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An Investigation of the Plant Ecology of the Hawaan Forest, Natal, using an Ordination Technique

by

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Abstract

An account of the forest ecology using a slightly modified Wisconsin ordination technique (Bray & Curtis, 1957) is given. The river-facing slope is considered preclimax, and the sea-facing slope subclimax, to the climax forest on the flat land. In addition, a secondary element, resulting either from recent disturbance or, possibly, from recently drier environmental conditions, is shown to be present in the climax forest.

Introduction

In recent ecological literature there has been a swing away from traditional descriptive ecological accounts towards quantitative methods of analysis. One of these methods, the modified Wisconsin ordination technique developed by Bray & Curtis (1957), was investigated with the aim of testing its usefulness when applied to South African vegetation, particularly forest. This technique can be used to compare quantitatively floristic data for different stands or examples of vegetation, and assumes that the floristic composition of a site is an expression of the environment of that site. Vegetation samples are compared one with another, to obtain an Index of Similarity $C = \frac{2w}{a + b} \times 100$, where *w* is the sum of the lesser scores for each species common to both stands, and *a* and *b* are the sum of the scores for each sample.

The sample plots are then arranged along axes, in this study two axes X and Y, so that the linear distance between plots is an indication of relative similarity or dissimilarity between plots. Because the method of endplot selection used by Bray & Curtis (1957) did not make efficient use of factor space, endplots with high mean dissimilarities and high standard deviations of the mean were used (Morris, 1967; 1969).

Methods

Data, suitable for ordination, were collected during an investigation of the Hawaan Forest (Moll, 1968a). This Forest is situated close to the sea on the North Coast highway, approximately 10 miles (16·1 km) north of Durban at the intersection of co-ordinates 29° 42′ south and 31° 06′ east. The Forest occurs on a flat area which slopes eastwards down to the sea in one direction, and steeply northwards to the Mhlanga River in the other direction (Moll, 1968b). The area analysed consists of some 100 acres (40·5 ha) of Coast Forest on sandy dune soils. Density data for trees and shrubs, i.e. the number of stems per plot, were collected from fifty 33 ft (10·1 m) square plots constituting a total sample of approximately 1·3 per cent of the Hawaan Forest. Woody plants with a diameter at breast height (d.b.h.) of at least three inches (7·6 cm) or at least 15 ft (4·6 m) high, were considered trees. All smaller woody plants were considered shrubs. The fifty plots were located by restricted randomization, a grid being superimposed on a large scale map of the Forest, and three plots were located within each grid square by pacing out two random co-ordinates.

RESULTS

Two axes, X and Y, were sufficient to account for most of the floristic variation between samples of the trees and shrubs. The two-dimensional scatter diagrams, where points represent sample plots, are shown in Figs. 1–3. Isolines have been employed to draw attention to high and low values. Correlation coefficients between 200 randomly selected interpoint distances and their corresponding calculated dissimilarity values were found to be significant, with a value of 0·61 on the tree ordinations (Figs. 1 and 2), and a value of 0·50 on the shrub ordination (Fig. 3). This significant correlation indicates that most variation within the data is accounted for by the X and Y axes used.

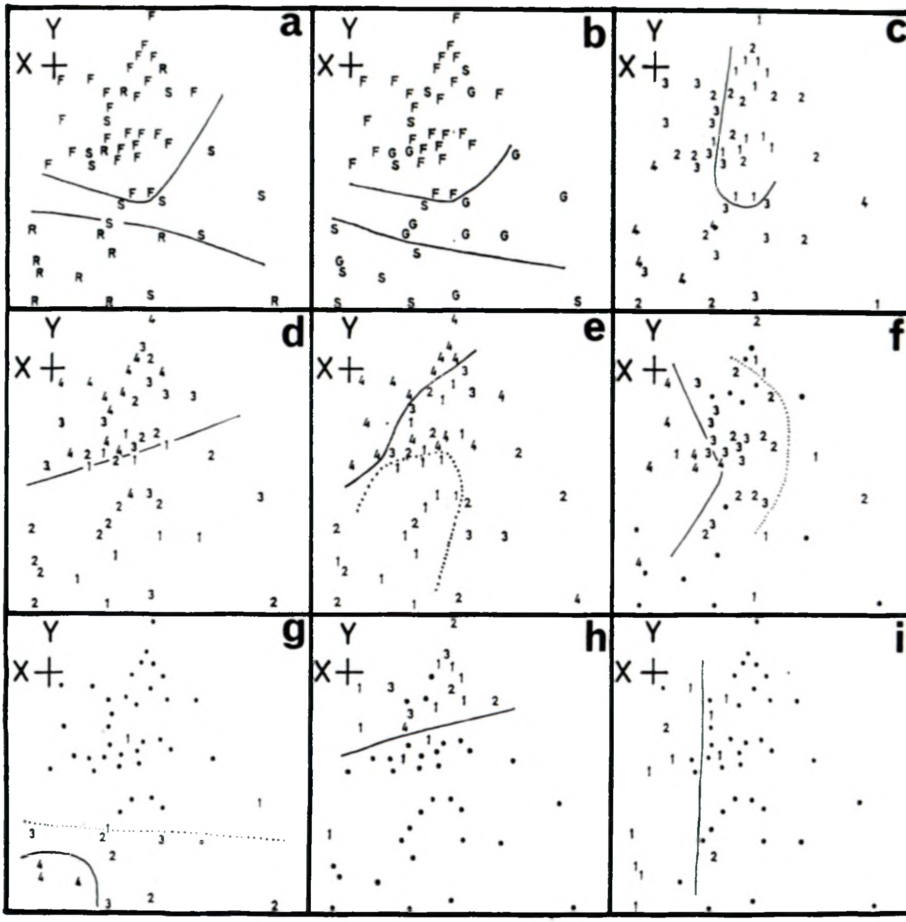

FIG. 1.—Tree ordination showing the distribution of: a, plot aspect (F = flat, S = sea, R = river); b, angle of slope (F = flat, G = gentle, S = steep); c, canopy tree density (1 = 2–4, 2 = 5–6, 3 = 7–10, 4 = 11–18); d, estimated mean tree height in feet (1 = 20–23, 2 = 24–26, 3 = 27–29, 4 = 30 and more); e, estimated d.b.h. in inches (1 = less than 4, 2 = 4–5·9, 3 = 6–8, 4 = 8·1 and more); f, **Cola natalensis** (. = absent, 1 = 1, 2 = 2, 3 = 3, 4 = 5–6); g, **Xylotheca kraussiana** (. = absent, 1 = 1, 2 = 2, 3 = 3, 4 = 4–5); h, **Cavacoa aurea** (. = absent, 1 = 1, 2 = 2, 3 = 3, 4 = 5); i, **Celtis africana** (. = absent, 1 = 1, 2 = 2).

Figs. 1a and 1b show the distribution of two environmental factors, aspect and angle of slope, which were estimated for each sample plot while in the field. The Y axis of the ordination is mainly responsible for separating the flat plots, the gentle sea-facing plots and the steep river-facing plots. There are, apparent however, certain anomalies which should be explained. The sea-facing plot and the two river-facing plots at the upper extreme of the Y axis are undisturbed forest. The remaining river-facing plot and three sea-facing plots, which are apparently similar to the flat plots, do in fact have high coefficients of dissimilarity, but a third axis would be necessary to expose these differences. Such discrepancies are understandable when one considers that a multidimensional system has been expressed in two-dimensions.

Fig. 1c shows that the tree densities are related to both the X and Y axes. The exact relationship between aspect and density is not clear, but it is apparent that the majority of the most dense plots are river-facing and sea-facing. Some flat plots do, however, have a high density.

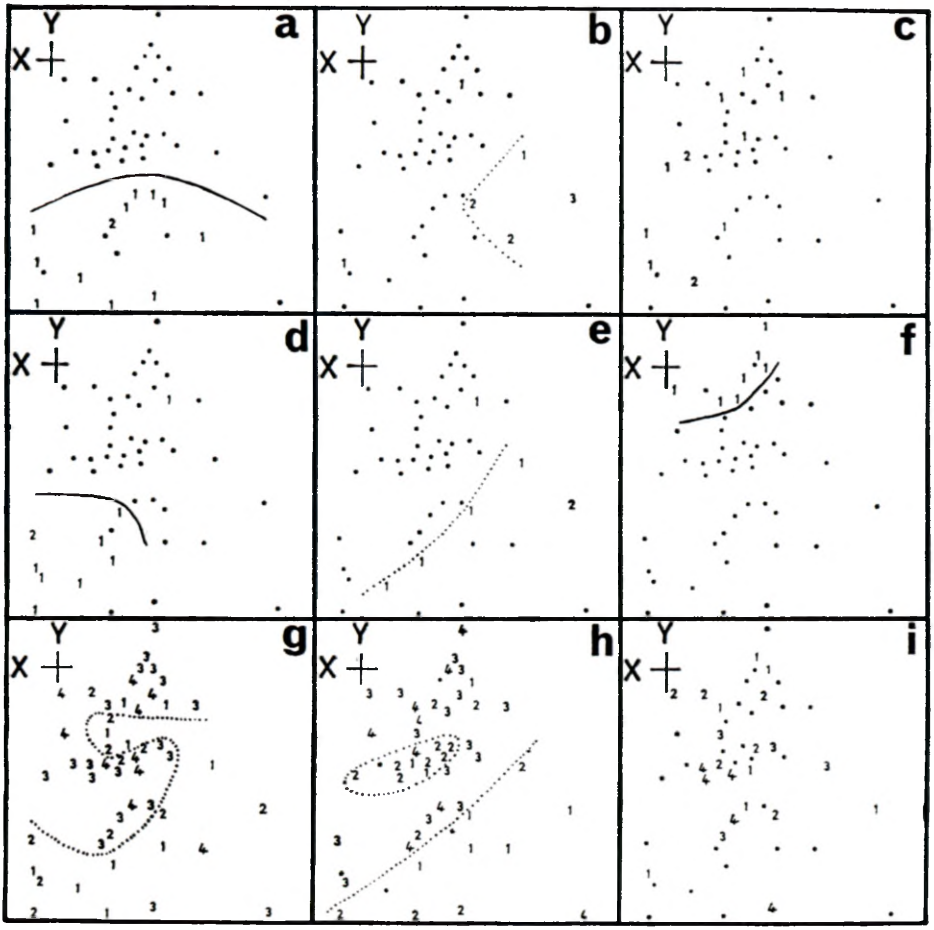

FIG. 2.—Tree ordination showing the distribution of: a, **Drypetes natalensis** (. = absent, 1 = 1, 2 = 2); b, **Teclea gerrardii** (. = absent, 1 = 1, 2 = 2–3, 3 = 5); c, **Dovyalis** sp. nov. (. = absent, 1 = 1, 2 = 2); d, **Deinbollia oblongifolia** (. = absent, 1 = 1, 2 = 3); e, **Mimusops obovata** (. = absent, 1 = 1, 2 = 2); f, **Strychnos decussata** (. = absent, 1 = 1); g, shrub density (1 = 6–18, 2 = 24–37, 3 = 41–69, 4 = 70–88); h, **Uvaria caffra** (. = absent, 1 = 1, 2 = 2–4, 3 = 6–9, 4 = 10–30); i, **Peddiea africana** (. = absent, 1 = 1, 2 = 2, 3 = 3, 4 = 4–12).

Estimated canopy height has been plotted in Fig. 1d, the tallest trees occurring in the flat plots. Fig. 1e shows the mean estimated d.b.h., the largest trees being in the flat plots.

Figs. 1f and 1i, and Figs. 2a–2f, show the distribution of the ten tree species with the highest densities on the ordination. One species, *Strychnos innocua*, is not illustrated here as it shows no relationship to the major environmental situations considered here and apparently has a random distribution. *Cola natalensis* (Fig. 1f) occurs mainly in those flat and sea-facing plots which have the highest tree density. *Xylotheca kraussiana* (Fig. 1g) occurs almost exclusively in the steep river-facing plots where the trees are generally small and with a high density, although two sea-facing plots and one flat plot do each contain only a single specimen. *Cavacoa aurea* (Fig. 1h) occurs in flat, sea- and river-facing plots which are gently sloping, though two steep-river-facing plots do each contain a single tree. The plots containing *C. aurea* vary in density, but contain the largest forest trees. *Celtis africana* (Fig. 1i) has a similar distribution on the ordination to *Cola natalensis*, but is confined mainly to the most dense plots. *Drypetes natalensis* (Fig. 2a) is generally limited to the sea- and river-facing plots, where the trees are predominantly small and fairly dense. *Teclea gerrardii* (Fig. 2b) is found mainly in the sea-facing plots with moderate density and medium-sized trees. *Dovyalis* sp. nov. (Fig. 2c) has a fairly random distribution on the ordination and is similar to *Cola natalensis*. *Deinbollia oblongifolia* (Fig. 2d) is limited entirely to river-facing plots and to two sea-facing plots where the trees are small and dense. *Mimusops obovata* (Fig. 2e) occurs mainly in the sea-facing plots, but also occurs in two of the river-facing plots. *Strychnos decussata* (Fig. 2f), with the exception of one river-facing plot, occurs exclusively in flat plots of low density and big trees.

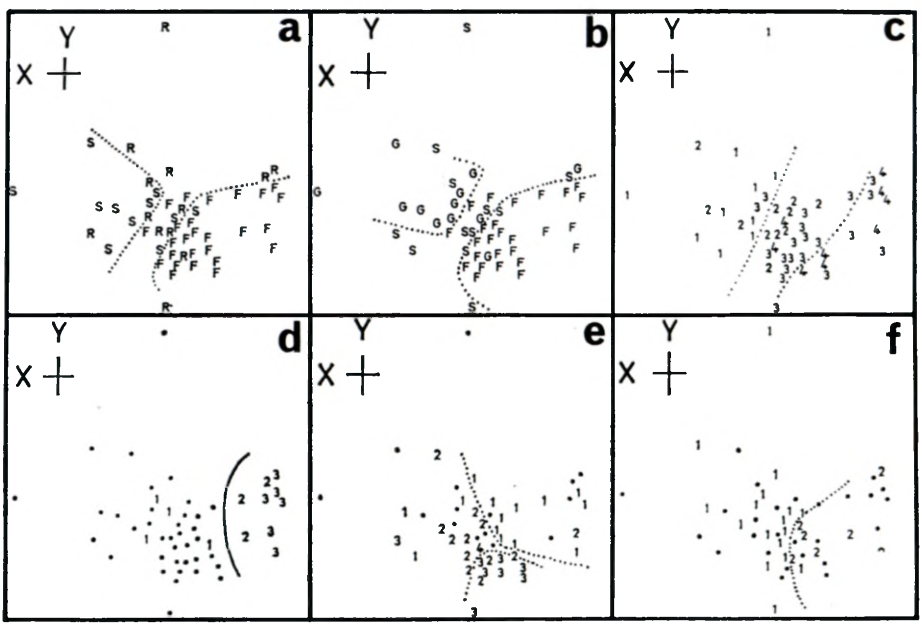

FIG. 3.—Shrub ordination showing the distribution of: a, plot aspect (F = flat, S = sea, R = river); b, angle of slope (F = flat, G = gentle, S = steep); c, shrub density (1 = 6–18, 2 = 24–37 3 = 41–69, 4 = 70–88; d, **Notobuxus natalensis** (. = absent, 1 = 1–5, 2 = 12–26, 3 = 34–52); e, **Baphia racemosa** (. = absent, 1 = 1–4, 2 = 5–10, 3 = 11–30, 4 = 61); f, **Carissa bispinosa** (. = absent, 1 = 1–2, 2 = 3–7).

Fig. 2g shows the shrub density data plotted on to the canopy tree ordination. No clear trends are discernible, but this is understandable because the shrub species are not as dependent on the external environment as are the tree species. It is apparent, however, that most river plots have a comparatively low shrub density.

Figs. 2h and 2i show the distribution of two selected shrub species, *Uvaria caffra* and *Peddiea africana*, on the tree ordination. Neither shows any marked relationship to the tree species performance. These two shrub species are given as examples of the unclear relationship between shrub and tree layers.

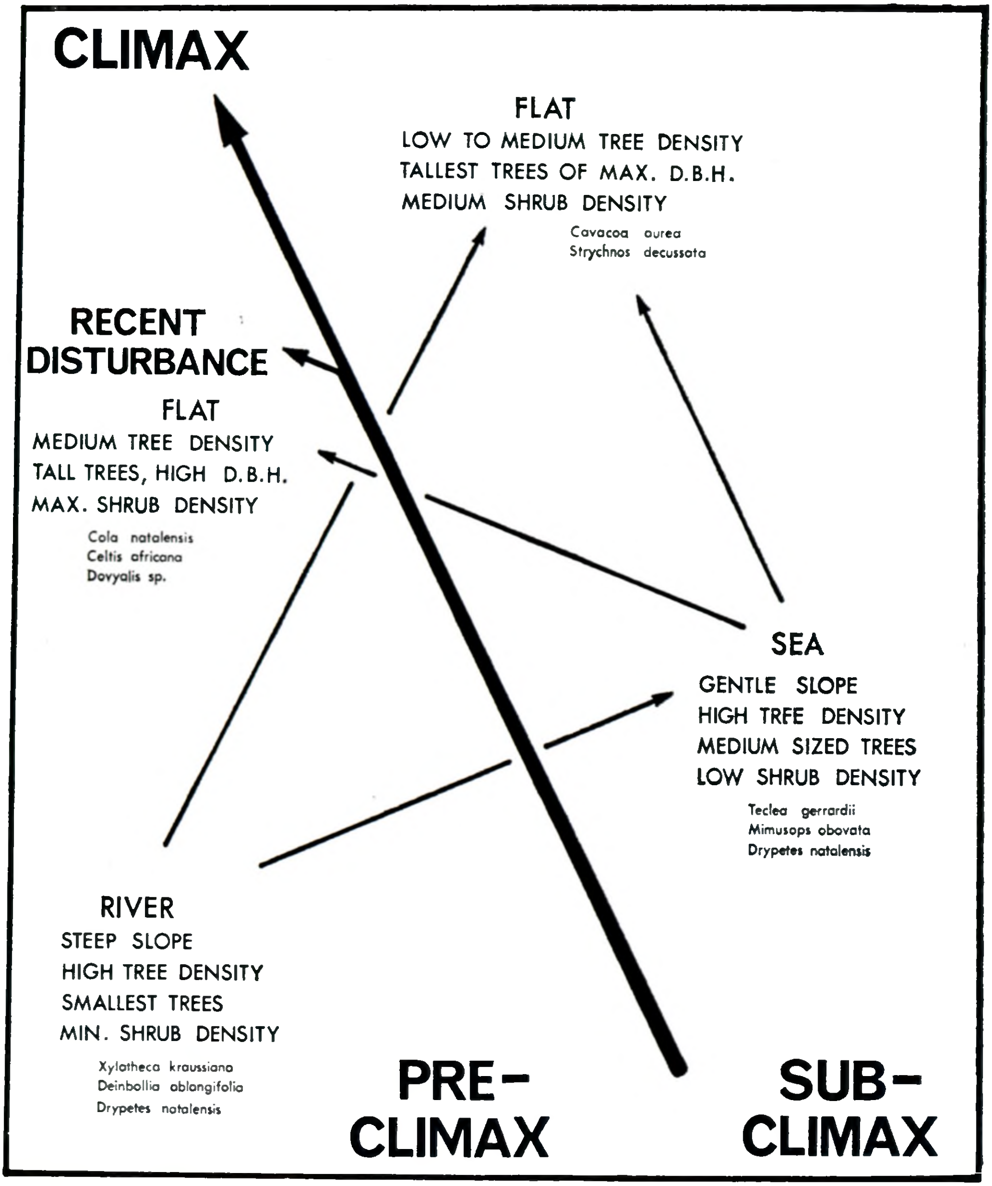

FIG. 4.—Diagrammatic summary, from the tree ordination, of suggested ecological gradients.

Figs. 3a and 3b show the distribution of aspect and angle of slope on the shrub ordination. The relationships between these two environmental factors are not as clear on the shrub ordination as they were on the tree ordination. A diagonal relationship to the two axes separates most of the gently-sloping to steeply-sloping, sea and river plots from the flat plots.

Fig. 3c shows the shrub density on the ordination. The relationships are not clear, but the flat plots tend to have the highest densities of shrubs.

Figs. 3d to 3f show the distribution of selected shrub species on the ordination. Only three species are shown. These are representative of the unclear shrub patterns on the ordination that appear to be unrelated to any of the major environmental data considered here. *Notobuxus natalensis* (Fig. 3d) is the one exception and shows a clear pattern, occurring in the flat plots where it contributes markedly to the high shrub density.

The results of the tree ordination are briefly summarized in Fig. 4, and suggested successional relationships are also given.

Discussion

By considering the limited environmental data that were collected in the field together with the tree density data and species behaviour, and with some experience of species performance in other parts of Natal, it is postulated that the forest on the flat sites represents the highest stage of development and can be considered climax. It is on the flat land that soils are deepest and where maximum penetration of rain water occurs. The rather varied tree density in some of the flat plots was at first a little perplexing but, when canopy tree species were plotted on to the ordination, it was apparent that either recent disturbance, by way of the occasional removal of a tree, or by a natural tree-fall, or recently drier environmental conditions, accounted for the much higher density in these plots. The shrub density data also indicated that there had been some recent disturbance, as many of the flat plots had a dense shrub layer indicative of a disturbed canopy. In fact, plots at the upper end of the Y axis may be considered as the best climax forest. The forest on the sea-slope may be considered a subclimax, limited by salt-spray, and the forest on the north-facing river slope, which is a xerocline, may be considered as preclimax.

Considering the canopy trees, it is postulated that *Cavacoa aurea* and *Strychnos decussata* (Fig. 1h and 2f) are true climax species in Hawaan.

Xylotheca kraussiana and *Deinbollia oblongifolia* (Fig. 1g and 2d) are heliophytes which occur almost exclusively in river plots. An occasional tree occurs on the sea-facing slope or on flat land, probably in an old gap.

Drypetes natalensis (Fig. 2a) occurs in an equal number of sea- and river-facing plots, and in two flat plots. It appears that this species prefers a fair amount of light, as the two flat plots where it is found are towards the seral end of the Y axis.

Mimusops obovata (Fig. 2e), a species that favours xeric sites, occurs mainly in the sea-facing plots, but is also present on the river slope. It occurs at the upper end of the Y axis and is probably indicative of subclimax forest.

Teclea gerrardii (Fig. 2b) has a similar behaviour to *M. obovata*, but is almost completely confined to sea-facing plots.

Cola natalensis has the highest density and is the most frequent species in Hawaan. Its distribution on the ordination (Fig. 1f) is across the successional trend postulated (see Fig. 4), being found mainly in flat plots, but it also occurs in sea- and river-facing plots. From field observations it was apparent that most *C. natalensis* trees were fairly small and I suggest that the frequency of *C. natalensis* is due to recent disturbance. This suggestion is partly supported by the shrub density data where the plots with the highest densities of shrubs are related to the distribution of *C. natalensis*.

The last two species, *Celtis africana* (Fig. 1i) and *Dovyalis* sp. (Fig. 2g), have a similar distribution to *Cola natalensis* although less well defined. *Celtis africana* is a fairly fast-growing tree which can tolerate both open canopy conditions and drier environmental conditions, as can also *Dovyalis* sp.

It is obvious that some relationship exists between the river xerocline and the sea-slope, the former probably bearing a seral relationship to the latter. This relationship is shown by the distribution of *Xylotheca kraussiana* (Fig. 1g), *Deinbollia oblongifolia* (Fig. 2d) and *Mimusops obovata* (Fig. 2e) on the ordination.

The distribution of shrub data on the canopy and the shrub ordinations was not clear and, at the present level of investigation, the shrubs are not as ecologically meaningful as the trees. A possible reason for this is that the shrubs, being partly protected by the trees, are not as dependent on the external environment. In addition, the shrub layer is more sensitive to local disturbance, such as the occasional removal of trees and natural treefalls. A combination of these factors has masked the shrub behaviour. Only the distribution of *Notobuxus natalensis* (Fig. 3d) was clear, this species being found exclusively in flat plots under the best canopy.

Conclusions

The climax forest species growing on flat sites are the tallest trees with maximum d.b.h. Most important climax species are *Cavacoa aurea* and *Strychnos decussata*. The forest of the gently-sloping sea slope is subclimax, and the most important sub-climax species are *Teclea gerrardii*, *Mimusops obovata* and *Drypetes natalensis*, the last species occurring on both the river and sea slopes (Fig. 4). The forest of the steep river slopes is at a preclimax to that on the flat sites, typical species being *Xylotheca kraussiana* and *Deinbollia oblongifolia*.

The modified Wisconsin ordination technique has given a good indication of the behaviour of the plant species considered. The manner in which this has been achieved is by simple, pictorial illustrations of the relationships of the plant species to certain environmental factors. The results of a previous investigation, based on density and frequency values, of the forest ecology (Moll, 1968a), were similar, but less obvious, in spite of the presence of the three distinct topographic sites in the Hawaan Forest. It is possible that if the size of the sample plot was manipulated to get the optimum size of sample, the results may have been even more informative.

Certain more refined statements concerning the plant ecology have been possible with the ordination technique than were possible with the previous study by Moll (1968a). A good example of this is that the ordination showed that *Cola natalensis*, *Celtis africana* and *Dovyalis* sp., although common in climax forest, are not true climax species, but can occur where there is comparatively recent disturbance. Such a conclusion was not easily drawn from a previous study of the Forest.

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