

# A quantitative description of some coast forests of Natal

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### ABSTRACT

Ten stands of subtropical forest in four areas along the coast of Natal, South Africa, were sampled using five 1/10 acre circular plots in each stand. A total of 101 woody species over one inch d.b.h. was encountered, with a range of 20 to 40 species per stand. Quantitative results, including numbers and sizes, are given for canopy, subcanopy, and understorey species as they occurred in these various layers. Specific size limits were used to recognize the three layers, thus putting all stands on a comparable basis. Relative basal area per acre figures were used as an indication of the relative dominance of the various species and layers, and the possibility of a biological principle to justify such usage is mentioned.

Although the stands are complex and are seemingly heterogeneous, there are definite patterns of species behaviour, and trends are indicated for the 10 stands and for the four forest areas. Relatively few species are dominant in each stand and the apparent diversity is mainly due to the high percentage of species that are relatively uncommon in each stand. The methods described in this paper should be applicable in a study of a broader range of Natal forests, an area from which quantitative studies have heretofore been virtually absent.

### INTRODUCTION

Few quantitative studies of subtropical forest vegetation have been made in South Africa. These forests have been described subjectively and profiles have been drawn to show the different layers. More specifically, virtually no quantitative studies have been made of the coast forests in Natal until recent studies in which Moll (1968a; 1968b; 1969) gathered density and frequency data for various *synusia* in large quadrats.

On the other hand, rapid techniques to sample large area of forest vegetation have been used in the temperate zone, for example the quarter method (Cottam and Curtis, 1956), where quantitative analytic techniques have been developed (Curtis, 1959). In temperate zone forests, however, the vegetation is more homogenous and the number of woody species is smaller compared to subtropical forests. The quarter method was briefly investigated in Natal forests, but was not considered suitable because it requires a larger homogenous area than was found to exist. Instead of the quarter method, this paper describes an area-method of sampling, which was applied in 10 stands of forest in Natal, and the subsequent quantitative analysis of these stands.

### STUDY AREA

The 10 stands of forest, from four areas of Coast Forest, were studied in December 1967. Table 1 gives a summary of various physical characteristics of the stands. Stands 1 to 3 were located in the Krantz-kloof Nature Reserve, 25 km northwest of Durban, and are shown as area A on the map of Natal (Fig. 1). Stand 1 was on a Table Mountain Sandstone slope

above a cliff. Stand 2 was just below the 100 m high cliff, and stand 3 was closer to the valley bottom than stand 2 (Fig. 2). The underlying rocks of stands 2 and 3 were granite, but many large sandstone rocks

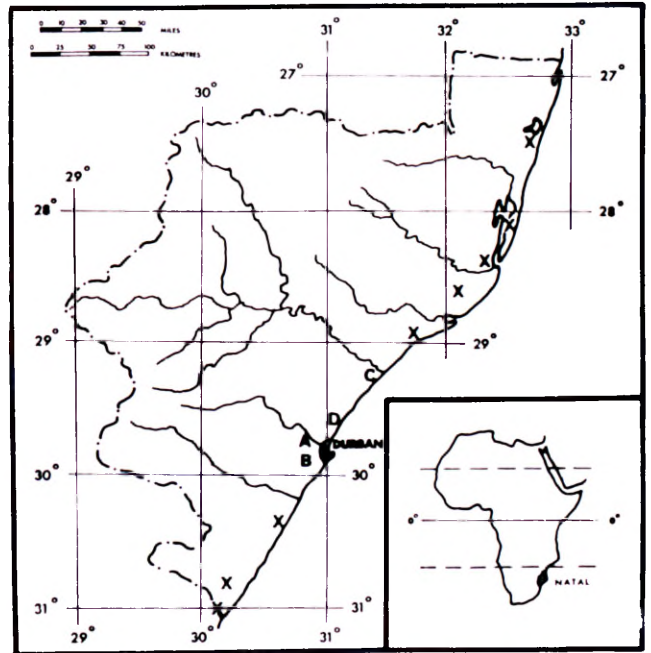


FIG. 1.—Map of Natal, South Africa, showing forests in which stands were studied. Latitude, longitude, and the location of Durban are shown for purposes of orientation. See Table 1 for location of stands in areas A to D. The few remaining similar natural forests along the Natal Coast are located in areas marked X.

TABLE 1.—Characteristics of the ten stands of Natal Coast Forest which were sampled

Stand	Forest (area)	Soil parent material	Altitude (m above sea level)	Slope	Aspect	Approx. height of canopy in m
1	Krantzkloof (A)	Sandstone	500	25°	SSW	12
2	Krantzkloof (A)	Sandstone on granite	400	30°	SW	18
3	Krantzkloof (A)	Sandstone on granite	350	20°	SW	18
4	Hlogwene (C)	Dune sand	30	8°	NNE	18
5	Hlogwene (C)	Dune sand	30	5°	NE	18
6	Hlogwene (C)	Dune sand	30	10°	NW	18
7	Hawaan (D)	Dune sand	30	4°	ENE	12
8	Hawaan (D)	Dune sand	30	3°	E	12
9	Stainbank (B)	Sandstone	120	45°	SSW	15
10	Stainbank (B)	Sandstone	100	5°	NE	12

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had fallen from the cliff, and weathered sandstone was probably the main soil parent material. Stands 9 and 10 were located in Stainbank Nature Reserve, 16 km southwest of Durban (area B on the map), and both stands were on Table Mountain Sandstone. Stands 4 to 6 were in the Hlogwene Forest, which is 80 km north of Durban near the town of Stanger

(area C on the map). The soil parent material was dune sand. This forest is owned and protected by Hulett's Sugar Co., and is pictured in Fig. 3. Stands 7 and 8 were in the Hawaan Forest, 19 km north of Durban (area D on the map). This forest is owned by Natal Estates (Pty) Ltd and is likewise on dune sand.



FIG. 2.—Krantzkloof Nature Reserve, looking east. Stand 1 is above the cliff on the left, stand 2 at the base of the cliff, and stand 3 to the left of the valley bottom. Note arid northwest-facing slopes in distance.



Fig. 3.—Aerial view of Hlogwene Forest, location of stands 4–6, looking south. The Indian Ocean is on the left, and the Tugela River in the foreground. Most dune forests of this type along the coast have been replaced by sugar cane plantations, or, near Durban, by housing development. (Photo: Natal Mercury).

Each stand was situated well within the forest to avoid any edge effect. The total forest in each of the four areas ranges from 50 to 250 ha.

The forests discussed here are classified by Acocks (1953) as Coastal Tropical Forest, although the Krantz/kloof stands are at the inland and altitudinal limits of this type. Edwards (1967) classifies the forests in this part of Natal from sea level to 500 m as Coast Lowlands Forest, and from 500 to 1 200 m above sea level as Semi-Coast Forest.

The four forest areas discussed in this paper are representative of the few remaining remnants of a once much more extensive and perhaps continuous forest along the coast dunes, in the lower valleys, and on east- and south-facing slopes inland to about the 500 m contour level. Approximately 90 percent of this forest type has been destroyed since the arrival of Bantu and European settlers in the last 400 to 500 years (Brookes and Webb, 1965).

The best climatic data available for the stands are statistics from Durban (Anonymous, 1954). The mean daily temperatures are 24 °C in February and 16.5 °C in July, with an annual mean daily temperature of 20.5 °C. The absolute minimum and maximum temperatures are 4 °C and 42 °C, respectively. Light frost is known to occur occasionally in the Krantz-kloof Forest, but the other forests may be considered frost-free. Average precipitation for Durban ranges from 28 mm in July to 121 mm in November, with a yearly average of 1 008 mm. These precipitation figures do not take into account the high humidity throughout the year, resulting in heavy dews in winter.

#### COMPLEXITY AND HETEROGENEITY

The number of species of vascular plants in a region gives an indication of the potential complexity of its plant communities. South Africa has an estimated 16 000 to 18 000 species of which some 5 000 species occur in Natal (Ross, 1972). Six hundred to 650 of the Natal species are woody, i.e., trees, shrubs and lianes (Ross, 1972; Ross and Moll, 1972).

Natal has rugged and diverse topography, rising from the Indian Ocean to over 3 300 m on the Drakensberg Range within a distance of 160 km. The many slopes and aspects, and the diverse climatic conditions associated with mountainous terrain lead to many microclimates. With the many species from which to select, the plant communities are extremely complex.

Since Natal forests are virtually unstudied quantitatively, and yet occur in such an interesting situation regarding topography, climate, and numbers of woody species, it was considered desirable to attempt a quantitative study. The 10 stands of Subtropical Coast Forest studied probably represent some of the most complex forests in Natal. If rapid quantitative methods could be devised which work in this region, a broader comparative study of the forest vegetation of Natal could be undertaken. The aim of these quantitative methods was to sample and describe a larger area of forest, rather than to describe only one plot at a time, as has usually been done in studies of tropical and subtropical forest. A further aim was to assess the degree of complexity and heterogeneity. The samples consequently represented the vegetation of one or two hectare, which is still much smaller than those Curtis (1959) and his associates sampled in the temperate forests of Wisconsin where their samples usually represented vegetation of 5 to 8 hectare.

#### FIELD METHODS

The following criteria were followed in the selection of stands. The stands were in upland situations free from standing water at any time of the year, and were free from any recent disturbance by man or domestic animals. The prime criterion for selection was

topographic homogeneity: an area of one to two hectare in size with the same slope, aspect and soil parent material was selected. The vegetation had "visual homogeneity" from a structural standpoint, in that the age or size classes of species, the physiognomy, and the density were relatively uniform throughout the stand. It was also determined that certain of the prominent tree species did occur throughout the stand. However, an actual estimate of vegetational homogeneity could not be determined until analysis of the samples. There was no attempt to study the full range of successional stages and all the stands sampled were relatively mature.

Each stand was sampled with five 1/10 acre circular plots. A 1/10 acre plot has an area of 4 356 square feet, and therefore a radius of 37.2 feet.\* The worker who recorded the data (Rogers) stood in the centre of the plot and determined the outer perimeter of the circle using a field rangefinder. A rope marked with the exact radius was also used in dense situations, and for trees located near the perimeter. The other worker (Moll) identified the species, and measured them with the aid of an assistant, Bernard Mkhize.

Two categories of woody species were recorded. Saplings and large shrubs were those individuals having a diameter at breast height (4.5 feet) of one to four inches. Trees, measured with a basal area tape giving readings in square inches, were those individuals having a d.b.h. of more than four inches, i.e., a basal area of more than 12 square inches. The basal areas of occasional trees with buttresses at 4.5 feet were measured above the buttresses. Basal area of the tree trunk is a common measure of size or dominance (Curtis, 1959), and is an easier and more objective measure than height or canopy spread in a closed forest. Herbs, lianes, epiphytes and small shrubs were not sampled.

The information recorded in the field for each stand, therefore, was altitude, slope, aspect, soil parent material, and measurement or listing of woody species of over one inch in d.b.h. In addition, a soil sample was collected in each of the five plots per stand; these were then combined to give one soil sample for each stand.)

#### RESULTS AND DISCUSSION

It would have been possible to assess each tree regarding its presence in the canopy or other subordinate layers. However, whether a tree is in the canopy or not is relative and varies with site, topography, age of the stand, which other species are present and interpretation of the observer. Therefore, canopy individuals were characterized arbitrarily as those having a basal area of 100 square inches or more. This size was not only convenient, but gave a reasonable separation. It was empirically determined in the stands that trees exceeding this size class formed the canopy layer a remarkable number of times. Trees having a basal area of less than 100 square inches were classified as subcanopy. Those of less than 12 square inches were listed as understorey, a category which includes saplings of canopy and subcanopy trees and large shrubs. Using these criteria we found a good correlation in our study with the same species subjectively assigned to the various layers by Henkel (1934) and Moll (1967).

In Table 2, the data recorded for the canopy, subcanopy and understorey species are shown for various layers. The order in which the stands are listed is based on an ordination which will be discussed later.

\* Feet and acres have been retained here because the work was completed before metrication, and because comparisons of basal areas (in square inches) were to be made with previously-published data from temperate forests.



TABLE 2.—Number of individuals per acre and basal area per acre, in square inches, for 77 species, by layer, in the 10 stands  $\frac{\text{(number)}}{\text{(basal area)}}$ . Canopy, subcanopy and understorey layers are designated by C, S and U respectively. Various totals and averages for layers as well as percentage relative dominance are also shown. X signifies that a species was present in the stand, but was not recorded in the sample. Not included in this table are 24 species which occurred in one stand only, although they are included in the totals. These species are listed in the appendix. For each of the three categories of species, the dominant in each layer, in each stand, is indicated by parentheses

Species	Stand 1			Stand 3			Stand 2			Stand 9			Stand 10			Stand 4			Stand 5			Stand 6			Stand 7			Stand 8				
	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U		
<b>CANOPY SPECIES</b>																																
1. <i>Podocarpus latifolius</i> .....		$\frac{2}{76}$	$\frac{6}{30}$		$\frac{10}{(404)}$		$\frac{2}{1560}$	$\frac{6}{274}$	$\frac{4}{20}$																							
2. <i>Ficus natalensis</i> .....				$\frac{2}{420}$	$\frac{2}{44}$	$\frac{6}{30}$	$\frac{2}{1260}$																									
3. <i>Sapium ellipticum</i> .....				$\frac{14}{2908}$	$\frac{4}{186}$		$\frac{2}{760}$																									
4. <i>Drypetes gerrardii</i> .....				$\frac{2}{344}$		$\frac{6}{30}$	$\frac{(16)}{(2408)}$	$\frac{46}{1976}$	$\frac{56}{280}$																							
5. <i>Commiphora woodii</i> .....		$\frac{4}{106}$									$\frac{2}{520}$		$\frac{2}{10}$																			
6. <i>Maytenus acuminata</i> .....		$\frac{8}{292}$	$\frac{8}{40}$					$\frac{2}{42}$			$\frac{2}{236}$	$\frac{2}{120}$																				
7. <i>M. peduncularis</i> .....			$\frac{2}{10}$	$\frac{6}{1022}$	$\frac{4}{116}$								$\frac{2}{10}$																			
8. <i>Brachylaena uniflora</i> .....		$\frac{4}{112}$	$\frac{4}{20}$			$\frac{2}{10}$					X		$\frac{2}{236}$	$\frac{10}{732}$																		
9. <i>Combretum kraussii</i> .....		$\frac{36}{1518}$	$\frac{34}{170}$	$\frac{4}{1144}$										$\frac{6}{446}$	$\frac{2}{10}$																	
10. <i>Erythroxylum pictum</i> .....	$\frac{2}{340}$													$\frac{6}{180}$																		
11. <i>Protorhus longifolia</i> .....	$\frac{(22)}{(4492)}$	$\frac{44}{2617}$		$\frac{(14)}{(3350)}$			$\frac{6}{1310}$			$\frac{(8)}{(2274)}$			$\frac{(24)}{(4822)}$	$\frac{24}{1062}$	$\frac{4}{20}$																	
12. <i>Harpephyllum caffrum</i> .....		$\frac{6}{312}$	$\frac{2}{10}$				$\frac{2}{284}$				$\frac{8}{360}$	$\frac{2}{10}$			$\frac{2}{10}$																	
13. <i>Manilkara discolor</i> .....	$\frac{4}{720}$	$\frac{4}{122}$	$\frac{4}{20}$							$\frac{2}{214}$	$\frac{8}{520}$	$\frac{2}{10}$	$\frac{2}{268}$	$\frac{6}{350}$																		
14. <i>Rhus chirindensis</i> .....	X			$\frac{4}{807}$							$\frac{2}{200}$			$\frac{2}{174}$																		
15. <i>Apodytes dimiata</i> .....	$\frac{4}{250}$	$\frac{4}{20}$			$\frac{2}{50}$									$\frac{4}{670}$																		
16. <i>Canthium ventosum</i> .....	$\frac{22}{672}$	$\frac{(48)}{(240)}$		$\frac{2}{216}$	$\frac{2}{40}$		$\frac{2}{476}$	$\frac{2}{160}$			$\frac{6}{118}$		$\frac{2}{66}$	$\frac{(8)}{(40)}$		X				$\frac{2}{120}$												
17. <i>Scolopia zeyheri</i> .....			$\frac{2}{10}$	$\frac{4}{428}$																	$\frac{2}{10}$	$\frac{4}{744}$	$\frac{2}{60}$									
18. <i>Trichilia dregeana</i> .....			$\frac{2}{10}$	$\frac{4}{920}$			$\frac{2}{1640}$							$\frac{12}{1940}$	$\frac{(12)}{(618)}$	$\frac{2}{10}$	$\frac{14}{3108}$	$\frac{6}{348}$			$\frac{4}{744}$	$\frac{2}{60}$	$\frac{14}{3140}$	$\frac{2}{130}$								
19. <i>Chrysophyllum viridiflorum</i> .....						$\frac{2}{10}$	$\frac{2}{1400}$						$\frac{2}{1600}$	$\frac{2}{28}$	$\frac{2}{10}$						$\frac{4}{112}$	$\frac{4}{20}$		$\frac{2}{92}$								
20. <i>Strychnos henningsii</i> .....			$\frac{2}{10}$								$\frac{8}{298}$																					
21. <i>Cola natalensis</i> .....				$\frac{2}{360}$		$\frac{(8)}{(40)}$	$\frac{8}{534}$	$\frac{10}{50}$			$\frac{2}{90}$																		$\frac{2}{236}$	$\frac{2}{76}$	$\frac{2}{40}$	
22. <i>Chaetacme aristata</i> .....					$\frac{2}{60}$		$\frac{2}{110}$				$\frac{2}{460}$						$\frac{4}{516}$	$\frac{2}{206}$			$\frac{2}{1450}$	$\frac{2}{74}$	$\frac{2}{806}$	$\frac{2}{52}$	$\frac{2}{748}$							
23. <i>Celtis africana</i> .....							$\frac{2}{420}$										$\frac{(22)}{(4312)}$	$\frac{8}{502}$			$\frac{6}{1144}$	$\frac{2}{108}$	$\frac{4}{960}$	$\frac{2}{120}$	$\frac{8}{3000}$					$\frac{6}{1850}$		
24. <i>Millettia grandis</i> .....										$\frac{2}{1320}$	$\frac{(38)}{(2472)}$	$\frac{2}{10}$	$\frac{2}{380}$	$\frac{(44)}{(2158)}$																		
25. <i>Cordia caffra</i> .....											$\frac{2}{112}$					$\frac{2}{540}$		$\frac{2}{10}$		$\frac{2}{134}$												
26. <i>Canthium obovatum</i> .....											$\frac{4}{156}$												$\frac{2}{720}$									



TABLE 2.—(Continued)

Species	Stand 1			Stand 3			Stand 2			Stand 9			Stand 10			Stand 4			Stand 5			Stand 6			Stand 7			Stand 8				
	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U	C	S	U		
19. <i>Taberaemontana ventricosa</i> .....					16			4	2									2			12	14										
					584			200	10									44			268	70										
20. <i>Cassipourea gerrardii</i> .....		2	28		2			2	4		10	24		12														4	(2)			
		30	140		52	10		24	20		262	120		60														20	(200)			
21. <i>Mimusops obovata</i> .....		4	12					2			14	8																		2		
		70	60					96			368	40																		10		
22. <i>Baphia racemosa</i> .....					6	2					16	20	4	48														4	(14)			
					146	10					280	100	48	240														20	(70)			
23. <i>Drypetes arguta</i> .....						4			2			(88)	29	(186)													6	12				
						20			10			(440)	284	(930)													30	60				
24. <i>Cassine aethiopoica</i> .....											6	16		6																		
											136	80		30																		
25. <i>Orcia bachmannii</i> .....											6	22		6																		
											142	110		30																		
26. <i>Cussonia sphaerocephala</i> .....											2					2					2											
											252					128					72											
27. <i>Turraea floribunda</i> .....														2							2											
														10							70											
28. <i>Cassipourea gummiflua</i> .....																					2	2										
																					28	10										
29. <i>Deinbollia oblongifolia</i> .....															(50)	46				(52)	46	28	44									
															(1146)	230				(974)	230	600	220									
30. <i>Diospyros natalensis</i> .....																4					2											
																20					10											
31. <i>Linociera peglerae</i> .....																4					6											
																20					30											
32. <i>Ochna natalitia</i> .....																4						2										
																20						56						2				
33. <i>Drypetes natalensis</i> .....																											(4)	2		2	2	
																											(132)	10		194	10	
34. <i>Sapium integerrimum</i> .....																												2	6			
																												64	38	30		
35. <i>Vangueria chartacea</i> .....																2	8					4	22						4		2	
																28	40					78	110						20		10	
36. <i>Teclea gerrardii</i> .....																					2	2						6	2			
																					36	10						20	104			
37. <i>Suregada africana</i> .....																												2	(8)		2	
																												88	40		10	
Totals: Subcanopy species....	74	348		180	248		100	146		136	498		78	426		112	212		114	530		136	538		10	34		8	40			
	2664	1740		4522	1240		3372	730		4240	6490		1914	2130		2480	1060		2510	2650		3218	2690		398	170		536	200			
UNDERSTOREY SPECIES (SHRUBS)																																
1. <i>Tricalysia capensis</i> .....		(372)		(128)		(50)		28					16		(6)								(18)									
		(1860)		(640)		(250)		140					80		(30)								(90)									
2. <i>Cassine papillosa</i> .....				2				4															2									
				10				20															10									
3. <i>Erythroxylum emarginatum</i> .....		2																			(38)		4		(14)					(20)		
		10																			(100)		20		(70)					(100)		
4. <i>Cussonia nicholsonii</i> .....								24					18																			
								120					90																			
5. <i>Dracaena hookeriana</i> .....								(84)					(24)																			
								(420)					(120)																			
6. <i>Pancovia golungensis</i> .....																																
Totals: Understorey species..		414		142		52		144					100		6																	
		2070		710		260		720					500		30																	

The number of trees per acre in the canopy ranged from 26 to 82 in the 10 stands. Trees per acre for the canopy species in the subcanopy layer ranged from 22 to 134, while trees per acre of subcanopy species in the subcanopy layer ranged from eight to 180, etc.

Summary totals and averages for the layers, and for each stand as a whole, are listed at the bottom of Table 2. The total number of species appearing in the various layers ranges from 20 to 40 species per stand.

*Basal area as a measure of relative dominance*

Relative dominance, based on basal area figures, is used as a measure of importance because it bears a fairly direct relationship to the amount of light intercepted or shade cast, the amount of water and nutrients taken up, photosynthesis, litter dropped, etc., which are underlying reasons for attempting to assess importance of the individual species.

Note then at the bottom of Table 2 that although the total number of stems per acre ranges from 268 to 1116 (with an average of  $658 \pm 60\%$ ), the total basal area per acre ranges only from 16 438 to 24 514 square inches (an average basal area of  $19 714 \pm 20\%$ ). This same pattern was found in a study of 86 stands of deciduous forest in southern Wisconsin which showed all degrees of cutting from heavy to light (Rogers, 1959), where the number of stems per acre ranged from 231 to 1 454, while the average basal area was  $18 391 \pm 25\%$ . It appears that there may be some phenomenon similar to "carrying capacity" operating in temperate and subtropical hardwood forests, i.e., as a forest matures from a large number of small stems to a smaller number of larger stems, the amount of ground actually occupied by the trees does not change nearly as much as the number of trees. Furthermore, the approximate average of 20 000 square inches is measured at breast height. Measurement of the basal area of a tree at ground level is usually a little over twice as great as at breast height, i.e., a basal area figure at

ground level would approximate 40 000 square inches per acre. With approximately 6,3 million square inches to an acre, this means that less than one per cent of the ground is actually occupied by the trunks of saplings and trees. These statistics are mentioned to illustrate that there may be some biological principle involved in basal area figures. If this is true, the use of basal area figures as an indication of relative dominance for species would be more than a convenience, and, in fact, might have some absolute significance.

The canopy species vary in relative importance from 61% in stand 9 to 97% in stand 7. In five of the 10 stands (1, 9, 10, 7, 8), canopy species dominate in the subcanopy layer. Only in one stand (stand 1) do understorey species, i.e., shrubs, dominate the understorey layer. In every other stand it is the subcanopy species which predominate in the understorey layer. Using basal area as an indication of importance, the canopy layer is shown to be the dominant layer in all but stands 1 and 9. If more stands covering a broader successional range of forests were studied, it is possible that these relative dominance values could be used to indicate successional trends. On the basis of relative dominance of canopy layers and canopy species, for example, stands 1, 5, 6, 9 and 10 may be more immature or pioneer stands, whereas stands 2, 3, 4, 7 and 8 may be more mature or climax stands. It is not implied, however, that these stands are part of the same successional series.

In Table 3 the dominant species of each layer for each category are shown. The figures indicate importance as a percentage of the total basal area for the stand, and are determined as shown in the following example: *Protorhus longifolia* is the dominant canopy layer tree in stand 1, having a basal area of 4 492 of the total 5 552 square inches (see Table 2); 4 492 is 23,9% and 5 552 is 29,5% of 18 792, the total basal area for stand 1. By comparison of Tables 2 and 3, the importance of each species in relation to the layer it dominates and to the stand as a whole can be seen.

TABLE 3.—Dominant species of each category for each layer. The basal area of each species as a percentage of the total basal area for each stand is used as the indication of importance. The species indicated by initials can be determined by reference to Table 2. Also listed are the three leading species for each stand with their relative importance values totalled. To indicate trends for the most important species the fourth leading species is shown for stands 4, 6, 7 and 8; the fifth leading species is shown for stand 5 and the sixth for stand 2

Stand	Species category	Canopy layer	Subcanopy layer	Understorey layer	Leading species
1	C.....	<i>Pr. l.</i> ... 23,9	<i>Pr. l.</i> ... 14,4	<i>C. w.</i> ... 1,3	<i>Protorhus longifolia</i> ..... 38,3
	S.....		<i>A. i.</i> ... 9,4	<i>C. w.</i> ... 1,4	<i>Anastrabe integerrima</i> ..... 10,5
	U.....			<i>T. c.</i> ... 9,9	<i>Tricalysia capensis</i> ..... 9,9
					58,7
3	C.....	<i>Pr. l.</i> ... 16,8	<i>Po. l.</i> ... 2,0	<i>C. n.</i> ... 0,2	<i>Bequaertiodendron natalense</i> ..... 20,3
	S.....		<i>B. n.</i> ... 15,0	<i>B. n.</i> ... 5,3	<i>Protorhus longifolia</i> ..... 16,8
	U.....			<i>T. c.</i> ... 3,2	<i>Sapium ellipticum</i> ..... 15,5
					52,6
2	C.....	<i>D. g.</i> ... 12,0	<i>D. g.</i> ... 9,8	<i>D. g.</i> ... 1,4	<i>Drypetes gerrardii</i> ..... 23,2
	S.....		<i>B. n.</i> ... 7,8	<i>B. n.</i> ... 3,3	<i>Bequaertiodendron natalense</i> ..... 11,1
	U.....			<i>T. c.</i> ... 1,2	<i>Podocarpus latifolius</i> ..... 9,2
					43,5
					( <i>Protorhus longifolia</i> , 6,5%)
9	C.....	<i>Pr. l.</i> ... 11,9	<i>M. g.</i> ... 12,9	<i>M. g.</i> ... 0,1	<i>Millettia grandis</i> ..... 19,9
	S.....		<i>A. i.</i> ... 6,2	<i>D. a.</i> ... 2,3	<i>Protorhus longifolia</i> ..... 11,9
	U.....			<i>D. h.</i> ... 2,2	<i>Anastrabe integerrima</i> ..... 6,5
					38,3





TABLE 5.—Average percentage similarity of the four forests with one another

	A	B	C	D
A.....	52	40	26	15
B.....		61	26	22
C.....			65	37
D.....				86

TABLE 6.—Average percentage similarity of the more inland forests (A+B) compared to the dune forests (C+D)

	AB	CD
AB.....	40	22
CD.....		37

slopes, compared to (CD), the stands along the coast on dune sand and generally on more gradual north- and east-facing slopes (see Table 1).

#### Patterns of species distributions

*Strychnos madagascariensis* is one of three leading species in forest areas C (stands 4–6) and D (7–8), and *Celtis africana* is one of the four leaders in these two areas, except for stand 5 in which it was fifth. *Cola natalensis* and *Cavacoa aurea* are dominants in area D (Fig. 4), but are absent from area C. Conversely, *Trichilia dregeana* and *Bequaertiodendron natalense* are dominants in area C (Fig. 5), but are absent from area D.

Species patterns are less distinct in areas A (stands 1–3) and B (9–10), although *Protorbus longifolia* is first or second in each stand, except stand 2 in which it is sixth. *Tricalysia capensis*, a shrub present in seven of the 10 stands, actually achieved a rank of third leading dominant in stand 1 (Fig. 6). *Millettia*

FIG. 4.—View inside Havaan Forest (area D). The two dominant species having a combined relative importance of 55 to 60% in stands 7 and 8 were *Cavacoa aurea* (right) and *Cola natalensis* (left centre).



FIG. 5.—View inside Hlogwene Forest (Area C). *Ekebergia capensis* (left) has a somewhat buttressed base. Most of the smaller trees are *Bequaertiodendron natalense*, one of the four leading dominants in this forest, having an average relative importance in the three stands (4, 5, 6) of approximately 15%.

We may therefore conclude that the first order of similarity is within one forest area (1, 2, 3) (9, 10) (4, 5, 6) (7, 8). The second order of similarity is (AB), the stands farther inland, altitudinally higher, on rocky soil, and in a topographically more mesic situation with generally fairly steep southwest-facing

*grandis* appears as a dominant in stands 9 and 10, the only stands in which it is ever present. *Podocarpus latifolius*, a very conspicuous tree in the forest, is present only in stands 1–3, and is a dominant only in stand 2 (Fig. 7).



FIG. 6.—View inside Krantz-kloof Forest (area A, stand 1). The dark-boled trees are *Protorhus longifolia*, perhaps the most characteristic dominant species of areas A and B. Most of the shrubs are *Tricalysia capensis*, which was very common in this stand.

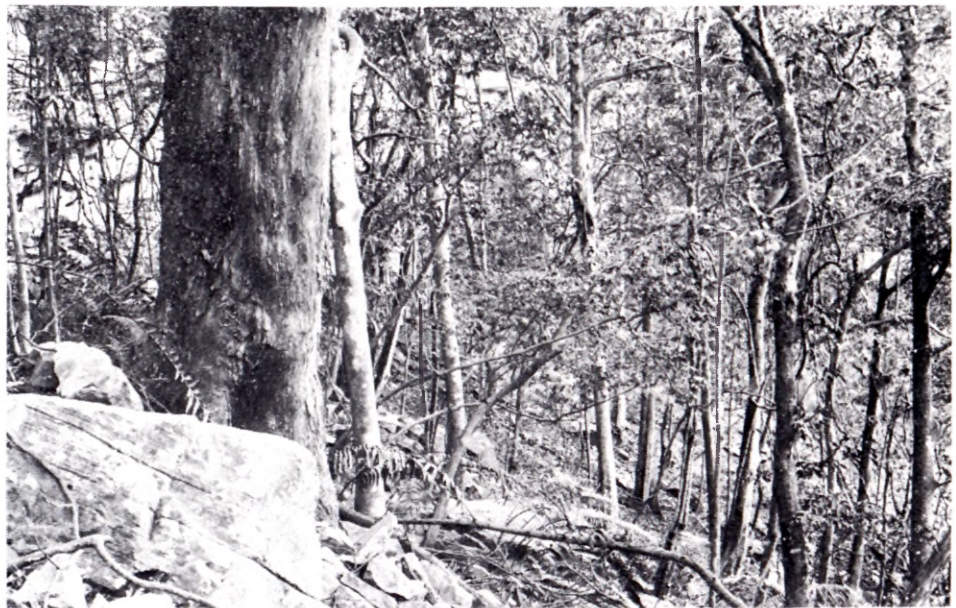


FIG. 7.—View inside Krantz-kloof Forest (area A). The three leading dominants in stand 2 are shown. The large tree is *Podocarpus latifolius*, the smooth-barked trees are *Drypetes gerrardii* and the small trees with fluted trunks are *Bequaertiodendron natalense*. Note the presence of sandstone rocks fallen from cliffs to the left (see Fig. 2) and the cycad, *Encephalartos villosus*, in the ground layer.

*Strychnos madagascariensis* is one of the three leading dominants in six of the 10 stands studied and may therefore be considered as the single species most likely to be a dominant in these Coast Forests. *Bequaertiodendron natalense* is present in eight of the 10 stands, the highest frequency for any species. Only two species appear in all four forest areas however: *Chaetacme aristata* and *Tricalysia capensis*.

The distribution patterns of other species may be seen in Table 2. The number of species of the various layers as appearing in the two main groups of stands, the inland, rocky areas (A and B) and the coast dunes (C and B), may be summarized as follows:

Species group	(A or B)	(A/B and C/D)	(C or D)
Canopy.....	14	16	4
Subcanopy....	13	14	10
Understorey..	2	3	1
Totals.....	29	33	15 = 77
Percentage...	38%	43%	19% = 100%

Although there are definite patterns in the distribution of species in the various stands and forest areas, no definite groups of species with identical patterns are obvious. It appears likely that the behaviour

indicates a continuum rather than an association interpretation. Further studies covering a wider range of successional conditions are desirable before we can fully understand these distribution patterns.

*Soil analysis*

From an analysis of the soil samples there were a few trends apparent within the groups of stands. The soils of areas A and B had more coarse sand, more clay, lower pH (4,2 to 5,0), and higher water-retaining capacities, while those of areas C and D had more medium and fine sand, higher pH (6,0 to 7,0), and lower water-retaining capacities. The soils of forest area D had the highest total bases, but the results for the other areas varied with the stands. Area D, likewise, had the highest cation exchange capacity, followed by areas A, C and B. Results concerning specific nutrients varied from stand to stand with no real pattern. If a larger number of stands were studied, it is possible that presence or absence of certain species might be correlated with certain nutrients.

*Heterogeneity and homogeneity of stands*

The terms heterogeneity and homogeneity are relative. It is possible to prove that a stand is heterogeneous, but it is unlikely that a stand of any size can be demonstrated to be homogeneous. Consequently, we can speak only of higher or lower degrees of heterogeneity.

Table 7 gives an indication of the relative degree of heterogeneity of each stand. Some stands may be considered less heterogeneous than others. The left hand columns show the decreasing rate at which new species were sampled in the successive plots of a stand. While the figures are similar to a species area curve, it is realized that chance may have influenced

limits to recognize the layers, rather than determining each individual subjectively in the field, the time spent in sampling a stand is shortened. Likewise, the relative contribution of the canopy, subcanopy and understorey species to the various layers can be readily assessed and is on a comparable basis for all stands.

TABLE 7.—Relative degrees of heterogeneity for the stands on the basis of species appearance in the sample plots (see text for discussion)

Stand	No. of new spp. sampled in successive plots					Total no. of spp.	No. spp. occurring in indicated no. of plots (5 plots freq. of 100%)					% of spp. in 1 plot only (F. of 20%)	% of spp. in 3 or more plots (F. over 60%)
	1	2	3	4	5		1	2	3	4	5		
1	24	8	1	2	5	40	14	4	4	4	7	35	55
3	17	9	3	4	4	37	16	11	5	2	3	43	27
2	17	6	2	2	—	27	16	2	4	1	4	59	33
9	26	8	4	2	3	43	15	4	5	9	10	35	56
10	20	8	4	4	—	36	8	8	8	7	5	22	56
4	12	3	4	3	2	24	10	5	3	1	5	42	37
5	13	7	3	2	2	27	11	6	1	2	7	41	37
6	18	2	4	3	—	27	11	5	6	2	3	41	41
7	7	5	7	1	2	22	9	6	3	2	2	41	32
8	13	1	1	4	1	20	8	5	3	1	3	40	35

the results. However, the results are intended to show that there is probably some degree of vegetational unity in each stand. Completely heterogeneous stands would perhaps show a relatively constant rate of encountering new species in successive plots. With this interpretation, stand 7 may be more heterogeneous than the others.

The right hand columns of Table 5 illustrate the frequency with which species appeared in the plots of each stand. Relatively more species having high frequencies indicates relatively less heterogeneity. Stands 1, 9 and 10 could be considered as the least heterogeneous stands by this method. A high percentage of species occurring in one plot only would imply that a stand is relatively more heterogeneous, as is stand 2 by this interpretation.

A relatively large number of species may indicate complexity for a stand, but does not necessarily indicate heterogeneity. For example, stand 1 had 40 species, yet seems less heterogeneous than most stands as 55% of its species have a frequency of 60% or more. Conversely, stand 7 has only 22 species yet may be more heterogeneous than most stands.

CONCLUSIONS

The aim of this paper was to demonstrate the feasibility of applying quantitative phytosociological techniques in fairly complex subtropical forest. From the results obtained it is apparent that such a quantitative description is feasible and yields useful results.

The phenomenon of layering, or stratification, is generally considered to be more pronounced in tropical and subtropical than in temperate forests. Although discontinuous layers were not looked for in this study, the species have inherent growth properties which permit or do not permit them to become large canopy trees. Stratification, as a structural characteristic of these forests, was described by using specific size limits to classify species as to those commonly found in the canopy, subcanopy, or understorey. In the 10 stands, a total of 101 species was found, of which 38 were classified as canopy species, 49 as subcanopy species, and 14 as understorey species (i.e., shrubs). By using objective, indirect

Basal area in square inches per acre was used as an indication of the relative dominance of the species and of the various layers. Basal area is an objectively-determined measure which reflects both the size and the number of trees, and each species and layer can be expressed as a percentage of the total basal area of the stand. The relative basal area figures are considered to give an approximation of the relative influence on the environment of the various species and layers.

The subtropical forests of the Natal coast were found to be complex, having a large number of species, genera, and families, and this complexity is enhanced by layering (Table 2 and Appendix). The forests were all found to be fairly heterogeneous (Tables 2 and 3). There are definite trends in the distribution of species, with certain species tending to occur together with other species in similar habitats (Table 2). There is, therefore, a pattern in the variations from stand to stand and from area to area as illustrated in the similarity figures (Tables 4, 5 and 6). Only a few species are relatively important in each stand, and many of the same species are dominant in several stands (Table 3).

The 10 stands studied were in four forest areas. In each case the stands within one forest area had the highest degree of similarity with each other. Two of the forest areas were located on coast dunes and the other two were farther inland, altitudinally higher, and on steeper, rocky slopes. As would be expected, the dune forests were more similar to one another, as were the inland forests to each other. We may, therefore, conclude that the first order of similarity was geographical proximity, and that the second order was topographic and soil similarity (Tables 4, 5 and 6). *Protorhus longifolia* was the dominant canopy species most characteristic of the inland forests, while *Strychnos madagascariensis* and *Celtis africana* were most characteristic of the dune forests. There is an indication that the inland and dune forests represent two different communities, and that the five stands in each community represent some sort of successional trends. However, of the 77 species occurring in more than one stand, 43% of them occurred in both inland and dune stands, and no indication of discontinuous species groups or associations was noted.

An interpretation of the behaviour of the species is that of all the species present in a stand only a small percentage of them is dominant and present throughout the stand, while a large percentage occurs in very small numbers. The relatively large number of individuals appearing only occasionally in the stands leads to the interpretation of the stands as being heterogeneous. However, as seen in Table 3, only two or three species are required to attain more than 50% dominance in eight of the stands, compared with the total of 20 to 40 species found in each of the 10 stands. Four species are necessary in stand 2 and six species in stand 9 to attain 50% dominance. It is likely that this same situation regarding dominants prevails in temperate zone forests, with two or three species being dominant. However, in temperate forests, only a few other species would constitute the remainder of the stand, compared with these subtropical forests in which a large number of species constitute the remainder.

The sampling method described in this paper is relatively rapid in the field and requires a minimum of field equipment (a range-finder and a basal area tape). The analytic methods are relatively simple, yet much information is derived. The use of several smaller plots is preferable to one large one in that this avoids basing judgement on one atypical area and allows for variability within a stand. Plots of 1/10 acre are not too large to use and simplify the analytic methods. Circular plots have a smaller perimeter-to-area ratio than any polygon with the same area, which helps reduce heterogeneity. By use of a range-finder to delimit the plots, the difficulty of staking out quadrats is avoided. Sampling of smaller shrubs and herbs could easily be incorporated into the study by using several small quadrats per plot. With data from a larger number of stands, a statistical treatment of the forest communities of a larger region could be achieved.

The first criterion of stand selection was topographical homogeneity, and then visual vegetational homogeneity from a structural standpoint. Sampling and analysis of these stands then followed, and we believe that floristically defined vegetation units have been demonstrated to exist despite some heterogeneity. We therefore conclude that the analysis was justified and that the methods described offer the possibility of a broader comparative study of the relatively complex subtropical forests of Natal.

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#### UITTREKSEL

Tien subtropiese woud stande is in vier gebiede langs die kus van Natal, in die Republiek van Suid-Afrika, gemonster. Vyf 1/10 acre sirkelvormige persele binne elke stand is hiervoor gebruik. 'n Groot-totaal van 101 houtagtige spesies met stamdeursneeë groter as een duim d.b.h. is aangeteken, met 'n variasie van 20 tot 40 verskillende spesies per stand. Kwantitatiewe resultate, met inbegrip van aantal en grootte, word gegee vir die kroon, sub-kroon en onderkroon spesies soos hulle in die verskillende strata voorkom. Spesifieke grootteklasse is gebruik om die verskillende strata te

identifiseer om sodoende al die stande op 'n vergelykbare basis te plaas. Getalle van relatiewe basale bedekking per acre is gebruik as 'n aanduiding van die relatiewe dominansie van die verskillende spesies en strata. Die moontlikheid van 'n biologiese beginsel om hierdie gebruik te regverdig word vermeld.

Ten spyte van die komplekse struktuur van die stande asook die feit dat hulle heterogeen voorkom, toon die spesies van die verskillende stande nogtans soortgelyke gedragspatrone. Die ontwikkelingstendense vir die 10 stande en vier woudegebiede word aangedui. R latief min spesies kom dominant in elke stand voor en die oënskynlik hoë floristiese verskeidenheid is grotendeels toe te skryf aan die hoë persentasie spesies wat relatief skaars is. Die metodes wat hier beskryf word, behoort bruikbaar te wees in 'n studie van die breër verspreidings-gebied van woude in Natal; 'n gebied waar kwantitatiewe studies tot nou toe feitlik ontbreek het.

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#### APPENDIX

A total of 101 species in 78 genera and 39 families was sampled in the 10 stands and the taxa are listed in systematic order (Phillips, 1951). The 24 species which were omitted from Table 2 are included here, and in parentheses after each of these species is the letter C, S, or U, indicating the layer, and a number referring to the stand in which it occurred.

- PODOCARPACEAE: *Podocarpus latifolius* (Thunb.) R. Br. ex Mirb.
- AGAVACEAE: *Dracaena hookeriana* K. Koch
- ULMACEAE: *Celtis africana* Burm.f., *C. gomphophylla* Bak. (C-2), *Chaetacme aristata* Planch.
- MORACEAE: *Ficus capensis* Thunb. (C-2), *F. natalensis* Hochst.
- LAURACEAE: *Cryptocarya woodii* Engl.
- CAPPARACEAE: *Maerua racemulosa* (A. DC.) Gilg & Ben.
- LEGUMINOSAE: *Albizia adianthifolia* (Schumach.) W. F. Wight, *Baphia racemosa* (Hochst.) Bak., *Millettia grandis* (E. Mey.) Skeels.
- ERYTHROXYLACEAE: *Erythroxylum emarginatum* Thonning, *E. pictum* E. Mey. ex Sond.
- RUTACEAE: *Fagara davyi* Verdoorn (S-1), *Vepris undulata* (Thunb.) Verdoorn & C. A. Sm. (S-10), *Teclea gerrardii* Verdoorn, *Oricia bachmannii* (Engl.) Verdoorn.
- BURSERACEAE: *Commiphora harveyi* (Engl.) Engl. (S-9), *C. woodii* Engl.
- PTAEROXYLACEAE: *Ptaeroxylon obliquum* (Thunb.) Radlk. (C-9).
- MELIACEAE: *Turraea floribunda* Hochst., *Ekebergia pterophylla* (C. DC.) Hofmeyr (S-1), *Trichilia dregeana* Sond.

- EUPHORBACEAE: *Drypetes arguta* (Muell. Arg.) Hutch., *D. gerrardii* Hutch., *D. natalensis* (Harv.) Hutch., *Antidesma venosum* L. Mey. ex Tul. (S-6), *Croton sylvaticus* Hochst., *Acalypha glabrata* Thunb. (U-3), *Suregada africana* (Sond.) Kuntze, *Sapium ellipticum* (Hochst. ex Krauss) Pax, *S. integerrimum* (Hochst. ex Krauss) J. Léon., *Cavacoa aurea* (Cavaco) J. Léon.
- BUXACEAE: *Buxus natalensis* (Oliv.) Hutch. (U-7).
- ANACARDIACEAE: *Harpephyllum caffrum* Bernh., *Protorhus longifolia* (Bernh.) Engl., *Rhus chirindensis* Bak.f. forma *legatii* (Schonl.) R. & A. Fernandes.
- CELASTRACEAE: *Maytenus acuminata* (L.f.) Loes., *M. peduncularis* (Sond.) Loes., *M. undata* (Thunb.) Blakelock (U-1), *Cassine aethiopica* Thunb., *C. papillosa* (Hochst.) Kuntze.
- ICACINACEAE: *Apodytes dimidiata* E. Mey. ex Arn.
- SAPINDACEAE: *Allophylus dregeanus* (Sond.) De Wint., *A. melanocarpus* (Sond.) Radlk. (S-3), *Denbollia oblongifolia* (Sond.) Radlk., *Pancovia gongensis* (Hiern) Exell & Mendonca.
- RHAMNACEAE: *Ziziphus mucronata* Willd.
- STERCULIACEAE: *Cola natalensis* Oliv.
- OCHNACEAE: *Ochna arborea* Burch. ex DC., *O. natalitia* Engl. & Gilg.
- CLUSIACEAE: *Garcinia gerrardii* Harv. ex Sim (U-2).
- VIOLACEAE: *Rinorea angustifolia* (Thouars) Baill. (S-9).
- ELACOURTIACEAE: *Rawsonia lucida* Harv. & Sond., *Xylothea kraussiana* Hochst. var. *glabrifolia* Wild., *Scolopia zeyheri* (Nees) Harv., *Homalium dentatum* (Harv.) Warb. (S-9), *Dovyalis longispina* (Harv.) Warb.
- THYMELAEACEAE: *Peddiea africana* Harv. (U-1).
- RHIZOPHORACEAE: *Cassipourea gerrardii* (Schinz) Alston, *C. gummiflua* Tul.
- COMBRETACEAE: *Combretum kraussii* Hochst., *C. molle* R. Br. ex G. Don (S-10).
- MYRTACEAE: *Eugenia natalitia* Sond., *E. zuluensis* Dummer.
- ARALIACEAE: *Cussonia sphaerocephala* Strey, *C. nicholsonii* Strey.
- SAPOTACEAE: *Chrysophyllum viridifolium* Wood & Franks, *Bequaertiodendron natalense* (Sond.) Heine & Hemsl., *Minusops obovata* Sond., *Vitellariopsis marginata* (N.E. Br.) Aubrev., *Manilkara discolor* (Sond.) J. H. Hemsl.
- EBENACEAE: *Euclea natalensis* A. DC., *Diospyros natalensis* (Harv.) Brenan, *D. scabrida* (Harv. ex Hiern) De Wint. (U-1).
- OLEACEAE: *Schrebera alata* (Hochst.) Welw., *Linociera peglerae* (C.H. Wr.) Gilg & Schellenb., *Olea woodiana* Knobl. (S-4).
- LOGANIACEAE: *Strychnos decussata* (Pappe) Gilg, *S. henningsii* Gilg, *S. madagascariensis* Poir., *S. usambariensis* Gilg.
- APOCYNACEAE: *Carissa bispinosa* (L.) Desf. ex Brenan (U-9), *Tabernaemontana ventricosa* Hochst. ex A. DC., *Rauvolfia caffra* Sond. (C-3).
- BORAGINACEAE: *Cordia caffra* Sond.
- VERBENACEAE: *Clerodendrum glabrum* E. Mey.
- SCROPHULARIACEAE: *Anastrabe integerrima* E. Mey. ex Benth.
- RUBIACEAE: *Xeromphis obovata* (Hochst.) Keay (S-10), *Gardenia amoena* Sims, *Rothmannia globosa* (Hochst.) Keay., *Oxyanthus latifolius* Sond. (U-10), *Tricalysia capensis* (Meisn.) Sim, *Vangueria chartacea* Robyns, *Canthium ventosum* (L.) S. Moore, *C. mundianum* Cham. & Schlecht. (S-9), *C. obovatum* Klotzsch, *Pavetta lanceolata* Eckl., *Psychotria capensis* (Eckl.) Vatke.
- COMPOSITAE: *Brachylaena uniflora* Harv.

