaps are typically ephemeral in that they will be filled by lateral growth of trees to one side or growth from below by **understory** trees (these, however, may occur repeatedly in the same place; Young & Hubbell 1991). Gaps are critical not only to forest tree succession but also to the growth and turnover of **canopy** plants (which contribute to gap filling), and in diverse ways to the lives of **canopy** animals (*e.g.,* Endler 1993, Young 1995). Gaps can likewise be important in nonforest **terrestrial** ecosystems (Platt 1975, Hobbs & Mooney 1991, Moloney & Levin 1996).

Other kinds of openings in vegetation range from intervals between stems and leaves (*e.g.,* **crown shyness**) to the corridors between vegetative strata, and are best described by an ecologically more neutral term than gap, such as "space." In some cases, it may pay to concentrate less on **canopy structure** and more on the space between structures (Lieberman *et al.* 1989; see a possible example discussed under "**glide**"). Mapping open space and understanding its use by various canopy taxa has been difficult, but see for example Aluja *et al.* (1989), Brady *et al.* (1989), Cuthill and Guilford (1990), Cannon and Leighton (1994), Brigham *et al.* (1997), and Aylor (1999).

Leaf area index (LAI).—A measure of leaf density in which the mean total *leaf area* (leaf surface area measuring one side of each leaf only) lying above a given unit of horizontal ground surface area is estimated for a community. The *branch area index*

(BAI) is the total area of (or projected branch area) nonleaf plant surfaces per unit ground area, and the *plant area index (PAI)* combines BAI with LAI. *Leaf area density (LAD)* is the mean leaf area per unit of **canopy** volume. A *foliage height profile* shows the distribution of leaf area (or mass) with height.

OUTER CANOPY.—The uppermost surfaces in a **canopy,** and particularly the leaves immediately adjacent to the open atmosphere. For some researchers, **canopy** *sensu stricto.*

OVERSTORY.—The **stratum** of trees that have outgrown the other vegetation in a forest to have their uppermost **crown** foliage largely or fully in direct sunlight, usually as a relatively continuous layer (excluding **gaps**); **emergent** trees may be either included or assigned to a separate **stratum.** For some researchers, synonymous with **canopy**. An "overstory tree species" is any species for which individuals reach maturity with their **crowns** in the overstory; the term "overstory tree" typically describes any individual tree (mature or not) that has its **crown** in that **stratum.** Foresters refer to overstory tree individuals or species as *dominant* (fully illuminated from above) or *codominant* (illuminated in part from above, with some lateral shading). Of course, "dominant" alternatively can be used to indicate the ecological importance or abundance of a species. Any tree that is *overtopped* (*i.e.,* fully shaded by other trees) can be described in the forestry literature as *suppressed.* It is more ecologically relevant, however, to exclude **understory** specialists by restricting use of the term "suppressed" to those individuals that are surviving for a time in shade for which continued growth would require a light **gap** or other sunlit conditions.

PHYSIOGNOMY.—The gross form and structure of a plant community (*i.e.,* the concept of "morphology" applied at a community level), which is largely determined by the dominant plant growth form in the community's uppermost **stratum** (Whittaker 1962). The overall form of single plants is sometimes described (I suggest secondarily) by this term.

RESIDENT.—A **canopy organism** specialized on a particular **host** plant or plant species (compare **tourist**) or specialized on a particular plant organ (as in a resident of flowers or bark), often across many plant species. The term "canopy resident" is used more generally as a synonym for **canopy organism.**

STRATIFICATION.—Any nonuniform vertical distribution within vegetation. Stratification can be either continuous (as in gradients in midday humidity from ground to **outer canopy**) or discontinuous; if the latter, individual **strata** can be defined.

Stratification can be measured in leaf, stem, or total surface area or biomass of the **terrestrial** rooted plants; in the diversity or abundances of **canopy** plants, animals, and other taxa; in gradients of humidity, light, temperature, and other meteorological conditions, and the physiological responses of species to such gradients; in airborne concentrations of CO_2, pollutants, particulate matter, and **aerial plankton**; in terms of penetration of mist, rain, and turbulence; and in the occurrence of open space within vegetation, and so on. The most common (and primary) use of the term, however, concerns the **terrestrial**-rooted plants of a community, notably the stratification of leaf mass, of individual plants, or of plant species (Smith 1973). Distinct strata could exist for any one of these features, and at the same time not for the others.

Parker and Brown (2000) have critiqued the ways "stratification" has been defined for **terrestrial**-rooted forest plants, and fault many applications for their lack of clarity, testability, and logic. As they point out, the term has been used to describe both strata and gradients. I think it is best defined loosely to accommodate a variety of research interests. For example, just as **architecture** determines at what level a plant or its parts are perceived as patches by foragers (Casas 1991), so different parameters of vertical change and different scales of such changes will influence different **canopy organisms.** Thus how one views stratification may depend on the **resident** or attribute under consideration. At the same time, some standardization of methodologies is necessary to allow for general community descriptions and the accurate comparison of sites or ecosystems (Parker & Brown 2000).

Perhaps because the height of forests aids human perception of any **strata** in them, most studies of stratification (*e.g.,* Smith 1973) have considered only these ecosystems. Yet other **terrestrial** communities show complex stratification patterns, both of their ground-rooted plants (*e.g.,* Monteith 1975–1976) and their **residents** (*e.g.,* Denno & Roderick 1991). Indeed, it is not clear how overall vegetation height might be relevant to stratification. Even communities as short as a mowed lawn show a complex stratification (Roxburgh *et al.* 1993).

A review of stratification literature reveals furthermore that absolute height within a plant community is seldom important per se to the organisms in question (although relative height can be important, as when one plant shades another). This is true both for **canopy organisms** (excluding the costs of **climbing** or falling or requirements for **gliding** or **brachiation**, and even in these cases the importance of substantial height is often overstated) and for their **hosts** (except for certain problems of biomechanics and fluid transport; *e.g.,* Vogel 1988). A couple of examples making use of different approaches to the concept of stratification should make this clear. The stratification of *Anolis stratulus* in Puerto Rico is not a matter of a preference for height per se, but this lizard's choice of perches that happen to be stratified. Thus the lizards are found higher wherever their favored perches are distributed higher in the vegetation (Reagan 1992). Other *Anolis* species stratify in relation to their distance from the **outer canopy**, but again not because of any height (depth) preference. Instead, the lizards select certain temperatures, and temperature is stratified. The *Anolis* ascend or descend as temperatures change (Schoener 1970). Many **epiphytes** at a specified site tend to grow within a certain height range in relation to a diversity of different patterns in the stratification of variables critical to their own establishment and survival, such as microclimate, substrate characteristics, and the distribution of dispersal agents (consider some examples that pertain to cryptogams: Hosokawa & Kubota 1957, Harris 1971, Kelly & Becker 1975, Tobiessen *et al.* 1979, Shirazi *et al.* 1996).

Parker and Brown (2000) have argued that the concept of stratification could be discarded. Yet a basic research approach in **canopy** biology is well demonstrated by the examples mentioned in the paragraph above, i.e., to compare stratification patterns of **canopy residents** to patterns in microclimate or other **canopy** attributes (*e.g.,* bark pH for lichens) in order to make hypotheses about organismal preferences. If confirmed by further studies, such hypotheses could lead to more general explanations for **canopy** species distributions, and for even gross community organization. In a sense this is no different from how scientists handle horizontal distributions. (Of course, patchiness in all three axes is rendered topographically fine-grained within vegetation by **canopy structure.**) A common finding is that short distances traversed vertically in **canopies** are equivalent in effect to changes that occur over much greater horizontal distances in most regions (*e.g.,* Geiger 1965, Russell *et al.* 1989), demonstrating the critical importance of the height dimension as an environmental determinant. The vertical richness in microhabitat may be the primary reason so much diversity packs into structurally complex ecosystems. This could explain the high alpha diversity and low beta diversity of **epiphytes** in relation to other plants (McCune & Antos 1981), intimating the utility of quantifying a vertical component to beta diversity (DeVries *et al.* 1999).

STRATUM.—The presence of a distinctive vertical range within a plant community, either in the distribution of leaf mass, plant individuals, or species, or in any other **canopy** feature, revealed by studies of **stratification** and delimited by predictable changes in character at its upper and lower limits. Also *level, story, layer* or *tier.* These terms often are used incorrectly to describe relative position on a plant, as in an upper stem versus a lower stem (*e.g.,* "higher strata," which commonly means simply "higher"). Of course, depending in part on their locomotor abilities and their fractal scale of perception (*i.e.,* what may be a distinct space or barrier to one organism may be perceived as a continuum to another larger or differently adapted organism; Morse *et al.* 1985), **canopy organisms** are likely to respond to different "strata," so that the way strata are defined must be chosen carefully for each study. A stratum can be a widespread or a universal attribute of an area, but it will more likely be a product of localized conditions (*e.g.,* varying jaggedly in a patchwork of vegetation types or successional stages), and even in a uniform environment, it need not exist at one height above ground but rather may occur relative to the distance from the **outer canopy**. Many terms have been applied to forest strata; see **emergent, overstory,** and **understory**. The other two often mentioned vegetational strata, the *shrub layer* and *herb layer,* are self-explanatory. Terborgh (1985) modeled a way that the **understory** stratum could arise.

Foliage height diversity is the application of the Shannon-Wiener formula to the proportions of the total foliage that lie within each of several selected height ranges of a community (MacArthur & MacArthur 1961). August (1983), Maurer and Whitmore (1981), and others have used this formula as an index of vegetation **stratification** or *complexity.* From this perspective, communities with uniform densities of vegetation at all height intervals would be most "complex" and have the most "strata," counter to the definition proposed in this article; however, if height boundaries are carefully chosen with reference to growth form (*e.g.,* herb, shrub, and tree) as MacArthur and MacArthur (1961) attempted to do, then relative densities of foliage within each height range could at least bear on **canopy** "complexity" (Shrewsbury & Raupp 2000; *cf.* Erdelen 1984).

SUPPORT.—Any structure bearing an organism's weight. *Substrate* and *perch* are similar in meaning, without the connotation of "weight." See **suspension**.

SUSPENDED SOIL.—Soil on or in aboveground plant parts. Equivalently, "**canopy** humus," "epiphytic soils," and other similar terms.

TERRESTRIAL.—Can be used generally to refer to the ground, as opposed to the **canopy**, or anything existing, forming, or living in the ground (*e.g.*, rooted there), as distinct from something that is **aerial** (canopy-dwelling, *e.g.*, **arboreal** or epiphytic). A ground-rooted plant taken as a whole can be described as "terrestrial" (*e.g.*, in comparison to an **epiphyte**) or its roots can be described as terrestrial and its leaves as **aerial**. Context should make it clear whether these definitions or one of the other definitions of "terrestrial" or **aerial** is intended (*i.e.*, land as opposed to "aquatic," or earth as opposed to "extraterrestrial").

TOURIST.—A species occurring fleetingly on a plant with little or no feeding or other effects (compare **resident**). Originally used loosely as suggested here (Murphy 1973), the term can be applied more specifically to nonpredatory (*e.g.*, herbivorous) insects presumed to be passing through the plant on their way to the **host** species to which they are specialized (Moran & Southwood 1982).

UNDERSTORY.—The **stratum** of trees that (barring **gaps**) lies in the shade immediately below the **overstory**. Also loosely applied to all woody strata below the (directly sunlit) **overstory**. An "understory tree species" is any species in which individuals reach maturity with their **crowns** in the understory, whereas the term "understory tree" typically describes any individual tree (mature or not) that has its **crown** in that **stratum**. While "understory" commonly has been used to describe all vegetation up to a specific height, this approach is problematic because it does not conform clearly to the definition of the understory as a vegetational **stratum**.

HOST PLANT-SPECIFIC TERMS

ARCHITECTURE.—In **canopy** biology, the size, angles, distributions, and spatial relations of leaves, stems, **branches**, reproductive organs and other **aerial** parts of a plant, and the generation of these attributes by patterns of intra-plant development, **reiteration**, and death in a given environmental regime. Some researchers include plant size as architecture (*e.g.*, Lawton 1983). Classically, tree architecture is described in part (*e.g.*; Sachs & Novoplansky 1995) by the models of Hallé *et al.* (1978); the system can be extended to herbs (Bell & Tomlinson 1980). Deviation from the generalized models as a result of the history and local microsite conditions (*e.g.*, Oldeman 1990, Valladares 1999) can be described as each individual tree's *crown structure*. Beyond the architectural models, **physiognomy**, and other structural details mentioned above, such characteristics as longevity, resilience, hardness, strength, insulation properties, capacity to transmit vibration, chemistry, pH, absorbency, texture, surface stability, and color, in combination with local meteorological conditions (Freiberg 1997) and the plant's spatial relation to others in its community, create each plant's environment and determine its potential as a **host** of a **canopy** species. The crucial challenge of quantifying the distributions of **residents** in reference to plant architecture was first crudely attempted by Hazen (1966), and has since been accomplished more completely for **epiphytes** (Nychka & Nadkarni 1990, Engwald 2000), **vines** (Castellanos *et al.* 1992), and insects (Casas 1990).

BRANCH.—Typically indicates a (woody) "axis of lesser stature to that on which it is located" (Bell 1991; *cf.* Tomlinson 1987); in some contexts, can include all subordinate axes borne by the axis under consideration. Recently Ng (1999) defined branches in relation to **trunks** as "throw-away shoots which are going to be shed," as distinguished from *limb*, which he applied more narrowly to any stem that is not shed and that, when broken off, leaves behind a large stub. The distinction is difficult or unnecessary in most contexts. *Terminal branches* are distal woody plant shoots (*e.g.*, the smallest—and youngest—stems). These are referred to topologically by some botanists as *first-order branches* (*e.g.*, Steingraeber *et al.* 1979; *cf.* Bell 1991). "Terminal branch" is preferred by botanists and primatologists (*e.g.*, Grand 1972) over *twig*, a less formal word connoting a thin terminal branch. *Bough* lacks a botanical definition, but a few primatologists follow Fleagle (1976) in applying the word to branches too broad to grasp (*e.g.*, >10 cm in diameter for adults of Fleagle's study species); others apply it to branches greater than some specified (large) diameter.

CANOPY ROOT.—Any adventitious root produced by a tree from a **trunk** or **branch** junction. Generally identical in gross morphology to the tree's **terrestrial** roots, canopy roots extend into **suspended soils** or in some cases downward and to the ground (Nadkarni 1981). *Aerial root* is a more general term that can be applied to any root occurring at least in part aboveground, including the stilt roots and prop roots of trees and the various roots typical of **canopy** plants (for additional terms, see Benzing 1991).

CORTICOLOUS.—Any species residing on bark (including in or under bark in spaces open to the air, thereby mostly excluding **endophytes**, which live within plant tissues). The term has been used for species on logs (*e.g.*, Barkman 1958) but is more typically reserved for those on the bark of live **hosts**. I recommend the latter, narrower usage, but in keeping with the definition of **epiphyte**, I suggest that the term also applies to **residents** of the bark of **snags** or dead portions of the aboveground **host** surface. Other useful terms are *ramicolous* (residing on **branches**) and *epiphyllous* (plants, fungi, or microbes residing on unshed leaves; see **epiphyll**).

CROWN.—Aboveground parts of a tree or shrub, and particularly its topmost leaves and limbs. The term **canopy** is often erroneously used as an alternative to "crown" in modifying the word "plant." Plants have "summits" or "crowns" and plant communities have "canopies," but see Sillett and Van Pelt (2000) for an example of an exceptional tree with a **canopy** for a "crown."

CROWN SHYNESS.—A clear, although usually narrow and often regular separation between neighboring tree **crowns** or between adjacent **branch** systems within a tree. This separation may result from mutually inhibited growth or from physical abrasion (Franco 1986). Many plants other than trees show inhibited or directed growth in relation to neighbors (Hutchings & de Kroon 1994, Aphalo & Ballaré 1995).

DOMATIUM.—A cavity or largely enclosed structure constructed of living plant tissue that can be presumed to be largely or exclusively adapted for occupancy by mutualists, such as ants or mites, but at times taken over opportunistically by nonmutualists. Domatia develop as a normal product of plant growth, although some are modified by **residents** (*e.g.*, the removal of pith from internodes). Domatia are known so far only for **aerial** plant organs. See the discussion in O'Dowd and Willson (1989).

HOST (HOST PLANT).—Any plant on or in which another species resides, either for extended periods or briefly, for a particular and specialized activity (*e.g.*, feeding or reproduction). The term "phorophyte" has been applied to plants on which an **epiphyte** resides (Ochsner 1928; *basibiont* in marine systems), but no parallel word exists for long-term animal **residents** of **terrestrial** plants; I find this alternative term awkward and unnecessary. As in animal parasitology, the term "host" (applied to the larger of the two associated organisms) can be used regardless of the occupying species' phylum, and regardless of whether the relation is parasitic, commensalistic, or mutualistic. **Canopy organisms** can be host generalists, widespread on varied plant taxa, or **residents** limited to one or a few species. The latter may either be adapted to a particular host clade or be restricted to any plant species that happen to offer the correct habitat (*e.g.*, bark of a certain texture, stability, pH, or chemistry; Barkman 1958). For some **residents**, habitat selection within plants may be more limited than the species of host.

PHOROPHYTE.—see **host plant**.

PHYLLOPLANE.—The surface of an unshed leaf. The *phyllosphere* is the open space around a leaf that has a microclimate strongly affected by that leaf. Freiberg (1996) proposed the term *caulosphere* to refer to the open space next to a bare **branch** surface strongly affected by the **branch's** presence, *ramosphere* to refer in a similar fashion to the space around a **branch** bearing humus or **epiphytes**, and *aerosphere* to refer to the remaining air spaces within a **canopy**.

PHYTOTELMATUM.—A plant-held pool, that is, a body of liquid held more or less exposed to open air in an aboveground containerlike plant structure. The word applies regardless of whether the water is excreted by the plant (as in pitcher plants) or accumulates from external sources such as rain (as in tree holes). The term is valid whether the structure is adapted to hold water (as in bromeliad leaf axils) or results from an accident of **architectural** growth or death (Kitching 2000).

Reiteration.—A **branch** system within a plant that comes about from activation of a dormant bud, in which development recapitulates that of the seedling of that species, causing a replication of the "**architectural** model" of the plant (for this and other terms, see Hallé *et al.* 1978, Oldeman 1990, Bell 1991, and Valladares 1999). Unique in this process is the replication of functional equivalents of the **trunk** itself. As Ng (1999) has written, "a reiteration is any shoot [within a plant] apart from the main **trunk**, that has the potential to form a **trunk**." Normally, the potential is suppressed, maintaining the singularity of the dominant **trunk**. A reiteration can be triggered by stress (*e.g.*, structural damage) or favorable conditions (*e.g.*, improved light environment).

Snag.—A standing dead tree **trunk** and any attached **branches.** Used by nonbiologists, "snag" can also describe small dead portions of live trees or pruned **branch** stumps (sometimes applied inappropriately to fallen trees). A classification of snags was attempted by Cline *et al.* (1980). A sufficiently short (*ca* <5 m tall; Winters 1977) broken section of standing **trunk** can be called a *stub* (a term also used to describe broken-off **branches** attached to a bole [*e.g.*, for those ≤50 cm long]; Cline *et al.* 1980). When it is sufficiently short (shorter than a person), the stub should be called a *stump.* A general term for dead trees or tree parts, whether **arboreal** or on the ground, is *woody debris.*

Stemflow.—Water from mist or rain flowing to the ground along the outside of stems (for comments, see **throughfall**).

Throughfall.—Water from mist or rain dripping from foliage to the ground, as opposed to **stemflow**. Normally it is measured below the lowest foliage (*e.g.*, at ground level). A given water molecule is likely to variously drip, splash, and flow along **canopy** surfaces in its descent. The part of throughfall that passes through a **canopy** without ever interacting with it is called the *bypass flow. Interception loss* is the part of the precipitation falling on vegetation that does not reach the ground, including water evaporated from or absorbed within the **canopy**. For additional terms, see Parker (1983).

Trunk.—A single (excluding some apical forking), erect, columnar, often woody plant axis of substantial height. Height criteria to date have reflected commercial rather than functional distinctions. Trunks are formed when a plant develops a single vertical stem to which other stems (**branches**), if not suppressed completely, are subordinated by way of their lateral orientation, lesser degree of secondary thickening, and ultimate shedding (Ng 1999).

CANOPY PLANT-SPECIFIC TERMS

Climber (climbing plant, scandent plant).—Any **vine** that **climbs** (grows) a substantial distance upward from the ground, requiring the **support** of a **host plant** or other object to ascend. Source of nutrition is not a part of the definition. Many climbers not only root into the ground but also grow adventitious roots that absorb minerals from within the **canopy**. Climbers have never been categorized as *facultative* or *obligate*, although there are a number of ways this could be done. Most species may be "facultative" as climbers of plants, in that they freely use alternative substrates such as walls. In addition, some **vines** that are capable of **climbing** can also grow over the ground or on low vegetation. Finally, some gesneriads with a **vine** growth form, such as *Drymonia serrulata*, occasionally sprout in **suspended soils** and thus can be facultative **epiphytes** (Skog 1978; L. E. Skog, pers. comm.). None of these distinctions has been addressed in detail.

Methods of ascent (Putz & Mooney 1991) include *scramblers* or *hook climbers* that loosely sprawl over or ascend vegetation by leaning against it, typically aided by hooks or thorns; *tendril* bearers, in which lateral growths of varied derivation entwine **supports**; *twiners,* in which main stems spiral up (*circumnutate*) hosts; and *bole climbers*, which use diverse surface-gripping "adhesive" organs (adventitious roots in *root climbers*) to hold a **support** without entwining it. Attributing the term to B. J. Wallace, Kress (1986) described root climbing species as "semiepiphytic climbers," because root climbers absorb nutrients arboreally through their **aerial** roots. This category is of little value since such nutrients are taken up through leaves, **canopy roots**, and other **arboreal** parts in many **terrestrial**-rooted plants, including possibly the feeder roots of some other **vines** (Putz & Mooney 1991). While common usage suggests that only entwining organs should be considered "tendrils," certain nonroot bole-climbing organs without this property have been labeled *adhesive tendrils.*

Endophyte.—A plant, fungus, or microbe living inside a plant such that it is in contact with the plant's live tissues (excluding any necrosis caused by its presence; relevant to **canopy** study when it is **aerial**). Whereas I prefer to apply "endophyte" to organisms without access to external air, this issue is semantically unresolved (Clay 1995). Regardless, the distinction from **epiphyte** in terms of physical location can be unclear in some situations (Beattie & Lindow 1995). Limiting the term "endophyte" to cases in which an organism is not immediately or overtly harmful to the **host** (Hirsch & Braun 1992, Stone *et al.* 2000) is problematic (Clay 1995). Even in **parasites**, the onset of negative effect relates to **host** health and the **residents'** population density. Thus "endophyte" should be defined to encompass all *endoparasites* and other symbionts, approximating early usages (*e.g.*, De Bary 1866). Because of its location, any endophyte will probably be nutritionally dependent on its **host** to some extent, and therefore at least mildly parasitic. Some endophytes fruit or survive as saprophytes after **host** senescence and death. A few parasitic plants in the Loranthaceae are endophytic *sensu stricto,* except when they produce external reproductive organs. *Endobiont* is a more general term (*e.g.*, it can be applied to animals residing within plant or animal tissues) that is largely restricted to aquatic ecology.

Epiparasite.—An organism extracting nutrients from its **host plant** by means of intermediates (*e.g.*, **host** tissue-invading fungi; Benzing 1990) that potentially cause a disease called *epiphytosis* by Ruinen (1953). This kind of interaction needs verification for **canopy** dwellers. Epiparasite is also used to describe a *hyperparasite* (a **parasite** of another **parasite**) or as a synonym for *ectoparasite* (a **parasite** located externally except for its feeding organs, to contrast with *endoparasite*). For such meanings, these terms are less ambiguous than "epiparasite."

The epiparasitic "intermediates" act as the **parasites** of the **host** (Ruinen 1953). For Ruinen, epiphytosis connotes a mutualism (*i.e.*, between an epiphyte and its "intermediate" mycorrhiza). Such epiparasitisms *sensu stricto* could be difficult to distinguish from hyperparasitisms. For epiparasitisms *sensu lato,* other transphylum possibilities also come to mind, for example, "epiparasitic" yeast on leaf surfaces that is sustained by honeydew from aphids (Fokkema 1981, Dik 1991), not to mention any ants tending those aphids.

Epiphyll.—An **epiphyte** living on the **phylloplane**. Species growing only on unshed leaves are *obligate epiphylls;* those epiphytic as well on other surfaces I propose should be described as *facultative,* unless they are *accidental* (*i.e.*, unable to reach maturity or reproduce as epiphylls), as is the case for the seedlings of orchids, bromeliads, and some **parasites** (mistletoes). In at least the case of certain mistletoes, these presumptively "accidental" epiphylls may be able to send roots to the **host's** stem and save themselves from "certain death" (Kuijt 1964). How long the original epiphyllic portion remains intact after this occurs is unclear.

Epiphyte.—A plant, fungus, or microbe (Beattie & Lindow 1995) sustained entirely by nutrients and water received nonparasitically from within the **canopy** in which it resides (see **parasite**); an epiphyte can live on any aboveground plant surface, growing partly or entirely into the air (see **endophyte**), into **suspended soils**, or on (or in) **snags** or the dead parts of the live **host**, but it does not actively extract water or nutrients from the ground or from the live tissues of the **host**. Thus any negative effect on the **host**, if it occurs, is indirect (*e.g.*, its weight, either singly or combined with other epiphytes, perhaps increasing the chance of **branch** breakage). Nutrients and water are taken up entirely from **suspended soils** and other **aerial** sources such as dead **host** tissues, airborne dust, mist, and rain. This part of the definition excludes dormant stages such as cysts and diaspores. Mistletoe seedlings should not be described as epiphytes because they rely on minerals and water stored in their endosperm until the haustorium forms (Lamont 1983). "Epiphyte" can be applied to nonliving **canopy** features, as in "epiphytic soils" as an alternative to **suspended soils** or "epiphytic pools" instead of **phytotelmata**, but any use for "epiphyte" or "epiphytic plant" as a synonym of **canopy** plant (which encompasses **vines** and **hemiepiphytes**; see **canopy organism**) should be avoided.

In early discussions (Schimper 1898, Oliver 1930), the ground-connected stages of **hemiepiphytes** were termed "epiphytes." This is no longer the norm, except for Madison (1977), who includes as epiphytes plants that are connected to the ground by roots rather than by stems (presumably excluding the prop or stilt roots of trees). Elsewhere the focus has been on nutrient source, consistent with the distinction made between epiphyte and **parasite.**

Canopy-dwelling animals could be characterized as epiphytes (Barkman 1958) because sessile animals routinely are in marine biology. Yet the word has been traditionally limited to nonanimals in **terrestrial** ecosystems, perhaps because of a paucity of sessile animals on land. "**Canopy** animal" is the more appropriate general expression. In aquatic systems, *epibiont* and *basibiont* are applied to external macroscopic **residents** and their **hosts** respectively, regardless of either one's Kingdom, and without connoting any particular trophic interaction or degree of mobility (Wahl 1989). Such terms could be used in **terrestrial** ecology but seldom are (*e.g.*, Gressitt 1966).

So defined, "epiphyte" excludes **parasites** but not other effects on **host** fitness (see **piracy**). Any **resident** of another species can have both positive and negative effects on a **host**, even vertebrate **parasites** (*e.g.*, Munger & Holmes 1988). As in **parasites**, such effects should often be density or "dosage" dependent, changing with **resident** mass in relation to **host** mass, **resident** densities and positions, the health of the **host** or its **architectural** parts, and environmental factors. The net effect of epiphytes can undoubtedly be harmful to their hosts in certain situations (*e.g.*, see discussion in Montaña *et al.* 1997), as might be expected given the huge ecological and phylogenetic diversity of epiphytic species (Kress 1986, Benzing 1990).

Many terms have been proposed to describe epiphytes (*e.g.*, Oliver 1930, Barkman 1958, Benzing 1990). Four are particularly valuable. An epiphyte is *obligate* (or "typical") if it is exclusively epiphytic (a "holoepiphyte"), both sprouting and reproducing in the **canopy**; *facultative* (or "casual") if it sprouts and also reproduces on nonplant substrates (*occasional* applies if the species is relatively scarce in **canopies**); or *accidental* (or "ephemeral") if it fails to reproduce in **canopy** settings, and so has a low fitness regardless of **canopy** abundance (such species when common could be ecologically significant in **canopies**). A species fitting one of these definitions in one region or habitat may fit another definition in a different region or habitat (McCune 1993). In other words, it may be locally (regionally) obligate rather than universally obligate.

Some plants that are ordinarily considered "obligately" **terrestrial** in fact also show geographical patterns in epiphytism. Many old growth forests have moist **canopies** with thick accumulations of **canopy** soil. In such forests, stress-susceptible species (*sensu* Grime 1977, 2001) that elsewhere grow exclusively on the ground can survive in tree **crowns**, even though they not only lack discernible adaptations for epiphytism but also seem ill-designed for **canopy** life by being trees themselves (*e.g.*, Sillett 1999). Under ideal conditions, some of these "**terrestrial**" plants can be facultative (*i.e.*, reproductively successful) epiphytes. The converse is seldom true: most epiphyte species with manifest adaptations to tree **crowns** (usually related to water or nutrient stress; *e.g.*, Benzing 1990) occur exclusively as epiphytes, even when the forest floor offers widely disparate microclimates (light **gaps** included) and microhabitats (*e.g.*, varied soil and plant substrates). The scarcity with which these epiphytes sprout (let alone mature and reproduce) on the exposed tree roots that commonly extend over the ground in lowland rain forests seems to me a profound **canopy** mystery. An adjunct of McCune's (1993) "similar gradient hypothesis" is that stress-tolerant epiphytes should most likely range to the forest floor at the harsher (*e.g.*, xeric) extremes of their distribution. That this is not observed suggests uniquely **arboreal** factors (not just microclimate) confine these epiphytes to trees.

"Obligate" and "facultative" also can be used to describe parts of the life cycle in **nomadic vines** and **hemiepiphytes**, reflecting the likelihood that a normally epiphytic stage occurs in noncanopy settings. An epiphyte can still be considered "obligate" if individuals reproduce after falling to the ground, as long as that is not its only means of propagation. (Such a reproductive strategy remains undocumented, although a variant strategy occurs in the "accidental" epiphytic trees described in Putz 2000). An individual of a species ordinarily considered to be "obligately epiphytic" may still be labeled as an epiphyte if (by "accident") it grows on the ground (*e.g.*, Johansson 1974).

Epiphyte mat.—A carpetlike aggregation of **canopy** plants along with associated **suspended soils** and debris. Nonepiphyte species (*e.g.*, **climbing plants**) can be included (Nadkarni 1984). Also called a "moss mat" when mosses dominate.

Hemiepiphyte.—A plant adapted to sprout as an **epiphyte** that later develops **terrestrial** roots. Such plants need not lose their **aerial** roots. *Obligate* species always show this pattern, whereas *facultative* hemiepiphytes can bypass the epiphytic stage by sprouting on the ground (*e.g.*, Lawton 1983). Hemiepiphytes range from essentially commensal to overtly harmful in their impact on the **host** (Lawton & Williams-Linera 1996). While most are physically supported by the **host** throughout their life, **stranglers** are hemiepiphytes that outlive their **hosts** and replace them as freestanding trees. The term *accidental hemiepiphyte* can be applied to **epiphytes** surviving a fall to earth, or to ground plants that on rare occasions sprout in trees and manage to root to earth. In temperate rain forests of North America, western hemlock (*Tsuga heterophylla*) trees fall into the second category (S. C. Sillett, pers. comm.). Barkman (1958: 11) has given other examples of "accidental" species lacking clear adaptations to hemiepiphytism.

I have chosen to follow the original terminology of Schimper (1898), which was applied with regard to "hemiepiphyte" by most other early English-language authors until Barkman (1958) and particularly Putz and Holbrook (1986). The term "hemiepiphyte" has also been used for the **vine**-like strategies common among aroids (*i.e.,* "secondary hemiepiphyte"; Putz & Holbrook 1986; see **nomadic vine**), the rationale being that as in the species just discussed, part of the life cycle is spent as an **epiphyte** and the other part is spent rooted to ground (with secondary hemiepiphytes sprouting on the ground rather than in the **canopy**). Yet this dual usage of hemiepiphyte has confounded life cycles for plants in which even the "shared" epiphytic parts of their lives are radically different. Most troublesome in viewing such "secondary hemiepiphytes" as epiphytic is that many aroid species grow adventitious roots that are difficult to trace but that frequently extend to the ground. Furthermore, a **terrestrial** life cycle phase is also not a necessity for this strategy: certain aroids may on occasion germinate in **suspended soils** rather than on the ground (T. Croat, pers. comm.). The term Schimper (1898) selected for these vinelike plants, "pseudo-epiphytes," may be less misleading, but I have chosen the term **nomadic vine** because it indicates the relation to and likely derivation from taxa with a **vine** (or **climbing plant**) strategy. Another reason to adopt a new phrase is to avoid confusion. Where "hemiepiphyte" has been used without a modifier, it is common to find, but often difficult to discern, that only hemiepiphytes *sensu stricto* (*i.e.,* the "primary" forms) are being described.

HEMIPARASITE.—A **parasite** simultaneously capable of photosynthesis.

LIANA.—A **vine** with a woody stem. Sometimes the word is limited to species in the tropics, but I follow Putz and Mooney (1991) in encouraging its global application.

NOMAD (NOMADIC VINE, NOMADIC CLIMBER).—A plant that shifts position many times its relatively unchanging length over its lifetime, such that the organism as a whole moves toward and often clearly orients to specific distant localities. Described for some Cyclanthaceae, Marcgraviaceae, and Araceae (Ray 1979), in which nomadism is a modification of the **vine** habit. Best studied are the aroids, which lose their initial root and, remaining largely unbranched, grow ahead and die behind while changing little in overall configuration and mass (beyond an initial growth phase; Ray 1992; see **hemiepiphyte**). The initial root is replaced by adventitious roots that often extend to the ground. Nomadic vines lack a single, stable locus one could call a "home root," much like nomadic people. Nomadism is a spectacular example of plant foraging (as defined in Hutchings & de Kroon 1994), and contrasts with suckering trees, rhizomatous plants, fairy-ring mushrooms such as *Marasmius,* and others that shift more locally and diffusely from their point of origin (*e.g.,* germination site). A few **arboreal parasites** may qualify as nomads (*e.g., Ileostylus micranthus*; Kuijt 1969).

PARASITE (PLANT PARASITE).—A plant, fungus, or microbe that actively extracts nutrients or water from live **host plant** tissues, typically by means of intrusive organs (*e.g.,* haustoria), or by living internally. See entries for **endophyte** and **epiparasite**; for a discussion of animal "parasitisms" of plants, notably insect herbivores, see Price (1977). Generally, "parasite" is applied only to species in which individuals are faithful over their lifetime to a single **host** individual (as distinguished from predatory species), but in fact some mistletoe individuals "prey" on several **hosts** simultaneously or sequentially (Kuijt 1969). The *Oxford English Dictionary* (2nd edition) extends the meaning of "parasite" to "animals or plants that live as tenants of others, but not at their expense (strictly called commensal or symbiotic)," but tradition among ecologists (and indicated in the *O.E.D.* by fiat) has been to call such plants **epiphytes**. In this dictionary, as in Webster's 3rd, the currency of **host** "expense" is nutrition (see the excellent discussion in Kerner von Marilaun 1888). For a few expedient phrases helpful in describing a **resident's** other negative effects on its **host**, see **piracy**.

Most **canopy** parasites are mistletoes. Indeed, the terms are often treated as synonyms, but some nonmistletoe taxa that might otherwise be described as **epiphytes** (including **epiphylls**) appear on close inspection to be parasitic or show transitional characteristics (Berrie & Eze 1975, Legaz *et al.* 1988, Yagüe & Estévez 1988). Mistletoes have been described as **hemiparasites**, because their photosynthetic capacities were thought to limit reliance on the **host** to water and minerals (Kuijt 1969). Actually carbon uptake from the **host** occurs in some mistletoes (Marshall & Ehleringer 1990), but **hemiparasite** remains expedient in describing any chlorophyll-bearing parasite (as contrasted with *holoparasite*). The presence or absence of haustorial links to the phloem may be a better measure of host dependency (*e.g.*, Lamont 1982). The possibility that parasites can be *facultative* (meaning that some individuals live as **epiphytes**) has been suggested by some researchers. This has yet to be confirmed for mistletoes under natural conditions (Kuijt 1969). Certain fungi, however, survive on incidental nutrients on the surface of a living plant and then infect their **host** as it senesces, or they are parasitic on the leaves of one plant species and commensal on those of another (Leben 1981, Beattie & Lindow 1995; see **epiparasite**).

An apparent difficulty for the definition of "parasite" is the active transfer of nutrients from mistletoe to **host** claimed by Rediske and Shea (1961). While both the methods and the results of that paper may be flawed (J. D. Marshall, pers. comm.), it is hypothetically possible for parasites to be beneficial, at times making up for a **host's** net nutrient loss with other attributes (related nomenclatural issues are addressed in Goff 1982, Margulis 1990, and Smith 1992).

Piracy.—A term variously useful in describing a **canopy resident's** negative effects on a **host** (other than **parasitism**): *nutritional pirate* (Benzing & Seeman 1978) for a **canopy** plant in which **aerial** organs intercept minerals nonparasitically, with the net effect of reducing nutrient flow to the **host**; *light pirate* for a **canopy** plant that reduces **host** photosynthesis through shading; *structural pirate* for a **canopy** plant that weighs down or physically impedes the growth of its **host** (calling it a "mechanical parasite" is inappropriate; see **parasite**), and so on. The effects will often depend on **resident** densities on a **host**. The term "pirate" can apply to **parasites**, as when the weight of a *Struthathus orbicularis* plant snaps a tree **crown** (Kuijt 1964).

Strangler.—A **hemiepiphyte** that outlives its **host** as part of its normal life cycle, at which point it becomes a freestanding tree itself. At this stage, its **trunk** is formed by the coalescence of what had originally been its descending (hemiepiphytic) roots. Because the primary cause of **host** death often may be old age (Holbrook & Putz 1996), the definition does not specify that there must be negative consequences to the **host** tree from carrying a strangler. Nevertheless, a strangler may accelerate the demise of its **host** by mechanically impeding its growth, splitting its wood, shading its foliage, or root competition. Large, clinging **hemiepiphytes** dependent on a **host** for lifelong **support** should not be called stranglers (Moffett 1994: 184). Whereas I follow most authors in treating stranglers as a type of **hemiepiphyte**, Richards (1996) considers **hemiepiphytes** and stranglers to be separate, potentially overlapping categories.

Vine.—A growth form distinguished by indeterminately elongate, often frail stems requiring external **support** to grow upward. Often treated as synonymous with **climbing plant**, many vines grow recumbent on the ground and a few may sprout opportunistically in the **canopy** (see **climber**). Some vines lose their initial rooted connection to the ground (see **nomad**). Vines can be woody (see **liana**), and some species that habitually grow as **lianas** are freestanding when young or develop as shrubs if no **supports** are available.

ANIMAL-SPECIFIC TERMS

Climb.—Can be applied (*senso lato*) to any movement on uneven surfaces, although context often implies more (*e.g.*, "climb a tree" [ascend] vs. "climb in a tree" [move about arboreally]). Biomechanically "climb" can be defined for both plants (see **climber**) and animals in terms of any change in potential energy; in the field it is more meaningful to designate as a climb any sufficient interval of relatively continuous increase or decrease in height. There can be more stringent criteria. Hunt *et al.* (1996) have suggested limiting "climb" to ascent or descent of **supports** angled ≥45° from horizontal, in parallel with the arbitrary distinction made between **parachute** and **glide**. McGraw (2000) discussed problems arising from disparate research applications of the word, and limits "climb" to ascent of upright boles (*vertical climb*). Cant *et al.* (2001) developed finer subcategories. Regardless, this term confounds many activities that have yet to be adequately distinguished and studied (*e.g.*, Rose 1979) (see **locomotor behavior**).

Most climbing terminology is descriptive of kinematics (limb motions) rather than the underlying forces that make organisms move without falling. As an example, for unknown reasons anole lizards climb (*senso lato*) most effectively by walking on narrow **supports** and running on wide ones (Irschick & Losos 1999). In biomechanical terms, *walking* involves fluctuations in potential energy out of phase with fluctuations in kinetic energy, compared with *crawling*, in which potential energy (height) varies little. On vegetation, such fluctuations are overwhelmed by **support** irregularities in ways not yet understood. On this basis (and because some species commonly said to crawl actually walk; Farley & Ko 1997), the word "walk" is preferred.

Depending on the species and situation, the difference between locomotion in **canopies** and in other environments can blur. A fossorial species might burrow through the moss-covered soil on tree **trunks** and thereby ascend several meters without "climbing" in the typical sense (except insofar as animals can be said to "climb" when moving upward through soil). Worm-size blind snakes (Typhlopidae), considered overwhelmingly subterranean, have been found several meters high in trees, perhaps following ant columns (Shine & Webb 1990); other species climb routinely (Gaulke 1995). S. C. Sillett (pers. comm.) has seen a 7-cm earthworm of a predominantly **terrestrial** species rapidly ascending 60 m up a Sitka spruce **trunk**. A further challenge to any preconceived ideas about what constitutes **arboreal** "climbing" is the discovery by Sillett and colleagues (pers. comm.) of copepods belonging to an obligately aquatic taxon (although often an interstitial inhabitant of the saturated sediments in or beside water bodies) at a height of 68 m in a California redwood (*cf.* Reid 1986). They think the copepods swam to this height through the water that seeps from **epiphyte mats**, forming a constant **stemflow** along the **trunk** of this tree in dry weather. Scaled up from the copepod's <1 mm length, this feat would surpass a salmon "climbing" Mt. Everest. Certainly it is debatable at what point accidents end and adaptations begin: ground-dwelling arthropods are routinely driven up trees during annual flooding of the Amazon River (Adis 1997), whereas **suspended soils** harbor numerous arthropods typical of ground soils (although often of distinct taxa) for which life cycles are not known.

Locomotor behavior.—**Positional behaviors** involving motion. See discussion in Prost (1965). There is a large vocabulary to describe kinematics, especially in primates, many categories of which intergrade. I mention a few terms based largely on Hunt *et al.* (1996). See **suspensory behavior** and **climb**. *Leaping* (*saltation*) occurs if contact with **supports** is lost during propulsion between **branches** (the *aerial phase*), and most commonly indicates a jump from a position above a **support**; *hopping* and *bounding* refer to small leaps, in the former case generally in a series (although more specific definitions for both words exist; *e.g.*, Hildebrand 1985, Günther *et al.* 1991). *Vertical clinging and leaping* is clinging to and leaping between vertical **supports**. To *drop* is to fall upon release of a **support**; in an *arrested drop*, the animal catches its fall and remains suspended below the original **support** by its limbs or tail. An animal may *hoist* itself from such a **suspensory** position to the top of the **support**. Space can be crossed without a leap by maintaining contact between (*bridging*) **supports**. *Tree sway* occurs if an animal oscillates or deforms a **support**, often to reach a new one. In a *cantilever*, weight is held by the hind limbs or tail, and the body is stretched toward a goal; if a new **support** is gripped, the animal is making a *transfer*. *Clambering* is simultaneous and protracted use of multiple **supports** requiring all four limbs, either during **quadrapedalism** or vertical **climbing** (Cant 1988). *Scramble* typically implies rapid clambering. Snakes show *lateral undulation* by moving over continuously shifting, widely separated points of contact. *Concertina* describes a snake using static points of contact with **supports**, either by progressing between **branches** in a series of cantilevers using the tail or hind body, or by wedging its posterior into surface irregularities with short-radius bends, extending its anterior to grasp more irregularities, then pulling up the posterior. *Scansorial* usually describes species adept both at **canopy** and **terrestrial** locomotion, but it can also be used more generally to describe species capable of **climbing** or to indicate adaptations for **climbing**. Others limit the term to "**quadrupedal** progression using the tegulae along large vertical **supports**" (Youlatos 1999), whereas herpetologists apply scansorial to species that **climb** on rocks.

Positional behavior.—**Postural behaviors** and **locomotor behaviors** considered jointly. Body orientation is described as *orthograde* (perpendicular) or *pronograde* (parallel) in relation to level ground.

Postural behavior.—Stationary **positional behaviors** such as sitting or standing. To *sit*, an animal on a largely horizontal **support** puts most of its weight on its haunches; in **canopies**, *sprawl* refers to lying on the belly with the limbs dangling. To *cling*, an animal grips **supports** with its limbs. Typically the word is applied when **supports** are vertical, although animals can also cling to slippery horizontal **supports** or under **branches** if they grasp them tightly; the latter example can be viewed as a form of **suspensory behavior.**

Quadrupedalism (arboreal quadrupedalism).—Positioned on or moving above a **support** using four limbs (compare **suspensory behavior**). Applied to movements on relatively horizontal **supports** (*e.g.*, <45°, as contrasted with **climb**).

Suspensory behavior (suspension).—Hanging or moving below a **support.** Such behavior is described more fully by indicating the limbs used in supporting body weight (*e.g.*, "tail suspend"). In suspensory behavior, a **support** is typically called a *superstratum*, although given the precise definition of **stratum**, a more appropriate descriptor might be *supersupport*. The problem of balancing above a **support** faced by species with **quadrupedalism** is often avoided by spreading body weight between **supports**. Hanging by four limbs should be referred to as *quadrumanous-suspend* (Hunt *et al.* 1996) rather than as **quadrupedalism**. *Suspensory feeding* describes hanging from **supports** to reach food on terminal **branches**. *Brachiation* is prolonged swinging under **supports** using only the forelimbs. *Ricochetal brachiation* incorporates leaps (see **locomotor behavior**) from below one **support** to below the next; leaps are absent from *continuous contact brachiation* (Bertram *et al.* 1999). *Arm swing* is a more general term that includes species managing only a few arm-over-arm strokes or for which a prehensile tail helps the arms. *Semibrachiation* is a term with little utility (*e.g.*, Mittermeier & Fleagle 1976).

AIRBORNE LOCOMOTOR TERMS

Aerial plankton.—Minute airborne organisms en masse, including mites, thrips, ballooning spiders, cysts, and many plant and fungal reproductive structures small enough to remain suspended in the air for potentially long intervals. The term is analogous to plankton in water, although most **aerial** plankton stay aloft only temporarily (Johnson 1969).

Alignment.—A leap or fall is considered "aligned" if adaptations exist to maintain a constant vertical orientation in the air (compare **free fall**) typically so that drag or lift is enhanced. The term covers all species with **controlled descent** (since these require alignment to orient; *e.g.*, Möhl 1989) and passively dispersing organisms. Among many of the latter taxa, however, **parachuting** can occur without body alignment if a fall is slowed by drag due to structural features or by low body density. This description may apply to many insects and diaspores. Alignment can serve several functions, such as increasing the precision of an animal in reaching targets or the speed of its recovery from jumps or falls (*e.g.*, Belt 1874, Losos *et al.* 1989, Demes *et al.* 1991, Wassersug *et al.* 1993) or causing seeds to strike the ground and "plant" themselves at an angle conducive to germination (Sheldon 1974).

Controlled descent.—Jumping or falling by organisms that use any active means, other than flapping wings, to influence direction and velocity in the air. Thus midair shifts in speed and course can represent locomotion rather than passive dispersal. Initial directional biases imposed by the takeoff are excluded. Critical to the concept of controlled descent is orientation in relation to the exterior environment, which requires **alignment**. Some species with controlled descent may be limited to **parachuting**, whereas many **gliders** can choose to descend steeply and so can **parachute** as well. The term applies regardless of whether an organism leaps or falls routinely to traverse either primarily horizontal or vertical distances, or if it does so only accidentally or as an escape response. Controlled descent has been analyzed for a few species (*e.g.*, Emerson & Koehl 1990) but is not necessarily an attribute of all animals that fall regularly from a height. It may be absent in coqui frogs, which **parachute** as part of a daily activity cycle (Stewart 1985; M. M. Stewart, pers. comm.). Coqui descent appears at times to be indifferent to **canopy structure**, since frogs often strike vegetation en route.

Free fall.—To leap or fall without behavioral or morphological adaptive mechanisms that maintain a constant posture in the air. Free fall can be either accidental, as when an animal is knocked from foliage (Schlesinger *et al.* 1993, Haemig 1997), or intentional, as when insects descend from trees in a daily cycle (Adams 1941, Costa & Crossley 1991). It is unclear from most reports, however, whether these species free fall or show **alignment**. Free-falling organisms are said to **parachute** if they develop a high level of drag because of low density or structural features. Some free-falling **parachuters**, such as lichen lobules (Rhoades 1983), still manage substantial horizontal transits by breaking free of the substrate in high winds (*i.e.*, a "wind-blown free-faller"; Boucher & Nash 1990). Free-falling species without **parachuting** characteristics can be said to fall *ballistically* (R. Dudley, pers. comm.). In aerodynamics, the distinction between **parachuting** and ballistic descent is relative: *e.g.*, one object with a lower density than another but that is otherwise identical can be said to **parachute** in relation to the second object. For most uses of this term in biology, the existence of adaptive mechanisms is a key feature.

GLIDE.—To leap or fall at a shallow angle of descent (*e.g.*, <45° from horizontal), without the use of flapping wings. These criteria must be met under windless conditions such that the organism's own morphological or behavioral adaptations determine the steepness of descent, unlike organisms that specialize at moving over extreme horizontal distances carried by wind (see **parachute**). Most gliders are animals capable of **controlled descent**. Plant dispersal could likewise be enhanced by gliding, but very few seeds glide (*e.g.*, Augspurger 1986), perhaps because gliding is more dependent than parachuting on an ability to steer and remain stable in turbulent air (McCutchen 1977) and on having a sufficiently high mass (Niklas [1992], however, has pointed out that even pollen grains and spores can develop appreciable forward motion in stagnant air as a result of structural asymmetries). Gliding often requires a minimum descent speed, so that the organism must initially **parachute** some distance before it achieves appreciable forward motion.

Gliding and **parachuting** are most usefully distinguished for species operating at the extremes of descent angle. This is because Oliver's (1951) 45° demarcation is arbitrary (except at this angle, lift = drag, *e.g.*, consider Fig. 3.8 in Dudley 2000) and frustrating to assess, owing to the unpredictability of air currents and the flexibility available to many organisms in choosing their downward angle and continuously changing this angle during the course of descent. Of greater biological merit than tests of the 45° criterion is the question of how (and how well) an organism influences its descent (*e.g.*, Emerson & Koehl 1990). One solution would be to redefine "glide" to coincide with **controlled descent**. Another would be to distinguish organisms that develop aerodynamic lift from those that purely increase drag (even though lift and drag become indistinguishable under certain conditions; M. H. Dickinson, pers. comm.). I decided against these options because in common parlance, "glide" is used for largely horizontal airborne travel and because for species operating at the extremes of descent angle, **parachuting** and gliding as defined here are likely to have different ecological functions (*e.g.*, transits exclusively from **stratum** to **stratum** as compared to a facility with movements also from tree to tree within a **stratum**). In general, however, the capacity to generate aerodynamic lift gives an organism far greater possibilities for control (S. Vogel, pers. comm.).

The high diversity of Indo-Malayan gliders has been attributed to the relatively great height of many Asian trees, which may allow longer glides (Dudley & DeVries 1990), and to the paucity of **vines** in that region, which may drive the evolution of gliding behavior as a substitute means of crossing from tree to tree (Emmons & Gentry 1983). Yet with descent angles of 10° in some cases (Thorington & Heaney 1981), many gliders require so little height that some of them stratify (MacKinnon 1978; T. Laman, pers. comm.). Furthermore, gliding is less risky and more efficient than **clambering** long distances along **vines** (Norberg 1983, Norberg 1985) to reach the highly dispersed foods eaten by these animals (Goldingay 2000; T. Laman, pers. comm.). I propose that the converse of these hypotheses is more accurate: as a result of being both tall and sparsely interconnected, many Indo-Malayan forests are characterized by large uncluttered spaces that are conducive to gliding.

PARACHUTE.—A falling or jumping organism having behavioral or morphological mechanisms to increase drag. Associated with descent at a sharp angle (*i.e.*, 45–90° from horizontal; Oliver 1951). Zoologists typically apply the term "parachuting" to species with **controlled descent** that show vertical **alignment** in the air, but other organisms can parachute (see **free fall**). Some species that **glide** can also choose to parachute, but many parachuters do not have the morphological adaptations needed to descend at a shallow enough angle to **glide**. Ballooning arthropods (*e.g.*, Suter 1999) and wind-dispersed diaspores such as autogyros or plumed seeds (Augspurger 1986) also parachute, but they are most likely to fall free during wind (Greene & Johnson 1989), resulting in notable horizontal movement (Matlack 1987) such that their angle of descent may often meet the criterion for gliding. I suggest this be called "windblown" parachuting. The ability of wingless insects to parachute is critical to certain theories of the origin of insect flight (Kingsolver & Koehl 1994), but rarely has been observed in nature (Murphy 1973, Dudley 2000).

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APPENDIX. *INDEX, WITH FOREIGN TRANSLATIONS. The following is an index of the terms discussed in this article (excluding sub-terms like "obligate epiphyte," which for example is defined under "epiphyte"). Translations are given into Panamanian Spanish (S), Brazilian Portuguese (P), French (F), and German (G), representing the simplest "best fit" for each term. Translations seldom have exactly the same meaning as their English "equivalent" at the level of detail addressed in this article, and words such as "canopy" and "vine" can have very different connotations from language to language. No foreign terms are provided for some basic vocabulary words with numerous alternative translations and for a few words specific to English (e.g., "arm swing").*

English	Spanish	Portuguese	French	German	Page
adhesive tendril	zarcillo adhesivo	gavinha	vrille adhésive	Haftranke	578
aerial	aéreo	aéreo	aérien	Luft...	572
aerial phase	fase aérea	fase aérea	phase aérienne	Flugphase	583
aerial plankton					584
aerial root	raíz aérea	raíz aérea	racines aériennes	Luftwurzeln	577
aerosphere	aerofera	aerosfera	aerosphère	Ärosphäre	577
alignment					584
arboreal	arbóreo	arbóreo	arboricole	arborikol, baumbewohnend	572
architecture	arquitectura	arquitetura	architecture	Architektur	576
arm swing					584
ballistic fall	caída balística	queda balística	chute balistique	ballistischer Fall	584
basibiont	basibionte	basibionte	basibionte	Basibiont	579
bole climber	enredadera			Stammkletterer, Stammkletterpflanze	578
bound					583
brachiation	braquiación	braquiação	brachiation	Schwinghangeln	584
branch	rama	galho, ramo	branche	Ast	576
branch area index	índice del área de las ramas	índice de área cortical	indice surfacique de branche	Borkenflächenindex	573
bridge	puente	ponte	pont	Brücke	583
bypass flow			pluie directe	durchfallender Niederschlag	578
canopy	dosel	dossel	canopée	Kronenraum, Baldachin	572
canopy biology	biología del dosel	biologia de dossel	biologie de la canopée	Kronenbiologie	572
canopy root	raíz del dosel	raiz de dossel	racines de canopée	Baumkronenwurzeln	576
canopy structure	estructura del dosel	estrutura do dossel	structure de la canopée	Kronenstruktur	573
cantilever	cantilever, ménsula	pulvino	console	Ausleger	583
caulosphere	caulosfera	caulosfera	caulosphère	Kaulosphäre	577
circumnutate	circumnutante	circumnutação	volubile	Windebewegung, winden	578
climb					582
climber (climbing plant)	planta trepadora	trepadeira, cipó	plante grimpante	Kletterpflanze	578
cling					583
closed canopy	dosel cerrado	dossel fechado, dossel contínuo	couvert fermé, canopée dense	geschlossenes Kronendach	573
codominant	codominante	codominante	codominant	codominant	574
complexity	complejidad	complexidade	complexité	Komplexität	575

APPENDIX. *Continued.*

English	Spanish	Portuguese	French	German	Page
concertina	concertina		accordéon	ziehharmonikaähnliche Bewegungen	583
controlled descent	descenso controlado	descida controlada	descente contrôlée	kontrollierter Abstieg	584
corticolous	corticícola	corticícolo	corticole	rindenbewohnend	577
cover	cobertura	cobertura	couverture	Deckungsgrad	573
crawl	arrastrar, trepar	arrastar	ramper	kriechen	582
crown	copa	copa	couronne, cime	Krone	577
crown shyness	intervalo de copas	intervalo de copas	timidité des cimes	Kronenvermeidung, Kronenscheu	577
crown structure	estructura de la copa	estrutura da copa	structure de la cime	Kronenstruktur	576
domatium	domacio	domácea	domatie	Domatium	577
dominant	dominante	dominante	dominant	dominant	574
drop					583
ectoparasite	ectoparásito	ectoparasita	ectoparasite	Ektoparasit	579
emergent	emergente	emergente	émergent	Überständer	573
endobiont	endobionte	endobionte	endobionte	Endobiont	579
endoparasite	endoparásito	endoparasita	endoparasite	Endoparasit	579
endophyte	endófito	endófito	endophyte	Endophyt	578
epibiont	epibionte	epibionte	épibionte	Epibiont	579
epiparasite	epiparásito	epiparasita	epiparasite	Epiparasit	579
epiphytosis	epifitosis	epifitose	épiphytose	Epiphytose	579
epiphyll	epifilia	epífilo	épiphylle	Epiphyll	579
epiphyllous	epifila	epífila	épiphylle	epiphyllisch	577
epiphyte	epífita	epífita	épiphyte	Epiphyt	579
epiphyte mat	alfombra de epífitas		tapis d'épiphytes	Epiphytenmatte	580
foliage height diversity					575
foliage height profile	perfil vertical de hojas	distribuição vertical de folhas	profil vertical de répartition foliaire	Belaubungshöhenprofil	573
free fall	caída libre	queda livre	chute libre	freier Fall	584
gap	claro, apertura	clareira	chablis	Lichtung, Gap	573
glide	deslizarse, escurrirse, planear	planar	vol plané, planer	gleiten	585
hemiepiphyte	hemiepífita	hemiepífita	hémiépiphyte	Hemiepiphyt	580
hemiparasite	hemiparásito	hemiparasita	hémiparasite	Hemiparasit	581
herb layer	estrato herbáceo	estrato herbáceo	strate herbacée	Krautschicht	575
hoist					583
holoparasite	holoparásito	holoparasita	holoparasite	Holoparasit	581
hook climber	gancho de subir	gancho para escalada	plante grimpante à crochets	Hakenkletterer	578
host	hospedero	hospedeiro	hôte	Wirt	577

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English	Spanish	Portuguese	French	German	Page
hyperparasite	hiperparásito	hiperparasita	hyperparasite	Hyperparasit	579
interception loss	pérdida por intercepción	chuva interceptada pelo dossel	perte par interception	Interzeptionsverlust	578
jump (see leap)					
lateral undulation	ondulación lateral	ondulação lateral	ondulation latérale	schlängelnde Bewegungen	583
layer (see stratum)					
leaf area density	densidad del área foliar	densidade de área foliar	surface foliaire par unité de volume de la canopée	Blattflächendichte	573
leaf area index	índice del área foliar	índice de área foliar	indice [de surface] foliaire	Blattflächenindex	573
leap	saltar	saltar	sauter	springen	583
level (see stratum)					
liana	liana	liana	liane ligneuse	Liane	581
limb (see branch)					
locomotor behavior	comportamiento de locomoción	comportamento locomotor	comportement locomoteur	Fortbewegungsverhalten	583
mechanical parasite	parásito mecánico	parasita macânico	parasite mécanique	mechanischer Parasit	582
nomadic vine	bejuco nómada	liana nômade	liane nomade	nomadische Kletterpflanze	581
open canopy	dosel abierto	dossel aberto	voûte ouverte, canopée ouverte	offenes Kronendach	573
orthograde	ortógrado	ortógrado, ortogonal	orthograde	aufrecht	583
outer canopy	dosel superior	dossel superior	canopée supérieure	äußere Kronenschicht	574
overstory	dosel	dossel	couche supérieure, canopée	oberes Stockwerk im Wald, Kronenschicht	574
parachute	paracaídas	páraquedas	parachute	Fallschirm	585
parasite	parásito	parasita	parasite	Parasit	581
perch	percha	pouso, poleiro [bird]	perchoir	Sitzplatz, Hochsitz, Ansitz [bird]	576
phorophyte	forofita	forófito	phorophyte	Trägerbaum, Phorophyt	577
phylloplane	fitoplano	fitoplano	phylloplan	Blattoberfläche	577
phyllosphere	filosfera	filosfera	phyllosphère	Phyllosphäre	577
physiognomy	fisonomía	fisionomia		Physiognomie	574
phytotelmatum	fitotelma	fitotelma	phytolème	Phytotelme	577
piracy	piratería	pirataria	piraterie	Piraterie	582
plant area index	índice del área vegetal	índice de área vegetal	indice surfacique végétal	Deckungsgrad	573
positional behavior	comportamiento de posición	comportamento de posicionamento	comportement positionnel	Positionierungsverhalten	583
postural behavior	comportamiento de postura	comportamento de postura	comportement postural	Ausrichtungsverhalten	583
pronograde	nivelación del cuerpo	corpo nivelado	pronograde	auf vier Beinen stehend	583

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English	Spanish	Portuguese	French	German	Page
quadrumanous suspend	suspensión cuadrúmana	suspensão quadrumana	suspension par les quatre membres	vierfüssiges Hängen	584
quadrupedalism	cuadrupedal	quadrupedalismo	quadrupédisme	Vierfüßigkeit	583
ramicolous	ramícola	ramículo	ramicole	astbewohnend	577
ramosphere	ramosfera	ramosfera	ramosphère	Ramoshäre	577
reiteration	reiteración	reiteração	reitération	Reiteration, Wiederholung	577
resident	residente	residente	résident	Bewohner, Standvogel [bird]	574
root climber	raíz trepadora	raiz trepadeira	liane qui utilise ses racines pour grimper	Wurzelkletterer	578
scansorial		escansorial	grimpant	scansorial, kletterfüßig, Klettervogel [bird]	583
scramble					583
scrambler	trepador	trepador		Spreizkletterer, Spreizklimmer	578
shrub layer	estrato arbustivo	estrato arbustivo	strate arbustive	Strauchschicht	575
sit	sentar	sentar	s'asseoir	sitzen	583
snag	árbol muerto	árvore morta	chandelle	stehendes Totholz, Dürrständer	578
sprawl					583
stemflow	flujo caulinar	água de escorrimento	ruissellement le long des troncs	Stammabfluss	578
story (see stratum)					
strangler	estrangulador	estrangulador	étrangleur	Würger	582
stratification	estratificación	estratificação	stratification	Stratifikation, Stratifizierung	574
stratum	estrato, nivel, capa	estrato	étage, strate, couche, niveau	Schicht, Stratum, Niveau, Level	575
stub	tocón	toco	souche	Stumpf	578
substrate	sustrato	substrato	substrat	Substrat, Nährboden	576
superstratum	superestrato	estrato superior	strat supérieur	Deckschicht	584
supersupport					584
support	sostén, apoyo	suporte	support	Stütze, Träger	575
suppressed	supreso	suprimido	réprimé	unterdrückt	574
suspended soil	suelo suspendido	solo suspenso	sol suspendu	Baumkronenhumus	576
suspensory behavior	comportamiento suspensorial	comportamento suspensório	comportement de suspension	schwebend	584
suspensory feeding	alimentación en suspensión	alimentação em suspensão	se nourrir en étant suspendu	Ernährungsweise hängend unter Ästen	584

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English	Spanish	Portuguese	French	German	Page
tendril	zarcillo	gavinha	vrille	Ranke	578
terminal branch	rama terminal, rama pequeña	ramo terminal, galho terminal	branche terminale, rameau ultime	Endzweig	576
terrestrial	terrestre	terrestre	terrestre	terrestrisch	576
texture	textura	textura	texture	Textur	573
throughfall	flujo del follaje	água de gotejamento	pluie atteignant le sol	Kronentraufe	578
tier (see stratum)					
tourist	turista	transeunte	touriste	Tourist	576
tree sway	balanceo del árbol	balanço da árvore	balancement d'un arbre pour atteindre le suivant	Baumkrümmung	583
trunk	tronco	tronco	tronc	Stamm	578
twig	rama pequeña	ramo pequeno	rameau, petite branche	Zweig, Ästchen	576
twiner	zarcillo	plantas acopladas	liane volubile	Schlingpflanze	578
understory	sotobosque	sub-bosque	sous-bois	Unterwuchs	576
up					571
vertical clinging and leaping	saltas y sujetación vertical	ejeção	saut en position verticale	vertikales Anklammern und Springen, Springkletterer	583
vine	bejuco	cipó	liane	Kletterpflanze	582
walk	caminar	caminhar	marche	gehen	582
woody debris	escombros leñosos	escombros lenhosos	débris de bois	Ansammlung von Totholz, holzige Pflanzenreste	578