Tropical Rain-Forest: The Leeds Symposium, pp. 15–24 (1982)

Strata in tropical rain-forest at Taï (Ivory Coast)

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SUMMARY

1 In the course of a study of the light regime of the undergrowth of the Taï-forest in the Ivory Coast a set of fish-eye photographs has been taken and analysed. The photographs reveal that the cover presents a higher mid-elevation hole-density than expected. This is discussed and a model is suggested to account for the observations.

2 It is proposed that forest layering is explained by the existence of a densely shaded 'exclusion volume' for other trees beneath each existing tree crown.

INTRODUCTION

Since the publication of 'The tropical rain forest' by P. W. Richards in 1952 the question of tropical rain-forest stratification is certainly one which has greatly occupied tropical ecologists.

The reason of this interest is, of course, that whilst the structure of the forest cover has important bearings on every aspect of the forest ecology, the forest strata are very difficult to distinguish.

No doubt, secondary forests and some almost monospecific forests have obvious strata. For most mature tropical rain-forests, however, this is not the case.

After Richards, Newman (1954) made an important contribution to the understanding of TRF stratification: he pointed out that young trees still growing quickly have to be considered separately from adult trees which show almost no growth in height. This author states also that the height of the lower branches is one of the most distinctive features of stratification. This distinction between young and adult trees has been further developed by Oldeman (1974) who introduced a new concept: the 'surface d'inversion'. The inversion surface may be of two kinds: structural or ecological; in a young forest the morphological inversion starting at the lowest living branch is at the same height as the ecological inversion which empirically may be at or about half the total height of each tree, but the author gives no further justification of that particular height. When the forest gets older the inversion surface continues to ascend whilst the ecological surface does not and both get further and further apart. Later on Hallé *et al.* (1978, p. 333) wrote: 'Strata (and inversion surfaces) should not be confused. Our opinion is that there are no strata in the forest as subdivisions of the total population but in certain plots there are demonstrable horizontal "sets" composed of trees of the present.' Following personal communications from Horn, Hallé *et al.* (1978) explained why trees of the present should form horizontal sets. They describe (p. 338) a model where tree crowns separated by gaps are opaque, globular and form a single layer. They write: 'Through the gaps between two

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*Present address: ORSTOM BP 165, 97305 Cayenne France trees light enters and illuminates zones below. Immediately under each crown there is dense shade . . . At some distance from the crowns there are atmospheric cells receiving light from one gap, two gaps and three gaps . . .'. The point here is: why should this apply to the trees of the present and not to those of the future? This is not obvious, as trees of the future can be as old and as large as those of the present. Trees of the future keep to the basic models described by Hallé & Oldeman (1970) and have a narrow crown ('lollipop trees'). The trees of the present are those that profit from an increased amount of energy by the process of the 'reitération' and have a wide crown.

Kahn has developed Oldeman's concepts and has introduced the concept of volumes defined by homogenous content; these volumes are called 'hoplexols' (Guillaumet & Kahn 1979). In Kahn's terminology a volume usually filled with leaves of mature trees of the present is called 'palyphyse'. In this system there are words for any volume with respect to its content. A volume containing mainly leaves of submature trees (trees of the future) is called 'prophyse'.

All these views concern the same fact, i.e. the difficulty of defining real strata in the sense of particular tree height classes, whether these concern total tree heights or heights of parts of trees. For example, in the Ivory Coast Huttel (1967) and more recently van Doorn (1973) have studied tree height in 'The Banco' forest near Abidjan in an attempt to define strata. Neither found any particular height frequency for their 0·25 ha sample plots. At Pasoh forest Kato *et al.* (in Kira 1978) measured leaf biomass and leaf area on a clear-felled plot 20 × 100 m. Their results clearly show two strata: a tree stratum, with a bell-shaped distribution having a mean height around 30 m and a ground layer with an L-shaped distribution having an abundant occurrence of seedlings and Monocotyledons, mainly Palmaceae.

Except for the ground stratum, which may be present and well defined, we may now conclude that the tropical rain-forest is not, in general, layered. However, it may well be structured. Is it structured and if so, how?

For structurally-simple stands, like corn fields, the simplest way to predict the light intensity profile inside the vegetation may be to study the cover structure but conversely light intensity profile studies may give insight into cover structure and this may be particularly useful in the case of a high forest, the structure of which is difficult to observe directly.

METHODS

Fish-eye photographs offer a tool which permit an indirect access both to light intensity profile and to stand structure. This technique has given good results within certain limits: even with the best available film the negative area of a 35 mm camera is very small and one cannot completely record the multitude of tiny holes in a dense forest cover.

In 1979 we tried to take fish-eye photographs, in a regular sample pattern, from a station of Taï forest we were studying (Alexandre 1982).

The film was developed and high-contrast positives prepared on 18 cm wide paper. The pictures were divided in 9 concentric coronae and the gap area in each corona was evaluated and expressed as a proportion of the total corona area. (Fig. 1)

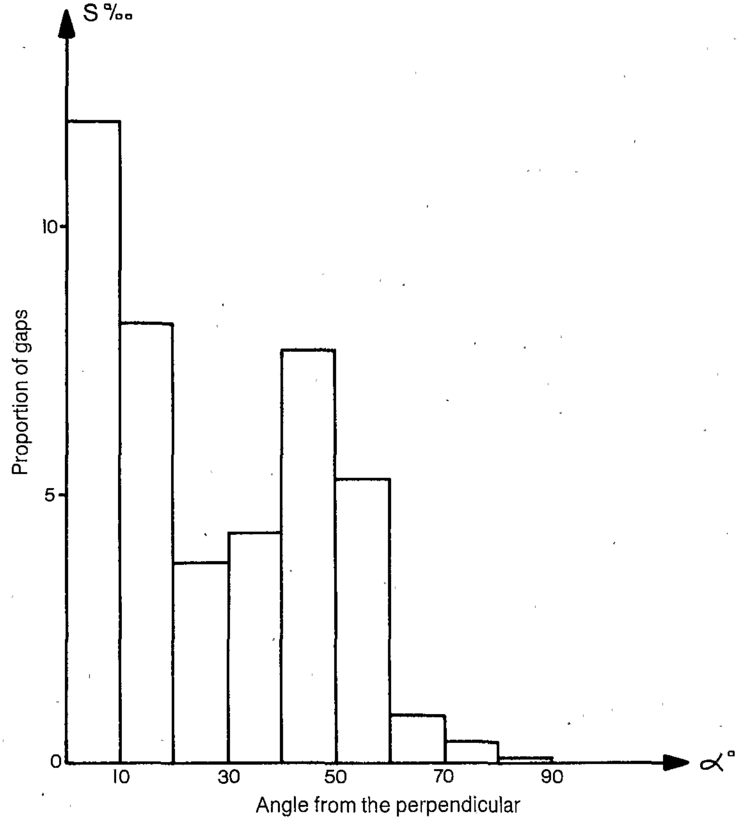

FIG. 1. Mean angular densities of the gaps in the cover of the Taï forest, computed from 12 fish-eye photographs expressed as ‰ of surface occupied by gaps in each of 9 concentric coronae.

Owing to technical limitations, this gives a rather crude estimate of the angular gap-density. It is, however, sufficiently precise to serve as a basis for a discussion about the forest structure.

RESULTS AND DISCUSSION

With regard to angular gap-density, the photographs allow the sampling points to be ordered in two sets. In the first set we have those which show a high density of holes in the central corona, corresponding to vertical or near-vertical light beams. The second set, on the other hand, show densities at high elevations which are low or zero. However, it is important to note that both sets of sampling points show a high gap-density at mid-elevations when photographed from the ground.

If the leaves were arranged at random, whichever direction or inclination they had, the angular gap-density would appear to decrease smoothly from high elevations to low elevations.

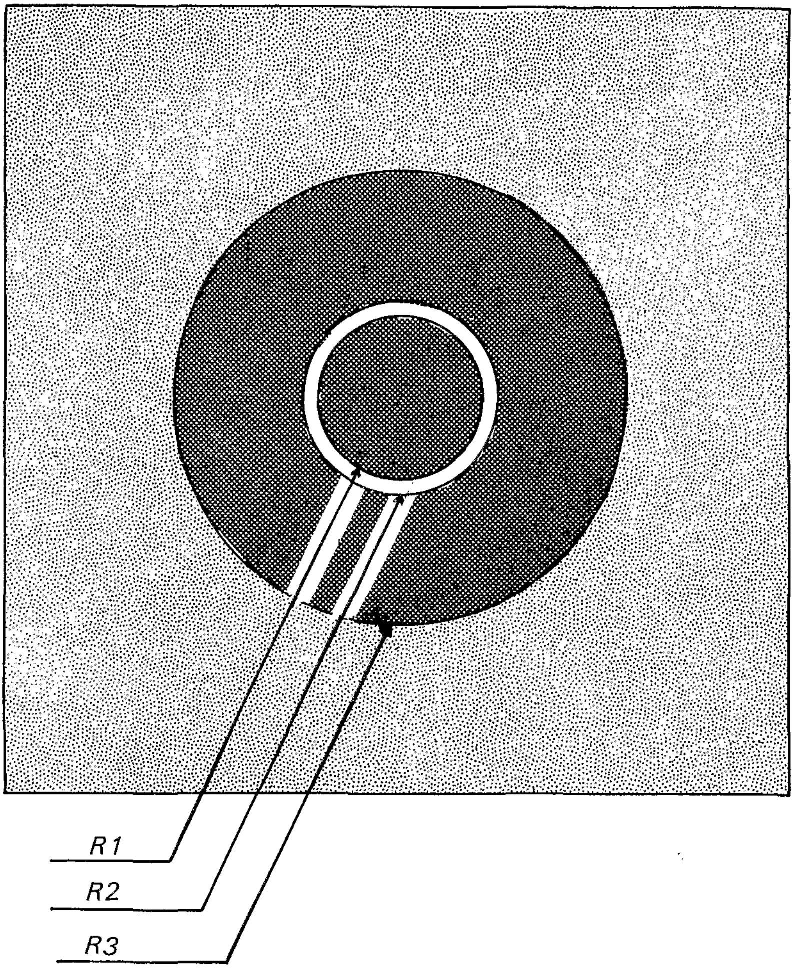

FIG. 2a. Light, dense shade and diffuse illumination under a tree crown.

Hence, Taï forest leaves are not distributed at random. The same is certainly true of other forests: similar observations have been made in *Chamaecyparis* forests in Japan (Tamai 1976).

The fact that leaves are not distributed at random, though obvious, must be stressed (e.g. Anderson 1966): *in a forest, leaves are, of course, clumped around tree crowns!*

Dense crowns are almost opaque while adjacent to them there are spaces without any leaves that are transparent except for the branches and trunks. Voids between crowns are frequent and sometimes are maintained by the motions of the trees caused by the wind (E. F. Brunig, pers. comm.).

Thus the simplification by Horn (1971) is legitimate and we may compute the light profiles from below in simple cases. For a point in the middle of a cylindrical hole of radius r and height H the light available is approximated by the view factor

$F = \sin^2 \text{arc tan}\,(r/H)$ w~~here $H \gg r$.~~

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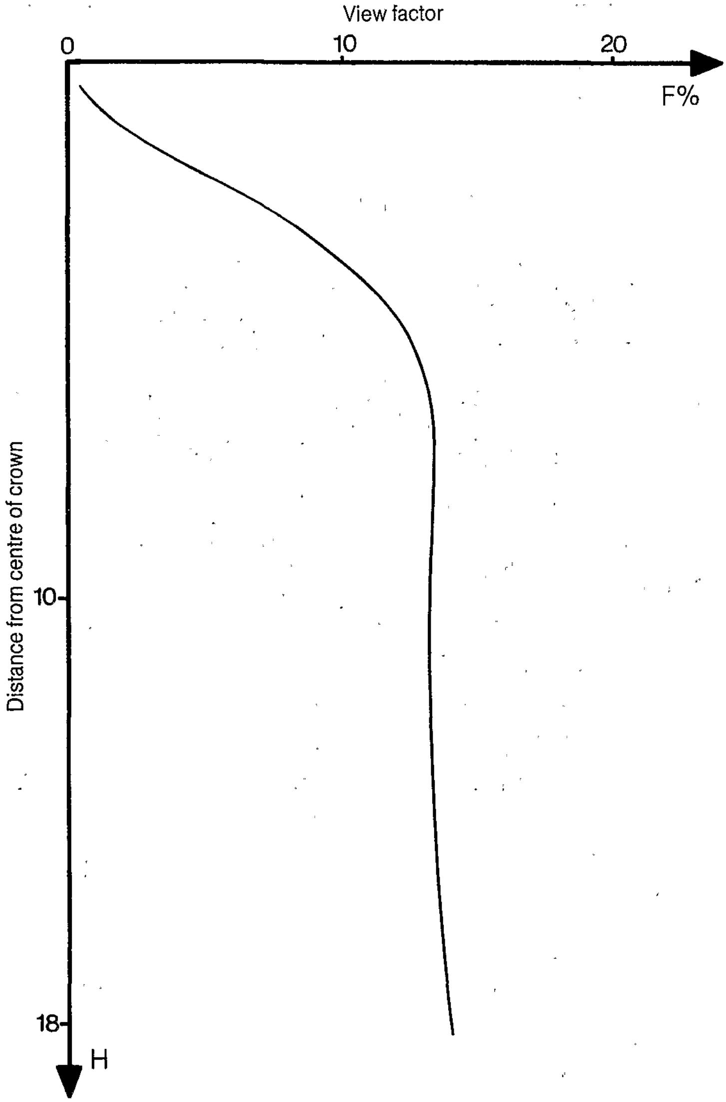

FIG. 2b. Computation of the light profile at the plumb of a tree crown.

$$F = \sin^2 \arctan.(r2/H) - \sin^2 \arctan.(r1/H) + (1 - \sin^2 \arctan.(r3/H))\,T$$

wheare F is the view factor (100% un-obstructed illumination) and T is the mean transparency of the cover, here $T = 0{\cdot}18$; $r1$ is the radius of the tree crown, $r2$ the radius to the nearest trees and $r3$ the mean radius to the rest of the cover ($r1 = 5$; $r2 = 6{\cdot}2$; $r3 = 15$)

Let us now consider two situations. First we will consider the light available under the central point of a crown (Fig. 2). We can represent the forest cover by a black disk surrounded by a transparent corona, a second black corona for the nearest trees, then a grey zone for the rest of the cover (Fig. 2a). The values of the different radii and the transparency of the whole cover are hypothetic and chosen empirically in accordance with our experience in the Ivory Coast. Here *r*1 = 5, *r*2 = 6·2 and *r*3 = 15 m; the transparency of the whole cover is taken as 0·18.

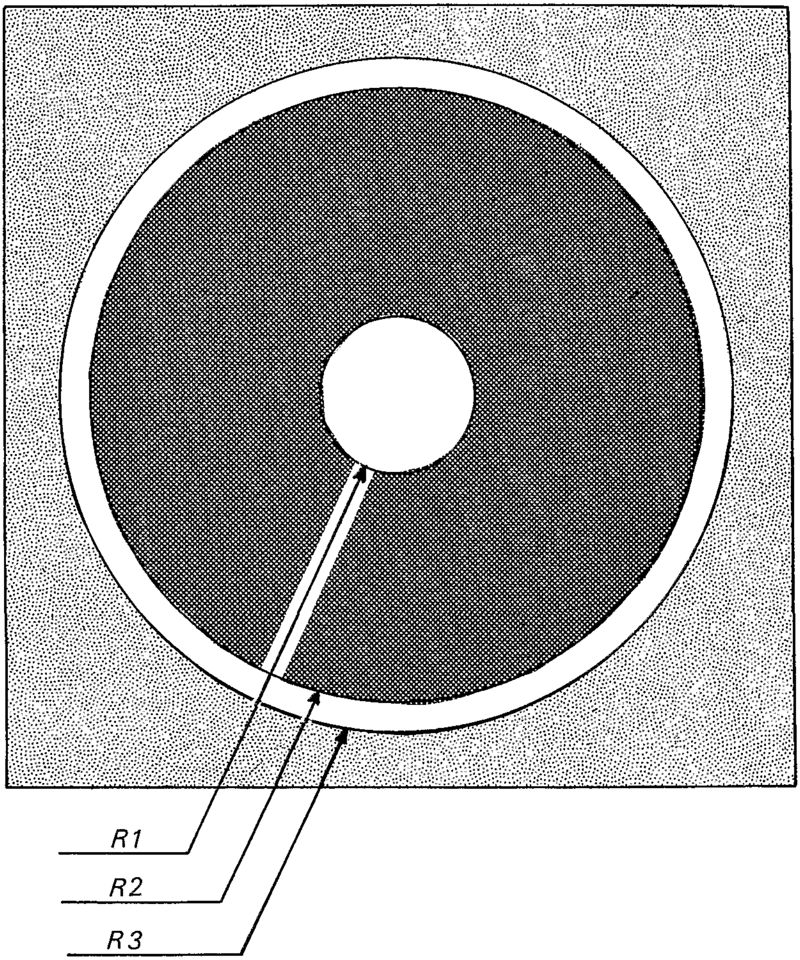

FIG. 3a. Light, dense shade and diffuse illumination under a canopy hole

In order to simulate the conditions below the middle of a hole we take a hole surrounded by a black corona, then a transparent corona, lastly the grey zone (Fig. 3a). Here the hole diameter has great importance, which is why we have taken three empirically observed combinations of diameters (see legend to Fig. 3).

We see from Figs 2b and 3b that at a distance of the crown equal to its radius (here 5 m) the light conditions become uniform. Immediately underneath the crown there is deep shade and it is likely that no tree could live under such conditions. Downwards from the centre of a hole the light diminishes rapidly. In some cases, when the hole is small, light intensity reaches a minimum then can grow again as one passes downwards owing to the increased lateral light. This supports Horn's theory quoted before. If a hole in the canopy is large enough a sapling in its middle will grow slowly for a long time, till it reaches the height where light increases rapidly. At that point the sapling may grow quickly and have a chance to reach the adult stage. If the hole is smaller the same sapling will never reach the height where the light starts to increase for it would have to overcome a zone of very dense shade first.

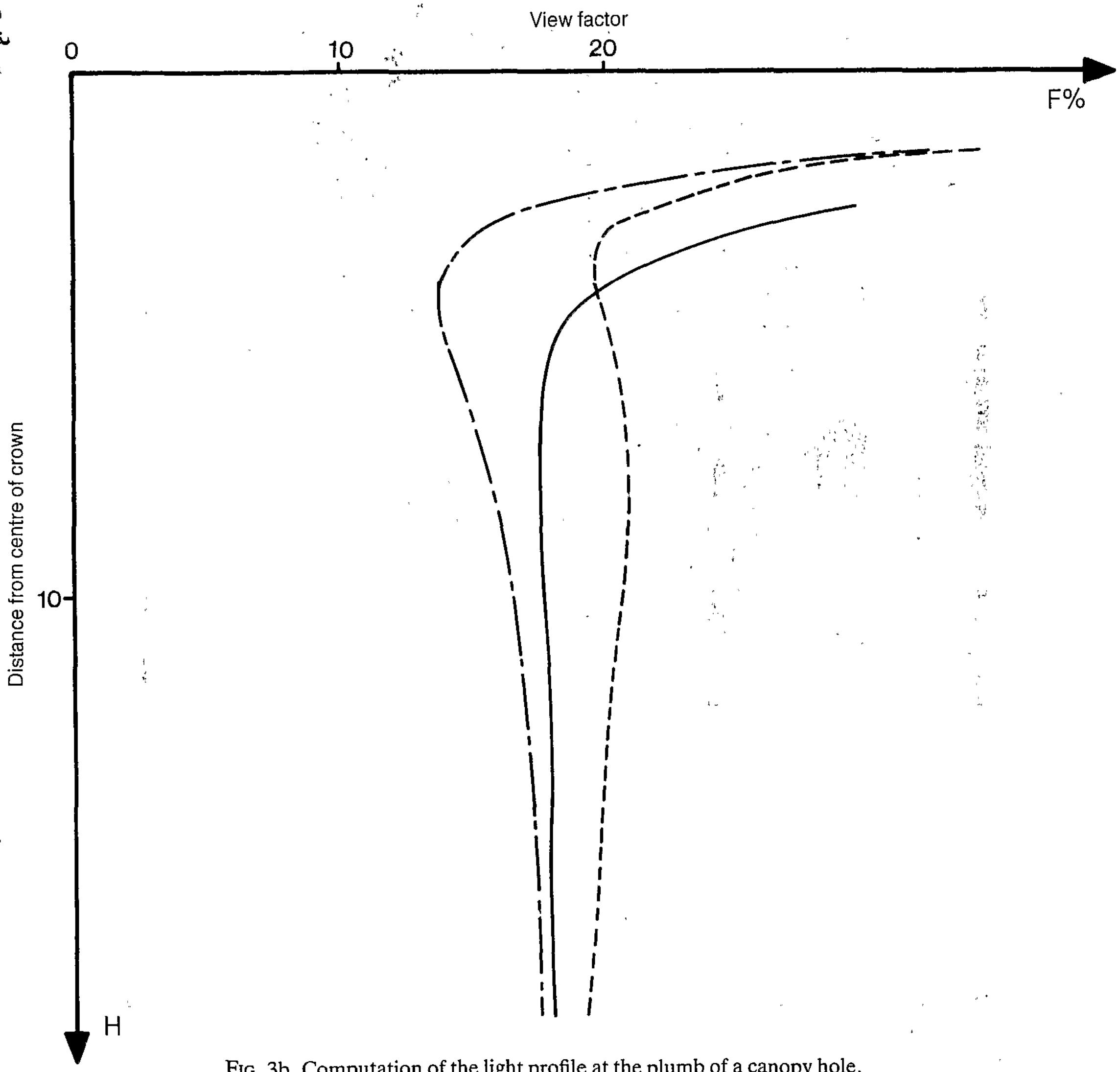

FIG. 3b. Computation of the light profile at the plumb of a canopy hole.
$F = \sin^2 \text{arc tan.}\ (r1/H) - \sin^2 \text{arc tan.}\ (r2/H) + (1 - T)\cdot(\sin^2 \text{arc tan.}\ (r3/H)) + T$
$r1$ is the radius of the hole, $r2$ the radius to the next holes and $r3$ to the rest of the cover.

——— $r = 1{\cdot}5$ $r2 = 6{\cdot}2$ $r3 = 6{\cdot}7$
— – — $r1 = 1$ $r2 = 6{\cdot}2$ $r3 = 6{\cdot}7$
- - - - - $r1 = 1$ $r2 = 5$ $r3 = 6$

In the case where a stable storey of canopy trees is found, another storey of small trees must exist below. The distance between the two should be approximately equal to half the mean diameter of the upper tree crowns.

FIG. 4. Schema of the exclusion volume created by a dense crown. In the hatched zone the light is dim enough to preclude the presence of another crown.

This is not normally the rule, however. Let us assume that under each tree, with a dark enough crown, there is a pear-shaped volume where no other tree can find enough energy to survive (Fig. 4). This volume is here called the 'exclusion volume'. It is postulated that a salient feature of the exclusion volume is that it must be slightly wider than the crown that produces it, in order to explain the observed gap-angle maximum frequency. When the crown of a growing tree reaches the exclusion volume either its growth must stop or its crown must bend. Thus, by virtue of their location, the upper trees control the location of the lower ones and these in turn control the location of those still lower. Of course, as long as a tree grows upwards, the trees underneath can grow also, unless the upper crown also widens. It is in this sense that the trees of the present control the layering of the forest and, in my opinion, all the lower trees must be affected by the upper ones.

Fish-eye photography produces proof that Taï forest, although not layered, is definitely structured.

This particular structure results in a very high frequency of gaps under 45° in the undergrowth. It is possible, even probable, that dicotyledonous plants utilize completely the dominant vertical component of the penetrant illumination below the forest canopy. The remaining oblique component may then be used by monocotyledonous plants with tilted leaves (A. de Rouw, pers. comm.).

Observed facts of forest tree growth have been explained here by postulating the existence of an exclusion volume under each crown. This hypothesis must now be tested in various forests by appropriate measurements of structure and light-intensity profiles.

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