Forest Canopy Stratification—Is It Useful?

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Submitted February 16, 1999; Accepted November 22, 1999

abstract: It has long been recognized that the forest canopy has a complex structure that is significant for environmental interactions, regeneration, growth, and biotic habitat. Not only is the structure variously complex, but also there are many ways to conceptualize that complexity. Yet the persistent theme when considering the structure of canopies continues to be that of stratification: whether structural units are arranged in layers above the ground. We examined the use of the terms "stratification," "layering," and others in connection with canopy structure and found they had various meanings (often only implied) that were difficult to reconcile and to measure. We applied the definitions to the structure of a single, well-studied canopy located in Virginia, U.S.A., and found they failed to define consistently and clearly the presence, number, or location of strata. Additionally, we found the concept had limitations related to scale dependence, point of reference, and spatial averaging. Thus, asserting that a forest is stratified or naming the number of layers generally provided no guide to its structure. We propose alternative ways of conceptualizing and studying the forest canopy that avoid most of the problems associated with stratification. Among these are direct measurement and mapping of structural and environmental variables that have clear potential connections with canopy functions and viewing the distribution of structures or environmental conditions within the canopy as ecological gradients.

Keywords: forest, canopy, layer, stratification, stratum.

> There opened to my view one of the most magnificent prospects that forest scenery could afford; the gigantic measure of some of the trees was altogether surprising, but yet, on account of their various heights, their foliage lay as if it were in strata, and the denseness of the ramification wove the branches into a chaos as picturesque as it was inextricable. (Schweinfurth 1874, p. 488)

Traveling through Africa in 1870, G. A. Schweinfurth saw forest canopies in what seem like modern terms, as both "stratified" and "chaotic." He also seized upon the elements of much confusion and argument about forest canopy structure in twentieth-century ecology.

"Stratification," "layering," and related terms have long been used by ecologists to describe the simultaneous variety and organization they see when looking up into the forest canopy. With these words, they have generally asserted that there can be different things—be they structures, species, or environments—at different heights in the canopy, to a degree that they might define identifiable zones, and that canopies can differ in this organization. For example, several recent papers have examined interactions between strata (Craig 1993; Gilliam and Turrill 1993; Wilson et al. 1995). Terborgh (1985) discussed the hypothesis that there are more strata in tropical than temperate forests. Mimicking the "stratification" of natural forests has been one goal in designing some agricultural (Hart 1980; Altieri et al. 1983; Ewel 1986) and agroforestry (Unruh 1991) systems. In the wet forests of Oregon and Washington, efforts have recently focused on recreating "multilayered" canopies—one of the distinguishing characteristics of old-growth Douglas-fir (*Pseudotsuga menziesii*) forests (Franklin and Spies 1991). In short, stratification is often presented as a scientific system for classifying or measuring canopies.

The popularity of stratification has reached beyond academic journals to appear in "coffee-table" books (Ayensu 1980; Middleton 1992; Terborgh 1992; Moffett 1993), undergraduate texts (Gerking 1974; Kimmins 1987; Smith and Smith 1998), and encyclopedia entries on forests (Encyclopaedia Britannica 1982; Goulding 1997). It is one of the first concepts many people are taught about forests.

But in the scientific literature, the popularity of the term has produced neither clarity nor agreement. Disputes about exactly what kind of organization is implied by stratification are practically as old as observations of canopy structure, and still remain unresolved despite an emotional debate in some circles. Richards (1952, p. 22), in the classic citation on the concept, describes an argument going on back to the 1920s: "There are also authors who state, or imply, that any grouping of the trees according to their

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Am. Nat. 2000. Vol. 155, pp. 473–484.

height is arbitrary and that 'strata' have no objective reality. This is the point of view of Mildbraed (1922)." Subsequently, there were occasional calls for clarification and precision (Newman 1954; Grubb 1966). Smith (1973, p. 671) wrote in *The American Naturalist*, "Vertical stratification of plant and animal communities has been a basic concept in forest ecology; yet it has seldom received critical examination." He went on to discuss several ways that canopies could be considered stratified, and the possible ramifications of those patterns. Despite these thoughtful efforts, definitions have continued to multiply in recent years.

With stratification growing in importance but not in clarity, we believe it deserves another kind of assessment. We will not enter into any arguments about whether stratification exists (it surely does in some cases), whether canopy structure changes as forests develop (it does), nor whether structure has ecological consequences (it likely does). Instead, we will review the current definitions of canopy stratification and related terms. To help evaluate the tractability and utility of each definition, we will then attempt to apply each one to the canopy of one well-studied forest. This review and trial will be the basis for a discussion of the many problems involved in the application of stratification as a scientific system of classification or measurement of canopies. Finally, we will suggest several alternative approaches to the subject of canopy structure and environment that avoid most of the problems we have identified.

References to layering and stratification cross several disciplines. We make a broad review but limit most of our discussion to terrestrial plants. Though canopies change with time (e.g., Aber 1979; Oliver 1981; Waring and Schlesinger 1985; Oliver and Larson 1990), we limit our discussion to structure described at one time. There remains a large literature that uses "stratification" to describe the vertical zonation of animals in terrestrial vegetation (e.g., de Vries 1988; Reagan 1992) and of various organisms in aquatic and littoral environments.

Varieties of Stratification

Many things may be meant when an author writes about a "layer" or "level" or "stratum" or "tier" or "story" or that a canopy is "stratified." Here we list some recent usages of the terms in the ecological literature. Note that, since the terms are often used without being explicitly defined, we often had to deduce the meaning from the context.

Definition 1: Stratification = A Synonym for Height. One of the most common usages is one of the most subtle. Sometimes "layer," "level," "stratum," and so forth are used without further qualification or description and can logically be interpreted as synonyms for the elevation above the ground or other reference level. For example, "black-backed Woodpeckers ... were found to excavate mainly on logs and at the base of large-diameter tree trunks. In contrast, Three-toed Woodpeckers ... preferred higher strata and smaller diameter trunks" (Villard 1994, p. 1957) and "linear relations between foliar dry matter and cross-sectional area of first-order branches in lower, middle, and upper crown strata also were examined. Branches in the lower stratum had less foliar dry matter per unit of cross-sectional area than branches in the other two strata" (Valentine et al. 1994, p. 576). The last sentence could be rephrased as "branches in the lower height class had less foliar dry matter per unit of cross-sectional area than branches in the other two height classes," without any loss of meaning.

Definition 2: Stratification = Different Life Forms or Age Classes at Different Heights. A second very common usage for "layer" or "stratum" is to indicate a plant life-form group, for example, the tree, shrub, and herb layers (Hussain et al. 1994), or an age class, such as the tree, sapling, and seedling layers (Craig 1993), that tend to exist at a characteristic height. Sometimes the relative coverage of these different forms is used to describe stands (Cain and de Oliveira Castro 1959; Spies 1991; Okuda 1994).

Definition 3: Stratification = General Variability in Plant Matter. When a large variety of sizes and types of plant matter, usually including some especially large items, is observed, the stand is called "multilayered" or "stratified," without specifying what the layers are. Shorter, usually younger forests with a more consistent look are called "monolayered" or "unstratified." In this definition, there are often no special measurements or analyses: for example, "diversification of tree structure may begin early. Many 90- to 130-year-old stands begin to show greater ranges in size of trees and a multilayered canopy. Time for development can also vary.... The broad range of sizes and varied canopy (as opposed to the monolayer of Douglas-fir canopies in young-growth stands) do not generally become well developed, however, until stands reach 200 to 250 years of age" (Franklin et al. 1981, p. 19).

Definition 4: Stratification = A Continuous Vertical Distribution of Foliar Surfaces. Franklin and Spies (1991, p. 76) later extended the previous definition for cases where leaves are found at all heights: "Multiple canopy layers or, more specifically, the continuous distribution of foliar surfaces from the top of the crown to the ground, is another stand-scale structural feature. Such canopy distributions are significant in creating greater quantities and greater diversity of animal habitat."

Definition 5: Stratification = The Vertical Distribution of Foliage. In this usage, the question, Is the canopy stratified? does not have a yes/no answer. Rather, stratification refers to the vertical distribution of foliage; thus, a graph of leaf area index or merely leaf presence or absence within different height categories, would be a picture of stratification (e.g., Hubbell and Foster 1986; Malcolm 1994). Though this usage often depends on height categories, like 0–2, 2–5, 5–10, 10–20, 20–30, and 30–40 m above ground (Malcolm 1994), no particular functional or structural difference between the height categories is necessarily presumed.

Definition 6: Stratification = A Set of Crown Limits. Richards (1952, p. 23) defined a stratum as "a layer of trees whose crowns vary in height between certain limits." The choice of these strata often came from exquisitely drawn "profile diagrams" (e.g., Davis and Richards 1933), and the subjectivity of these choices caused a lot of debate (Hallé et al. 1978; Brünig 1983; Whitmore 1984). He later acknowledged the technique was illustrative rather than statistical (Richards 1983, 1996). The use of profile diagrams has been continued by some, who argue that thoughtfully prepared illustrations are more valuable than random sampling, given the current poor knowledge of canopy structure (Kuiper 1988).

Definition 7: Stratification = Clumped Leaf Area with Height. Other ecologists following the lead of Richards adopted a slightly more refined definition: a clumped distribution of leaf area, leaf area density, or crown cover in vertical space (Koike et al. 1990; Terborgh and Petren 1991; Ashton and Hall 1992; Koike and Syahbuddin 1993). Stratification should be detectable as modes on a graph of leaf area against height; the number of strata would be equivalent to the number of modes. Koike and Syahbuddin (1993) used ANOVA to try to locate these modes in some subalpine forests. This usage is common in some ecosystem and physiological studies (e.g., Hollinger 1989; Nobel et al. 1993). Note that this definition is the opposite of definition 4, which implies a somewhat even distribution of leaf area with height.

Definition 8: Stratification = Species with Different Leaf Heights. While the previous definition lumps all species together, some ecologists have measured the leaf heights or crown cover of different species by height class. Strata are composed of species cohorts or dominance categories with significantly different mean leaf heights or cover heights (e.g., Wierman and Oliver 1979; Bicknell 1982; Guldin and Lorimer 1985; Oliver and Larson 1990).

Definition 9: Stratification = Species with Different Top Heights. Another group of ecologists more concerned with interspecific competition has defined stratification as significant differentiation in tree heights between species (e.g., Palik and Pregitzer 1993). Sometimes this assessment is made without absolute height measurements; here, stratification refers to a trend in the relative positions of adjacent crowns of different species (e.g., Smith 1962; Oliver and Larson 1990; Whitney 1990).

Definition 10: Stratification = An Index of Vertical Structure. Some have combined attributes of canopy structure to create indices to represent structural variability. Mills et al. (1993) calculated a "canopy layering index," a sum of canopy cover in height intervals 2–10, 10–20, 20–30 m, to predict the suitability of a site as a habitat for spotted owl. Terborgh and Petren (1991) suggest that the number of superimposed crowns is the correct measure of stratification. Spies and Cohen (1992) defined an index of "canopy height diversity," which increased with both stature and variance in crown size and position. Ashton and Hall (1992) devised a "stratification index" that increased with the disparity in crown coverage between the most and least dense parts of the canopy. Though not labeled as a measure of stratification, the "foliage height diversity index" (MacArthur and MacArthur 1961) increases when there are many layers or great differences in foliage density among layers (e.g., Unruh 1991).

Trial Application of These Definitions

We applied each of these definitions to a forest stand that we have studied in detail, the Twin Springs permanent plot (TSP), in a successional, mixed-oak forest in southwestern Virginia (described in Parker et al. 1993). For each definition, we attempted to answer, Is the TSP canopy stratified? And if so, is there a numerical summary of the stratification, such as the number of strata?

Most of the definitions could be evaluated using the results in figure 1, which shows Twin Springs leaf area by height, or figure 2, which shows stem density by tree height. We supplemented those results with other field observations (e.g., Parker et al. 1993).

The results, presented in table 1, differed in their evaluations of the definitions of stratification. Definitions 1, 3, and 6 could not be meaningfully applied (see comments below). The Twin Springs stand was not stratified by definition 4 but was stratified according to definitions 2, 7, 8, and 9. Furthermore, definitions 7, 8, and 9 provided answers ranging from 3 to 6 regarding the number of strata. In one application of definition 10, the "stratification index" (Ashton and Hall 1992) was 2.5. Definition 5 did not produce a yes/no evaluation of stratification or a number of layers; however, the relevant distribution of foliage by height is shown in figure 1, *left*.

Immediate Problems with the Definitions of Stratification

Beyond finding a lack of consistency in results (table 1), the exercise of compiling and attempting to apply the def-

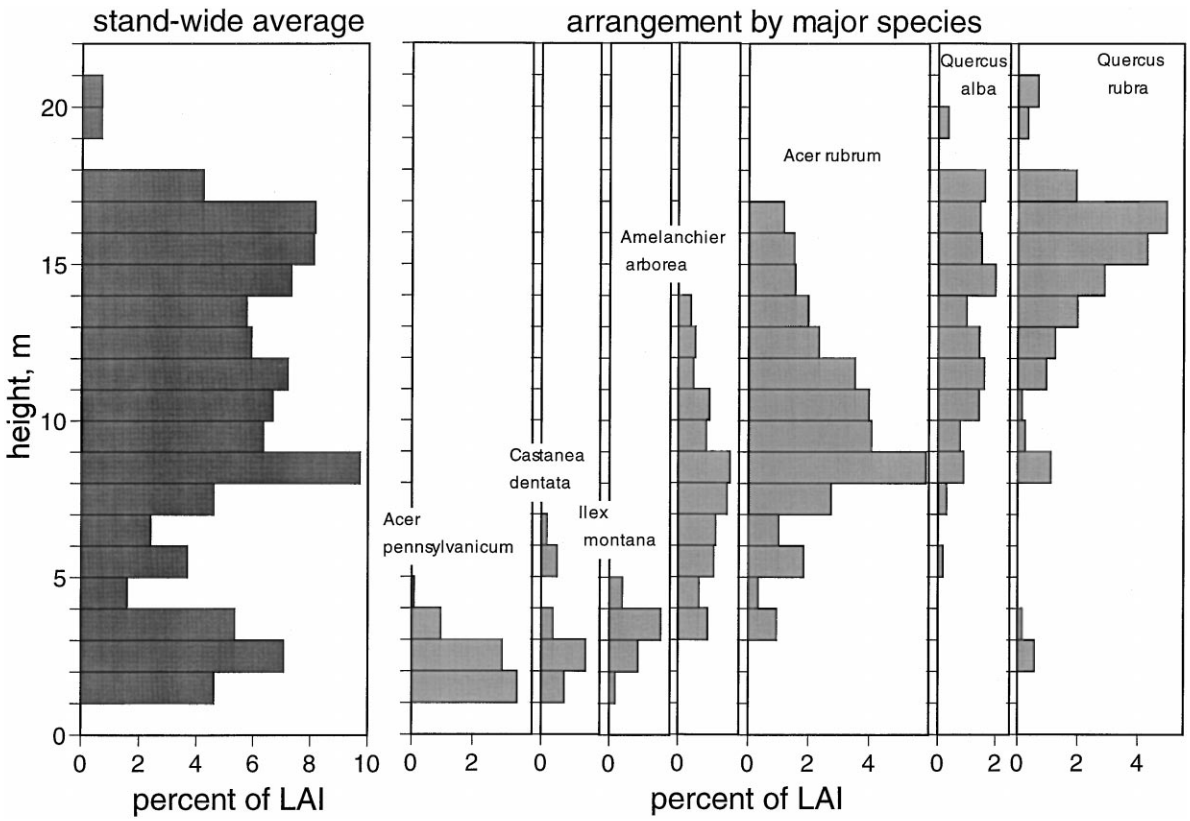

Figure 1: Foliage height profile for the Twin Springs plot, giving the percentage of the total leaf area index (*LAI*) in each vertical meter band (obtained using the method of optical point quadrats; MacArthur and Horn 1969). The left panel gives the pattern of foliage density with height when species are lumped together, and the right group of panels shows the corresponding distribution for each of the major species.

initions revealed some immediate difficulties in using stratification to compare and to contrast canopies or the conditions within them.

Exaggeration of Terms

Definitions 1 and 5 use "strata" or "stratification" to provide an extravagant name for otherwise straightforward measurements: height or the distribution of leaves by height. Like some other jargon, this kind of special vocabulary muddies clear communication by implying that something very important changes with height but without naming what it is.

Vague or Unrepeatable Methods

Definitions 3 and 6 bring forward potentially more discriminating concepts: that some canopies can be composed of a wider variety of objects than others and that crowns can be grouped by height class. However, the evaluation of those characteristics is based on no specific reproducible measurements or observations.

Highly Abstract Definitions Leading to Vague Predictions

Definitions 4 and 7 look for a rather conceptual kind of vertical organization: a continuous or clumped distribution of foliage against height. These definitions are evaluated objectively, on the basis of detailed measurements (such as fig. 1, *left*), and the judgment of stratification is clear (sometimes the result of a statistical test). Nonetheless, these definitions have little power to describe how a canopy is organized. There are many diverse ways that a canopy might have a clumped or continuous distribution of foliage against height, but the definitions cannot discriminate between them.

Some indices of stratification (definition 10) suffer the same kind of problem: they produce the same index value

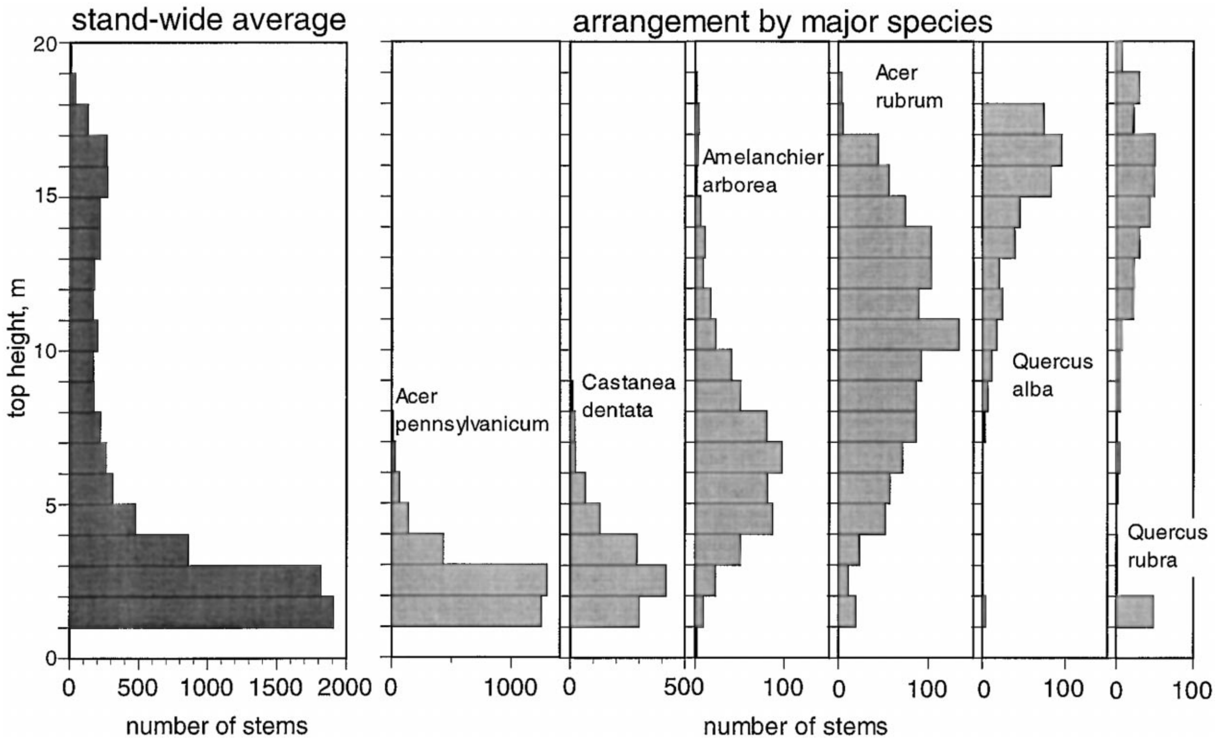

Figure 2: Height distribution of the tops of live stems in the 3.0-ha Twin Springs plot, estimated from species-specific allometric equations relating top height to stem diameter. At left is the distribution for all stems in the plot and at right is the corresponding distribution for each the major species. The major species differ from those in figure 1 because the foliage height distribution was measured at a subset of the plot locations.

for a wide variety of structures. Computed for our stand in the southern Appalachians, Ashton and Hall's (1992) "stratification index" is 2.5, similar to values those authors computed for tropical stands in northwestern Borneo. Though the numbers are close, it is difficult to see in what sense the stands are similar.

Weak Null Hypotheses

Definitions 2, 8, and 9 evaluate stratification depending on how canopy objects are sorted in relation to height. The heights of different life forms or species attributes are tested, and stratification is "confirmed" when one disproves the (often unlikely) null hypothesis that everything is the same at every height. Thus, by such criteria, most canopies will turn out to be stratified in some sense.

In short, to say that a forest is "stratified" or to say that a forest canopy is composed of a certain number of strata rarely provides a consistent or testable indication of its structure. Though stratification is referred to as if it were a system of classifying or measuring forest structure, the definitions are often incapable of clearly distinguishing places within a canopy, distinguishing canopies from one another, or both.

The number and poor quality of definitions creates a miasma of meaning where interesting, disprovable statements—the kind required for the testing of hypotheses (Peters 1991)—are difficult to make. In this sense, canopy stratification, and all the argument over it, really is not useful.

Further Conceptual Problems with Stratification

Evaluations of stratification are also constrained by their perspective and methods.

Scale Dependence

The perception of stratification depends strongly on the scale of measurement. Consider our trial evaluation of definition 4, where a stand is stratified if there is a con-

Table 1: Results from attempts to apply 10 definitions of canopy stratification to the Twin Springs plot (TSP) canopy, Virginia

Definition of stratification	Is the TSP canopy stratified?	Number of strata or other summary at TSP
1. Synonym for height	NA	NA
2. Different life forms at different heights	Yes	Tree cover 91%, shrubs 10%, herbs 30%
3. General variability in plant matter	Unknown[a]	NA
4. Continuous vertical distribution of foliar surfaces	No[b]	NA
5. Vertical distribution of foliage	NA	NA
6. Set of crown limits	Unknown[c]	NA
7. Nonrandom (clumped) leaf area against height	Yes[d]	3 strata[e]
8. Species with different leaf heights	Yes[f]	4 strata[g]
9. Species with different top heights.	Yes[h]	6 strata[i]
10. Index of vertical structure	NA	SI = 2.5[j]

[a] Definition does not state a required level of variability.
[b] Figure 1, *left*, shows that there is a zone between 18–19 m height where no leaves were detected.
[c] Definition is subjective; results depend on what crown limits were chosen.
[d] Figure 1, *left*, shows strong peaks and valleys of leaf area. No formal analysis was performed.
[e] Based on peaks in figure 1, *left*, at 2.5, 8.5, and 16.5 m.
[f] Figure 1, *right*, shows the vertical distribution of leaf height by species. ANOVA showed a significant effect of species on leaf height ($P < .001$).
[g] ANOVA showed that the six major species had leaf heights in four significantly different groups ($P < .05$).
[h] Figure 2, *right*, shows the top heights of trees at Twin Springs. ANOVA showed that species as a significant predictor of top height ($P < .001$).
[i] ANOVA showed the mean heights of the six major species were all significantly different ($P < .05$).
[j] Several indices are used to evaluate stratification in the literature. Here we give Ashton and Hall's (1992) "stratification index" (SI).

tinuous vertical distribution of foliar surfaces. In the Twin Springs stand, we measured leaf density within 1-m height intervals. Because there were no leaves between 18 and 19 m, the stand is unstratified. However, if we had used larger intervals, such as 2 or 5 m, the stand would be considered stratified by definition 4. In general, the strata apparent at one resolution may change or disappear at another resolution.

Loss of Valuable Information to Averaging

Efforts to evaluate stratification often involve the laborious collection of very interesting data, which are then averaged to produce a less interesting, and sometimes deceptive, result. A set of simple observations from the Twin Springs stand illustrates these effects. We established a large number of vertical transects, along which we noted the presence or absence of foliage in each of three vertical zones: 1–6, 6–12, and >12 m above the ground. The results from these transects could be summarized in two ways: by averaging the presence or absence within each zone across all transects to produce an average picture of leaf density by height, and by defining eight structural types (based on the presence or absence of leaves at each of three heights, $2^3 = 8$) and counting how many of the transects fell into each of those eight types (Connell et al. 1997).

Figure 3, *left*, shows the average presence of leaves in each zone across the entire stand. Note that the 5–7-m bands, though not unusually broad for studies of forest structure, are too wide to show the detail and "stratification" apparent in similar graphs with 1-m bands (figs. 1, 2). At the standwide level, this view of canopy structure is vertically rather even and, according to an informal application of definition 7, unstratified.

Figure 3, *right*, shows a vastly different picture: the variety of vertical structures that make up the average in figure 3, *left*. Only 28% of the transects had the "average" structure (some foliage in all zones), with its suggestion of a relatively even density of foliage against height. The remaining 72% had foliage in two or fewer zones, which usually suggested a more clumped or stratified arrangement. While only 3% of transects had the classic gap structure (no foliage in any zone), these areas may be disproportionately important, for example, for forest regeneration (Runkle 1985; Denslow 1987). Averaging may hide ecologically interesting diversity.

Weakness of Height as a Meaningful Proxy Axis

Many of the definitions of stratification use height as an essential measurement. But distance from the ground has little ecological meaning on its own; rather, it is a con-

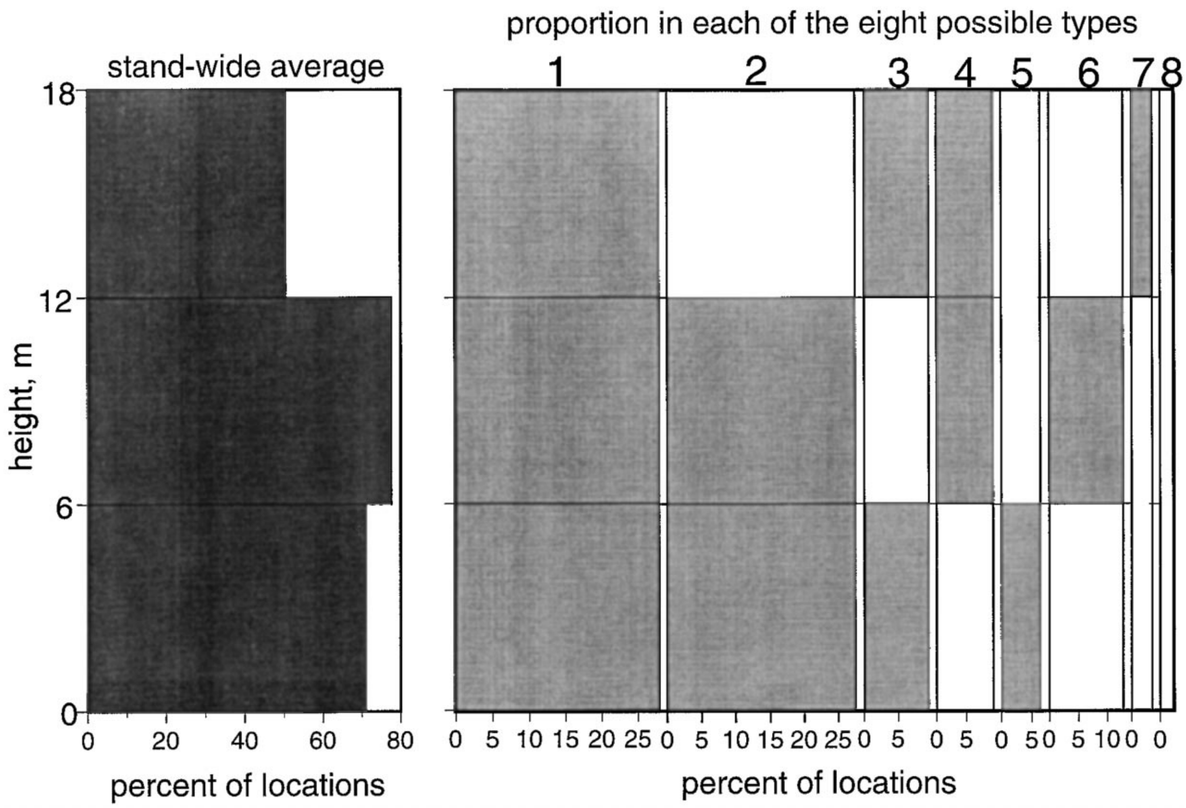

Figure 3: Foliage presence in three vertical layers at the Twin Springs plot, from observations at 517 locations (following the method of Connell et al. 1997). The left panel summarizes the frequency of foliage presence in each of three layers over all observations. The panels to the right depict the eight types of vertical structure (defined by the presence or absence of leaves in three layers). The widths of the individual columns at the right are proportional to the representation of that type of structure in the stand—note that the classical "gap" structure, with no leaves at any level (type 8), is the least common.

venient proxy for a complex gradient that spans conditions from the "outside" of the canopy (its interface with the atmosphere) to those of a more protected interior (Parker 1995). This gradient does not always correspond well with the vertical axis.

McCune (1993), working in western conifer forests, found that, at lower elevations in tree crowns, lichens could be found either both on the bole and far from it on extended branches. Higher up in the crown, they were found only on the bole. The suggestion is that there is a practical equivalence in habitat (probably conditions of temperature, humidity, etc. brought on by the protective influence of branches, leaves, etc.) between the two kinds of locations. This equivalence can explain the observed distribution of lichens, whereas height alone does not.

Similarly, Reagan (1991, 1992) found that anoles (lizards) were predominantly detected at high elevations in a Puerto Rican canopy, perched on small diameter branches. However, when a hurricane brought many small diameter branches to the ground, the anole distribution shifted toward the ground as well. The lizards preferred or depended on the small diameter perches, not on a particular height.

In short, height can be deceptive because it is only a rough substitute for structures or environments that have more ecological importance. A researcher who rigidly associated height and stratification may fail to understand the basic biological relationships suggested by the results.

Alternatives to Stratification

Many of the problems we have discovered in our review could be ameliorated. Methods and definitions could be standardized, weak null hypotheses could be strengthened, and inevitable limitations such as dependence on scale and problems with averaging could be explicitly recognized and accommodated.

However, such efforts do not change the powerful underlying presumption that canopies are, or in some sense should be, stratified. It may be more fruitful to discard

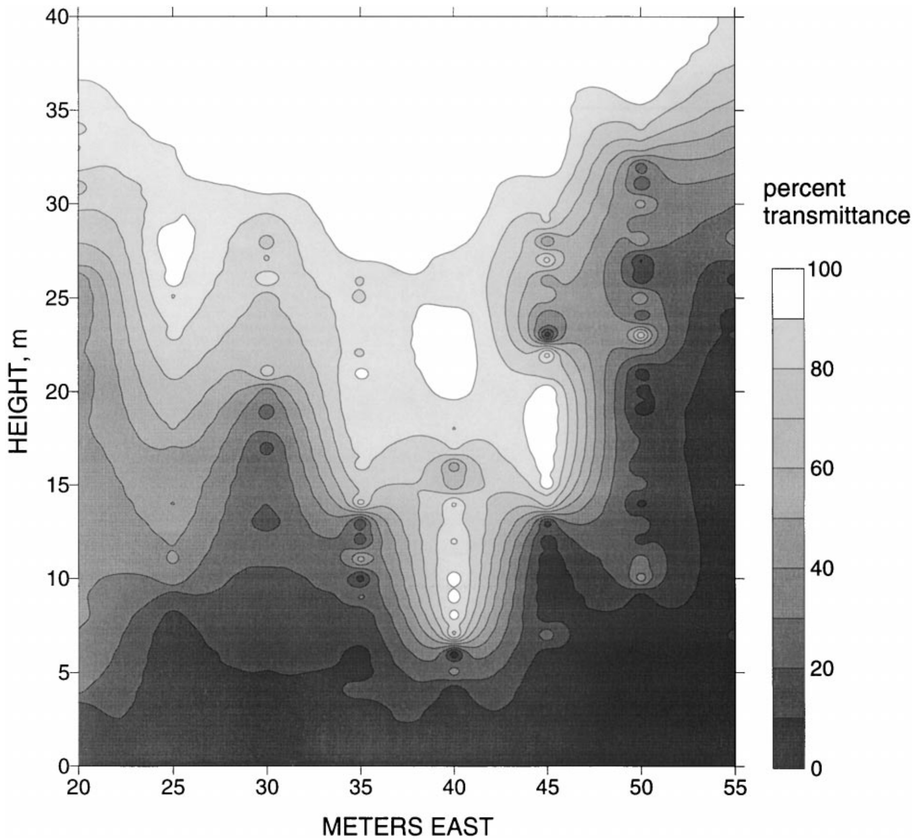

Figure 4: Transmittance of photosynthetically active radiation (PAR) in a vertical cross section of a large forest gap on the Maryland coastal plain, obtained with vertical transects with a balloon-mounted quantum sensor. The percentage of transmittance is presented as a contour graph with heavier shading indicating darker conditions.

that presumption entirely. In this section, we suggest some ways that might be done.

Use Existing Stand-Level Variables

Stratification is an attribute of a whole stand or canopy. For the purpose of comparing whole stands to one another, one simple alternative to stratification is to fall back on commonly accepted and understood attributes of whole stands, such as tree diameter, age, leaf area index, and variants thereof.

Such simple measurements rarely depend on the height axis as a proxy or presume some sort of stratification. Nonetheless, they may still be valuable for advancing ecological understanding. For example, the density of large-diameter standing dead trees helps indicate the habitats for many vertebrate and invertebrate animals (Franklin and Spies 1991); the mean diameter of standing dead trees can be a predictor of bird populations (Mills et al. 1993). The simple presence or absence of a tree-fall gap (and its unique environment) affects the composition of the bat community because the "clutter" of leaves and branches in the canopy affects how effectively bats of different morphology can fly (Crome and Richards 1988).

Map the Distributions of Relevant Structures, Environments, and Functions

Even when giving up the goal of identifying strata, basic efforts to illustrate the distribution of relevant structures across space are still essential. Though the vertical distribution of foliage (fig. 1) is one of the most common illustrations of this kind, other canopy structures are largely unexplored. The example of the Puerto Rican lizards, discussed earlier, suggests that the density of fine diameter perches may be an interesting structural attribute to map. Similarly, in a tropical forest, epiphyte seedling abundance may depend on particular sorts of crotches, where survival is based on water or nutrient availability (T. Laman, per-

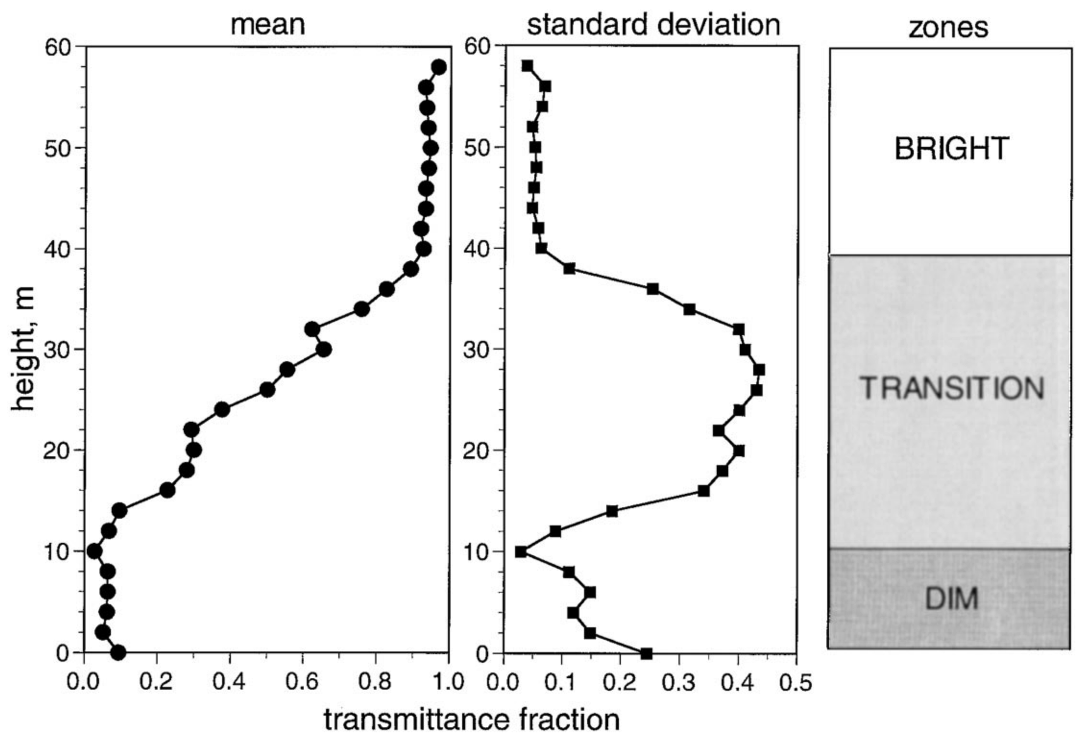

Figure 5: Vertical zonation of light environments in the canopy of an old-growth Douglas-fir/western hemlock forest in southern Washington (adapted from Parker 1997). The left and middle panels give the mean and spatial variation in the transmittance of photosynthetically active radiation (PAR) estimated from measurements in 16 vertical transects. The right panel shows the height limits of three light environment zones based on these.

sonal communication); this suggests crotches may be an interesting structural attribute to map.

The literature about canopy stratification has traditionally emphasized studies of structure. However, this article's examples concerning lizards, lichens, and epiphytes strongly suggest that our comprehension of the canopy can be greatly increased if we also map (or at least consider) the arrangement in the canopy of related functions (such as providing habitat for lizards, photosynthetic capacity, and others) and environments (such as the microclimate conditions, which support lichens, the intensity and quality of light, and others).

These maps of structure, function, and environment are illustrations of ecological gradients within the canopy system. Though these gradients will often be summarized along a vertical axis, they are not necessarily dependent on or restricted to the vertical. Figure 4 displays one such gradient in a two-dimensional cross section: the extinction of light (photosynthetically active radiation) in a forest gap. Light is obviously a critical resource for plants, and yet in this case the gradient has a complex and variable relationship with height.

Such gradients have characteristics that provide a way to compare and to distinguish canopies from one another. Gradient characteristics like length, shape, and slope can be objectively evaluated and compared. For example, Brown and Parker (1994) found that a collection of canopies varying greatly in stature and leaf area index had very similar light conditions at the forest floor. Accordingly, these stands must vary in the shape or slope of their gradients of light extinction. Exploring this kind of variation can lead to new hypotheses about forest processes.

If Necessary, Define Strata as Segments of Gradients

One of the goals of stratification analysis is to identify distinct, meaningful zones within the canopy (e.g., Smith 1973). Gradients of structure, function, and environment offer a clear basis for defining such zones when they are desirable or necessary. Much as we arbitrarily identify colors by marking off a particular region in a continuous gradient of wavelengths, a ecological zone or stratum might be objectively defined as all the locations that happen to be within a range of specific structural, environmental, or functional conditions (see Whittaker 1975, p. 157).

For example, in oceanography and limnology, the "euphotic" zone is sometimes defined as the region where light transmittance is greater than the "compensation point," where phytoplankton respiratory losses match photosynthetic gains (e.g., Parsons et al. 1984). One could make similar definitions for canopy environments, such as the overstory is the zone with >50% light transmittance, the understory is the zone with <10% light transmittance, and the midcanopy is the zone with light levels between these.

Strata defined this way have appealing properties. They can be based on variables that are standardized, commonly understood, and easily comparable between sites. They may be simple or complex in conception, relying on single or multiple variables. They are not fixed to the vertical axis, as figure 4 shows. They can also vary in time, shifting as both the forest and the external environment change. Such strata could reveal unexpected equivalences between disparate times and locations.

Use, Do Not Discard, Information about Variability

The variability inherent in observations of canopy structure, environment, and function need not be discarded through averaging. The variation itself can be useful in a description of canopy environments; differences of variation between situations may reveal distinct ecological features. For example, figure 5 defines three potentially relevant zones for an old-growth Douglas-fir/western hemlock (*Pseudotsuga menziesii*/*Tsuga heterophylla*) stand, based on both the mean and standard deviation of the transmittance of light. The "bright" zone is a region of high transmittance, with little variation; the "dim" zone is a region of low transmittance, with some variation. In between, the "transition" zone is a region of great variability in transmittance.

These ideas and examples offer just a few ways that the forest canopy might be conceptualized and studied without reference to the traditional notion of stratification. There are surely many more.

Conclusion

The forest canopy is still a little-known environment and still engenders the same impressions of simultaneous chaos and order that Schweinfurth (1874) described so well. The various concepts of stratification aimed, admirably, to spell out that order but were too ill defined to be of much help.

The drive to number the strata in the forest was probably premature. It helped us ignore significant aspects of how forests are organized and how structure can relate to ecologically interesting environments and functions. In a sense, stratification has not provided an approach for understanding Schweinfurth's "chaos" but rather a means to avoid it.

Acknowledgments

We thank M. Moffet for bringing Schweinfurth's work to our attention. R. Hansing gave helpful background information about oceanography. B. Boelts, J. Connell, R. Dueser, and S. Dunbar made useful comments on an earlier version of this manuscript. Support came from the James Smithson Society and the Smithsonian Environmental Science Program. This is a contribution to the Global Change program of the Smithsonian Environmental Research Center.

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Associate Editor: David A. Wedin