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A quantitative technique for the identification of canopy stratification in tropical and temperate forests

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Abstract

Canopy stratification is one of the oldest concepts in tropical forest ecology. However, there has been considerable debate over the existence and identification of strata. Much of the confusion arises from the differing definitions of strata (i.e. vertical stratification of phytomass, individual crowns, or species) and the methods used to evaluate them (e.g. profile diagrams). In this paper, a quantitative technique for identifying stratification of individual tree crowns in the forest canopy is presented. Strata are identified by comparing sorted tree heights to a moving average of height at the base of the live crown. Height and crown measurements were obtained from 21 published profile diagrams of forests, representing many biogeographic regions and covering a wide variety of forest types. The technique provides an objective measure of canopy strata allowing for a valid comparison of stratification between the different profile diagrams. Neither the original author's estimates of strata nor the number of strata detected by the quantitative technique support the premise that tropical forests have more strata than temperate forests. With the sole exception of a mono-layered European Douglas-fir plantation, all forests in this study had two or three layers. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Canopy stratification is one of the oldest concepts in tropical forest ecology, dating as far back as the early 19th century (Richards, 1996). Nonetheless, there has been considerable debate regarding the existence and measurement of strata in the forest (Richards, 1996; Smith, 1973; Whitmore, 1985). Some authors have found canopy strata in forests they studied (e.g. Davis and Richards, 1933; Ashton and Hall, 1992); others have not (e.g. Mildbraed, 1922; Paijmans, 1970); while some authors have cryptically suggested that whether canopy strata exist or not, the concept of stratification is a useful organizational tool for the study of the vertical distribution of plants and animals (e.g. Halle et al., 1978).

Perhaps the most important sources of confusion regarding the nature of stratification are its definition and the relatively subjective methods traditionally used to identify it. The term 'stratification' has been used to characterize three distinct, though closely

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allied, phenomena (Smith, 1973): vertical stratification of phytomass (e.g. Ashton and Hall, 1992), vertical stratification of individual crowns (e.g. Grubb et al., 1963), and vertical stratification of species (e.g. Oliver, 1978). Strata may exist by one definition, but not another. For example, phytomass may be stratified in a forest even if individual crowns are not; or, individual crowns of the same species may be found in different strata.

The oldest and most widely used method to study stratification is the profile diagram, which was introduced to the literature by Watt (1924) in a study of beech forests in England. Davis and Richards (1933) were the first to apply the profile diagram technique to a tropical forest. A profile diagram is created by establishing a plot (usually 40–70 m by 10 m wide, although this may vary depending on tree density), measuring the height, the crown length, and the crown width for all trees, and later converting these measurements to a scale drawing of the plot seen in profile. From the diagram one can visually assess whether or not strata exist. In some cases, histograms of height class or phytomass have supplemented profile diagrams (e.g. Grubb et al., 1963; Ashton and Hall, 1992). Confirmation of the presence of strata from profile diagrams or histograms of height or phytomass is visual and qualitative. Grubb et al. (1963), discussing the lowland rain forest of Ecuador, claimed that the number of strata in a given forest was more a matter of 'personal preference' than objective criteria.

Ashton and Hall (1992) presented the first quantitative measure of stratification, the stratification index. The stratification index is the ratio of phytomass in the height class with the greatest amount of phytomass to that of the height class with the least amount. The resultant number provides a normalized index of stratification that can be compared among stands. However, the stratification index does not identify how many strata exist, where they are found in the vertical profile of the stand, nor which trees are found in which strata. In addition, Ashton and Hall's stratification index requires measures of individual tree crown width, a relatively time-consuming procedure in dense tropical forests.

Recently, Latham et al. (1998) proposed a quantitative model, TSTRAT, for identifying stratification within stands. Their methodology was developed to facilitate structural classification of temperate conifer forests of the Inland Northwest region of the USA (Montana, Idaho, Oregon, and Washington). TSTRAT estimates the number of strata in a given stand using individual tree height and live crown ratio data. The trees are sorted by height and crown ratio and the upper 60% of the tallest tree crown—described as the competition zone (Latham et al., 1998)—is used as the basis of inclusion for the first strata. All trees with heights greater than or equal to the lower limit of this competition zone are included in the first stratum. The tallest tree not included in the first stratum is used as the guide for inclusion in the next stratum, and so on, until all trees have been assigned to strata. While this approach provides a repeatable estimate of the number of strata and requires only height and live crown ratio measures, we believe that the number of strata may often be overestimated. The causes of this bias are considered in the discussion.

In this paper, we present a simple quantitative technique for identifying stratification of individual tree crowns (Smith, 1973). We have adopted this definition of stratification in developing the technique because of the relative ease and accuracy of measuring individual crowns vs. the distribution of phytomass, and because it permits comparison of patterns of stratification among forests of differing species composition.

1.1. Stratification algorithm

The stratification algorithm identifies discontinuities in the vertical distribution of crowns by comparing the height of a tree (HT) to the mean height of the base of the live crown (HBLC) of all taller trees (McCarter et al., 1996). The algorithm proceeds by the following steps:

1. Sort the trees by HT and HBLC in descending order.
2. Beginning with the tallest tree (t_1), calculate the mean HBLC [for t_1, mean HBLC $=$ HBLC (t_1), for later trees within the same stratum mean HBLC is the mean HBLC of all preceding trees].
3. Compare the height of the next tallest tree [HT(t_2)] plus the constant of overlap (k_o) to the mean HBLC. [The constant, k_o, defines a threshold distance between the mean HBLC and HT(t_2) (see Section 1.3.]

4. If $\mathrm{HT}(t_2) + k_o$ is greater than the mean HBLC, then t_2 is in the same stratum as t_1. The mean HBLC is recalculated using t_1 and t_2.
5. If $\mathrm{HT}(t_2) + k_o$ is less than the mean HBLC, then t_2 is in a stratum below t_1. The calculation of mean HBLC is reinitialized beginning with t_2, ignoring HBLC values from the preceding stratum.
6. The decision rules (steps 4 and 5) are repeated for all trees in the plot.

1.2. Data

To evaluate and parameterize the algorithm we used tree height and crown length data obtained from profile diagrams in the published literature, supplemented by our own unpublished data (Table 1). The data represent a wide range of forest types (both temperate and tropical), species compositions, and stand structures. The sole criterion for inclusion of a profile diagram was a minimum of 30 visible trees. Each profile diagram was enlarged with a photocopying machine to facilitate measurement. Height and HBLC were measured for each tree in the profile diagram for which both the top and bottom of the crown were visible. This criterion excluded between 10% and 20% of the trees in the profile diagrams. A detailed evaluation of several profile diagrams found neither systematic exclusion of trees in particular strata nor a bias toward missing crown tops or crown bottoms. The stratification algorithm was run for the data obtained from each profile diagram and the number of predicted strata was then compared to the original author's estimates.

1.3. Evaluation

We performed a sensitivity analysis of the constant k_o to determine a standard value that could be used when comparing stratification in different stands. For each profile diagram the constant, k_o, was evaluated using both simple distance measures and percentages of the maximum height of the stand. The distance measures ranged from the height of the tallest tree for each stand to $-1 \times$ (the height of the tallest tree). The height ratios ranged from -100% to 100% of the height of the tallest tree in the stand. The range of distance values for k_o are plotted against the number of strata detected for each profile diagram in Fig. 1 (the results from the height ratio values for k_o were nearly identical and are not shown). To estimate the 'best-fit' value for the parameter k_o, we used the sum of squares method (Neter et al., 1989) as follows:

$$\mathrm{Error} = \sum_{i=1}^{n} (S_{\mathrm{obs}} - S_{\mathrm{est}})^2 \qquad (1)$$

where S_{obs} is the strata observed by the original authors, S_{est} the strata detected by the algorithm for each value of k_o, and n the number of profile diagrams.

The 'best-fit' value of k_o is that value which minimizes the error estimate.

To illustrate the results of the stratification algorithm, we have included a profile diagram (Fig. 2; Paijmans, 1970) and a graph of the output from the stratification analysis (Fig. 3). Note that in Fig. 3 the discontinuities in the mean HBLC at trees 6 and 15 are the beginning of new layers.

2. Results and discussion

The goodness-of-fit profile for k_o (Fig. 4) shows that a value of 1.5–2.0 m overlap in the stratification algorithm resulted in the minimum estimation error. Above $k_o = 5$ m, the number of strata in all forests becomes asymptotic at one stratum (Fig. 1). When $k_o = -10$ m, the number of strata in each stand approaches the number of trees included in the stand analysis (Fig. 1). Of the values for k_o that we tested in each profile diagram, $k_o = 1.5$ m routinely identified levels of stratification consistent with the published accounts, irrespective of biogeographic region or forest type (Table 1). Using a k_o equivalent to 4% of the maximum tree height in a stand identified a similar number of strata as $k_o = 1.5$ m, suggesting that identification of strata is less sensitive to variation of k_o in forests with taller maximum heights.

In contrast, TSTRAT uses a fixed proportion of the crown length which, in the uppermost stratum of the example shown in Latham et al. (1998) (see Fig. 5, p. 163, Latham et al., 1998), is roughly equivalent to an overlap of -3 m or 10% of the tree height. As Fig. 1 shows, such a low k_o will tend to overestimate the number of strata. Another potential weakness of the TSTRAT model (Latham et al., 1998) is that the definition of strata is highly dependent on the crown

Table 1
Profile diagrams used in the stratification analysis

Author	Location	Forest Type	Profile Diagram	N	Maximum height (m)	Published strata [a]	Estimated strata [b]
Davis and Richards (1933)	British Guiana	mixed forest	Fig. 6	102	34.1	2–3	2
		mixed forest	Plot 1	107	37.8	2–3	2
		mixed forest	Plot 2	46	34.0	2–3	2
Richards (1936)	Sarawak	mixed rain forest (ridge)	Fig. 2	60	43.0	3	2
		mixed rain forest (mid-slope)	Fig. 3	38	40.0	3	3
Richards (1939)	Nigeria	mixed rain forest	Fig. 4	51	32.5	3	2
		mixed rain forest	Fig. 5	60	46.5	3	2
Beard (1946)	Trinidad	Mora forest	Fig. 2	62	35.0	2	2
		Carapa–Eschweilera forest	Fig. 3	40	44.0	2–3	3
Richards (1996)	Zaire	Gilbertiodendron forest	Fig. 2.10	88	33.5	3	3
Grubb et al. (1963)	Ecuador	montane rain forest	Fig. 2	51	28.0	1	3
		lowland rain forest	Fig. 3	43	32.9	3+	3
Paijmans (1970)	New Guinea	plateau forest	Fig. 3	64	67.0	2+	3
		plateau forest	Fig. 4	55	39.0	2+	3
Halle et al. (1978)	Massachusetts, USA	oak/hemlock forest	Fig. 93	29	22.0	2	2
Oosterhuis et al. (1982)	Virginia, USA	mixed mesophytic cove forest	Fig. 4	32	28.5	2	2
		mixed mesophytic slope forest	Fig. 5	30	32.0	2	2
Kuiper (1988)	Pacific Northwest, USA	Douglas-fir/western hemlock	Fig. 2.6	45	77.0	3	3
		Douglas-fir/western hemlock	Fig. 4.5	55	76.0	3	3
Kuiper (1994)	Netherlands	Douglas-fir plantation	Fig. 7.1	30	23.0	1	1
Richards (1996)	Brunei	heath forest	Fig. 2.11	73	40.5	–	2
Baker, unpublished data	North Carolina, USA	mixed oak–hardwood forest	Plot HTR-1	33	32.8	2	2
		mixed oak–hardwood forest	Plot HTR-2	52	33.3	3	3
		mixed oak–hardwood forest	Plot RP-1	62	30.2	3	3

[a] Published strata are taken from the original author's interpretation of profile diagrams.

[b] Estimated strata is the number of strata identified by the stratification algorithm using a k_o of 1.5.

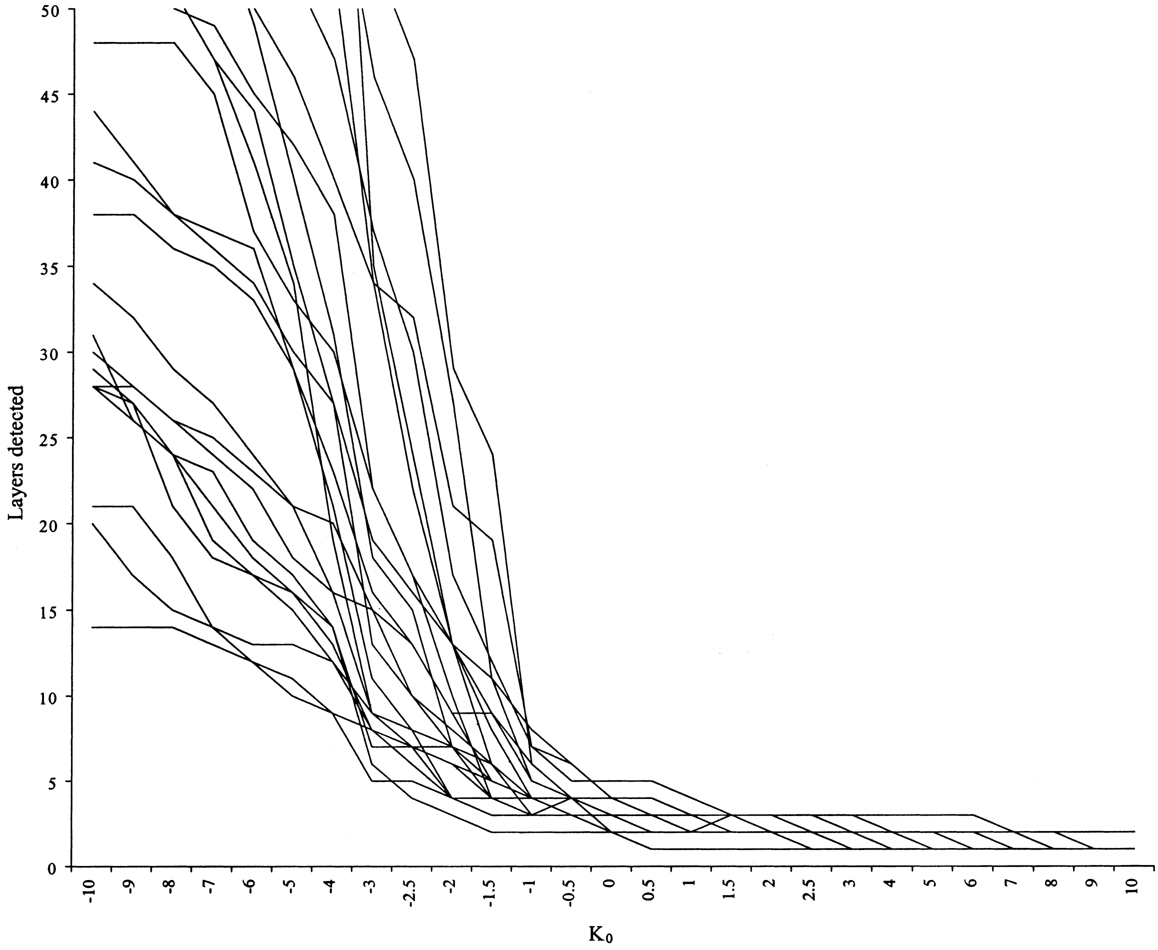

Fig. 1. The range of distance values for k_0 plotted against the estimated number of strata for each profile diagram (Please note the x-axis is not linear).

length of the tallest tree in each stratum. Using a moving average in the stratification algorithm dilutes the influence of tree order in the estimation of number of strata.

In those cases where a discrepancy existed between the observed and identified number of strata, the algorithm showed no systematic bias toward more or less strata. The largest difference in the number of observed vs. identified strata occurred for the profile diagram of the montane forest in Ecuador as described by Grubb et al. (1963) (one stratum observed by the original authors vs. three strata identified by the stratification algorithm); however, the third stratum for this diagram, as identified by our algorithm, contained only three trees. These trees were the shortest in the profile diagram and may be better considered as dominant individuals in the ‘shrub’ layer (i.e. below 5 m), which is not typically included in profile diagrams. Of the 17 profile diagrams with unambiguous number of strata (i.e. excluding those profile diagrams for which the authors provided a range of values, such as 2–3 strata, or a lower limit of strata, such as 2+ strata), only four (24%) had discrepancies between the number of observed strata and the number of strata identified by the algorithm.

Our analysis is limited to 24 data sets and, therefore, cannot resolve fundamental questions related to the nature, extent, and proximate causes of stratification;

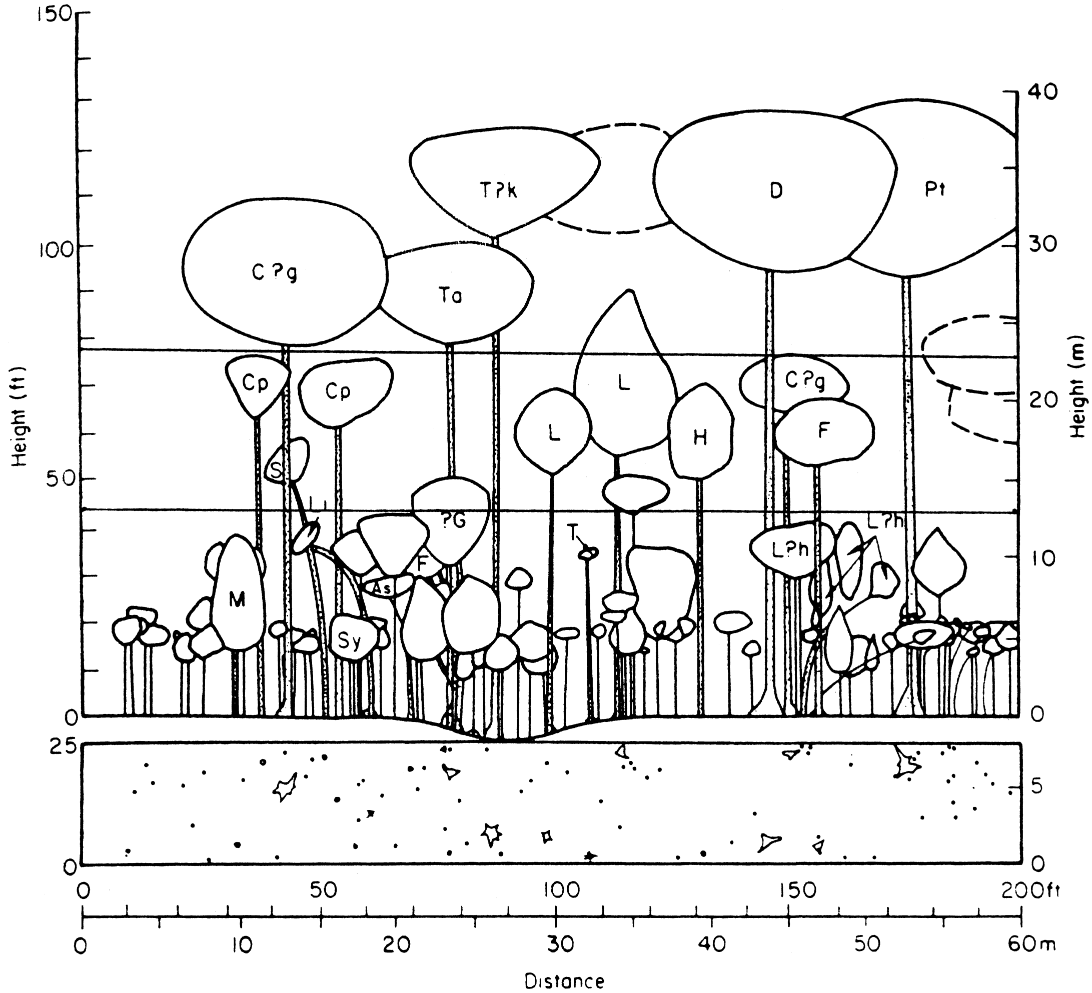

Fig. 2. Profile diagram of plateau forest from Paijmans (1970). The horizontal lines added to the diagram represent the height of the tallest tree in the second and third strata as identified by the stratification algorithm.

however, three areas do emerge that may be used to focus more extensive investigations:

1. differences in the number of strata in tropical and temperate zone forests;
2. the relationship of stand height to number of strata; and
3. the influence of species composition, in particular the relative proportion of shade-tolerant species in the canopy, on the number of strata in a stand.

Some authors have suggested that there are more strata in tropical forests than in temperate forests (Newman, 1954; Holdridge, 1967). For example, Allee et al. (1949) suggested that in the forest of Barro Colorado Island, Panama, there were as many as six strata of vegetation, at least four of which would be included in a standard profile diagram. The stratification algorithm provides an objective method of detecting canopy strata allowing for valid comparisons between the different profile diagrams. In the profile diagrams analyzed, neither the original author's estimates of strata nor the more directly comparable output from the stratification algorithm support the premise that tropical

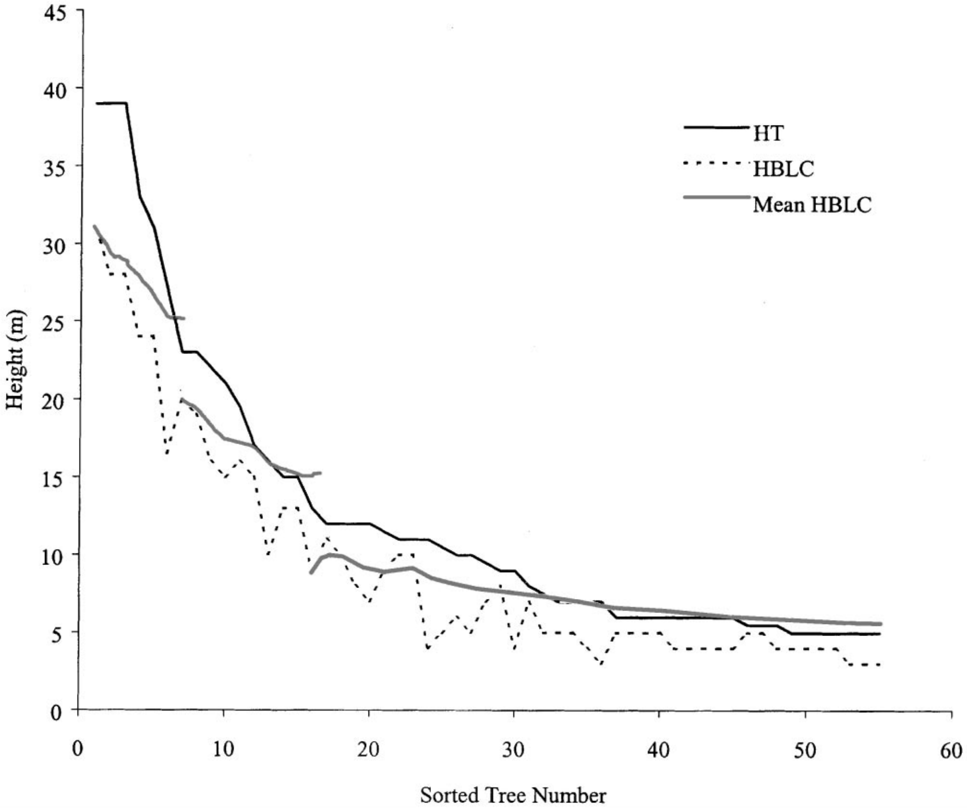

Fig. 3. Height (HT), height at the base of the live crown (HBLC), and mean HBLC for the Paijmans (1970) profile diagram (see Fig. 2). Discontinuities in the mean HBLC indicate new strata. Note that the mean HBLC exceeds HT after tree 38; however, the difference is less than the constant of overlap ($k_o = 1.5$ m).

forests have more strata than temperate forests (Table 1). All forests in this study had either two or three layers. The sole exception was a Douglas-fir plantation from the Netherlands that was in the stem exclusion phase of development (Oliver, 1981) and had only one stratum.

The number of strata identified by the algorithm was not significantly correlated with total height ($r_s = 0.32$, $p = 0.125$) (Fig. 5). At the extremes of height, three strata were identified in each of the three profile diagrams with trees taller than 65 m, while the sole profile diagram with one stratum had the second shortest total canopy height among the profile diagrams. There was great overlap in the total height of forests that had two or three strata. However, the sample of profile diagrams is somewhat biased in that single-stratum forests, being relatively simple in canopy structure, are not commonly described with profile diagrams.

Species composition of the canopy should affect the number of strata in a stand. Shade-tolerant trees typically have longer crowns than their shade-intolerant neighbors (Lorimer, 1983). As longer crowns create a more continuous distribution of foliage throughout the vertical profile of the stand, stands with a greater proportion of shade-tolerant species in the canopy should have fewer strata. In those cases where the stratification algorithm identified fewer strata than were enumerated by the original authors, the cause was invariably the presence of midstory trees with deep crowns. The long crowns lowered the mean HBLC, creating more overlap of midstory crowns with the understory, thus preventing identification of a third, lower stratum.

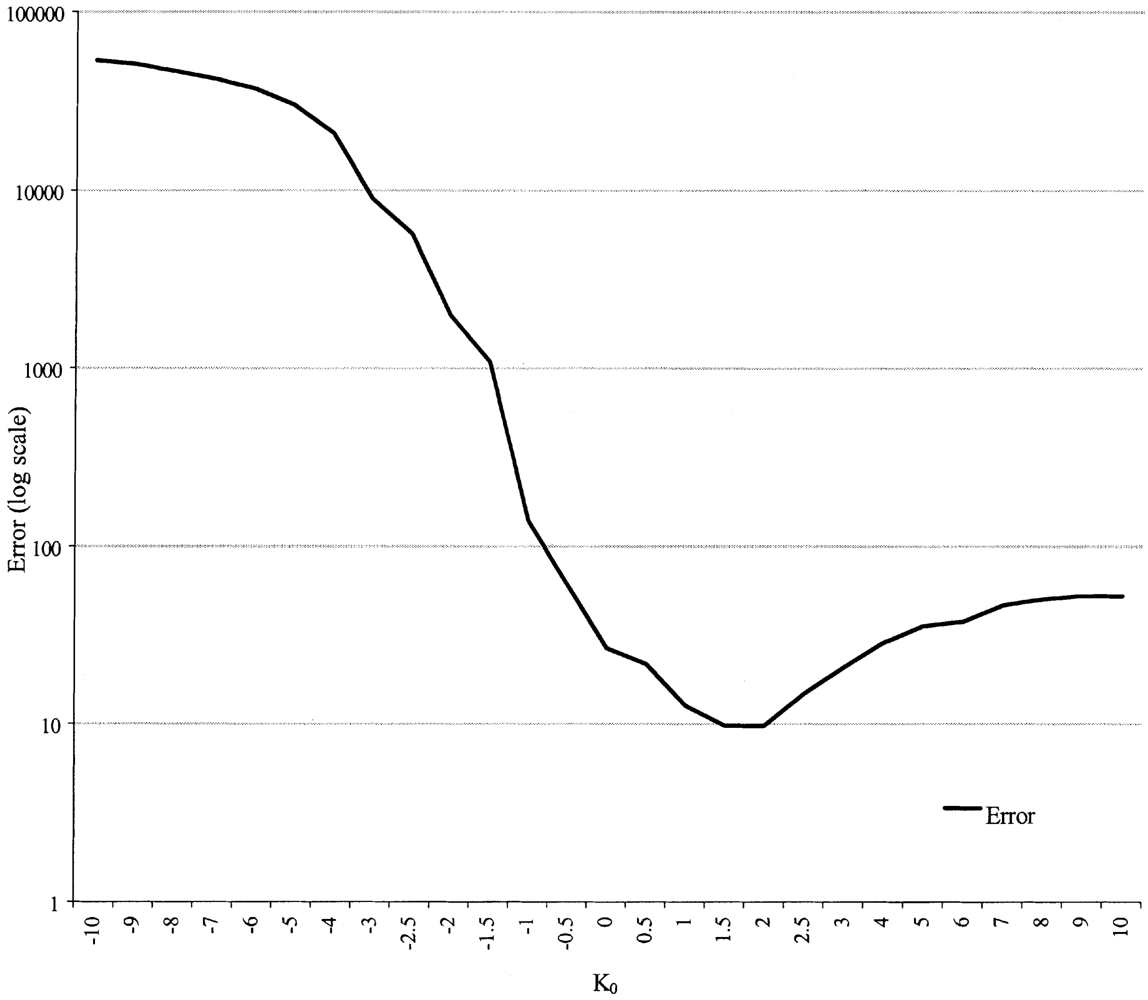

Fig. 4. Goodness-of-fit profile for parameter k_0. Goodness-of-fit determined from sum of squared error between predicted and observed number of strata for each profile diagram. The minimum is the 'best-fit' value of k_0 (Please note the x-axis is not linear).

3. Conclusion

Profile diagrams have been the standard means of identifying stratification in forest canopies, yet they have three principal drawbacks as tools for analyzing stratification, namely, their interpretation is subjective, they are labor-intensive, and spatially restrictive. The approach for identifying stratification described here liberates researchers from all three problems. The algorithm is objective, allowing for a valid comparison of stratification between forest plots. Because a drawing of the forest canopy in profile is not required, relative horizontal and vertical positions of tree crowns and stems do not need to be measured. Only height and crown length are necessary and even in tropical rainforest they can be obtained relatively efficiently. The restrictive spatial constraints that accompany the development of profile diagrams are avoided as well. In order to avoid excessive overlap of tree crowns when seen in profile, plots used to develop profile diagrams are typically long, narrow rectangles rarely >10 m wide. Our approach requires only a list of the total height and height of the base of the live crown for each tree. Trees may be obtained from plots of any dimension; however, a word of caution regarding stand spatial scale and structure is warranted. If a

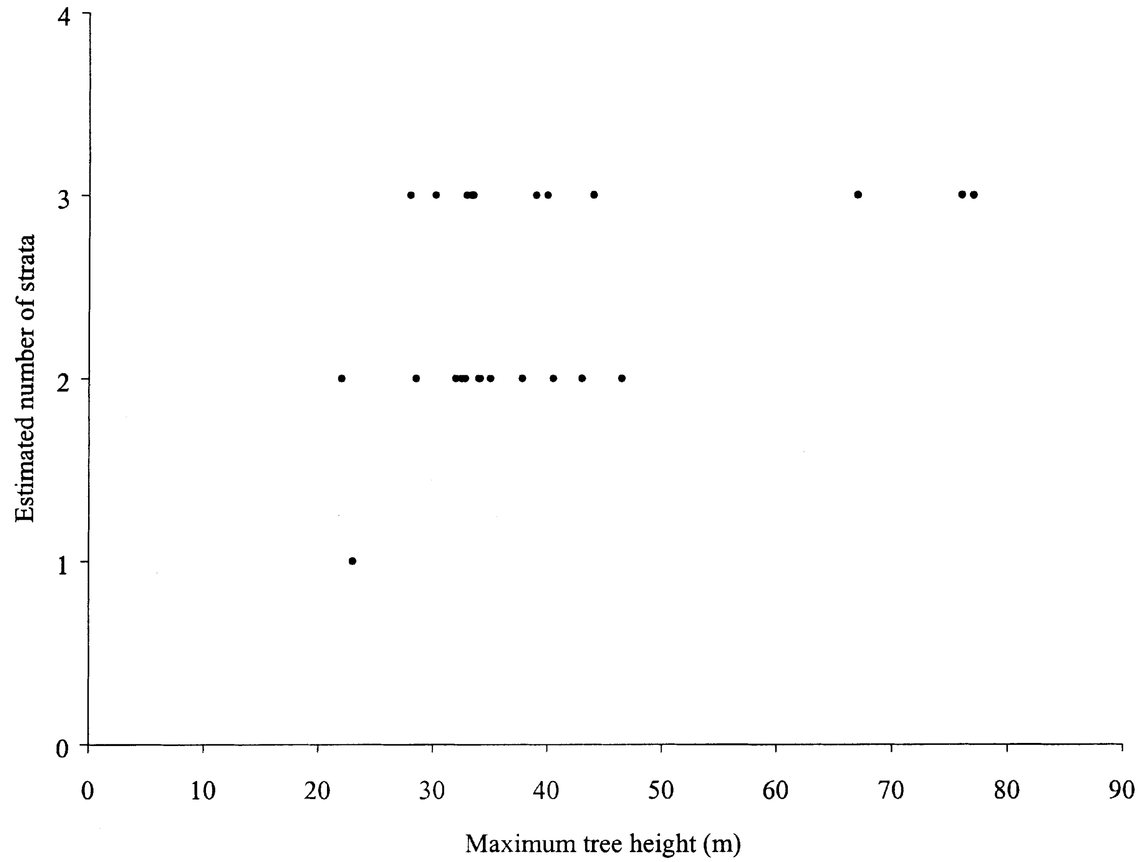

Fig. 5. Maximum height vs. estimated number of strata for each of the profile diagrams measured.

study plot used for measuring stratification includes gaps or portions of two stands with differing structures, the results obtained from the stratification algorithm will be confounded. For example, if a plot overlaps the edge of two adjacent stands, one with a single stratum of 35–50 m and another with a single stratum of 10–15 m, the stratification algorithm would identify two strata, an inappropriate conclusion in this case. Taking care to identify an area of homogenous forest structure for analysis will insure against spurious results.

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