

The Rate of Forest Tree Growth and a Forest Ordination at Xumeni, Natal

by

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ABSTRACT

The rate of increment in circumference at breast height of canopy tree species in the southern temperate, Mist-belt forest at Xumeni, Natal, South Africa, is very slow. The mean for all trees calculated from measurements in 1929 and 1966 is 0.201 ± 0.015 inches per year.

Results from an ordination analysis of 39 plots were interpreted in terms of a successional gradient from seral sites on steep ground, characterized by *Kiggelaria africana*, *Xymalos monospora* and *Fagara davyi*, to climax sites on flatter ground with *Podocarpus* spp. Two climax types are indicated, with *P. henkelli* on moist soil and *P. falcatus* on drier soils.

INTRODUCTION

The Xumeni forest lies 110 km south-west of Pietermaritzburg in the Polela magisterial district of the Natal midlands. The indigenous forest is under the control of the Government Forestry Department.

The forest occurs on the south-facing slopes of a dolerite ridge. The topography is rugged and the soils are shallow. Boulder-strewn areas are common.

The most important canopy tree at Xumeni is *Podocarpus henkeli* but generally the canopy, which has an average height of about 30 m, is of mixed composition (Moll and Haigh, 1966). The area is classified as southern temperate (Köppen's Cwb division; Schulze, 1947). According to Acocks (1953), Xumeni is Mist-belt forest, and is rich in epiphytic bryophytes, ferns and angiosperms which festoon tree boles and rocks.

In 1929 the resident forester laid out a line through the forest and on it recorded all canopy trees in 40 one chain square, systematically placed, plots (Cook, 1929). He took various measurements including circumference at breast height (CBH). In 1966 the same trees were re-measured for this parameter.

RESULTS

1. TREE GROWTH

In Fig. 1 the tree CBH measurements for 1929 have been plotted against their CBH 1966. A regression line fitted for all species, shows that the average CBH increment rate over 37 years is very small. Regression lines were also calculated for the six most common species, and with the exception of *Fagara davyi* these were almost identical to the regression line for all species.

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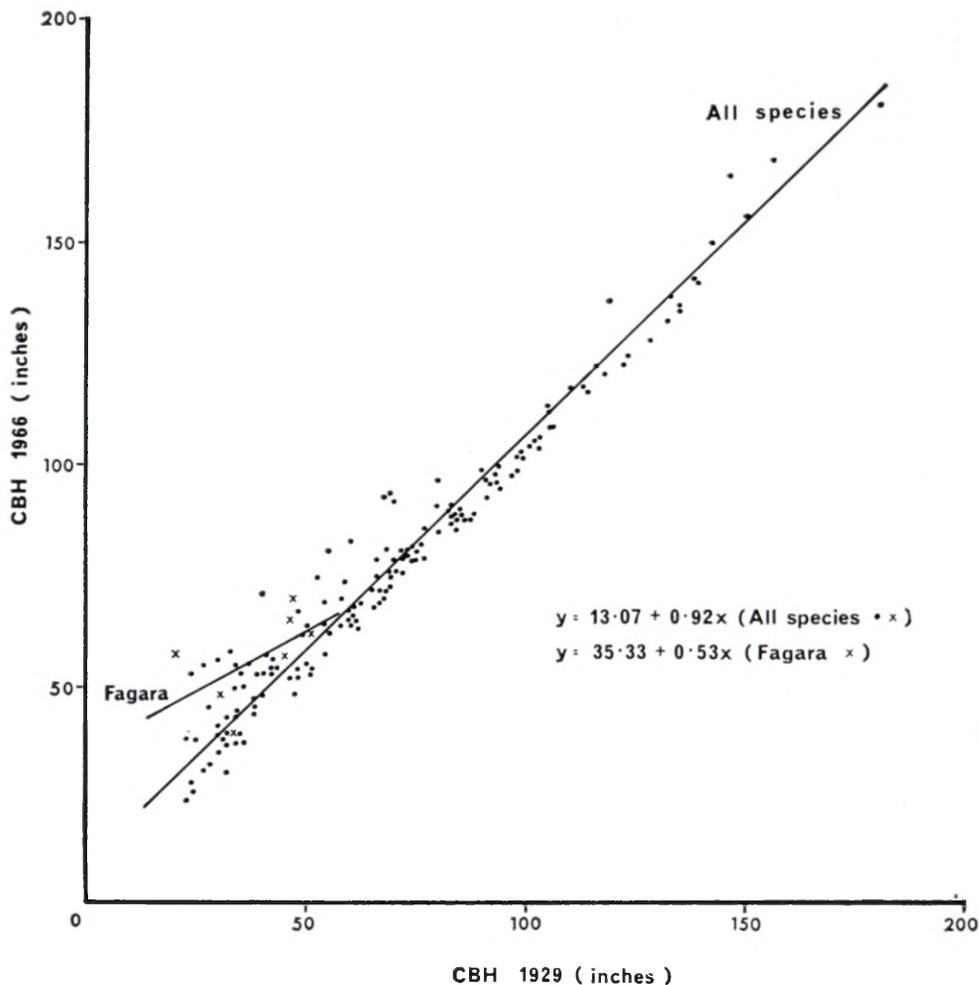


FIG. 1. — CBH increment 1929—1966 for all species in all plots, and *Fagara davyi* alone.

The regression line for *F. davyi* probably reflects that this species has the fastest rate of CBH increment of all species when young, but that the older individuals approximate to the behaviour of all species. This conclusion though tentative, there being only seven trees encountered, is in keeping with field observations on *F. davyi*.

P. henkelii exhibits a very slow rate of CBH increment (all the individuals being mature), while *F. davyi* shows the most rapid rate of CBH increment (all the individuals being comparatively young).

The rate of CBH increment of forest trees at Xumeni is very slow averaging 0.201 ± 0.015 inches* ($n = 160$) per year. Phillips (1931) quotes average increment of CBH per year in the Knysna Forest, Cape Province (Table 1). Comparing the data shown for the two species in common, the rate of increment

* As the original measurements were in feet and inches, these units have been retained rather than adopt the metric system for the recent measurements.

of *P. henkelii* in both Knysna and Xumeni is similar. The other common species, *Kiggelaria africana*, has twice the increment rate of this species in Knysna.

TABLE 1. — Mean annual CBH increment rate (in inches) of selected forest tree species at Knysna and Xumeni.

Species	Observed Rate Knysna (1924-5)	Estimated Rate \pm S.E.M. Xumeni (1929-66)
<i>Podocarpus henkelii</i>	0.139	0.132 \pm 0.017 (n = 68)
<i>Xymalos monospora</i>	no data	0.191 \pm 0.064 (n = 13)
<i>Podocarpus falcatus</i>	no data	0.231 \pm 0.049 (n = 15)
<i>Kiggelaria africana</i>	0.131	0.267 \pm 0.036 (n = 26)
<i>Fagara davyi</i>	no data	0.459 \pm 0.113 (n = 7)

In Fig. 2 the mean plot increment 1929—1966 was plotted against the mean plot CBH 1929, and a regression line fitted. The results indicate that the plots with the smallest mean CBH 1929 exhibit maximum increment, reflecting that CBH increment is inversely proportional to age of canopy tree species.

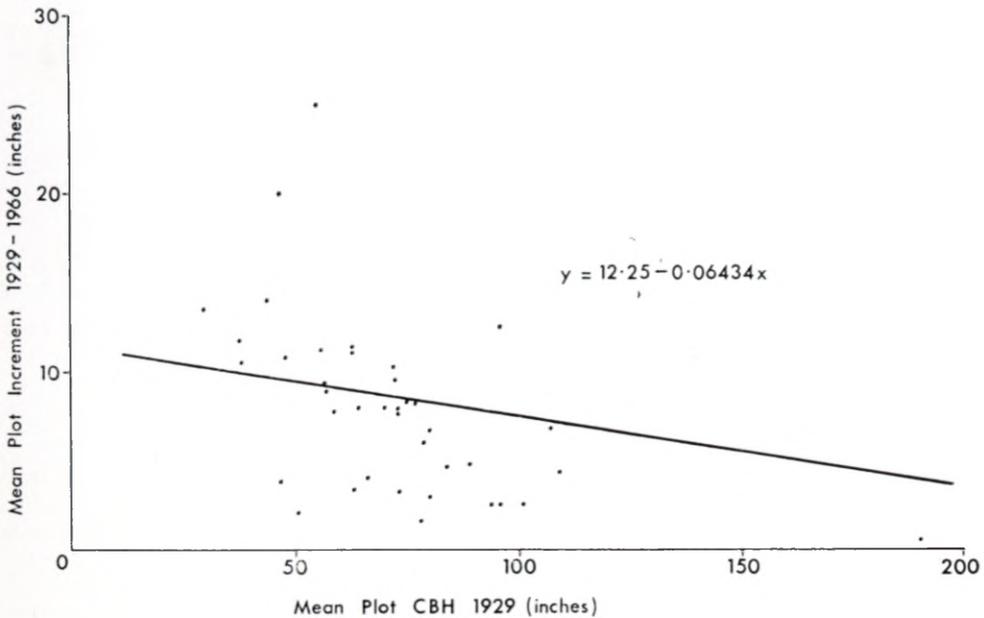


FIG. 2. — The relation of mean plot increment 1929—1966 to mean plot CBH 1929.

The CBH data were separated into 20 inch size classes and their increments drawn as a histogram (Fig. 3). As reflected in Fig. 2 the trees with the smallest CBH have increased the most, with one exception, CBH size class 141-160 inches. Upon further investigation of the four individuals in this size class, it was found that the unexpected high rate of increment was due entirely to two individuals, which were extremely fluted.

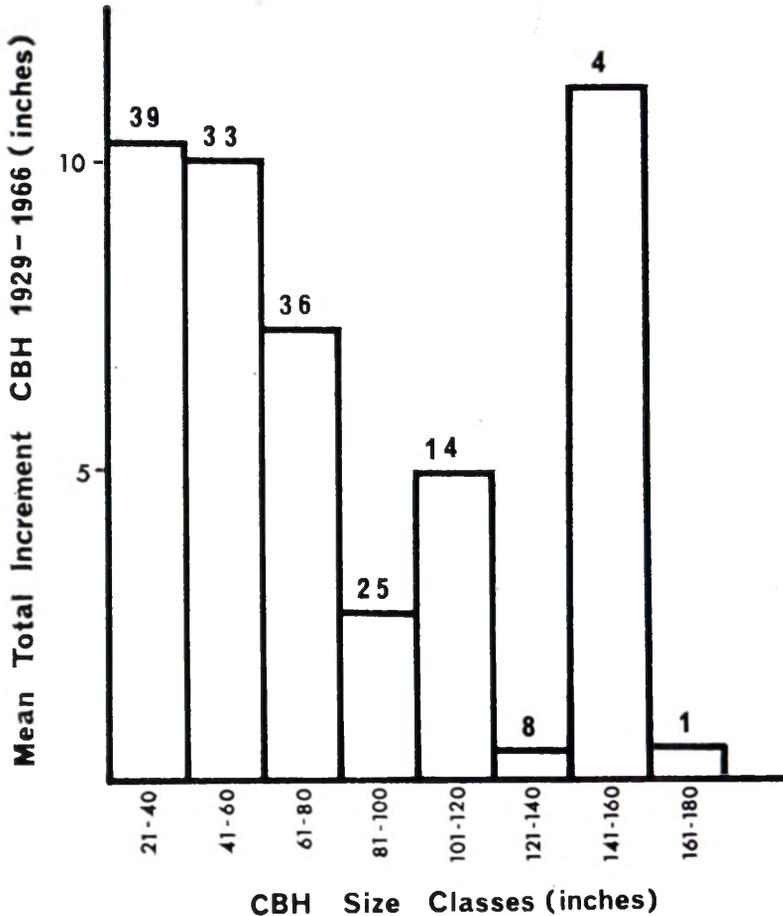


FIG. 3. — Histogram of CBH increment for 20 inch size classes (the number of individuals per size class are given above each bar).

2. ORDINATION

The floristic similarity of Cook's 1929 data for 39 plots (one plot was excluded because it contained no canopy tree species), was investigated using the ordination procedure developed by Bray and Curtis (1957). Two axes, X and Y, were sufficient to account for the floristic variability and the resultant two dimensional scatter diagram of points (representing plots) is shown in Figs. 4-16 (the orientation of the X and Y axes is given in each figure). Isolines are used to draw attention to (i.e. separate) high and low ratings, unless otherwise explained.

Canopy tree species (Figs 4—8)

Podocarpus henkelii and *P. falcatus* (Figs 4 and 5) separate off with centres of maximum density at the two extremes of the X axis, while *K. africana* and *X. monospora* (Figs 6 and 7) separate off at the upper end of the Y axis, the latter species being apparently unrelated to the X axis. *F. davyi* (Fig. 8) is intermediate between *K. africana* and *X. monospora*.

Canopy (Fig. 9)

Subjective estimates of canopy were made in 1966. Comparison of Figs 4 and 9, reveals that *P. henkelii* is the most important species contributing to plots with closed canopy.

Density and CBH (Figs 10 and 11)

Highest densities tend to occur in the *K. africana* and *P. henkelii* region of the ordination, while plots with trees of the largest CBH are found mainly in the *P. henkelii* and *P. falcatus* region.

Increment (Fig. 12)

Minimum plot increment 1929—1966 is found in the *P. henkelii* region and maximum increment is limited to *K. africana*, *X. monospora* and *F. davyi* at the upper region of the ordination.

Slope (Fig. 13)

At each site a subjective estimate of slope was made. Although the pattern is not altogether clear, the Y axis appears related to a gradient from steep plots with *F. davyi* and other species, through gentle and flat plots with predominantly *P. henkelii*.

Rocks (Fig. 14)

A subjective estimate of the amount of surface rocks in each plot was made. The most rocky plots are found in three groups: flat plots with *P. henkelii*, flat and gentle plots with, predominantly, *P. falcatus* and three plots with *K. africana*.

Mist (Fig. 15)

Nine plots are situated, approximately 100 m above the rest, on a ridge exposed to winds from the south. These plots receive most orographic mist. The soils are generally rocky and well drained, and the majority of these plots contain the highest densities encountered of *P. falcatus* (compare Figs. 5 and 15). Three plots isolated from the rest (Fig. 15), fall in the *K. africana* and *X. monospora* region of the ordination.

Selaginella kraussiana (Fig. 16)

The presence of this herb, recorded in 1966, reflects a high soil-moisture content and the majority of plots which contain this species are in close proximity to small flowing streams or noticeably dank. The distribution of this species in the ordination coincides with *P. henkelii* and the closed canopy region (Figs. 4 and 9).

FIGS. 4—16. — Distribution on the ordination of:-

4—8: Plot density of selected canopy tree species.

9: Canopy (c = closed, o = open and * = no canopy; isoline encloses region of closed canopy).

10: Plot density (absolute values plotted).

11: Mean plot CBH 1929 (CBH size classes in inches: 1 = < 60, 2 = 60—90, 3 = 91—110, 4 = > 110).

12: Mean plot increment 1929—1966 (CBH increment classes in inches: 1 = < 5, 2 = 5—10, 3 = > 10; isolines enclose regions of maximum and minimum increment).

13: Slope (S = steep, G = gentle, F = flat).

14: Rocks (R = rocky, S = semi-rocky, O = no rocks).

15: Mist (M = plots with most orographic mist).

16: *Selaginella kraussiana* present in the herbaceous field layer.

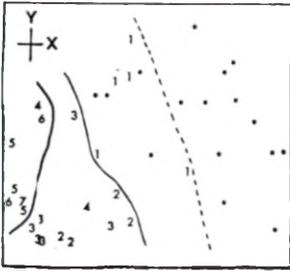


Fig. 4. *Podocarpus henckelii*

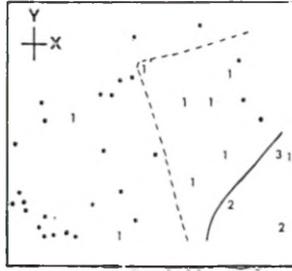


Fig. 5. *Podocarpus falcatus*



Fig. 6. *Kiggelaria africana*

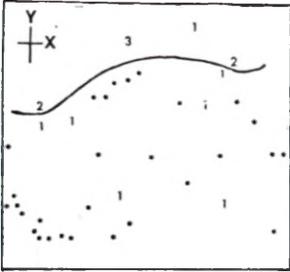


Fig. 7. *Xymalos monospora*

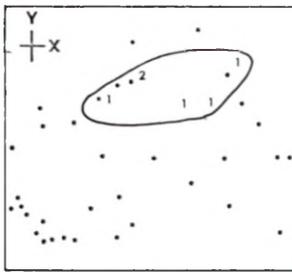


Fig. 8. *Fagara davyi*

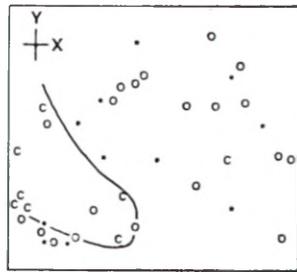


Fig. 9. Canopy

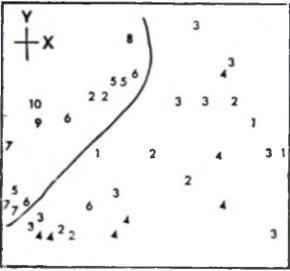


Fig. 10. Density

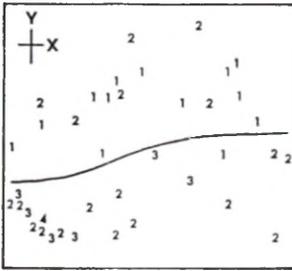


Fig. 11. Mean plot CBH 1929

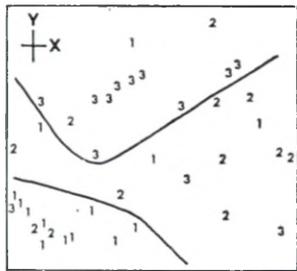


Fig. 12. Mean plot increment 1929-1966

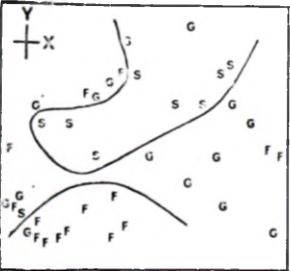


Fig. 13. Slope

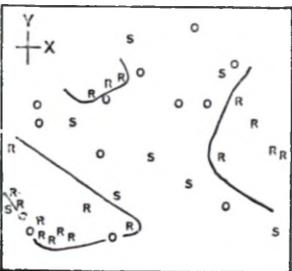


Fig. 14. Rocks

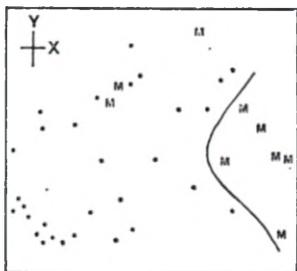


Fig. 15. Mist

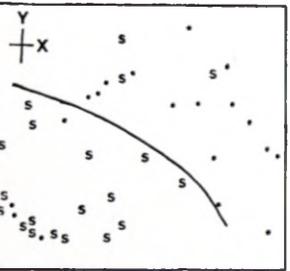


Fig. 16. *Selaginella kraussiana*

CONCLUSIONS

1. TREE GROWTH

- (a) Rate of forest tree growth at Xumeni is very slow, mean CBH increment for all species being 0.201 ± 0.015 inches per year.
- (b) *P. henkelii* exhibits the minimum increment, *X. monospora* a higher increment approximating to the average of all trees, and *P. fulcatus*, *K. africana* and *F. davyi* the highest. *F. davyi* shows the maximum CBH increment of all canopy species.
- (c) The inverse relationship between age and CBH increment rate, well known to foresters, is clearly demonstrated for this area of indigenous forest.

2. ORDINATION

(i) *Specific conclusions*

- (a) Two axes, X and Y, were sufficient to account for the floristic variability within the 39 plots.
- (b) Comparing Figs 4 and 13—16 it appears that *P. henkelii* occurs on moist, flat, rocky terrain situated below the level of most orographic mist.
- (c) Comparing Fig. 5 and Figs 13—16, it appears that *P. fulcatus* is associated with gently sloping, dry, rocky areas with most orographic mist.
- (d) From b and c, and with reference to Figs 10, 15 and 16, it is suggested that the X axis reflects a density gradient with *P. henkelii* and *P. fulcatus* at the two extremes from respectively flat, moist, rocky plots exposed to damper atmosphere at a higher altitude. This gradient is mirrored in decrease in canopy and the occurrence of *S. kraussiana*, the presence of *S. kraussiana* showing high soil-moisture and low light intensities.
- (e) The Y axis separates the two *Podocarpus* spp. from *K. africana*, *X. monospora* and *F. davyi* (Figs 4—8), the latter three species growing on the steeper, least rocky slopes, and appears to show an environmental gradient from steeper, drier sites to gentle and flat, wetter sites (Figs 13 and 16).
- (f) Figs 11 and 12 show the inverse relationship, stated previously, between mean plot CBH and increment, and the Y axis is related to these two measures of productivity.
- (g) With reference to Figs 4—9, 11—13, 15 and 16 it is suggested that the Y axis reflects a successional trend from seral sites with *K. africana*, *X. monospora* and *F. davyi* to climax sites with *P. henkelii* and *P. fulcatus*, the X axis showing the separation between the two climax species as described in (d).

(h) Fig. 17 summarizes the suggested site-succession relationships.

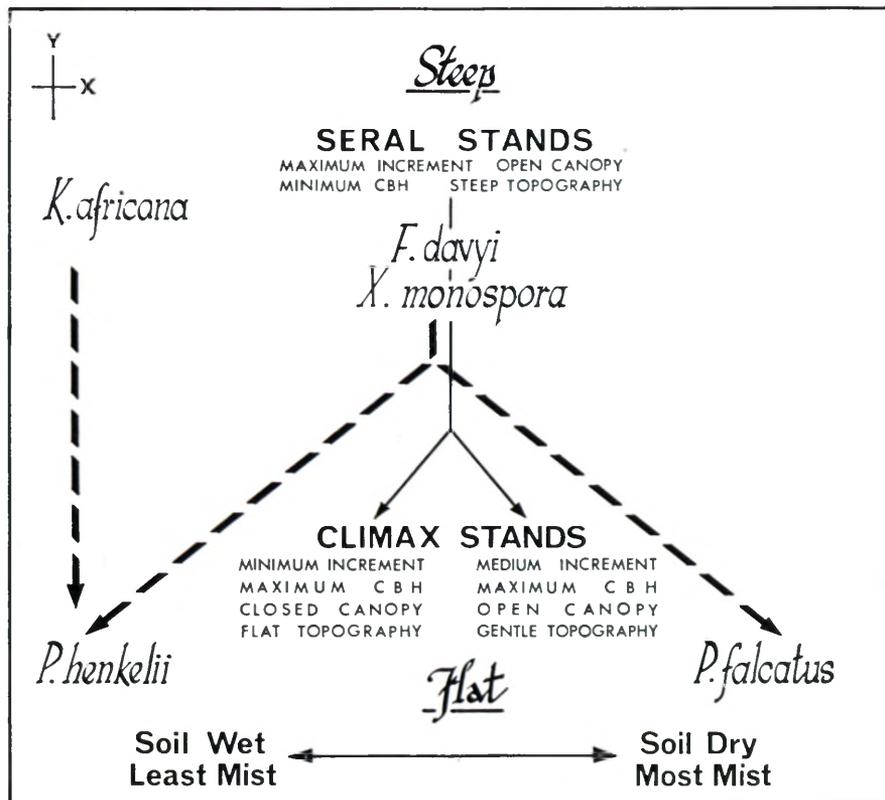


FIG. 17. — Diagrammatic representation of suggested environmental gradients and successional trend on the ordination.

(ii) *General conclusions*

- (a) The plotting of information collected in 1966 onto an ordination scatter derived from data collected in 1929, and the resultant correlations, indicate that the forest environment has remained stable over this period of years. The value of plotting information onto an ordination based on floristic data collected in previous seasons has been shown to have considerable use (*cf.* Woods, 1964).
- (b) Consider two hypothetical plots A and B, containing species a, b, c, d and e in the following densities:

Plot	Species	a	b	c	d	e
A		1	—	1	1	2
B		—	—	1	1	1

C (coefficient of similarity) between A and B = 75.0 per cent. Suppose species c were absent from plot B, then C would have a value of 57.1 per cent.

The plot density values at Xumeni for all species were low (Fig. 10), and it was initially suspected that such low values might have yielded little meaningful information in the matrix of similarity coefficients. However, the ordination technique employed proved

reasonably robust in view of the nature of the data used. The value of a correlation coefficient between 151 randomly selected inter-point distances and the respective dissimilarity ($100 - C$) values was 0.678.

- (c) In view of the relative inefficiency of the ordination technique used, compared with such a technique as principal components analysis (Orloci, 1966), it is realized that the Wisconsin ordination technique does not yield high correlations between inter-point distances and similarity coefficients. However, the actual distances between points are not necessarily of paramount importance unless, for example, it is desired to classify the samples. Numerous workers have shown that the Wisconsin technique yields a meaningful overall pattern of variation in vegetation samples analysed. It has the considerable advantages of not necessarily requiring electronic computation facilities and unlike such classificatory techniques as Association Analysis, ordination is primarily useful in the study of the autecology of species when overall trends, rather than inter-point differences, are studied.

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REFERENCES

- ACOCKS, J. P. H., 1953. Veld types of South Africa. *Mem. Bot. Surv. S. Afr.*, No. 28.
- BRAY, J. R. & CURTIS, J. T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-349.
- COOK, G., 1929. *Sample Area Records: Xumeni Forest*. Unpublished data, records in Natal Region of Forestry Department.
- MOLL, E. J. & HAIGH, H., 1967. A report on the Xumeni forest. Natal. *Forestry in S. Afr.* 7: 99-108.
- ORLOCI, L., 1966. Geometric models in ecology. I. Theory and application of some ordination methods. *J. Ecol.* 54: 193-215.
- PHILLIPS, J. F. V., 1931. Forest-succession and ecology in the Knysna region. *Mem. Bot. Surv. S. Afr.* No. 14.
- SCHULZE, B. R., 1947. The climates of South Africa according to the classification of Köppen and Thornthwaite. *S. Afr. geogr. J.*, 29: 32-42.
- WOODS, D. B., 1964. *A study of the ecology of selected annual and biennial species on sand-dunes*. Unpublished Ph.D. thesis. University of Wales.