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An Ordination of the Vegetation of Ntshongweni, Natal*

by

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ABSTRACT

The physiography, soils, climate and dense woody vegetation are briefly described for Ntshongweni, a cone-shaped hill in Natal, South Africa (29° 51′ S and 30° 43′ E). A primary ordination of the woody plants, based on Bray & Curtis's (1957) method, was carried out using 60 quadrats. Four stand noda were delimited and another four noda within a secondary ordination of a cluster of quadrats which could not be interpreted within the primary ordination. Edaphic and atmospheric moisture conditions and slope aspect were proposed as the main site factors correlated with species performance. Tables of density, local frequency and constancy for species occurring in each nodum were drawn up.

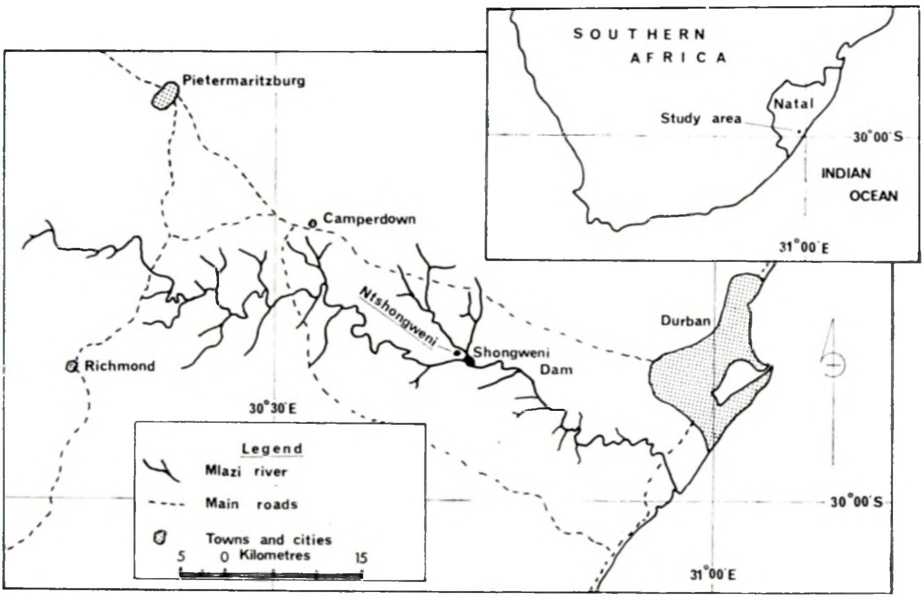

FIG. 1.—Location of Ntshongweni, the study area.

INTRODUCTION

Ntshongweni is the name of a steep-sided, cone-shaped hill situated in the Mlazi River Valley, Natal at the intersection of co-ordinates 29° 51′ S and 30° 43′ E (Fig. 1). The anglicized name of the hill is given to Shongweni Dam, completed in December, 1927, at the foot of the hill. Since construction, the dam and land in the vicinity, including Ntshongweni, have been controlled by the Durban Municipality.

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Gleason (1926) and Ramensky (cited in Whittaker, 1962), working independently at about the same time, first proposed the Individualistic Hypothesis of vegetation structure. The Hypothesis holds that no two communities are strictly identical in floristic composition. Instead, communities exhibit continuous variation in detailed composition and cannot be readily delimited as clearcut units. No discontinuities in compositional variation occur, except where there are discontinuities in the physical environment. Ordination studies by many ecologists, including Curtis & McIntosh (1951), Whittaker (1956 and 1960), Bray & Curtis (1957) and Curtis (1959), have shown that variation in composition is continuous, except where the environment is discontinuous, and have thus fostered the Individualistic Hypothesis. On the hill, Ntshongweni, there is a gradual change in slope aspect from north-west through north, east and south to south-west and an altitude gradient of over 200 m. It was considered that the effect of aspect and altitude on the vegetation of the hill was eminently suitable for study by ordination and that the vegetation was likely to conform to a continuum in the manner indicated by the Individualistic Hypothesis.

Ordination, the technique used in this account, is the uni- or multi-dimensional arrangement of stands so that a statement of stand position, relative to other stands or to the axis or axes of the model, conveys the maximum amount of information about its composition. It is thus an ecological tool for summarizing and ordering information about the distribution and relative abundance of plants. Rewarding use can be made of

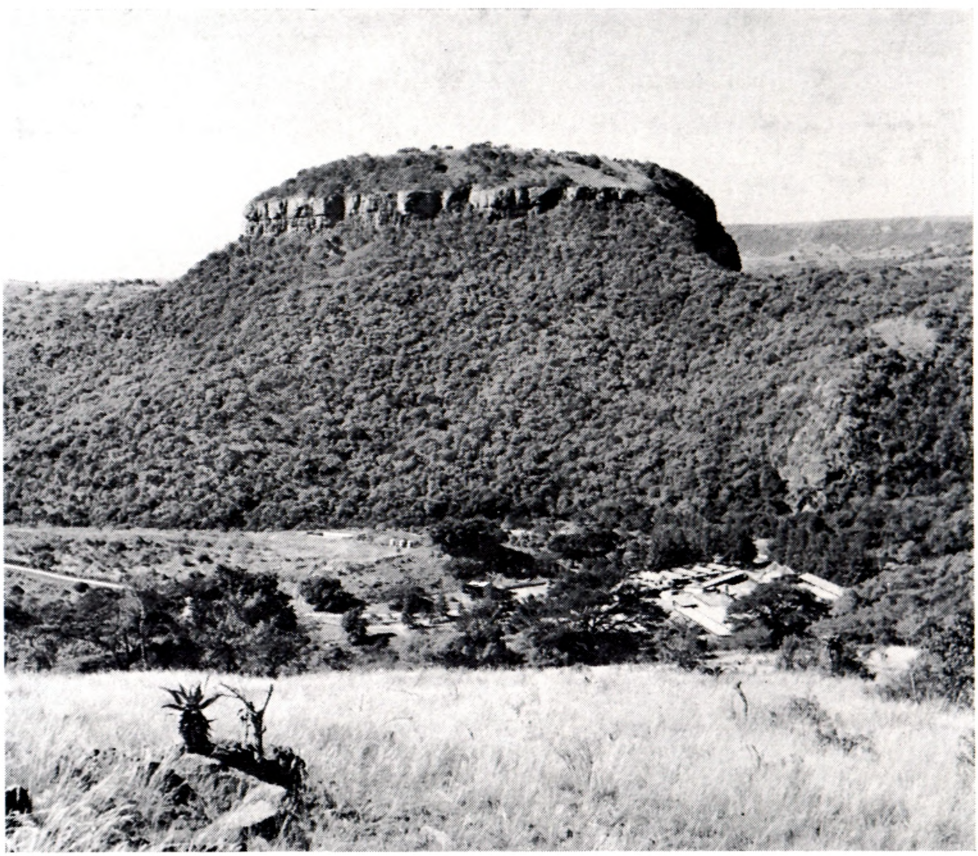


PLATE 1.—View of Ntshongweni from the north-west.

ordination as a framework for indicating potential environmental correlations because the complexity of environmental factors determining plant distribution may be better measured indirectly, through studying the plants, than by direct measurement of the environment.

Physiography and Soils

The hill, Ntshongweni, is bounded on its north and south sides by the deep valleys of the Sterkspruit and Mlazi Rivers. From the surface of Shongweni Dam at an altitude of about 300 m, the land rises, gently at first, and then steeply, to high sandstone cliffs that almost surround a small summit plateau at over 500 m above sea level (Fig. 2). The cliffs are composed of a band of fine-grained rock, the Orthoquartzitic Marker Band of the Table Mountain Series (Rhodes & Leith, 1966). The Marker Band is underlain by the sandstones, grits and shales of the Basal Zone of the Table Mountain Series that rests unconformably on Basement Complex Granite (Dodson, 1951). The narrow valley floors are of sandy alluvium.

The soils of the summit plateau and area east of the eastern fault (Fig. 2) are deep, grey- or red-brown, coarse, sandy loams with low organic-matter content. On the steep north- and south-facing slopes of Ntshongweni the soil is a shallow, greyish-brown, gritty loam. Large and small sandstone talus boulders add heterogeneity to the granite-derived soils. The influence of talus is most apparent immediately beneath the Marker Band cliffs.

Climate

Insolation and temperature

On account of the steep topography, the south-facing slopes of Ntshongweni are often in shadow and only intercept direct insolation in the early morning and late afternoon. West-facing slopes, receiving insolation in the afternoon, become hotter than east-facing slopes, because ambient temperatures are higher in the early afternoon than in the morning. Thus the north- and north-west-facing slopes, which receive most direct sunlight every day, become hotter and have a higher rate of evaporation than south-facing slopes. It was assumed that a gradient of insolation and temperature from high to low existed from the north-facing slopes to the south-facing slopes.

During the 25 year period when temperatures were recorded (Table 1), the absolute maximum was 43·9°C at the dam on the valley floor. During the same period, the absolute minimum temperature was 2·8°C. The difference in mean monthly temperature between summer and winter was less than 10°C. Frost was not observed by the writer at Shongweni Dam and is apparently rare.

Table 1.—Temperature data for Shongweni Dam Weathei Station, 1932 to 1946, from Weather Bureau (1954a)

	Mean monthly	Absolute maximum	Absolute minimum
January	22·5	40·6	7·2
February	22·6	38·9	11·1
March	22·3	39·4	11·1
April	20·8	36·7	8·3
May	18·4	35·6	5·0
June	16·0	33·9	4·4
July	15·5	32·8	2·8
August	16·5	36·7	3·9
September	18·2	40·0	6·1
October	19·7	41·7	8·3
November	21·2	41·7	7·2
December	22·0	43·9	9·4

Rain and fog

Nearly all geographers, according to Jackson (1952), and many ecologists have in the past explained wind direction and South Africa's summer rainfall in terms of a low pressure trough over the interior during summer and an anticyclonic circulation over the interior during winter. Jackson has shown, however, that this explanation is not consistent with known wind directions. During summer and winter an anticyclone is centred over the eastern Transvaal so that the normal air circulations are similar in summer and winter and the seasonal reversal of prevailing wind direction, as suggested previously, is not possible. The two prevailing winds at Shongweni Dam are north-east and south-west in approximately equal proportions throughout the year (Schulze, 1965). North-east winds blow during fair weather and south-west winds accompany cold fronts and rain.

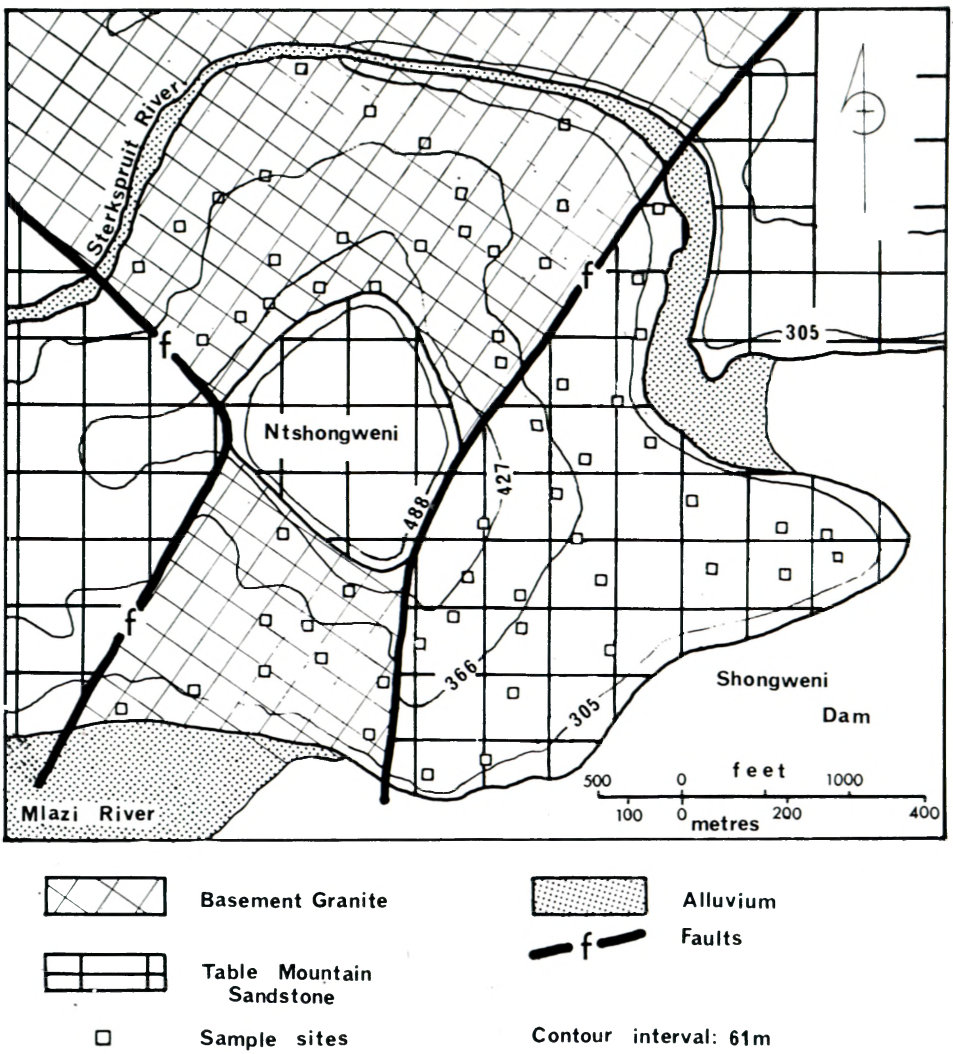


FIG. 2.—Geological map of Ntshongweni (partly after Dodson, 1951).

Accounts of the synoptic situations associated with frontal activity and thunderstorms in Natal are described by Tyson (1964a and b and 1965). Rain is brought by cold fronts which sweep along the east coast of South Africa throughout the year at two- to three-weekly intervals. Precipitation from these fronts is mainly confined to the summer months. Cold fronts are preceeded by hot, dry, gusty, north-west Berg Winds which blow for one to three days at a time. In summer, following the passage of a cold front, the wind becomes south-westerly, the temperature drops rapidly, a thick cloud cover builds up and gentle, continuous rain may be expected. In winter, a temperature drop follows a cold front and a cloud layer may develop but rain is unusual. Rain is also brought by summer storms of high intensity and short duration, during which 25 mm of rain, or more, may fall in two hours.

The rainy season at Shongweni Dam, during which 80 per cent of the mean annual precipitation may fall, extends from October to April. Mean annual rainfall for the period 1929 to 1950 was 773 mm (Weather Bureau, 1954b). The highest recorded rainfall of 1165 mm occurred in 1943, and the lowest of 519 mm in 1949.

In summer, fog may cover the higher slopes of Ntshongweni for two or three days at a time following the passage of a cold front. Exact frequencies of fog are not known but it was observed about four times per month during the summer of 1966. During the dry season, radiation fogs may form. These fogs were seen on only two occasions at Shongweni Dam during 1966. Radiation fogs are associated with the formation of inversions in valleys at night and are dispersed by the sun's warmth each morning.

VEGETATION

General description of vegetation

History

The vegetation of the study area was subjected to intense disturbance prior to the building of Shongweni Dam and the declaration of the catchment immediately above the dam as a Nature Reserve in about 1920. Comparison of the aerial photograph taken in 1937 (Plate 2: 1) with that taken in 1959 (Plate 2: 2) shows the change in cover which took place over 22 years in the absence of tree felling and cultivation by Bantu. Large portions of the peninsula surrounding the Bantu Kraal and areas south-east of the summit of Ntshongweni which lacked trees in 1937 had, by 1959, a good tree cover. Throughout the area, the cover of trees increased, the summit of Ntshongweni showing least increase although individual bush clumps appear bigger in the later photograph.

Major vegetation types

The edges of the flat summit of Ntshongweni and of the surrounding tableland form a sharp boundary between the physiognomically and floristically different plateau and valley vegetation types. Differences are a possible result of two major environmental factors. Firstly, the poorly drained, more-or-less level plateau differs with regard to soil moisture status from the steep, well-drained valley slopes. Secondly, the presence of summer fog on the upper slopes and plateau makes this environment moister than that of the lower valley slopes. The sandy soils of the plateau are underlain by the water-impermeable Orthoquartzitic Marker Band. Evidence for the presence of the Marker near the soil surface is given locally by the occurrence of *Syzygium cordatum*, a tree usually found along streams, but able to grow on the plateau where drainage is impeded and the water table is high.

Only the valley vegetation was analysed quantitatively. A brief description of the vegetation of the plateau and valley is given below, prior to an account of the quantitative study.

PLATE 2.—1, Aerial photograph of Ntshongweni taken in 1937; 2, same, 1959. Photos: Trigonometrical Survey Office.

1. *Plateau vegetation*

(*a*) Aristida junciformis *Grassland*

A grassland of perennial, tufted grasses up to 1 m high in autumn, is the principal plateau community. *Aristida junciformis*, which is unpalatable to cattle except in the early part of the growing season, is dominant in terms of cover. Other grasses include *Andropogon amplectens*, *Cymbopogon validus*, *Eragrostis capensis*, *E. chapelieri*, *E. plana*, *Panicum natalense* and *Trichoneura grandiglumis*. Spring aspect forbs are *Cassia plumosa*, *Eriosema salignum*, *Hypoxis* sp., *Pentanisia angustifolia*, *Polygala hotentotta*, *Rhynchosia totta*, *Tephrosia macropoda* and *Wahlenbergia undulata*. In autumn, tall, half-woody dicotyledons, such as *Pseudarthria hookeri* and *Leonotis dysophylla*, are prominent.

(*b*) Faurea saligna *Woodland*

The narrow-crowned tree, *Faurea saligna*, usually occurs on shallow, sandy soils in almost pure stands. Individuals are up to 4·5 m high with 2–6 m between crowns. Occasionally, *Acacia nilotica* and *Albizia adianthifolia* also occur. Many *F. saligna* trees, cut off about 20 cm above ground level, have produced a multiple-stemmed coppice. As *F. saligna* is prized as firewood by Bantu (pers. comm. Professor A. W. Bayer), it was probably felled for this purpose.

(*c*) Combretum molle-Acacia nilotica *Woodland*

Where the soil is deeper, a number of tree species form an open, deciduous, *Combretum molle-Acacia nilotica* Woodland. Distance between the flat, spreading crowns of the trees, which are up to 4·5 m high, varies from 1 m to about 6 m. *Combretum molle* and *Acacia nilotica* are dominant, but *A. robusta*, *Albizia adianthifolia*, *Syzygium cordatum*, *Apodytes dimidiata*, *Euphorbia ingens* and *Tarchonanthus trilobus* are also frequent. Shorter trees, growing to 3·5 m, include *Acacia gerrardii*, *Sapium integ rrimum*, *Maytenus heterophylla*, *Dichrostachys cinerea* and *Vangueria infausta*. Two herbaceous climbers of this community are *Clematis oweniae* and *Riocreuxia torulosa*. *Aristida junciformis* forms a continuous understory between the trees.

2. *Valley vegetation*

(*a*) *Rocky Hillside Scrub*

A scrub vegetation is found on the very steep, talus-littered slopes immediately beneath the cliffs which crown Ntshongweni. On the north-facing slopes, in the immediate vicinity of the sandstone cliffs, *Crassula portulacea*, *Tarchonanthus trilobus*, *Canthium ciliatum*, *Aloe arborescens* and *Urera tenax* are common. Where the soil is a little deeper, trees 4–5 m high from an open, uneven canopy. Trees on the north-facing slopes include *Euphorbia tirucalli* and *Combretum molle* as dominants, with *Brachylaena elliptica*, *Euphorbia ingens Hippobromus pauciflorus*, *Spirostachys africana*, *Commiphora harveyi*, *Dombeya rotundifolia* and *Grewia occidentalis* also occurring. The succulents, *Euphorbia ingens*, *E. tirucalli*, *Crassula portulacea* and *Aloe arborescens*, are a feature of this community. As rainfall runoff is high, the presence of these more drought-tolerant succulent species is possibly a response to the relatively dry edaphic conditions.

On the south-facing slopes, *Aloe arborescens* and *Euphorbia grandid ns* are common between rocks. Both are up to 1·5 m high. *Pavetta gracilifolia*, which is rarely over 30 cm high and is heavily browsed, is a common shrub of this community. *Iboza riparia*, *Sansevieria thyrsiflora* and *Senecio fulgens* are undergrowth herbs. An interesting herbaceous climber in an early stage of the woody plant succession on the south-facing slopes is the fern *Microgramma owariensis*, which appears to be restricted in distribution to this community. *Petopentia natalensis* is another common, herbaceous climber.

(*b*) Aloe-Dombeya *Woodland*

One of the most easily-distinguished communities of the study area is *Aloe-Dombeya* Woodland, found on the steep, lower, north-facing slopes of Ntshongweni on mineral soils derived from deeply weathered granite. The most conspicuous component of the community is *Aloe candelabrum* which grows to 2 m high and has large, succulent leaves. Other woody plants of the community are 2·5–4 m high and form an open woodland with a grass understory 60 cm high. Important species are *Dombeya rotundifolia, Combretum molle, Dichrostachys cinerea, Euphorbia tirucalli, Brachylaena elliptica* and *Cussonia spicata.* The largest tree clumps contain, in addition, *Spirostachys africana, Commiphora harveyi, Grewia occidentalis, Canthium locuples, Acacia gerrardii* and *Dalbergia obovata.* Common grasses of the field layer are *Sporobolus pyramidalis* and *Eragrostis curvula,* while *Tagetes minuta* and *Bidens pilosa* are common weeds. The presence of these four last-mentioned species indicates a previous history of disturbance.

PLATE 3.—**Aloe-Dombeya** Woodland.

(*c*) Acacia nilotica-A. karroo *Woodland*

The valley slopes east of Ntshongweni are occupied by *Acacia* spp. Woodland. The aspects are north-east-, east- and south-east-facing, but varying angle of slope and earlier interference by man throughout the area have produced a mosaic of plant communities. Soils, usually derived from Table Mountain Sandstone, are deep, except on steep slopes. The trees are usually 2–4 m high, but can be 6 m high occasionally. Many are deciduous and have widespreading crowns. Trees which reach the open or closed canopy in *Acacia* spp. Woodland include *Acacia nilotica*, *A. karroo*, *A.gerrardii*, *Dichrostachys cinerea*, *Grewia occidentalis*, *Acacia robusta*, *Clerodendrum glabrum*, *Combretum molle*, *Acacia caffra*, *Rhus chirindensis*, *Sclerocarya caffra*, *Strychnos decussata* and *Ozoroa paniculosa*. Shorter trees and shrubs include *Xeromphis rudis*, *Brachylaena elliptica* and *Sapium integerrimum*. On the mesic, south-east-facing slopes *Dombeya rotundifolia*, *Hippobromus pauciflorus*, *Maytenus heterophylla*, *Heteropyxis natalensis*, *Dombeya tiliacea*, *Protorhus longifolia* and *Erythrina lysistemon* are found in addition to the trees mentioned previously.

On parts of the south-east-facing slopes occur almost pure stands of *Heteropyxis natalensis*, a short tree 2 m high, together with a few *Acacia caffra* trees. This woodland may have resulted from the invasion of old fields on the south-east-facing slopes by *H. natalensis* and *A. caffra*.

(*d*) Euphorbia tirucalli *Succulent Scrub*

A small, dense stand of *Euphorbia tirucalli* on the peninsula which juts out from Ntshongweni into the dam now grows on the site of what was at one time a Bantu Kraal. The site of the abandoned kraal can be seen in the aerial photograph taken in 1937 (Plate 2: 1) and is still visible, as a ring of dark vegetation, in the 1959 photograph (Plate 2: 2). In this area, *Euphorbia tirucalli* trees are usually single-stemmed, about 6 m high, and average 1 m between boles. *Acacia nilotica* is found occasionally beneath the canopy as a straggly tree 3–4 m high and *Dalbergia armata* occurs as a woody climber. A few scattered herbs of Acanthaceae, including *Hypoestes aristata* and *Phaulopsis imbricata*, occur where the shade is not too dense. In view of the spread of *E. tirucalli* on the north-facing slopes of Ntshongweni and its dominance on the old Kraal site, the absence of *E. tirucalli* from the *Acacia* spp. Woodland is remarkable. *E. tirucalli* was probably planted at the Kraal as a hedge, a practice of the Bantu in the area to this day.

(*e*) Spirostachys africana *Woodland*

On the hot, dry, north-west-facing slopes of Ntshongweni *Spirostachys africana* Woodland occurs. These slopes are made up from a number of small gulleys separated by ridges. The ridges have drier soils as a result of higher runoff and better drainage than the gulleys, where both surface and subterranean water concentrates.

Spirostachys africana, with a thick, black, rough bark, and a diameter at breast height of up to 30 cm, is the dominant tree. Associated trees on the ridges are *Euphorbia ingens*, *E. tirucalli*, *Hippobromus pauciflorus*, *Combretum molle*, *Grewia occidentalis* and *Ptaeroxylon obliquum*. Commonly occurring small trees and shrubs, which form a discontinuous, short tree and shrub layer up to 3 m high, include *Brachylaena elliptica*, *Ehretia rigida* and *Tricalysia lanceolata*. Where the canopy is broken, *Aloe candelabrum* occurs. Components of the dense ground flora include *Achyranthes aspera*, *Sansevieria thyrsiflora*, *Hypoestes aristata*, *Hibiscus pedunculatus* and *Panicum deustum*.

The canopy is denser, there are fewer deciduous components, and the shade cast is much deeper in the gulleys than on the ridges. *Spirostachys africana* and *Acalypha sonderiana* are co-dominant in gulleys and other common components include *Combretum molle*, *Commiphora harveyi*, *Euclea natalensis* and *Euphorbia tirucalli*. The shade in summer would appear too dense for the development of a dense ground flora as the ground is usually almost bare.

(*f*) Hippobromus-Acalypha *Woodland*

This occurs on the south-facing slopes of Ntshongweni where insolation is lower and, as a result, temperatures and evaporation rates are lower than elsewhere in the study area. Soils are derived from granite with varying degrees of admixture from the sandstone above. Under the sandstone cliffs, slopes are steep and soils shallow, but at lower altitudes soils become deeper and slopes more gentle. The south-facing slopes, like the north-west-facing slopes, are made up of edaphically drier ridges with greater runoff and subsurface drainage than the intervening gulleys.

Canopy trees found on the ridges include *Hippobromus pauciflorus*, *Ziziphus mucronata*, *Heteropyxis natalensis*, *Dombeya rotundifolia*, *Rhus chirindensis*, *Euphorbia ingens*, *Grewia occidentalis*, *Combretum molle*, *Protorhus longifolia* and *Xylotheca natalensis*. A discontinuous layer of dark-green leaved shrubs, up to 2 m tall, includes *Euclea natalensis*, *Azima tetracantha* and *Maytenus undata* below the canopy. A 60 cm high, lush, ground flora of grasses and dicotyledonous herbs, includes *Panicum deustum* and *Sansevieria thyrsiflora*.

In the gulleys dense shade is cast by the thick, closed canopy of dark green leaves. Common trees include *Acalypha sonderiana*, *Dombeya tiliacea*, *Grewia occidentalis*, *Baphia racemosa* and *Euclea natalensis*. A large number of other species contribute occasionally to the canopy stratum. *Tricalysia lanceolata* and *Dovyalis rhamnoides* are common shrubs, while *Popowia caffra* occurs frequently as both a shrub and a climber. Common components of the herb layer are *Achyranthes aspera*, *Argyrolobium tomentosum*, *Crocosmia aurea*, *Cyathula cylindrica*, *Hypoestes aristata*, *Oplismenus hirtellus*, *Panicum deustum*, *Phaulopsis imbricata*, *Plectranthus purpuratus*, *Priva cordifolia* and *Sansevieria thyrsiflora*.

On the boundary between gulley and ridge, a dense, impenetrable tangle of woody lianes often develops. The lianes, including *Dalbergia obovata*, *D. armata*, *Scutia myrtina*, *Acacia ataxacantha* and *Capparis tomentosa* with stems up to 7 cm in diameter, form a dense tangled growth from ground level to a height of about 4 m. Emergent trees 4·5–6 m high, including *Grewia occidentalis*, *Clerodendrum glabrum* and *Dombeya rotundifolia*, occur occasionally. *Erythroxylum emarginatum* and *Popowia caffra* are evergreen shrubs or scramblers up to 2 m high that occur in the tangle. The ground flora is poor.

Quantitative analysis of valley vegetation

Methods

1. *Sampling*

The valley vegetation on the sides of Ntshongweni and on the peninsula which juts into Shongweni Dam were sampled for the quantitative study. Density values for trees over 1 m high were recorded from 60 square sample areas, which are termed stands, of side 30·5 m ($\frac{1}{4}$ acre). Stands were located by restricted randomisation, with the advantage of sampling the area efficiently and allowing statistically-valid comparisons of the samples to be made. Aspect, angle of slope, rock type and soil depth were the site factors recorded for each stand.

Species-area curves were plotted (Fig. 3) to determine a satisfactory sample size. The smallest size used was 2·3 sq m (25 sq ft) and increasing sizes were obtained by doubling the area to a maximum of 595·4 sq m (6,400 sq ft). The method is unsatisfactory according to Greig-Smith (1964) as the different sizes are not independent and, therefore, the number of species may be exaggerated. A more satisfactory method is the use of separate, randomly placed samples of each size (Greig-Smith, 1964). The latter method was not used at Ntshongweni, however, because the scale of pattern is such that samples located at random would almost certainly land in more than one community and thus overestimate the number of species per community. Although a marked change in the rate of increase of species number with increasing sample size occurs at the 74·4 sq m (800 sq ft) size the number of species continues to increase appreciably to the maximum sample area. It was thus decided to use samples larger than 595·4 sq m. The minimal area would not be reached before the sample was either too large for a density count to be made in a reasonable time, or more than one community would be included in the sample as a result of the pattern of gulleys and ridges. The 595·4 sq m sample size was eventually chosen, therefore, as being the largest stand consistent with the scale of pattern of the vegetation and that could be analysed within a reasonable amount of time.

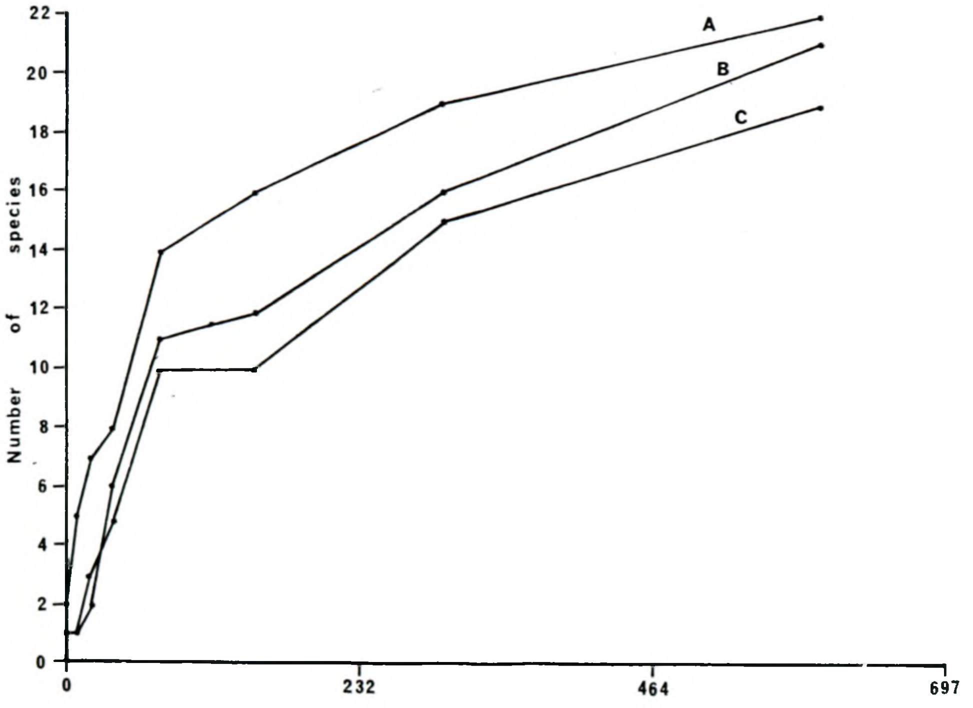


FIG. 3.—Species-area curves for three localities.

The square stands were divided into four strips [30·5 m by 7·6 m (100 ft by 25 ft)] and each strip into four squares of side 7·6 m (25 ft) for ease of sampling, so that local frequency data were available from the 16 sub-samples comprising each stand, and so that samples with areas from 7·6 m^2 to 30·5 m^2 were available for analysis.

2. *Ordination*

The ordination was based on that developed by Bray & Curtis (1957) and described in detail by Beals (1960). Initially, coefficients of similarity (C) between every possible pair of stands were calculated. Expressed as a percentage for two stands, M and N, the coefficient is given by:

$$C(\textsc{mn}) = \frac{2w}{a+b} \times 100$$

where a is the sum of the density values of all species in stand M, b is the sum of the values in stand N, and w is the sum of the lower values recorded for species common to stands M and N. The coefficient may have a value of 100 if the stands are identical in species composition and density, a value of zero if the stands have no species in common or an intermediate value dependent upon the degree of similarity of the stands.

The number of similarity coefficients in the matrix of 60 stands sampled at Shongweni Dam was 1770. Two hundred and eighty of these coefficients had values under 10 per cent, 756 under 20 per cent, and 1153 under 30 per cent. Applying Beals's criteria of end stand selection to these very low similarity coefficients resulted in tight clustering of stands in the centres of the first and second axes. Inspection of the coefficients of similarity between pairs of stands situated in the tight clusters showed that many were very dissimilar from each other and should not have been placed as close together as they were. The level of distortion was thus high and the axes inefficiently utilized.

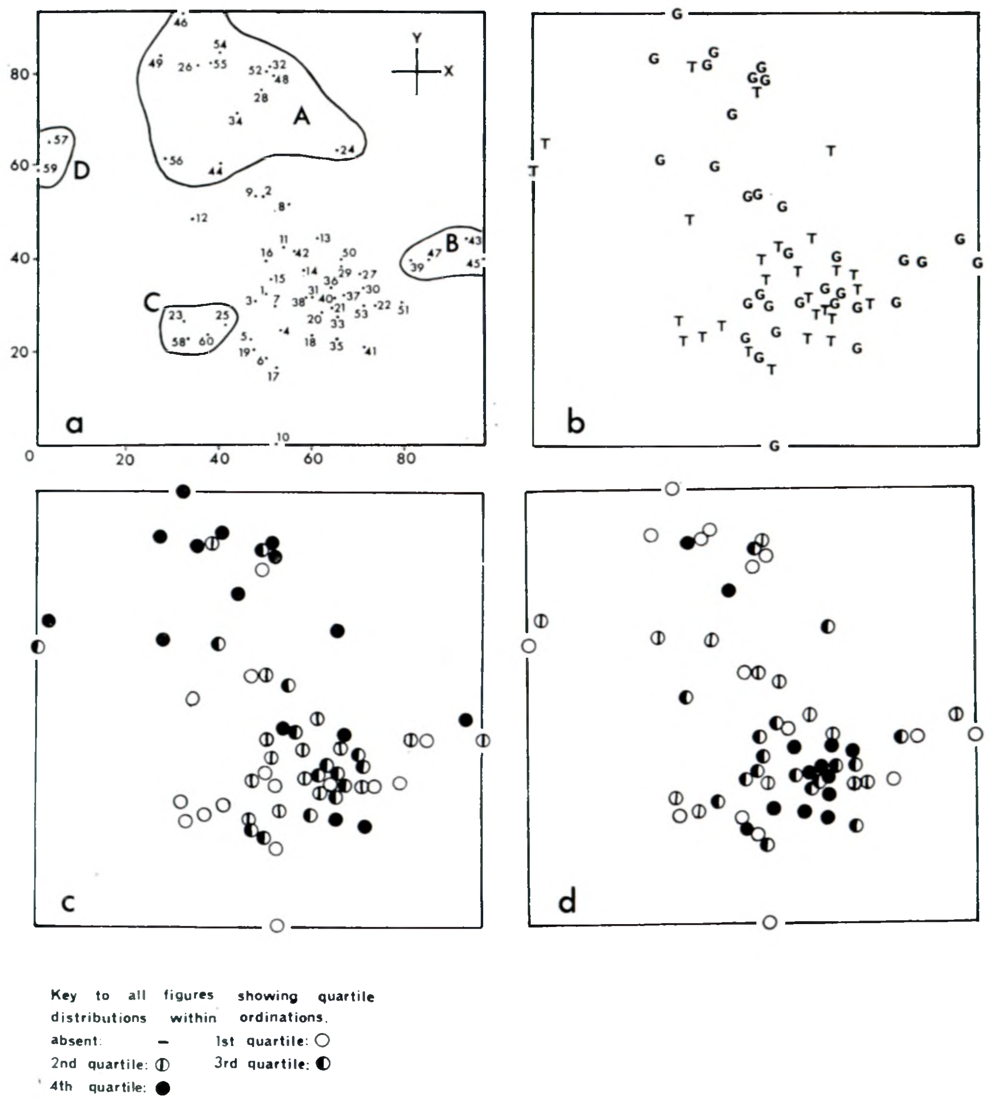


FIG. 4.—a, Primary ordination where numbers enclosed by solid lines refer to stands mapped in Fig. 5 Axes are in percentage dissimilarity. A = **Acalypha sonderiana** Nodum; B = **Aloe candelabrum** Nodum; C = **Euphorbia ingens** Nodum: and D = **Euphorbia tirucalli** Nodum: b, distribution of Table Mountain Sandstone (T) and Basement Complex Granite (G) within the ordination; c, quartile distributions of total density per stand within the ordination; d, quartile distributions of number of species per stand within the ordination.

The problem was not overcome by using three dimensions. These considerations lead to the modification of Beals's criteria for end stand selection as described below (see also Morris, 1967).

The sum of the similarities of each stand with every other one was found and the standard deviation of each mean similarity calculated. Stands with low sums of similarity but high standard deviations were chosen for end stands. Choosing stands with low sums of similarity ensured that the axis was relatively long while a high standard deviation meant that the stands were spread along the axis and not clustered in one section of the axis.

Results

1. *Primary ordination*

(*a*) *Assessment for noda*

Four groups of stands with similar floristic composition, termed noda, and named after the species with the highest mean density in the stands making up the group, are delimited within the primary ordination, shown in Fig. 4a and mapped in Fig. 5. The stands clustered in the centre of the ordination, between the delimited noda, are later shown to be heterogeneous and to form more than one nodum. A clear discontinuity exists between the stands of the *Euphorbia tirucalli* Nodum and all other stands (Fig. 4a). The other three noda grade into the central cluster and their delimitation was done after considering the positions of the stands, in the field and within the ordination, and of species distributions within the ordination. Other, equally justifiable delimitations are possible. The justification for the delimitation of the *Euphorbia ingens* Nodum, which appears inseparable from the stands of the central cluster, is given later. It is described in this section because of its close proximity in the field to the *Euphorbia tirucalli* Nodum. Noda are delimited to aid discussion and do not indicate that the Individualistic Hypothesis does not hold.

(*b*) *Relationships of noda to site factors*

Stands of the *Acalypha sonderiana* Nodum are located on the upper slopes of Ntshongweni facing north-west, north and east (Fig. 5). On the north-west-facing slope the Nodum extends down from the cliff surrounding Ntshongweni, and on the east-facing slope a tongue, terminated by stands 24 and 26, extends down from the cliff towards the Sterkspruit River. Investigations in the field and of the aerial photographs showed that these tongues follow gulley courses. From Fig. 4b, most stands of the community are seen to occur on Basement Granite. Most stands are located under the Table Mountain Sandstone cliffs on very steep slopes with shallow soils.

The four stands making up the *Aloe candelabrum* Nodum are found along the Sterkspruit River on the lower north-facing slopes of the hill. The shallow soils are derived from Granite (Fig. 4b). The convex ground form, in contrast to the concave form where stands of the *Acalypha sonderiana* Nodum are found at this altitude, suggests less favourable soil moisture conditions in the *Aloe candelabrum* Nodum.

The *Euphorbia ingens* Nodum is located on the peninsula which extends into Shongweni Dam, east of Ntshongweni, where the deep sandy soils are derived from Table Mountain Sandstone (Fig. 4b). The central portion of the peninsula, on which all four stands are located, is level.

Two stands, constituting the *Euphorbia tirucalli* Nodum, were found on the site of the old Bantu Kraal. Being so far removed within the ordination from all others, these stands have floristic compositions which are very different from all the other stands. Overall site conditions appear no different from stands of the surrounding area occupied by the *Euphorbia ingens* Nodum.

(*c*) *Species behaviour*

Instead of actual density values, quartile values are plotted within the ordination as species behaviour is then easier to comprehend. The total number of non-zero density values, arranged in order of magnitude, is divided into four groups (quartiles) containing, as near as possible, equal numbers of stands.

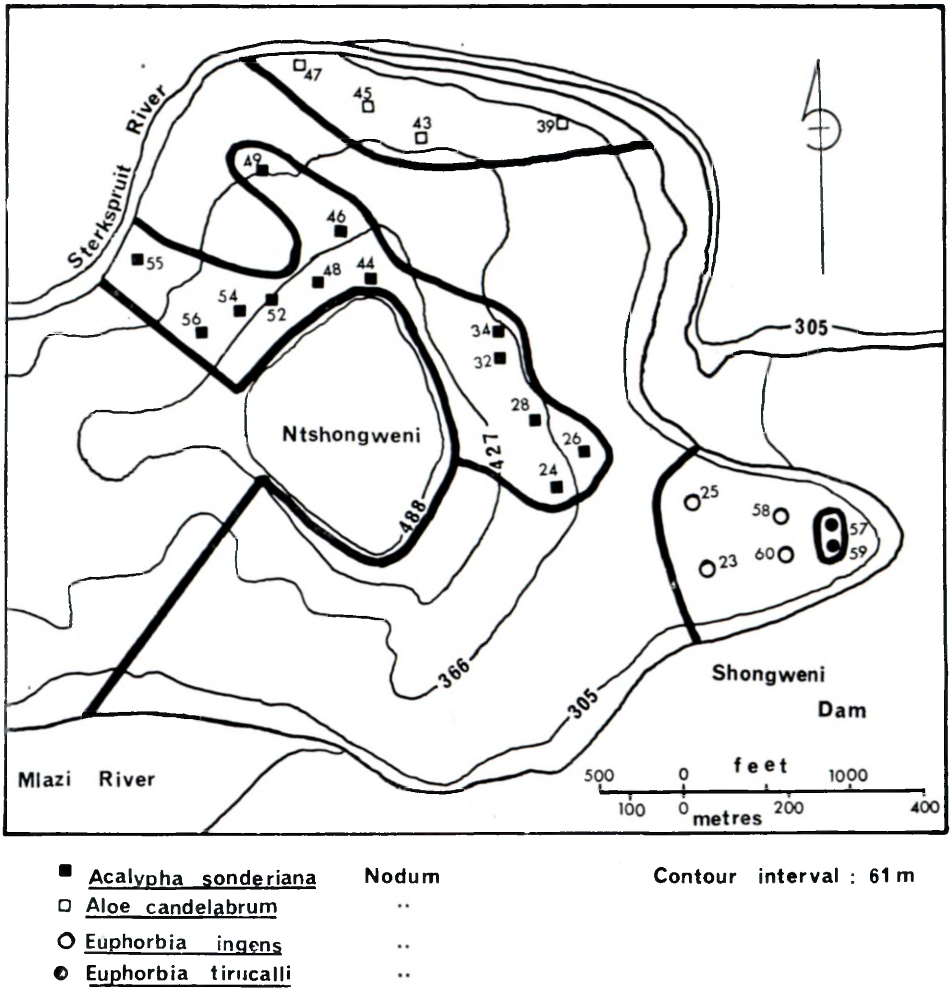


FIG. 5.—Map of Ntshongweni showing noda delimited in the primary ordination For clarity, stands delimited in the secondary ordination are omitted.

With few exceptions, high total densities (Fig. 4c) are found in the *Acalypha sonderiana* Nodum and in the *Euphorbia tirucalli* Nodum, whereas low total densities are found in the *Aloe candelabrum* Nodum and in the *Euphorbia ingens* Nodum. Stands of the central cluster have both high and low total densities. All four noda are notable for the low number of species per stand (Fig. 4d), while most stands of the central cluster have many species per stand. Stands of the *Acalypha sonderiana* and *Euphorbia tirucalli* Noda thus have high densities of a few species while the stands of the *Aloe candelabrum* and *Euphorbia ingens* Noda have low densities of few species.

Only selected species are plotted within the primary and secondary ordinations. Some unplotted species appear scattered at random within the ordinations while some show, less clearly, the patterns shown by species which are plotted.

Stands containing high densities of *Acalypha sonderiana* (Fig. 6a) are almost entirely restricted to the *Acalypha sonderiana* Nodum, while *E. tirucalli* (Fig. 6b) occurs in stands of the *Euphorbia tirucalli* and *Acalypha sonderiana* Noda but not in the *Euphorbia ingens* Nodum, which occupies the rest of the peninsula. Mean densities, mean local frequencies and constancy for species occurring in stands of the *Acalypha sonderiana* Nodum are given in Table 2. Mean density is per stand of 930·25 sq m (¼ acre) and local frequency is derived from the 16 sub-samples of which each stand consists. An idea of the variability about the mean values may be obtained from the standard deviations of each mean, given also in Table 2. Constancy is the frequency of occurrence of the species in the stands of the nodum, expressed as a percentage of the total number of stands in the nodum. The floristic composition of an " average " stand within the area occupied by the nodum is given by the table. The high densities of *A. sonderiana* and *E. tirucalli* in the *Acalypha sonderiana* Nodum suggest that site conditions are very suitable for their growth.

TABLE 2.—Mean density and mean local frequency, with standard deviations (s.d.), and constancy for species occurring in more than two of the 13 stands of the *Acalypha sonderiana* Nodum with a mean density greater than unity

Species	Density		Frequency		Constancy
	mean	s.d.	mean	s.d.	
*Acalypha sonderiana	151·6	87·2	12·8	5·3	92·3
*Euphorbia tirucalli	75·4	60·8	11·8	5·0	100·0
Spirostachys africana	25·4	18·4	10·3	6·0	84·6
Hippobromus pauciflorus	15·5	25·3	3·8	4·3	84·6
*Combretum molle	15·3	15·7	7·5	5·6	92·3
Grewia occidentalis	9·1	9·4	5·2	3·6	92·3
Canthium mundianum	8·5	20·6	2·5	3·6	69·2
Dombeya tiliacea	8·5	7·2	5·1	4·2	84·6
*Brachylaena elliptica	7·9	7·7	5·0	3·5	92·3
Ehretia rigida	5·9	4·9	4·5	3·4	84·6
Urera tenax	5·3	12·9	2·4	6·4	46·2
Euclea natalensis	4·7	4·2	3·8	3·4	84·6
Xeromphis rudis	4·0	4·6	2·9	3·2	69·2
Commiphora harveyi	3·8	2·2	2·8	2·0	100·0
Euphorbia ingens	2·7	2·7	2·2	2·3	76·9
Schrebera alata	1·9	3·9	1·5	3·1	46·2
Putterlickia verrucosa	1·8	3·1	1·5	2·6	38·5
*Aloe candelabrum	1·7	2·9	0·9	1·5	46·2
Ochna arborea	1·7	2·1	1·5	1·5	84·6
Cussonia spicata	1·4	1·5	1·2	1·2	61·5
Acacia robusta	1·2	1·5	1·0	1·4	61·5
Erythroxylum emarginatum	1·1	2·3	0·9	1·8	38·5
Total of 30 other species	14·7				
Total mean density	369·0				

* Plotted within the primary ordination

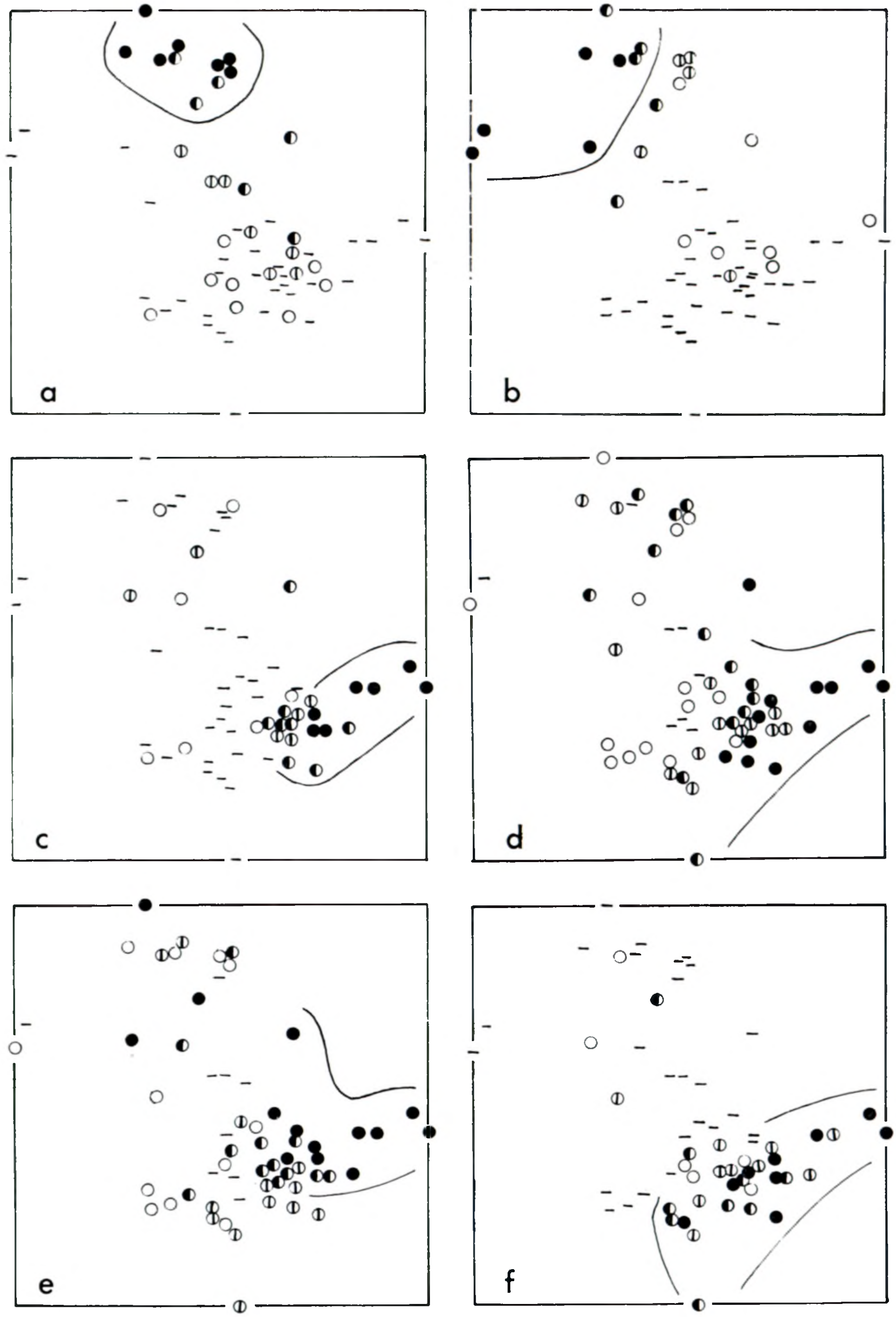


FIG. 6.—Quartile distributions of a, **Acalypha sonderiana**; b, **Euphorbia tirucalli**; c, **Aloe candelabrum**; d, **Brachylaena elliptica**; e, **Combretum molle**; f, **Dombeya rotundifolia** densities within the primary ordination. See Fig. 4 for key to symbols.

Stands on the upper slopes of Ntshongweni are shown by the ordination to be similar to stands in gulleys near the valley bottom. The floristic similarity between these altitudinally-distinct localities can possibly be explained by the compensatory effect of soil moisture and " atmospheric " moisture regimes. Run-off is rapid and drainage good on the steep upper slopes while gentler slopes and thus better moisture retaining capacities are found at lower altitudes. This gradient from dry to moist is compensated for by an atmospheric moisture gradient from moist to dry. The air is often moister and precipitation possibly higher on the upper slopes, through the presence of fog, than at the base of the hill.

Species which have distributions centred on stands of the *Aloe candelabrum* Nodum include *Aloe candelabrum*, *Brachylaena elliptica*, *Combretum molle* and *Dombeya rotundifolia* (Fig. 6c–f). No species is restricted entirely to the four stands making up this community but all extend into the central cluster and two extend into the *Acalypha sonderiana* Nodum as well. Reference to Table 3 shows that in addition to the four species mentioned above, *Spirostachys africana* has a high mean density value in these stands. The stands of the *Aloe candelabrum* Nodum were located in *Aloe-Dombeya* Woodland, described in the general account of the vegetation. Distributions within the ordination of species commonly occurring in the Nodum suggest that its boundaries are not as clearly defined as was indicated in the descriptive account.

TABLE 3.—Mean density and mean local frequency, with standard deviations (s.d.), and constancy for species occurring in more than one of the four stands of the *Aloe candelabrum* Nodum with a mean density greater than unity

Species	Density		Frequency		Constancy
	mean	s.d.	mean	s.d.	
*Aloe candelabrum	74·5	54·7	13·3	3·4	100·0
*Brachylaena elliptica	56·3	20·7	15·0	0·8	100·0
*Combretum molle	44·0	14·6	15·5	0·6	100·0
Spirostachys africana	25·5	15·3	9·3	2·4	100·0
*Dombeya rotundifolia	13·8	8·8	8·5	4·8	100·0
Hippobromus pauciflorus	9·5	10·5	3·8	2·4	100·0
Xeromphis rudis	5·5	5·3	3·8	3·2	100·0
Dichrostachys cinerea	4·8	4·8	3·8	3·4	100·0
Euphorbia ingens	4·8	2·9	4·0	2·6	100·0
Acacia caffra	4·3	2·9	3·8	2·1	100·0
Grewia occidentalis	4·0	4·7	3·3	3·2	100·0
Commiphora harveyi	3·8	3·5	3·5	3·0	100·0
Ehretia rigida	3·8	5·6	2·8	3·6	75·0
Dombeya tiliacea	3·5	4·7	1·3	1·5	50·0
Rhus pentheri	3·0	1·8	3·0	1·8	100·0
Cussonia spicata	2·7	0·9	2·8	0·9	100·0
Maytenus heterophylla	1·8	2·1	1·5	1·7	50·0
Acacia nilotica	1·3	1·5	1·0	1·2	50·0
Total of 17 other species	8·0				
Total mean density	274·5				

* Plotted within the primary ordination

Species with highest mean densities in the *Euphorbia ingens* Nodum (Table 4) are *Euphorbia ingens*, *Dichrostachys cinerea* and *Acacia nilotica.* The area covered by this Nodum was subjected to intense disturbance in the relatively recent past, a possible reason for the low total density and lack of species with high densities. *Acacia nilotica* and *Dichrostachys cinerea* are known to be secondary species and some other species occurring in this Nodum may also be secondary.

TABLE 4.—Mean density and mean local frequency, with standard deviations (s.d.), and constancy for species occurring in more than one of the four stands of the *Euphorbia ingens* Nodum with a mean density greater than unity

Species	Density		Frequency		Constancy
	mean	s.d.	mean	s.d.	
Euphorbia ingens	24·3	8·9	10·0	2·8	100·0
Dichrostachys cinerea	22·5	9·4	10·3	3·3	100·0
Acacia nilotica	11·8	8·9	5·8	4·6	100·0
Canthium ciliatum	9·8	9·4	5·8	4·9	100·0
Grewia occidentalis	8·3	5·1	4·8	2·1	100·0
Xeromphis rudis	7·0	6·1	4·8	1·7	100·0
Acacia robusta	6·5	8·5	3·8	3·9	75·0
Clerodendrum glabrum	6·3	1·3	4·8	1·3	100·0
Rhus pentheri	4·5	2·4	3·8	2·1	100·0
Acacia gerrardii	3·8	4·1	2·5	2·4	75·0
Sclerocarya caffra	3·5	2·4	2·5	0·6	100·0
*Combretum molle	3·3	4·5	2·5	3·0	100·0
Canthium ventosum	3·0	2·2	2·5	1·3	100·0
Euclea natalensis	2·8	3·1	2·0	2·2	75·0
Maytenus heterophylla	2·5	3·9	1·5	2·4	50·0
Ehretia rigida	1·8	2·1	1·8	2·1	50·0
*Brachylaena elliptica	1·5	0·6	1·3	0·5	100·0
Canthium mundianum	1·5	1·7	1·3	1·3	75·0
Commiphora harveyi	1·5	1·7	1·8	1·5	75·0
Total of 20 other species	10·2				
Total mean density	136·0				

* Plotted within the primary ordination

The most common species in the two stands of the *Euphorbia tirucalli* Nodum is *E. tirucalli* (Table 5). Its distribution, shown within the ordination in Fig. 6b, is limited to the stands of this Nodum and the *Acalypha sonderiana* Nodum. Species occurring in both stands but not mentioned in the general account of the vegetation are *Dichrostachys cinerea, Acacia robusta, Euphorbia ingens, Canthium ciliatum, Clerodendrum glabrum* and *Protorhus longifolia.* With the exception of *P. longifolia*, which has a low density anyway, these species are also components of the *Euphorbia ingens* Nodum, which surrounds the small *Euphorbia tircucalli* Nodum, so that the stands apparently bridge the ecotone between the two noda. The marked difference between the two noda is, however, still apparent by comparing Tables 4 and 5.

TABLE 5.—Mean density and mean local frequency, with standard deviations (s.d.), and constancy for species occurring in at least one of the two stands of the *Euphorbia tirucalli* Nodum with a mean density greater than unity

Species	Density		Frequency		Constancy
	mean	s.d.	mean	s.d.	
*Euphorbia tirucalli	285·0	65·1	16·0	0·0	100·0
Dichrostachys cinerea	14·5	16·3	6·0	4·2	100·0
Acacia robusta	10·5	2·1	7·5	2·1	100·0
Euphorbia ingens	6·5	7·8	3·0	2·8	100·0
Acacia nilotica	5·5	7·8	2·5	3·5	50·0
Canthium ciliatum	3·5	0·7	2·0	0·0	100·0
Clerodendrum glabrum	2·5	2·1	1·5	0·7	100·0
Acacia gerrardii	2·0	2·8	1·5	2·1	50·0
Azima tetracantha	2·0	2·8	1·5	2·1	50·0
Albizia adianthifolia	2·0	1·4	2·0	2·1	100·0
Trema orientalis	2·0	0·0	2·0	0·0	100·0
Dombeya tiliacea	1·5	2·1	1·0	1·4	50·0
Euclea natalensis	1·5	2·1	1·5	2·1	50·0
Grewia occidentalis	1·5	2·1	1·5	2·1	50·0
Protorhus longifolia	1·5	0·7	1·5	0·7	100·0
Ziziphus mucronata	1·5	2·1	1·5	2·1	50·0
Total of 12 other species	4·5				
Total mean density	348·0				

* Plotted within the primary ordination

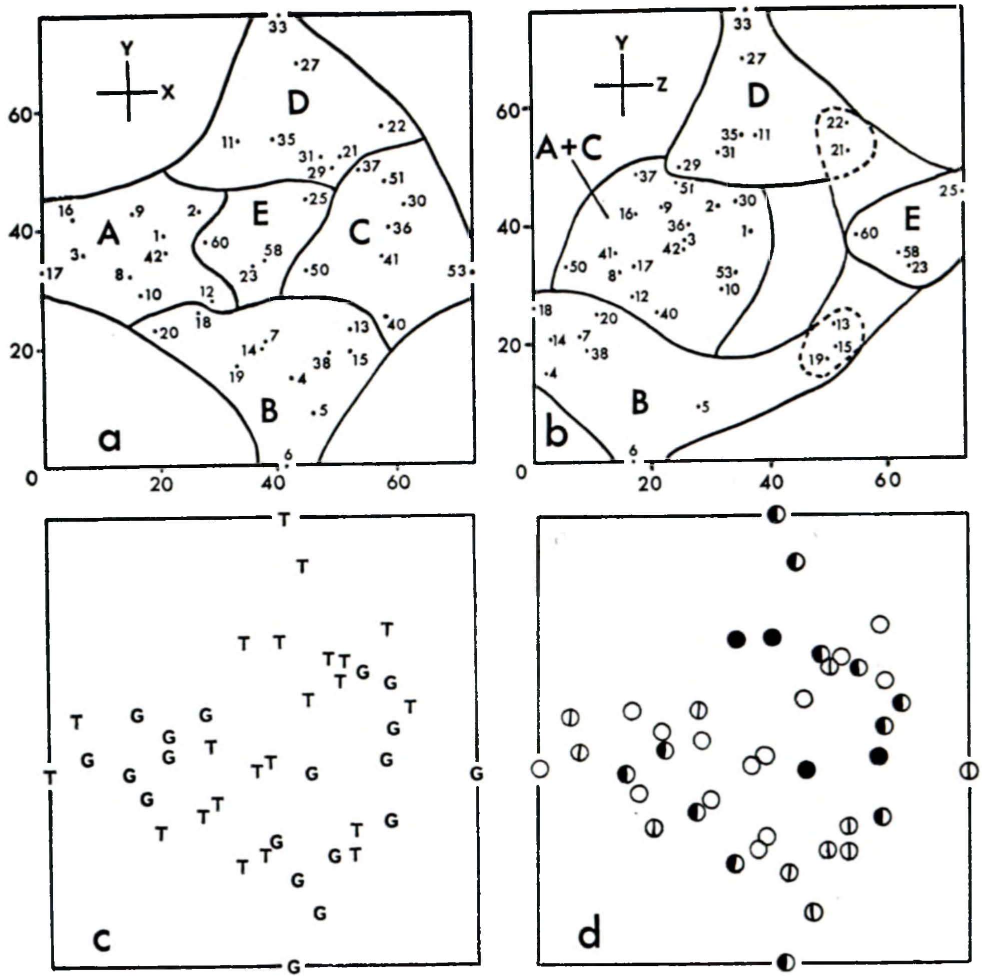
2. *Secondary ordination*

(*a*) *Assessment for noda*

A secondary ordination (Fig. 7a and b) with three axes, X, Y and *Z*, accounted for the variability between the stands constituting the central cluster of the primary ordination (Fig. 3a). Because three axes were required for the secondary ordination, it is not surprising that a meaningful arrangement of stands of the central cluster could not be obtained on the two-dimensional, primary ordination.

Five groups of stands, referred to as noda and named after the species with highest mean densities in the stands of the nodum, are delimited within the secondary ordination. The delimitation was made after inspection of stand position in the field (Fig. 8) and within the ordination, and after inspection of species distributions within the ordination in the same way as for the primary ordination.

As intermediate stands exist between neighbouring noda there are very few real discontinuities within the ordination and other, equally justifiable, delimitations are possible. The secondary ordination also supports the Individualistic Hypothesis of Gleason (1926).



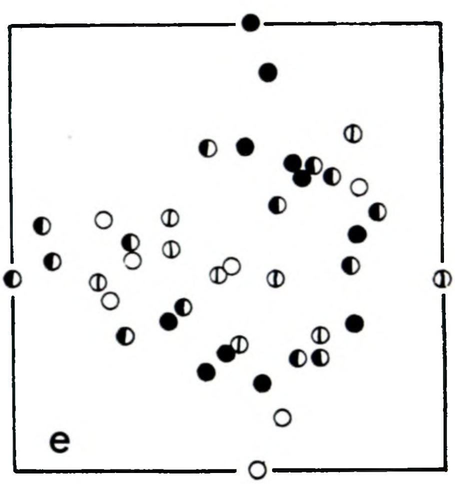


FIG. 7.—a, X–Y axes of the secondary ordination; b, Y–Z axes of the secondary ordination. Numbers refer to stands mapped in Fig. 8 and axes are in percentage dissimilarity. A = **Dombeya tiliacea** Nodum; B = **Hippobromus-Heteropyxis** Nodum; C = **Hippobromus-Spirostachys** Nodum; D = **Spirostachys africana** Nodum; and E = **Euphorbia ingens** Nodum (mapped in Fig. 5); c, distribution of Table Mountain Sandstone (T) and Basement Complex Granite (G) within the X–Y ordination; d, quartile distributions of total density per stand within the X–Y ordination; e, quartile distributions of number of species per stand within the X–Y ordination. See Fig. 4 for key to symbols.

The *Euphorbia ingens* Nodum is discussed under the primary ordination section. Within the X–Y ordination (Fig. 7a), it is centrally placed and would appear closely related to the four surrounding noda. On the Y–*Z* ordination (Fig. 7b), however, it is shown to be clearly separated from the other noda so that its separation on the primary ordination is justified. The *Euphorbia ingens* Nodum is most closely related to stands 21 and 22 of the *Spirostachys africana* Nodum and stands 13, 15 and 19 of the *Hippobromus-Heteropyxis* Nodum, according to Fig. 7b. The above-mentioned stands lie west and south-west of the peninsula which is covered by the *Euphorbia ingens* Nodum. Inspection in the field showed that, in addition to being close to the peninsula geographically, these five stands were similar, physiognomically and floristically, to the *Euphorbia ingens* Nodum. Being further from the Bantu Kraal site and, therefore, further from a centre of past disturbance, possibly accounts for stands 13, 15, 19, 21 and 22 being, in some ways, intermediate in floristic composition between the *Euphorbia ingens* Nodum and the *Hippobromus-Heteropyxis* and *Spirostachys africana* Noda.

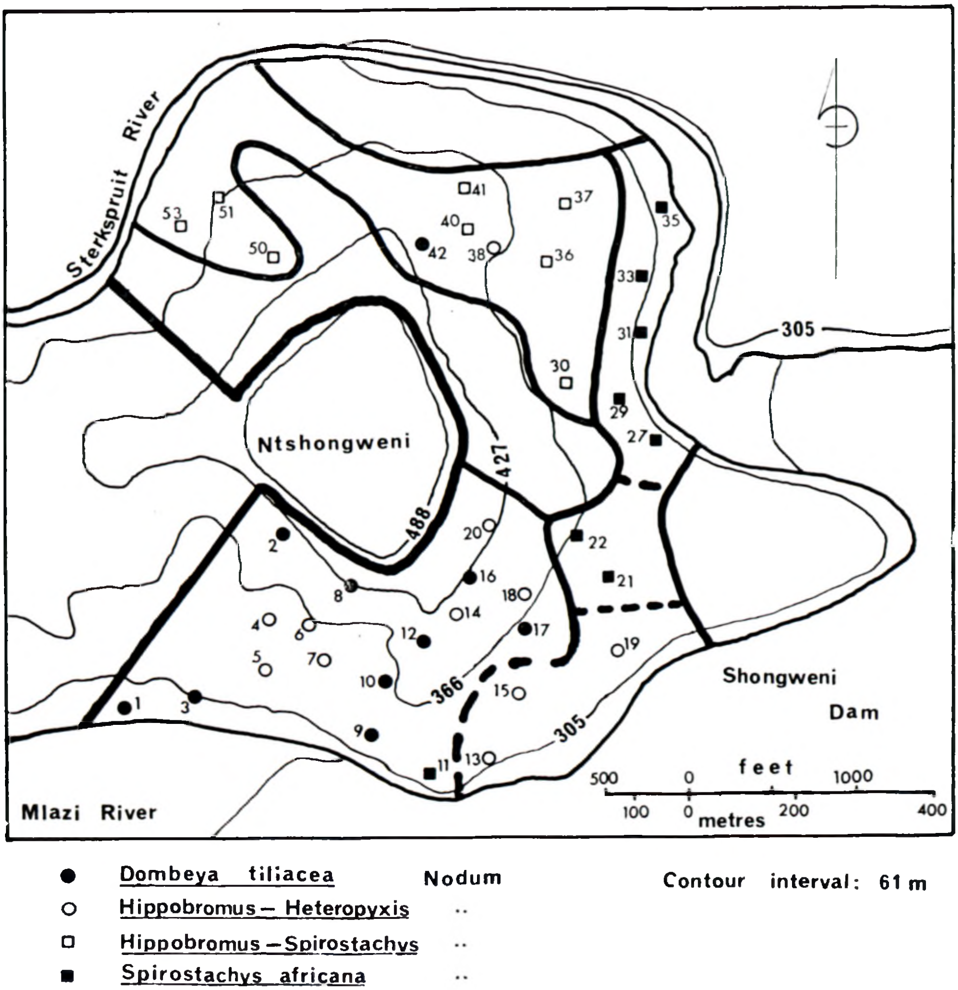


FIG. 8.—Map of Ntshongweni showing noda delimited in the secondary ordination.

The two-dimensional ordinations of Fig. 7a and 7b are two projections of a three-dimensional model of the actual forty-dimensional structure so that some distortion of relative stand positions is to be expected. On the Y–*Z* axes, the *Dombeya tiliacea* Nodum and the *Hippobromus-Spirostachys* Nodum are superimposed. The stands of these two communities are, in fact, not intermingled as they appear to be, but lie one behind the other, as shown by the X–Y axes. In the same way, the stands of the *Euphorbia ingens* Nodum on the X–Y axes should not be thought of as lying in the same plane as the other four noda but as either above or below the plane of the other four noda.

Bearing in mind that the *Euphorbia ingens* Nodum is distinct from the other four noda, only the X–Y axes need be used for further discussion of the secondary ordination. The Y–*Z* axes contain less information than do the X–Y axes, as two of the noda which can be recognized in a three-dimensional model overlap on the Y–*Z* axes. A further reason for using the X and Y axes in preference to the Y and *Z* axes is that the former are almost orthogonal while the latter are non-orthogonal.

(*b*) *Relationships of noda to site factors*

Stands 2, 8, 12 and 16 of the *Dombeya tiliacea* Nodum occur under the Ortho-quartzitic cliffs of Ntshongweni where slopes are very steep and soils are derived from both Table Mountain Sandstone and Granite (Fig. 7c). The other stands of this Nodum occur on Granite at lower altitudes, but a deep alluvium overlies the Granite where stands 1 and 3 occur on the edge of the Mlazi River floodplain. Stand 42 of the Nodum occurs on the north-facing side of Ntshongweni on the minor south aspect which can be seen in the aerial photographs (Plate 2). The south-aspect influence is sufficiently strong to give this stand a floristic composition similar to that of stands on the main south-facing slopes.

Surface and subterranean drainage is good on the steep, upper slopes but at lower altitudes where slopes are more gentle, movement of subterranean water is slower so that soil-moisture conditions are more hydric at lower than at higher altitudes. Conversely, atmospheric moisture conditions are more hydric at the higher altitudes because summer fogs, when present, usually clothe only the crest of Ntshongweni. The compensatory effect of soil and atmospheric moisture regimes discussed above is a possible explanation for the similarity, shown by the ordination, between stands from the upper and lower south-facing slopes. Low insolation is a characteristic of all the south-facing slopes.

The *Hippobromus-Heteropyxis* Nodum also occurs on the south-facing slopes of Ntshongweni. Some stands are located between the upper and lower groups of stands of the *Dombeya tiliacea* Nodum and the others occur south-west of the peninsula. Stand 38 occurs next to stand 42 of the *Dombeya tiliacea* Nodum. Most stands occur on Granite. Field inspection showed that the stands of this community occurred on ridges with good surface and subterranean drainage. Stands of the *Hippobromus-Heteropyxis* Nodum are thus probably more mesic, either edaphically or atmospherically, than stands of the *Acalypha sonderiana* and *Aloe candelabrum* Noda which were delimited within the primary ordination.

All but one of the stands of the *Spirostachys africana* Nodum occur on Table Mountain Sandstone, along the lower reaches of the Sterkspruit River. Stands are near a perennial, subterranean water supply and on gently sloping ground so that the moisture content of the soil is good. As most of the stands are east-facing insolation is of intermediate intensity.

(c) Insolation and soil moisture interaction

Measurements of actual soil-moisture content, atmospheric moisture content and quantity of insolation would have to be made to confirm the interactions suggested in Fig. 9. Being on the south-facing slopes, insolation is relatively low in the *Dombeya tiliacea* and *Hippobromus-Heteropyxis* Noda but soil moisture content is probably higher in stands of the *Dombeya tiliacea* Nodum than in those of the *Hippobromus-Heteropyxis* Nodum. Soil moisture content is probably also high in stands of the *Spirostachys africana* Nodum. Conversely, soil moisture content is low on the steep, north-facing slopes occupied by the *Hippobromus-Spirostachys* Nodum. Relatively high insolation is experienced by stands of the *Hippobromus-Spirostachys* and *Spirostachys africana* Noda as they occur on north-, north-west- and east-facing slopes.

Two gradients from hydric to zeric may be thus recognized (Fig. 9). The *Dombeya tiliacea* Nodum which is considered to be most hydric (low insolation and high soil moisture content) grades into the *Hippobromus-Spirostachys* Nodum which is con-

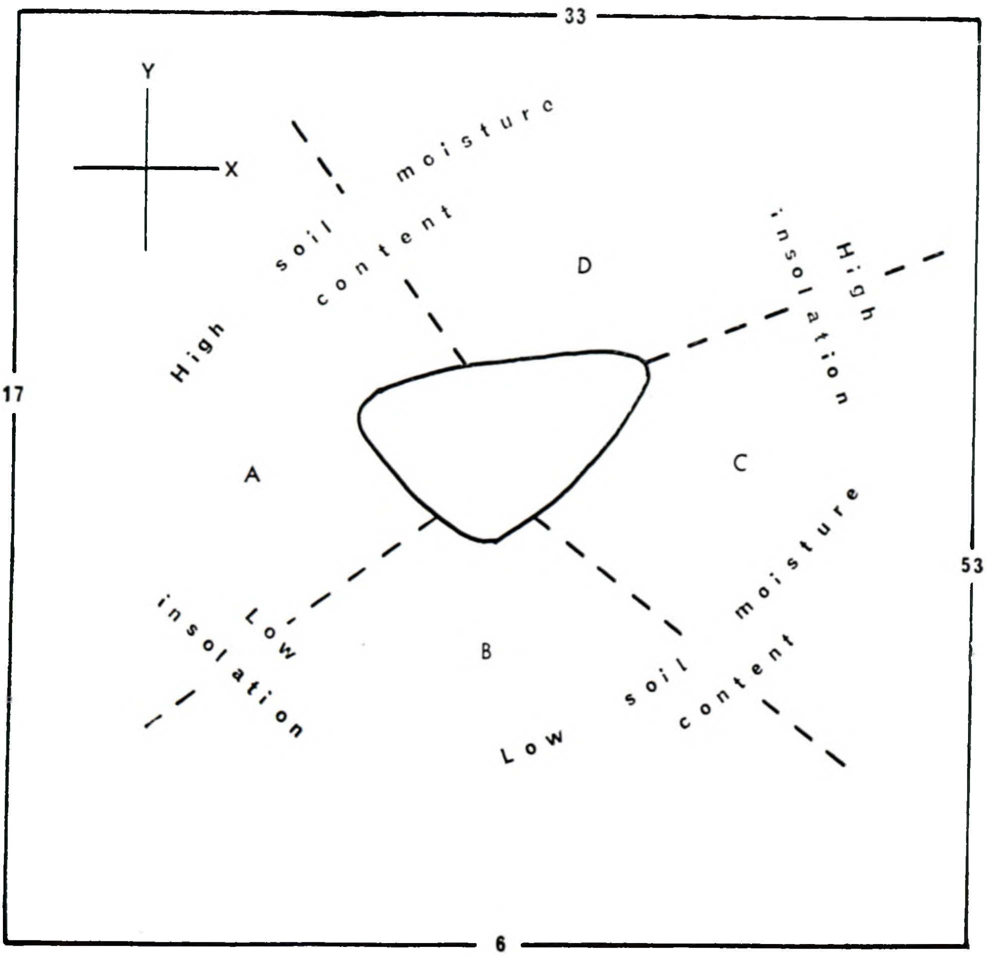


FIG. 9.—Summary of suggested interactions of insolation and soil moisture on the X–Y axes of the secondary ordination. Only positions of end stands are given. A = **Dombeya tiliacea** Nodum; B = **Hippobromus-Heteropyxis** Nodum; C = **Hippobromus-Spirostachys** Nodum; and D = **Spirostachys africana** Nodum.

sidered most xeric (high insolation and low soil moisture content) through the *Hippobromus-Heteropyxis* Nodum (low insolation and low soil moisture content) and the *Spirostachys africana* Nodum (high insolation and high soil-moisture content).

(*d*) *Species behaviour*

Stands of the *Dombeya tiliacea* and *Hippobromus-Heteropyxis* Noda generally have low total densities while high total densities are found in most stands of the *Hippobromus-Spirostachys* and *Spirostachys africana* Noda (Fig. 7d). Stands of all four noda have many species per stand, the lowest number of species per stand being found in stands of the *Dombeya tiliacea* Nodum (Fig. 7e). The *Dombeya tiliacea* Nodum is, therefore, characterized by relatively few species and low total densities. Many species occur in the stands of the other noda, stands of the *Hippobromus-Heteropyxis* Nodum having low total densities and stands of the *Hippobromus-Spirostachys* and *Spirostachys africana* Noda having high total densities. Very few species are restricted in distribution to the stands of any one nodum. As a rule, a species reaches it highest density in the stands of one nodum, but also occurs in the noda on either side.

TABLE 6.—Mean density and mean local frequency, with standard deviations (s.d.), and constancy for species occurring in more than two of the ten stands of the *Dombeya tiliacea* Nodum with a mean density greater than two

Species	Density		Frequency		Constancy
	mean	s.d.	mean	s.d.	
*Dombeya tiliacea	32·5	35·3	9·3	4·9	90·0
Grewia occidentalis	19·5	16·8	9·0	4·7	100·0
*Tricalysia lanceolata	15·7	21·2	4·6	5·5	80·0
Acalypha sonderiana	15·2	24·9	4·8	6·2	60·0
Euphorbia ingens	14·4	31·9	2·5	2·9	80·0
*Ehretia rigida	11·3	15·0	5·3	3·7	90·0
Euclea natalensis	11·1	9·3	6·5	4·5	90·0
*Hippobromus pauciflorus	8·1	10·8	3·9	4·0	80·0
*Brachylaena elliptica	4·9	6·1	2·8	3·0	60·0
*Erythroxylum emarginatum	3·8	3·8	2·8	2·4	70·0
*Azima tetracantha	3·4	3·4	2·8	2·6	70·0
Ptaeroxylon obliquum	3·4	7·8	1·7	3·2	50·0
Rhus chirindensis	3·2	3·5	2·4	2·0	90·0
Canthium mundianum	2·9	4·2	1·1	1·6	50·0
*Dovyalis rhamnoides	2·8	4·1	1·6	2·1	50·0
Xylotheca kraussiana	2·5	4·2	1·7	2·8	40·0
Acacia robusta	2·4	3·5	1·6	1·6	70·0
Maytenus heterophylla	2·4	2·9	1·7	1·8	70·0
Rhus pentheri	2·3	4·3	1·5	2·0	50·0
Ziziphus mucronata	2·3	2·6	2·0	2·2	60·0
*(Protorhus longifolia)	(1·8)	(3·7)	(0·9)	(1·6)	(50·0)
Total of 34 other species	33·8				
Total mean density	197·9				

* Plotted within the secondary ordination

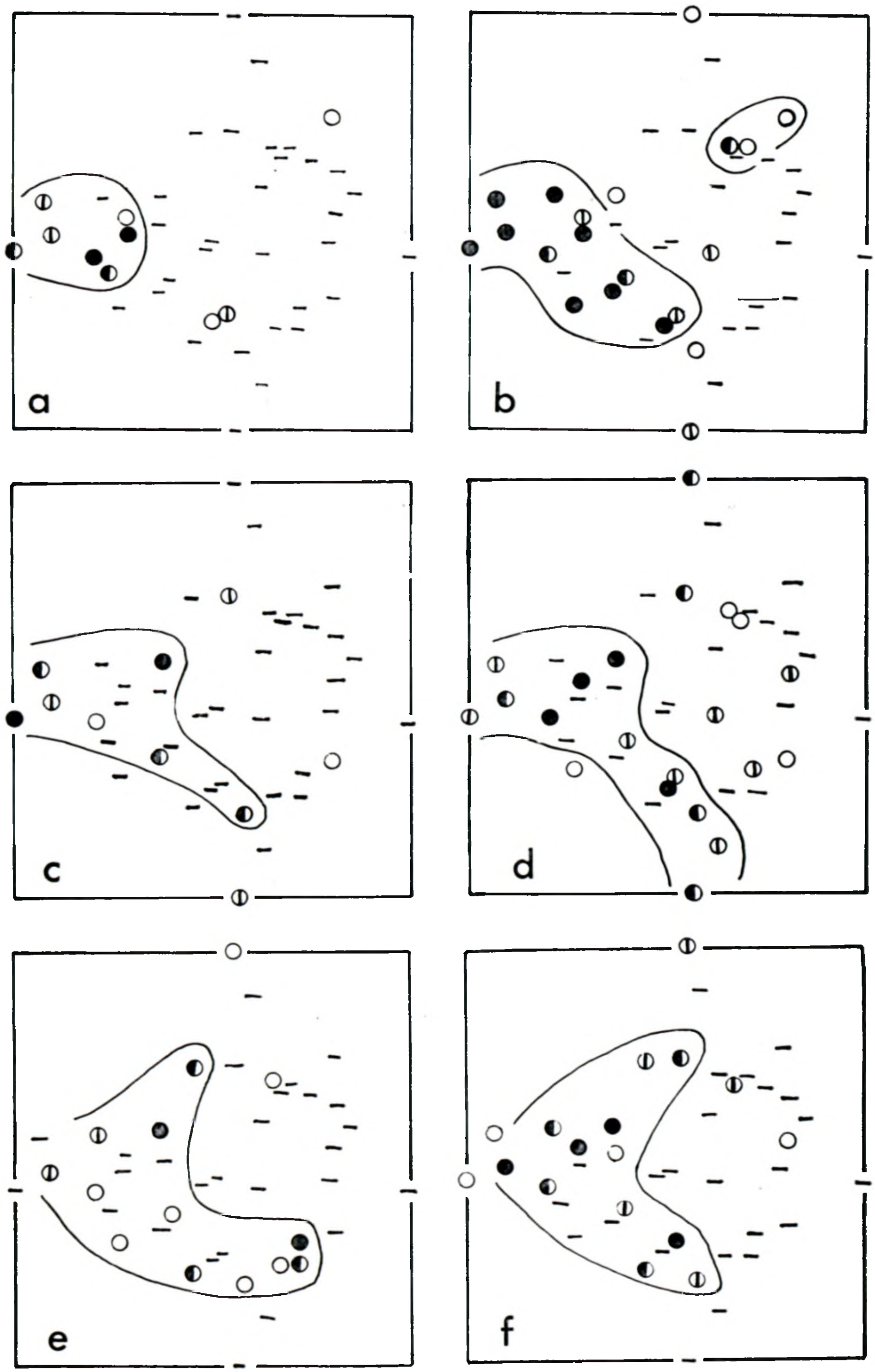


FIG. 10.—Quartile distributions of a, **Azima tetracantha**; b, **Dombeya tiliacea**; c, **Dovyalis rhamnoides**; d, **Erythroxylum emarginatum**; e, **Protorhus lo gifolia**; f, **Tricalysia lanceolata** densities within the X–Y ordination. See Fig. 4 for key to symbols.

Species which have distributions centred on the stands of the *Hippobromus-Heteropyxis* Nodum, for example, *Dombeya rotundifolia, Heteropyxis natalensis* and *Hippobromus pauciflorus* (Fig. 11 a–c) are widespread throughout the area covered by stands of the secondary ordination.

Species which have distributions centred on the stands of the *Dombeya tiliacea* Nodum include *Azima tetracantha, Dombeya tiliacea, Dovyalis rhamnoides, Erythroxylum emarginatum, Protorhus longifolia* and *Tricalysia lanceolata* (Fig. 10). Of these, only *Azima tetracantha* is restricted, almost entirely, to this Nodum. Because the stands of the *Euphorbia ingens* Nodum are in a different plane from those of the other communities, crescent-shaped distribution patterns are shown by many species within this ordination (for example: *Protorhus longifolia* and *Tricalysia lanceolata* in Fig. 10).

TABLE 7.—Mean density and mean local frequency, with standard deviations (s.d.). and constancy for species occurring in more than two of the eleven stands of the *Hippobromus-Heteropyxis* Nodum with a mean density greater than two

Species	Density		Frequency		Constancy
	mean	s.d.	mean	s.d.	
*Hippobromus pauciflorus	60·6	46·6	10·7	5·7	100·8
*Heteropyxis natalensis	38·0	44·0	7·4	6·8	81·8
Grewia occidentalis	26·8	18·5	11·2	5·0	100·0
Combretum molle	9·7	9·8	5·9	4·2	81·9
*Dombeya tiliacea	9·4	13·0	3·9	4·6	54·5
Dichrostachys cinerea	8·9	13·7	3·5	4·7	54·5
*Acacia caffra	8·0	14·7	3·6	5·2	45·5
*Tecomaria capensis	7·3	14·0	2·8	4·6	36·4
*Brachylaena elliptica	6·9	9·2	4·4	3·9	90·9
Acacia nilotica	6·6	8·0	4·1	4·1	81·8
*Dombeya rotundifolia	6·5	6·1	4·5	2·8	90·9
*Ehretia rigida	6·0	6·0	3·6	3·5	90·9
Euclea natalensis	5·6	5·8	3·8	3·6	81·8
Maytenus heterophylla	5·2	4·4	3·7	2·6	100·0
Euphorbia ingens	4·5	4·0	3·6	2·7	90·9
Putterlickia verrucosa	3·6	4·6	2·5	2·9	72·7
Ziziphus mucronata	3·1	3·1	2·6	2·4	100·0
Clausena anisata	2·8	3·3	1·8	2·2	63·6
Fagara capensis	2.5	4·6	1·8	2·9	54·5
*Xeromphis rudis	2.5	2·3	2·1	2·1	63·6
Canthium ciliatum	2.4	6·6	1·1	2·7	27·3
Commiphora harveyi	2.4	1·9	2·3	1.7	72·7
Canthium ventosum	2.2	2·4	1·6	1.9	63·6
Maytenus undata	2.2	3·4	1·7	2.5	45·5
*Tricalysia lanceolata	2.1	4·4	1·5	2·7	27·3
Vangueria infausta	2.1	3·6	1·9	3·1	45·5
Total of 29 other species	25.2				
Total mean density	262.7				

* Plotted within the secondary ordination

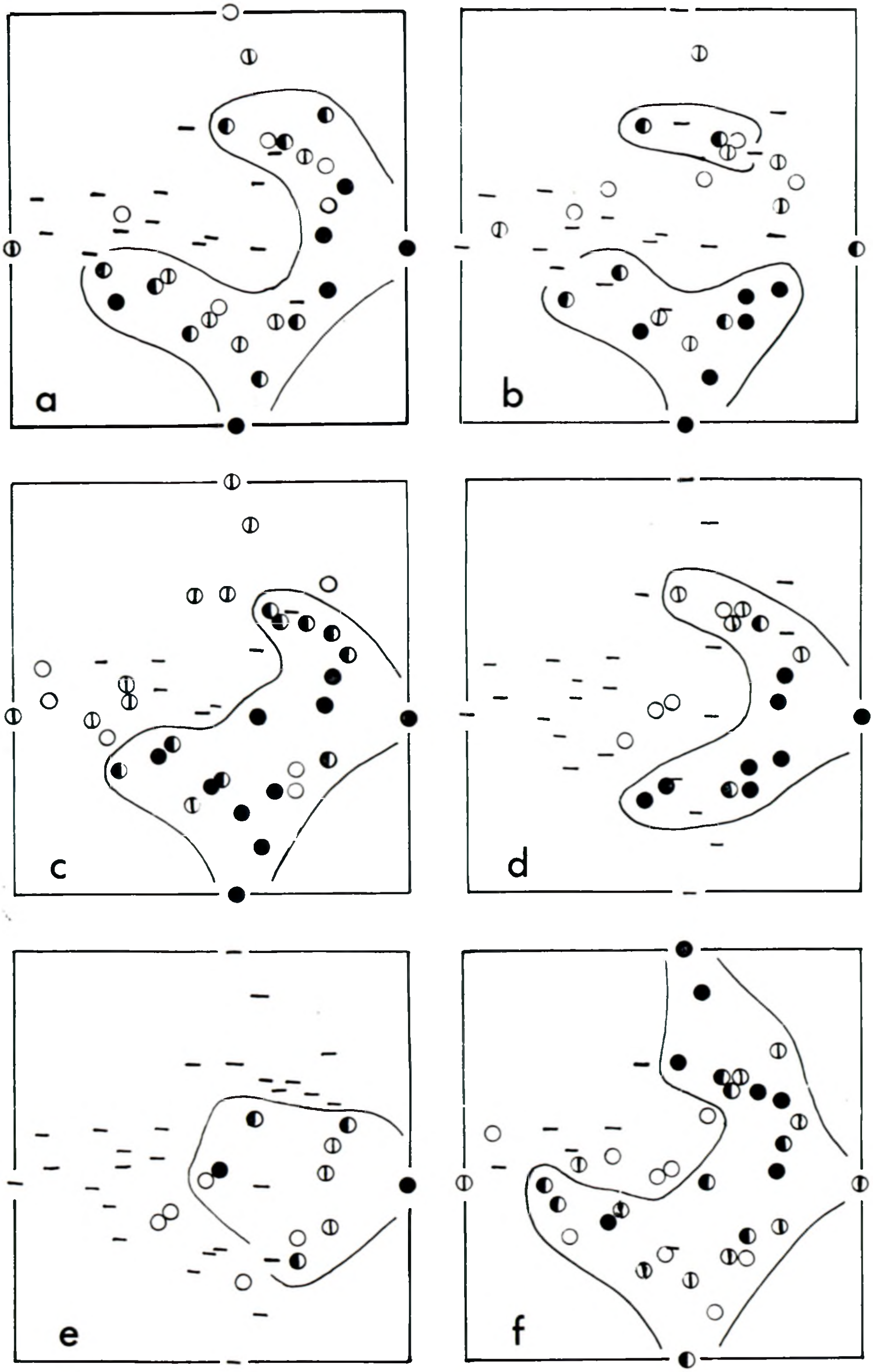


Fig. 11.—Quartile distributions of a, **Dombeya rotundifolia**; b, **Heteropyxis natalensis**; c, **Hippobromus pauciflorus**; d, **Acacia caffra**; e, **Acacia gerrardii**; f, **Brachylaena elliptica** densities within the X–Y ordination. See Fig. 4 for key to symbols.

Apart from species which are plotted within the ordination in Fig. 10, *Grewia occidentalis*, *Acalypha sonderiana*, *Euphorbia ingens* and *Euclea natalensis* have high mean densities in stands of the *Dombeya tiliacea* Nodum (Table 6). *Grewia occidentalis* is not pþotted, because it is ubiquitous through the study area, being absent from only two of the 60 stands. *Protorhus longifolia* is included in Table 6, even though it does not qualify for inclusion, as it has a clear pattern of distribution within the ordination and isknown to be a species appearing early in the succession to forest. Its distribution within the study area on the south-facing slopes indicates the area which, in the absence of disturbance, has the potential of being covered by forest.

Apart from the species whose distributions within the ordination are given, *Grewia occidentalis*, *Combretum molle* and *Dombeya tiliacea* have high mean densities in the *Hippobromus-Heteropyxis* Nodum (Table 7).

TABLE 8.—Mean density and mean local frequency, with standard deviations (s.d.), and constancy for species occurring in more than two of the eight stands of the *Hippobromus-Spirostachys* Nodum with a mean density greater than two

Species	Density		Frequency		Constancy
	mean	s.d.	mean	s.d.	
*Hippobromus pauciflorus	70·1	36·7	12·6	2·7	100·0
*Spirostachys africana	40·5	21·1	12·1	5·3	8·57
Combretum molle	23·1	13·8	10·0	4·1	100·0
Grewia occidentalis	21·9	13·5	10·6	2·9	100·0
*Brachylaena elliptica	16·8	11·2	8·5	3·9	100·0
*Aloe candelabrum	12·6	7·4	6·4	3·9	87·5
*Xeromphis rudis	11·5	6·4	7·5	2·8	100·0
*Ehretia rigida	10·9	8·4	6·3	3·3	100·0
*Acacia caffra	9·8	9·5	5·3	4·4	75·0
Acalypha sonderiana	8·8	8·7	2·0	3·5	37·5
*Dombeya rotundifolia	8·6	8·4	4·9	4·3	87·5
Maytenus heterophylla	7·5	7·0	5·5	3·4	75·0
Canthium mundianum	7·4	7·1	4·0	3·7	75·0
*Heteropyxis natalensis	7·0	5·8	2·4	4·8	62·5
Rhus pentheri	6·6	5·0	5·4	3·3	87·5
Dichrostachys cinerea	4·9	5·4	3·4	3·8	75·0
Euphorbia ingens	4·9	3·0	3·8	2·1	100·0
Euclea natalensis	4·3	1·9	3·9	1·9	87·5
Maytenus undata	4·1	4·7	3·5	3·7	62·5
Putterlickia verrucosa	3·5	3·6	2·3	1·8	75·0
Acacia nilotica	3·1	2·9	2·5	2·3	75·0
*Acacia gerrardii	2·9	3·1	2·4	2·3	62·5
Clausena anisata	2·6	4·6	1·8	3·1	37·5
Ziziphus mucronata	2·5	2·8	2·1	2·3	62·5
Fagara capensis	2·3	1·5	2·0	1·2	87·5
Total of 27 other species	19·2				
Total mean density	317·3				

* Plotted within the secondary ordination

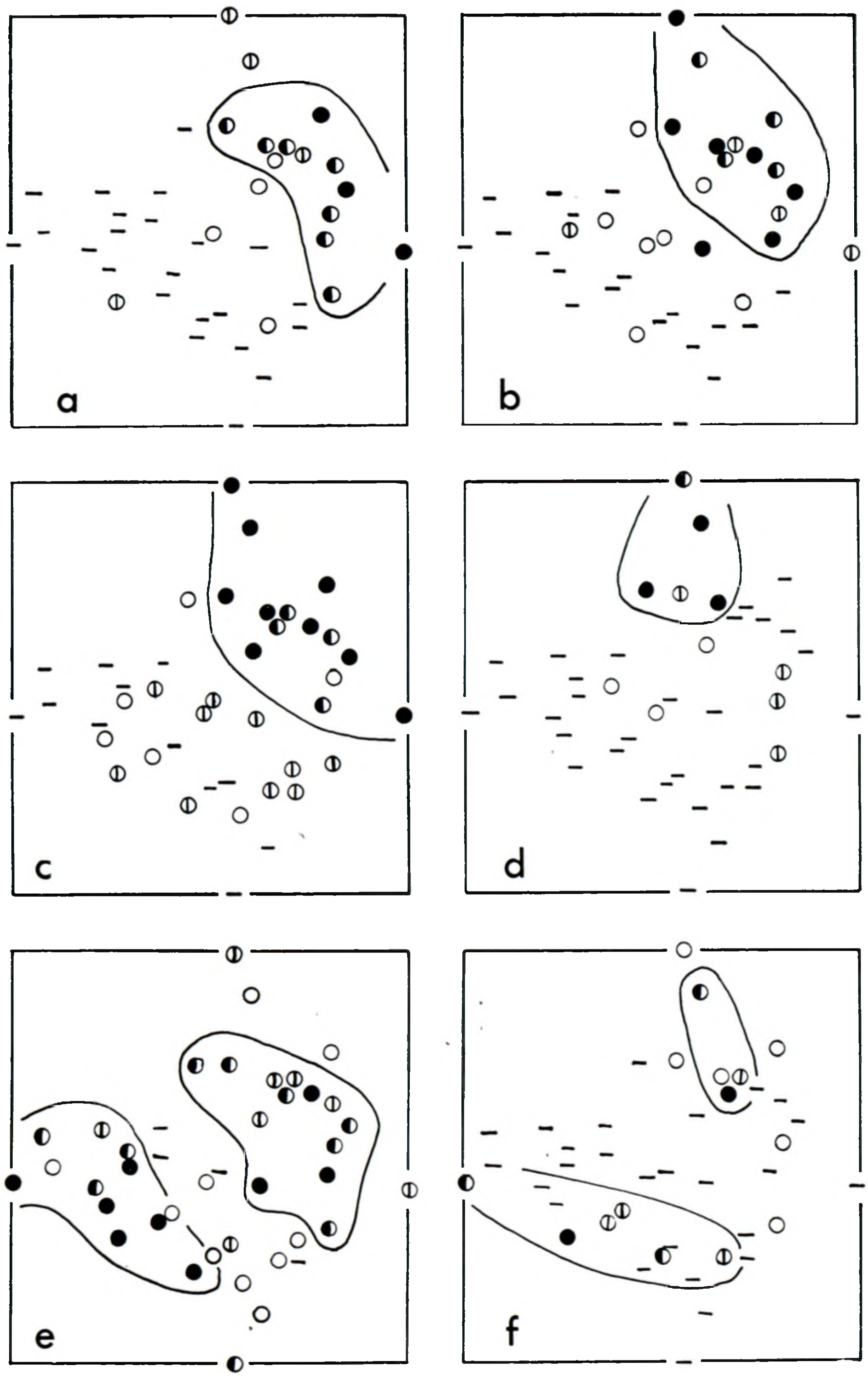


FIG. 12.—Quartile distributions of a, **Aloe candelabrum**; b, **Spirostachys africana**; c, **Xeromphis rudis**; d, **Canthium locuples**; e, **Ehretia rigida**; f, **Tecomaria capensis** densities within the X–Y ordination. See Fig. 4 for key to symbols.

Species with relatively high densities and high constancy values in the stands of the *Dombeya tiliacea* Nodum, but are absent from or have low densities in stands of the *Hippobromus-Heteropyxis* Nodum, are *Dombeya tiliacea* and *Tricalysia lanceolata*. *Acacia nilotica*, *Combretum molle*, *Dombeya rotundifolia*, *Heteropyxis natalensis* and *Hippobromus pauciflorus* are absent from, or rare in, the *Dombeya tiliacea* Nodum, but have relatively high densities in the *Hippobromus-Heteropyxis* Nodum.

Acacia caffra, *A. gerrardii* and *Brachylaena elliptica* have distributions centred on the stands of the *Hippobromus-Spirostachys* Nodum (Fig. 11 d–f). *Acacia gerrardii* is restricted, almost entirely, to this Nodum, while *Brachylaena elliptica* has a very wide distribution from the stands of the *Hippobromus-Heteropyxis* Nodum to the *Spirostachys africana* Nodum.

TABLE 9.—Mean density and mean local frequency, with standard deviations (s.d.), and constancy for species occurring in more than two of the eight stands of the *Spirostachys africana* Nodum with a mean density greater than two

Species	Density		Frequency		Constancy
	mean	s.d.	mean	s.d.	
*Spirostachys africana	43·1	27·4	12·4	4·6	100·0
*Brachylaena elliptica	19·1	16·2	8·9	5·9	87·5
*Xeromphis rudis	17·3	10·6	9·0	4·4	100·0
Combretum molle	14·5	8·2	7·8	2·3	100·0
*Hippobromus pauciflorus	14·0	15·6	5·1	4·6	87·5
Clausena anisata	13·0	13·2	4·5	3·5	87·5
Grewia occidentalis	12·9	7·3	7·5	2·2	100·0
*Aloe candelabrum	10·5	14·7	5·3	4·7	87·5
Canthium mundianum	9·1	9·4	4·5	2·9	100·0
Euphorbia ingens	8·1	5·3	4·6	2·5	100·0
Ochna arborea	7·3	8·4	4·0	4·0	75·0
Euclea natalensis	6·3	4·2	4·4	2·8	87·5
Xylotheca kraussiana	6·3	15·0	2·1	4·2	37·5
*Canthium locuples	6·1	7·3	2·9	3·6	62·5
*Tecomaria capensis	6·1	7·3	4·0	4·6	62·5
Dichrostachys cinerea	5·9	5·8	3·5	3·2	75.0
Acacia nilotica	5·5	5·1	4·6	4·4	62.5
*Ehretia rigida	5·5	3·0	4·6	2·5	100.0
Acalypha sonderiana	5·3	8·7	1·5	2·7	50·0
Maytenus undata	4·9	7·7	3·6	4·3	75·0
Maytenus heterophylla	4·6	5·7	2·9	3·2	62·5
Putterlickia verrucosa	4·4	4·1	3·3	2·6	87·5
Muriea discolor	4·1	10·9	1·1	2·5	37·5
Rhus pentheri	3·9	3·6	2·3	2·1	100·0
Canthium ventosum	3·5	3·7	2·6	1·9	87·5
*Heteropyxis natalensis	3·0	3·9	1·9	2·2	62·5
Canthium ciliatum	2·8	5·0	2·1	3·3	75·0
*Dombeya rotundifolia	2·7	2·6	2·5	2·3	75·0
Total of 27 other species	28·6				
Total mean density	278·3				

* Plotted within the secondary ordination

Apart from the species after which the *Hippobromus-Spirostachys* Nodum is named and species plotted within the ordination, *Grewia occidentalis*, *Combretum molle* and *Dichrostachys cinerea* have high mean densities (Table 8).

Aloe candelabrum, *Spirostachys africana* and *Xeromphis rudis* (Fig. 12 a–c) occur in both the *Hippobromus-Spirostachys* and the *Spirostachys africana* Noda. *Canthium locuples* (Fig. 12d) is restricted, almost entirely, to the *Spirostachys africana* Nodum while *Ehretia rigida* and *Tecomaria capensis* (Fig. 12e and 12f) occur in the stands of the *Spirostachys africana* Nodum and on the south-facing slopes of Ntshongweni. Apart from species plotted within the ordination, *Combretum molle*, *Clausena anisata* and *Grewia occidentalis* have high mean densities in stands of the *Spirostachys africana* Nodum (Table 9).

General Conclusions

Ordination was successful in aiding the writer's understanding of the vegetation and more knowledge was gained about the vegetation than if a descriptive survey alone had been carried out. Too much variation was inherent in the vegetation for it to be illustrated in two or three dimensions as used by Whittaker (1960) and by Bray & Curtis (1957). Two ordinations, using a total of five dimensions and a modified method of end stand selection, were required. Thus, used with discretion, ordination was a valuable tool in the study of this subtropical vegetation.

Correlations between species behaviour, illustrated by a stand ordination, and certain site factors were proposed. Actual measurements of factors, like quantity of insolation and soil moisture content, necessary to substantiate the proposed correlations, were precluded by a lack of time. Such measurements would have to be included in a more thorough investigation.

Evidence in support of the Individualistic Hypothesis is given, particularly by the secondary ordination. Although it was possible to delimit noda, it was shown that site factor and floristic gradients exist between noda.

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References

Beals, E., 1960. Forest bird communities in the Apostle Islands of Wisconsin. *Wilson Bull.* 72, 156–181.

Bray, J. R. & Curtis, J. T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325–349.

Curtis, J. T., 1959. *The vegetation of Wisconsin: an ordination of plant communities.* Madison: University of Wisconsin Press.

CURTIS, J. T. & MCINTOSH, R. P., 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32: 476–496.
DODSON, R. G., 1951. *Geology of the Shongweni District, Natal.* M.Sc. thesis, University of Natal, Durban.
GLEASON, H. A., 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53: 7–26.
GREIG-SMITH, P., 1964. *Quantitative plant ecology.* 2nd Ed. London: Butterworths.
JACKSON, S. P., 1952. Atmospheric circulation over South Africa. *S. Afr. Geogr.* J. 34: 48–60.
MORRIS, J. W., 1967. *Descriptive and quantitative plant ecology of Ntshongweni, Natal.* M.Sc. thesis, University of Natal, Pietermaritzburg.
RHODES, R. C. & LEITH, M. J., 1966. Lithostratigraphic zones in the Table Mountain Series of Natal. *Trans. Geol. Soc. S. Afr.* 71 (in press).
SCHULZE, B. R., 1965. *Climate of South Africa.* Part 8. *General Survey.* Pretoria: Government Printer.
TYSON, P. D., 1964a. Berg Winds of South Africa. *Weather, Lond.* 19: 7–11.
TYSON, P. D., 1964b. A summer storm over Pietermaritzburg. *J. Geog., Stellenbosch* 2: 23–29.
TYSON, P. D., 1965. Berg Wind over Durban. *Weather, Lond.* 20; 115–116.
WEATHER BUREAU, 1954a. *Climate of South Africa.* Part 1. *Climate Statistics.* Pretoria: Government Printer.
WEATHER BUREAU, 1954b. *Climate of South Africa.* Part 2. *Rainfall Statistics.* Pretoria: Government Printer.
WHITTAKER, R. H., 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26: 1–80.
WHITTAKER, R. H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30: 279–338.
WHITTAKER, R. H., 1962. Classification of natural communities. *Bot. Rev.* 28: 1–239.