Bothalia 14, 1: 127–130 (1982)

Dune advancement 1937–1977 at the Mlalazi Nature Reserve, Mtunzini, Natal, South Africa, and a preliminary vegetation-succession chronology

P. J. WEISSER*, I. F. GARLAND** and B. K. DREWS*

ABSTRACT

Foredune advancement on a 2 km coastline north of the Siaya Lagoon Mouth was studied using air photos. Between 1937 and 1977 the dunes advanced about 95 m (2,4 m per year). Vegetation was dated according to its position on a profile. If a 2,4 m per year seaward advancement of the dunes is assumed, the following succession chronology is obtained: *Scaevola thunbergii* Foredunes from 0 to 30 years; *Passerina rigida* Open Dune Scrub 30 to 60 years; Closed Dune Scrub 60 to 90 years and Dune Forest beginning at about 90 years. Variation in dune advancement rates on different coastal stretches and for different time intervals was observed and will be reported on later. This dune succession chronology should, therefore, only be seen as a first rough approximation.

INTRODUCTION

Huntley (1977), referring to vegetation mapping in South Africa, indicated that little effort had been expended in monitoring the rates and kinds of change taking place in vegetation. The availability of air photos (dating from 1937 to 1979) of Mtunzini, Natal, afforded the author the opportunity to contribute information in this neglected field. Objectives of this study were to evaluate the adequacy of air photos in monitoring dune advancement and vegetation changes; to measure foredune advancement and calculate advancement rates; and to infer a dune-succession chronology by dating the communities according to their position in a profile.

The two km coastline studied is part of the Mlalazi Nature Reserve and stretches from the Siaya Lagoon Mouth (latitude 28° 58' South, longitude 30° 45' 45" East) north-eastwards. The coast between Mlalazi Lagoon and the Tugela Mouth is one of the few coastlines in Natal where active sand deposition and foredune advancement is occurring. The dunefield there is formed by a series of about 16 phytogenic ridges parallel to the coast and is about 400 m broad. Edwards (1967) and Moll (1972) described dune communities of this region.

METHODS AND METHODOLOGICAL CONSIDERATIONS

The dune vegetation and its advancement were studied by direct inspection of air photos. The information was transferred onto a 1: 10 000 base map using a Bausch & Lomb ZT-4 Zoom Transfer Scope (=ZTS). This instrument was also employed to draw the base map from the orthophoto map 2831 DD 21 'Mtunzini' (1977). Interpretation of aerial photographs was aided by a Topcon Stereoscope. Roads were mainly used as matching lines. Limits of the foredunes were drawn onto overlays and their progression was measured with a 1/10 mm graduated ocular. About one hundred systematic sampling lines were drawn perpendicular to the coast on the base map starting at the Siaya Lagoon Mouth and going northwards. A north-eastward longshore advancement of the Siaya Lagoon Mouth of about 740 m from 1937 to 1977 was found, i.e. about 17,4 m per annum. Air photos 54693 (Job 117, of 1937.05.05), 6447 (Job 400, 1957.05.24), 5665 (Job 608, 1969.08.18) and the orthophoto 2831 DD 21 (Job 498/91, June 1979) were used. Ground truth was gathered on 1974.09.15, 1975.11.03, 1978.06.29, 1980.03.27, 1980.05.15, 1980.06.11 and 1980.06.12.

The potential and limitations of air photos in vegetation studies have been discussed by Edwards (1972) and, in relation to dune vegetation in Zululand, by Weisser (1979). Concerning this study the following points should be borne in mind. The photographs are at different scales, and were not taken at the same time of the year which impairs their comparability. Another factor is the differing resolution of the air photos, the 1937 photos being the weakest.

The evaluation of the results is complicated because dune advancement is not a linear process. It occurs in pulses, each pulse corresponding to the detection of an additional dune ridge on the air photo. There is a time lag between the establishment of *Scaevola thunbergii* seedlings, the accumulation of sand and the appearance of the new ridge on the air photo. These dunes are at first isolated and later colaesce to a coastal parallel ridge (Figs 1 & 2).

The distance between the dune ridges is not uniform. At Twinstreams, south of the Siaya Mouth, the average distance between the last four dune crests was 25 m. Distances measured on the transect published by Moll (1972) over the whole dune field suggest a distance of about 22 m between crests.

RESULTS AND DISCUSSION

Air photos of a scale equal to or less than 1: 30 000 were found adequate for monitoring and measuring the advancement of the foredunes provided matching lines or points were available. Air photos of 1977 and 1979 were discarded, because the small area covered provided insufficient matching points in the optical field of the ZTS.

Fig. 3 summarizes the distance measurements as interpreted from the photos. From 1937 to 1957 (20 years), the *Scaevola thunbergii* Foredunes advanced

*Botanical Research Institute, Department of Agriculture and Fisheries, Private Bag X101, Pretoria, 0001.
**P.O. Box 83, Mtunzini, 3867.

FIG. 1.—Foredunes at Twinstreams, Mtunzini (Nov. 1975). New *Scaevola thunbergii* dune being formed. First dune started in June 1973 (observation by I. Garland).

FIG. 2.—Picture taken from approximately same point as in Fig. 1. It shows how sand accumulation has progressed from November 1975 to June 1978. At this time, seedlings of *Scaevola thunbergii* were already colonizing the beach and starting a new dune ridge.

seawards by about 42 m, in 1969 (after 32 years) the distance had increased to 81 m and in 1977 (after 40 years) to 95,2 m. The average rate of advancement from 1937 to 1977 was 2,4 m per year. No advancement values could be obtained for other plant communities because their limits on the air photos are difficult to interpret consistently. While the seaward limit of the foredunes is well defined and corresponds to a *'limes convergens'* the others are of the *'limes divergens'* type (Van Leeuwen, 1966).

Space/time relations

The distance of dune ridges from the seashore is directly proportional to their age and *vice versa*. The foredune advancement rate of the last 40 years was 2,4 m per year north of the Siaya Mouth. Therefore, it is possible to date the ridges and their vegetation by measuring the distance from the beach.

This possibility of dating vegetation led us to extend our studies south to the farm Twinstreams. Whereas processes and dune advancement values similar to those north of the Siaya Mouth were encountered, the lack of matching points in the limited optical field of the ZTS made precise distance measurements difficult.

On a speculative level, and if the yearly advancement rate of 2,4 m is applied to the transect published by Moll (1972), the positions of the communities on the transect suggest the following succession schedule (Table 1):

(1) It agrees with Moll (1972) in that it takes about 10 years for a dune ridge to be formed under present conditions (Fig. 2).

(2) It will take about 30 years to become invaded and later replaced by the *Passerina rigida* Open Dune Scrub (Fig. 4).

FIG. 3.—In foreground, *Scaevola thunbergii* Community being invaded, and thereby phased out, by grass *Stipagrostis zeyheri* and shrubs such as *Passerina rigida, Colpoon compressum, Canthium obovatum, Apodytes dimidiata, Mimusops caffra* and *Brachylaena discolor*. Closed Dune Scrub lies at top of ridge, concealing Dune Forest (1978.07.29).

(3) It will take about another 30 years before this scrub is replaced by Closed Dune Scrub (Fig. 4).

(4) If protection against seawinds and saltspray is given by the seaward ridges and their vegetation, a Dune Forest could develop after about 90 years, beginning in the dune slacks and later spreading from there.

The reliability of the space/time relation is reduced by the variation in dune advancement rates on different coastal stretches and at different time intervals. In some places, e.g. in the northern part of the Mlalazi Reserve, there has lately been a tendency for the height of the existing dunes to increase instead of new ridge formation and dune advancement seawards taking place. The key factor to the differing deposition of sand, i.e. either in the formation of new ridges or in increasing the height of existing ones, is the establishment of *Scaevola thunbergii* seedlings on the beach and the accumulation of sand around these obstacles. If beach conditions do not allow establishment of *Scaevola thunbergii*, the landward-blown sand will tend to get trapped in the existing foredunes and contribute to their height increase. High and low ridges in Moll's profile suggest that they have held their position adjacent to the beach for varying periods of time before being replaced and outcompeted for sand by new ridges. High dune ridges suggest longer periods near the seafront, during which sand had time to accumulate. The occasional destruction of ridges by unusual storms and tides must also be considered.

A recent increase in the rate of sand deposition is likely, because of the increased sediment load of the Tugela River following agricultural malpractices in the catchment areas. Part of the sand is transported northwards by longshore drift (Orme in Begg, 1978). However, the LANDSAT satellite image No. 1190–07143 of 29th January 1973, shows the sediment plume of the Tugela extending mainly southwards.

The space/time relationships obtained here must be regarded as a first approximation and should be followed up by studies with permanent plots. C. J. Ward (pers. comm.) and MacDonald and Pammenter (MS) have laid out permanent vegetation plots and transects in the Twinstreams area and Mlalazi Nature Reserve which will allow future refinement of this interim dune vegetation-succession chronology.

TABLE 1.—Position and spatial range of dune vegetation and its inferred age assuming a seaward advancement of 2,4 m per year

	Distance of beginning of sere from first pioneer plants (Moll's transect)	Time taken for succession of community to commence	Range of community	Approximate duration of sere (assumed rate of vegetation advance 2,4 m per year)
	m	years	m	years
Pioneers	0		72	± 30
Passerina rigida Open Dune Scrub	72	30	74	± 31
Closed Dune Scrub	146	60	68	± 28
Dune Forest	214	89		

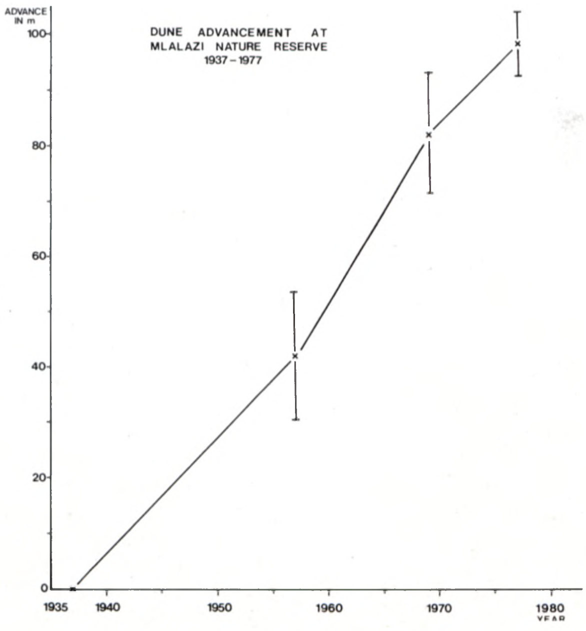

FIG. 4.—Foredune advancement at the Mlalazi Nature Reserve. Total distance of the dune advance 1937–1977 was 95 m and the average rate 2,4 m per year.

ACKNOWLEDGEMENTS

We would like to thank Drs J. C. Scheepers, D. Edwards and J. Walker, Messrs W. de Waal and P. Frost. Mesdames S. Frost and J. N. Weisser, and Miss R. J. Parsons for their valuable comments; Mr C. Buthelezi for his help during field work; Mesdames J. Mulvenna and S. Smit for typing the manuscript; Mr R. E. Crofts (Office of the Surveyor General), Prof. D. A. Scogings and Mr A. Bikaroo (Survey Department, University of Natal) for their collaboration in obtaining aerial photographs; Mrs A. Romanowski for photographic work; Mrs J. Schaap for the diagrams, and the Natal Parks, Game and Fish Preservation Board for their support during field work.

UITTREKSEL

Die voortgang van die voorste duine is bestudeer op 'n 2 km kuslyn noord van die Siaya strandmeermonding deur middel van lugfoto-interpretasie. Tussen 1937 en 1977 het die duine 'n afstand van ongeveer 95 m aangeskuif (2,4 m per jaar). Die plantegroei se posisie is ooreenkomstig hul posisie op die profiel gedateer. Indien aanvaar word dat die seewaartse voortskuiwing van die duine 2,4 m per jaar is, word die volgende chronologiese suksessie verkry: die voorste duine met Scaevola thunbergii *vanaf 0 tot 30 jaar;* Passerina rigida *Oopduinstruikgewas 30 tot 60 jaar; Geslote-duinstruikgewas 60 tot 90 jaar en Duinwoud begin ongeveer by 90 jaar. Verandering in die tempo van duinvooruitgang by verskillende kusstreke, sowel as teen verskillende tydintervalle, is waargeneem. Hierdie chronologiese suksessie van die sandduine moet gevolglik slegs as 'n eerste rowwe skatting gesien word.*

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Bothalia 14, 1: 131–138 (1982)

Aboveground biomass categories of woody plants in a *Burkea africana* – *Ochna pulchra* Savanna*

M. C. RUTHERFORD**

ABSTRACT

Aboveground peak season biomass is given for 11 woody species in each of five belt transects on the Nylsvley savanna study site. Mean aerial biomass for all species was 16 273 kg ha^{-1}, made up of 14 937 kg ha^{-1} wood, 236 kg ha^{-1} current season's twigs and 1 100 kg ha^{-1} leaves with an additional 1 859 kg ha^{-1} of dead wood attached to the individuals. Species which contributed most to total biomass were *Burkea africana* (8 687 kg ha^{-1}), *Ochna pulchra* (2 136 kg ha^{-1}) and *Terminalia sericea* (1 734 kg ha^{-1}). *Grewia flavescens* differed from all other species in having a proportionately larger mass of dead wood and current season's twig biomass. Shrub-sized individuals constituted 11,5% of mean total biomass and 29,7% of mean leaf mass for all species together. Values recorded in the five belt transects differed considerably, for example, leaf area index (LAI) ranged from 0,5715 in belt transect C to 1,0094 in belt transect A. The mean biomass data for the Nylsvley savanna site correspond with available biomass data for savanna vegetation elsewhere in southern Africa.

INTRODUCTION

The South African Savanna Ecosystem Project is being conducted on a portion of the Nylsvley Nature Reserve (3 120 ha in extent), 10 km south of Naboomspruit in the northern Transvaal. The basic ecological characteristics of the study area are described in Huntley & Morris (1978), while the projects overall objectives and research programme are outlined in Huntley (1978).

The study area lies on the edge of the Springbok flats on a slightly raised plateau at about 1 100 m above sea level. Most of the Waterberg System sandstone bedrock is covered by sandy soils belonging mainly to the Hutton and Clovelly forms (Harmse, 1977). Mean annual rainfall is about 630 mm and occurs mainly in summer. The mean annual air temperature is 18,6°C. The study site's past management has included light summer grazing by cattle with small populations of impala and fluctuating populations of kudu present. Fire has occurred irregularly at approximately five year intervals though there is evidence of more frequent fire in the south-western part (belt transects D, E) of the study area. The main vegetation type of the study area has been classified as *Eragrostis pallens* – *Burkea africana* Tree Savanna (Coetzee *et al.*, 1976) with the most extensive variation of this being the *Eragrostis pallens* – *Dombeya rotundifolia* variation with dominant trees *Burkea africana* and *Terminalia sericea* and dominant shrubs *Ochna pulchra* and *Grewia flavescens* (Fig. 1). Huntley (1977) suggests that the broad-leaved savanna of the study area is related to the mesic and moist broad-leaved savanna biome of Africa.

Scattered at several localities within the study area are small abandoned native settlement areas which now support a flora very different to that of the remainder of the study area.

The first objective of the Savanna Ecosystem Project has been to determine 'the structure and dynamics of the ecosystem as a whole' (Anon, 1975), and Phase I in the project includes 'the description and quantification of structural features of the ecosystem' (Huntley, 1978). The objectives of the study described in this paper fell within this first phase of the overall ecosystem project, and were to determine the biomass of the main aboveground categories of the woody species present and the variation from one part of the study area to another. This paper is largely limited to presentation of data and detailed discussion of methods is available elsewhere (Rutherford, 1979).

DEFINITION OF TERMS

Biomass is defined as oven dry mass of live, actively or structurally functional organic material and does not include the dead wood category. The categories which were determined included:

— Total biomass, the total living or functional mass.

— Biomass of the stem, mainly wood.

— Biomass of branches, mainly wood. Where stem and branch biomass were not separated, this is referred to as wood biomass.

— Biomass of current season's twigs.

— Biomass of leaves. Current season's twig mass together with leaf mass, that is the total mass of current terminal growth, is referred to as shoot biomass.

— Mass of dead wood (branches and twigs) still attached to the plant individual.

— Leaf area.

All shrubs and trees with stem diameters equal to or greater than one centimetre at 20 cm above ground level were included in the study. Individuals with stems less than one centimetre in diameter were clipped and included in an independent study of

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* This is a publication of the South African Savanna Ecosystem Project and is an abridged form of a report (No. 36) of the South African National Scientific Programmes.

** Botanical Research Institute, Department of Agriculture and Fisheries, Private Bag X101, Pretoria, 0001.

FIG. 1.—View of the vegetation in a part of Transect A in which aboveground woody plant dry mass (functional and dead) was estimated at 21 602 kg ha^{-1}.

herbaceous layer production. In terms of mass, in both the 1975/76 and 1976/77 seasons, flowering and fruiting was negligible compared to any of the other mass categories and was also very sporadic. Biomass of generative material is therefore not included.

Shrubs were defined as individuals with height less or equal to 2,5 m and trees were taller than 2,5 m. The use of 2,5 m height as a basis for separation of shrub- and tree-sized individuals is arbitrary but 2,5 m is a height above which virtually no browsing by larger herbivores present can take place. It is also a height below which shoot growth points are most commonly damaged after fire on the Nylsvley site.

METHODS

Survey areas

Lubke *et al.* (1976) have described how five belt transects were selected to best represent the woody vegetation of the ecosystem study site. These areas represent the three variations and the subvariations of *Eragrostis pallens* — *Burkea africana* Savanna of Coetzee *et al.* (1976). These selected areas do not include *Acacia* patches of old abandoned settlements, sandstone hills or occasional rocky outcrops, or fire-break areas. These five areas were used by Lubke *et al.* (1976) for an intensive survey of woody species structure including detection of pattern of distribution. The five areas are designated A in the north-east of the study area through to E in the south-west of the study area.

In the present study, all or part of each of these belt transects was used as basis for estimation of biomass of woody species, respective sample sizes being 0,875 ha in transect A, 1, 6 ha in transect B, 0,8 ha in transect C, 0,96 ha in transect D and 0,96 ha in transect E. The total area sampled for application of biomass relations was therefore 5,195 ha. Belt transects D and E have been set aside for destructive sampling with areas A, B and C being protected. Our own measurements of dimension were used for trees but data of Lubke *et al.* (1976) (using smaller parts of each sample strip) were used for shrub-sized individuals (except for *Grewia flavescens*).

Biomass estimation

The method used involved a destructive phase in which a number of individuals of each of the more important woody plant species were measured for various dimensions (see Appendix 1), then felled and the above defined parts of the plant weighed oven dry. All plant material was dried to constant mass at 85°C. A relational stage followed where dimensions were appropriately related to the various mass categories of the plant resulting in a predictive relation for each species (function types in Appendix 1). A third phase involved a large-scale field survey in which all individuals were measured for the predictor variables in plots of known size, whereupon the predictive relations were applied to give the mass of the various categories per unit ground area.

Because the number of different species involved was too large for equally intensive treatment of each, species were divided into convenient groups, based on plant abundance data available from early surveys.

The first group contained the four species, *Burkea africana, Ochna pulchra, Terminalia sericea* and *Strychnos pungens* in each of which a full size range of up to 49 individuals were processed in detail, providing from primary data, the predictive equations listed in Appendix 1. Leaf area data were obtained from leaf mass data by determination of Specific Leaf Area (cm^2/g) in each species. Stem wood was calculated by subtraction of all other biomass categories from total biomass.

The second group contained the next three, much less abundant species, *Vitex rehmannii, Combretum zeyheri* and *Dombeya rotundifolia*. The method was as in the first group except that the size of the field sample was much reduced, as little as three very carefully selected representative individuals being analysed in full. These restricted data were then plotted out together with relations for the species of the first group and used to determine what constants (if any) should be applied to the equations for the species of the first group to form new predictive equations. This method resulted in quantitative approximations of the biomass categories.

A third group comprised several distinctly rarer species. *Strychnos cocculoides* and *Combretum molle* were subjectively matched according to affinity at the generic level. Two *Securidaca longipedunculata* individuals were sampled in the field since matching here was less obvious. The two *Combretum* species *(C. zeyheri* and *C. molle),* from inspection of several individuals, appeared similar for each biomass category. *Strychnos cocculoides* appeared similar to *S. pungens* except in respect of the relations for total biomass and mass of dead wood.

A fourth group included all other rarer species for which no field mass data existed and there was no clear basis for matching with any particular other species. Here the combined relations of the group with the most reliable data (the first) were used. The above relations are valid for the peak of growth season (based on completion of terminal growth). Almost all field work was done in the 1975/76 season.

A fifth 'group' contained only the multi-stemmed shrub *Grewia flavescens*. The method described above for individual stems was found impractical to apply owing to the prohibitively large numbers of such stems in the enumeration-type survey. The alternative use of a 'whole individual' predictor for dimensions such as that of canopy diameter were found unsuitable owing to large variation in density and spacing of individual stems. Another test showed large scale harvest of all *G. flavescens* individuals over large areas, without recourse to predictive relations, was unacceptable due to several sampling problems. A further approach, which was finally accepted, made use of *G. flavescens* individuals stratified upon four modes of growth and die-back. Mean mass ratios were then applied to each of these different forms for shrub-sized and tree-sized individuals.

RESULTS

Biomass of different plant parts for tree- and shrub-sized individuals of each species is given in Table 1. Biomass proportions are summarized in Table 2. Shrubs had a far greater proportion of terminal growth than trees. It is particularly in current twig biomass of shrubs that exclusion of *Grewia flavescens* greatly reduced the relative contribution of this category. The other biomass categories are little affected by inclusion or exclusion of *G. flavescens*. However, in the dead wood mass category, it is important to differentiate between relative contributions with or without *G. flavescens*. It is particularly the shrub-sized individuals where the exclusion of *G. flavescens* causes a very large decrease in the relative contribution of dead wood mass. That *G. flavescens* differs from other species in respect of relative amounts of twig biomass and dead wood mass may not be merely fortuitous. These two aspects are likely to be linked since the large scale die-off of older parts allows for new self-supported shoot growth only from ground level. There are indications that proportions of dead wood mass in *G. flavescens* can vary greatly with season.

An example of a typical breakdown of biomass categories in a tree species is provided by *Burkea africana* (Table 3). For those species in which stem wood biomass and branch wood biomass were measured separately, that is in *B. africana, Ochna pulchra* and *Terminalia sericea* which make up more than three-quarters of the total biomass of all species, virtually twice as much stem wood as branch wood biomass was found, varying from 2,14 times more in *Burkea africana* to 1,37 times in *Ochna pulchra*.

Four species (Fig. 2) accounted for 81,9% of shoot mass or terminal production. A major contribution of 93,8% to dead wood mass was made by the same four species. Although *Burkea africana* comprised more than half the total biomass, its productivity (terminal) was only about one-third of the total. Conversely, the percentage contribution of *Ochna pulchra* to total terminal production is about twice that of its percentage contribution to total biomass while *Grewia flavescens* productivity rank position of 4 drops to 10 relative to total biomass.

Dead wood was also the only mass category where only three species accounted for more than 90% of the total amount. The mass of dead wood as a percentage of total mass was 79,3% for *G. flavescens*, 10,5% for *Terminalia sericea* and 5,6% for *Burkea africana*. The other separately considered species varied between 1,6 and 4,9%. Three of the four species with the greatest terminal growth capacity also had the highest percentage of dead wood mass. Leaf mass and leaf area differences between species followed the pattern of differences in shoot mass (Fig. 2), with the clear exception of *Grewia flavescens*.

Biomass and leaf area variation within the study site is summarized in Table 4. There were relatively large differences in woody species leaf area index (LAI) from one transect to another (Fig. 3) where, for example, LAI in transect A was 177% of that in transect C.

DISCUSSION

The mean woody species basal (at 20 cm above ground) area (excepting *Grewia flavescens*) is 6,26 m^2 ha^{-1} varying from 7,40 m^2 ha^{-1} in transect A to 4,52 m^2 ha^{-1} in transect C. This basal area is lower than the 8 m^2 ha^{-1} quoted for a long protected savanna woodland with *Burkea africana* dominant in north-eastern South West Africa/Namibia (Rutherford, 1978) and the 8,5 m^2 ha^{-1}, in a *B. africana* dominated community about 7 km from the Nylsvley study area, that had been protected from fire for several decades (Rutherford & Kelly, 1978). The Nylsvley study area has a lower woody species basal area than similar communities elsewhere possibly owing to the more frequent occurrence of fire on the Nylsvley site. This lower basal area is also reflected in a lower total biomass.

The mean total biomass for the Nylsvley site (16 273 kg ha^{-1}) is considerably less than the 22 300

TABLE 1.—Mean mass and leaf area data for the Nylsvley study site*

Species	Size Class	Biomass kg ha^{-1}					Dead Wood Mass kg ha^{-1}	Leaf Area m^2 ha^{-1}
		Total	Stem Wood	Branch Wood	Cur-rent twig	Leaf		
Burkea africana	Tree	8 495	5 560	2 512	59	364	462	2 597
	Shrub	193	47	102	8	36	57	257
	Total	8 687	5 607	2 614	66	400	519	2 854
Ochna pulchra	Tree	887	597	210	7	73	23	532
	Shrub	1 250	450	554	30	216	19	1 733
	Total	2 136	1 047	764	36	289	42	2 266
Terminalia sericea	Tree	1 631	1 007	470	9	145	195	889
	Shrub	104	35	53	1	15	9	88
	Total	1 734	1 042	522	10	160	204	977
Grewia flavescens	Tree	91	53		27	11	373	76
	Shrub	164	69		59	36	604	250
	Total	256	123		86	47	977	325
Vitex rehmannii	Tree	742	659		12	71	12	509
	Shrub	74	61		2	11	1	76
	Total	815	719		14	82	13	587
Combretum zeyheri	Tree	691	646		9	36	28	261
	Shrub	0	0		0	0	0	2
	Total	691	646		9	36	28	263
Dombeya rotundifolia	Tree	378	350		7	21	11	145
	Shrub	1	1		0	0	0	3
	Total	380	352		7	21	11	148
Combretum molle	Tree	351	334		3	14	12	104
	Shrub	2	1		0	1	0	4
	Total	353	334		4	15	12	107
Strychnos pungens	Tree	273	265		0	8	8	43
	Shrub	38	33		0	5	1	33
	Total	312	298		0	14	9	76
Strychnos cocculoides	Tree	446	433		1	12	23	57
	Shrub	2	2		0	0	0	2
	Total	448	435		1	12	23	59
Securidaca longipedun-culata	Tree	205	199		1	5	7	33
	Shrub	2	2		0	0	0	1
	Total	207	201		1	5	7	34
Remaining species	Tree	213	199		1	13	11	85
	Shrub	43	35		1	7	3	45
	Total	255	233		2	20	14	131
All species	Tree	14 402	13 493		135	773	1 165	5 331
	Shrub	1 872	1 444		101	327	694	2 495
	Total	16 273	14 937		236	1 100	1 859	7 826

*0 signifies a positive amount less than 0,5

In a few cases the independently estimated total biomass does not precisely equal the sum of the constituent biomasses. This is due to one or both of the following reasons depending on species and area: 1, All computer calculations from the application of the allometric formulae onwards were carried out retaining several decimal places. This was to reduce the magnitude of round-off error that would otherwise be propagated during calculation. To obtain minimum round-off error per separate mass category, data were converted to integer form only in the final presentation but this sometimes results in imperfectly additive matrices relative to the last significant digit; 2, For the smallest shrub of some species the estimate of its stem wood mass, through subtraction, becomes marginally negative owing to the predictor variables being applied at the extreme limit of regression range. Such estimates were automatically set to zero as the most feasible estimate of stem wood mass in such individuals. Only where such shrubs occurred in exceptionally large numbers did this setting to zero slightly affect the equality between total biomass and the sum of the constituent biomasses.

Two typographical errors which appeared in the prediction equations of the original report have been corrected. The biomass results remain unchanged.

TABLE 2.—Relative contribution of mass categories for tree- and shrub-sized individuals*

	Trees and shrubs	Trees	Shrubs
Percentage wood biomass	91,8	93,7	77,4
Percentage twig biomass	1,4 (0,9)	0,9 (0,8)	5,4 (2,4)
Percentage leaf biomass	6,8	5,4	17,5
Percentage dead wood mass (of total mass)	10,3 (5,2)	7,5 (5,2)	27,1 (5,0)

* Values in brackets are for all species omitting *Grewia flavescens* as a percentage of total biomass (or of total mass for the bottom line) of the non-*G. flavescens* group.

TABLE 3.—Biomass proportions in the *Burkea africana* population

	Stem wood	Branch wood	Leaf	Twig
Trees	65,5%	29,6%	4,3%	0,7%
Shrubs	24,5%	52,6%	18,7%	4,0%
Total	64,6%	30,1%	4,6%	0,8%

TABLE 4.—Mass and leaf area data for the woody plant component of different areas of the Nylsvley study site

Transect	Size Class	Biomass kg ha^{-1}				Dead Wood Mass kg ha^{-1}	Leaf Area m^2 ha^{-1}
		Total	Stem & Branch Wood	Current twig	Leaf		
A	Tree	17 062	16 029	146	887	1 202	6 153
	Shrub	2 963	2 368	93	502	378	3 941
	Total	20 022	18 397	239	1 388	1 580	10 094
B	Tree	14 767	13 868	135	764	1 155	5 211
	Shrub	1 568	1 187	115	266	925	1 989
	Total	16 335	15 055	250	1 030	2 079	7 200
C	Tree	11 040	10 418	102	520	836	3 652
	Shrub	1 605	1 240	90	277	614	2 063
	Total	12 647	11 658	192	797	1 450	5 715
D	Tree	14 065	13 081	137	847	1 201	5 798
	Shrub	736	510	74	152	649	1 135
	Total	14 800	13 591	210	999	1 850	6 933
E	Tree	15 073	14 069	157	847	1 431	5 841
	Shrub	2 483	1 915	131	438	903	3 346
	Total	17 555	15 984	288	1 285	2 334	9 187
ALL	Tree	14 402	13 493	135	773	1 165	5 331
	Shrub	1 872	1 444	101	327	694	2 495
	Total	16 273	14 937	236	1 100	1 859	7 826

kg ha^{-1} for the abovementioned South West African site although the 20 022 kg ha^{-1} of Nylsvley transect A is in closer agreement. Dayton (1978) found that the biomass of *Combretum apiculatum* and *C. zeyheri*, the two dominant woody plant species in a savanna community in the eastern Transvaal lowveld, was 16 909 kg ha^{-1}. The individuals of these species accounted for about 85% of the woody species crown cover of the community. Kelly & Walker (1976) determined woody plant biomass of nine sites in *Colophospermum mopane* dominated communities in a region with an annual rainfall of approximately 500 mm in south-eastern Zimbabwe. Woody plant biomass ranged from 8 726 to 30 782 kg ha^{-1} and averaged 19 694 kg ha^{-1}. This average value is very similar to the biomass value for transect A of the Nylsvley study site. The relative contributions of the first six ranking species to total woody plant biomass is given in Table 5 for comparison of the Nylsvley site with the South West African site (Rutherford, 1975) and the Zimbabwean site (Kelly & Walker, 1976). The Zimbabwean *C. mopane* site with the median total biomass value was selected for the comparison. It is clear that relative to the other given communities, a considerably greater proportion of the total biomass is unaccounted for by the six major contributing species on the Nylsvley site(s). This relatively lower degree of dominance on Nylsvley is also apparent when compared in terms of basal area to the long-term fire protected *Burkea africana* community seven kilometres from Nylsvley (Rutherford & Kelly, 1978). The relative contribution of shrub biomass to total woody plant biomass for the

Nylsvley site (12%) is virtually identical to the mean proportion (11%) of shrubs given for the Zimbabwean *C. mopane* sites.

The leaf production (1 100 kg ha^{-1}) or shoot production (1 336 kg ha^{-1}) of the Nylsvley site agrees well with data for other savanna areas (Rutherford, 1978), particularly with that of the South West African site. For their *Colophospermum mopane* sites, Kelly & Walker (1976) obtained an average shoot production of 1 506 kg ha^{-1} season $^{-1}$ which is 8% of the mean total biomass. This proportion is identical to that found for the Nylsvley site where shoot production was also 8% of total biomass. For the two dominant woody species in the abovementioned *Combretum apiculatum* and *C. zeyheri* savanna community, Dayton (1978) found shoot production to constitute 9% of the total biomass. On Nylsvlei, the terminal shoot production by the woody species was greater than for example, the

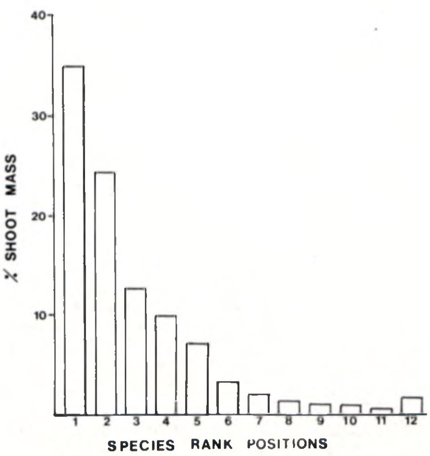

FIG. 2.—Relative contribution of different species to total current season's shoot biomass. Species rank positions are: 1, *Burkea africana;* 2, *Ochna pulchra;* 3, *Terminalia sericea;* 4, *Grewia flavescens;* 5, *Vitex rehmannii;* 6, *Combretum zeyheri;* 7, *Dombeya rotundifolia;* 8, *Combretum molle;* 9, *Strychnos pungens;* 10, *Strychnos cocculoides;* 11, *Securidaca longipedunculata;* 12, remainder.

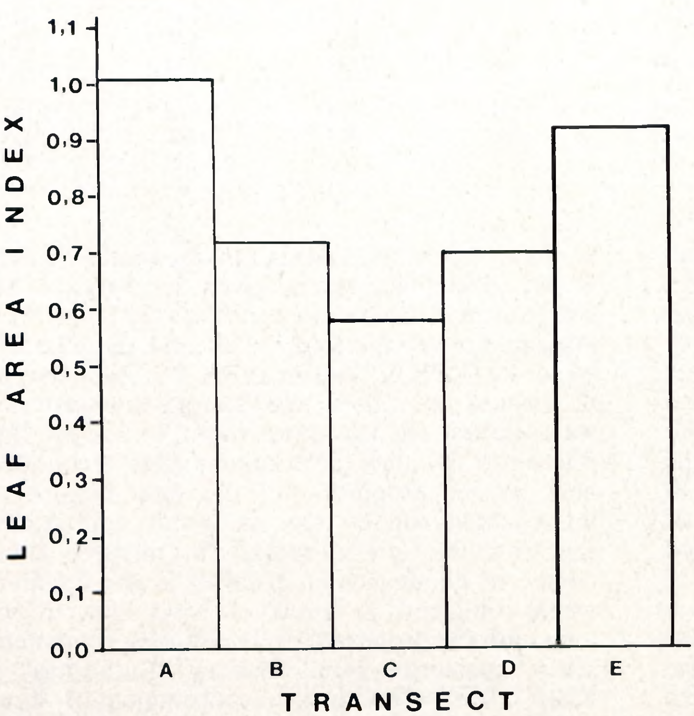

FIG. 3.—Leaf area indices for each transect of the study area.

TABLE 5.—Comparison of species' relative contributions to total woody plant biomass for selected southern African savanna communities (sources in text)

Nylsvley *Burkea africana* community (all transects)			Nylsvley *Burkea africana* community (Transect A)			South West African/Namibian *Burkea africana* community			A Zimbabwean *Colophospermum mopane* community		
Species	Biomass kg ha^{-1}	%	Species	Biomass kg ha^{-1}	%	Species	Biomass kg ha^{-1}	%	Species	Biomass kg ha^{-1}	%
Burkea africana	8 687	53,4	Burkea africana	9 957	49,7	Burkea africana	11 801	52,9	Colophosperum mopane	13 002	60,9
Ochna pulchra	2 136	13,1	Ochna pulchra	3 753	18,7	Terminalia sericea	6 153	27,6	Combretum apiculatum	7 812	36,6
Terminalia sericea	1 734	10,7	Combretum zeyheri	2 066	10,3	Combretum psidiodes	3 405	15,3	Acacia nigrescens	211	1,0
Vitex rehmannii	815	5,0	Terminalia sericea	1 932	9,6	Ochna pulchra	226	1,0	Cissus cornifolia	110	0,5
Combretum zeyheri	691	4,2	Dombeya rotundifolia	521	2,6	Combretum collinum	195	0,9	Dalbergia melanoxylon	100	0,5
Strychnos cocculoides	448	2,8	Grewia flavescens	275	1,4	Securidaca longipedunculata	160	0,7	Commiphora africana	79	0,4
Remainder	1 762	10,8	Remainder	1 518	7,6	Remainder	350	1,6	Remainder	53	0,2
Total	16 273	100,0	Total	20 022	100,0	Total	22 290	100,0	Total	21 367	100,0