Aboveground biomass subdivisions in woody species of the savanna ecosystem project study area, Nylsvley

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A report of the Savanna Ecosystem Project
National Programme for Environmental Sciences

SOUTH AFRICAN NATIONAL SCIENTIFIC PROGRAMMES REPORT NO

36

JANUARY 1979

Issued by
Cooperative Scientific Programmes
Council for Scientific and Industrial Research
P O Box 395
PRETORIA 0001
from whom copies of reports in this series are available on request.

Printed 1979 in the Republic of South Africa
by the Graphic Arts Division of the CSIR

ISBN 0 7988 1445 4

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PREFACE

The Savanna Ecosystem Project of the National Programme for Environmental Sciences is one of several national scientific programmes administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1970 by ICSU (International Council of Scientific Unions) to act as a focus of non-governmental international scientific effort in the environmental field.

The Savanna Ecosystem Project being carried out at Nylsvley is a joint undertaking of more than fifty scientists from the Department of Agricultural Technical Services, the Transvaal Provincial Administration, the CSIR, the Transvaal Museum, and eight universities. As far as possible, participating laboratories finance their own research within the project. The shared facilities at the study area and the research of participating universities and museums are financed from a central fund administered by the National Committee for Environmental Sciences and contributed largely by the Department of Planning and the Environment.

The research programme of the Savanna Ecosystem Project has been divided into three phases - Phase I (mid 1974 to mid 1976) - a pilot study of the Nylsvley study area, in particular the description and quantification of structural features of the ecosystem, Phase II (mid 1976-1979) - studies in the key components and processes including the development of mathematical models, and Phase III (1979-1984) - extension to other sites and the study of management strategies for the optimal utilization of Burkea savanna ecosystems.

The present report forms part of the description and quantification of the structural features of the ecosystem, namely the determination of the biomass of the main aboveground categories of the woody species present and the variation from one part of the study area to another.

ABSTRACT

Aboveground peak season biomass is given for 11 woody species in each of five belt transects under study. 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.

SAMEVATTING

Bogrondse biomassa word gegee vir elf houtagtige plantsoorte in elk van die vyf strooktransekte wat bestudeer is. Die gemiddelde bogrondse biomassa vir al die houtagtige plantsoorte was 16 273 kg ha^{-1}, bestaande uit 14 937 kg ha^{-1} hout, 236 kg ha^{-1} huidige seisoenlote en 1 100 kg ha^{-1} blare, asook 'n addisionele 1 859 kg ha^{-1} dooie hout aan die individue. Die plantsoorte wat die grootste bydrae tot die totale biomassa gelewer het, was *Burkea africana* (8 687 kg ha^{-1}), *Ochna pulchra* (2 136 kg ha^{-1}) en *Terminalia sericea* (1 734 kg ha^{-1}). *Grewia flavescens* het van die ander plantsoorte verskil deurdat dit 'n proporsioneel groter massa dooie hout en ook 'n groter biomassa van huidige seisoenlote gehad het. Individue van struikgrootte het 11,5% van die gemiddelde totale biomassa en 29,7% van die gemiddelde blaarmassa van al die plantsoorte uitgemaak. Die waardes wat bepaal is in die vyf strooktransekte het aansienlik verskil : die blaaroppervlakte-indeks het byvoorbeeld gewissel van 0,5715 in strooktransek C tot 1,0094 in strooktransek A. Die gemiddelde biomassa-data vir die Nylsvley savanna-studiegebied stem ooreen met beskikbare biomassa-data vir savanne-plantegroei elders in Suidelike Afrika.

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INTRODUCTION

The South African Savanna Ecosystem Project is being conducted on a portion of the recently established 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 and 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. Huntley (1977) suggests that the broadleafed savanna of the study area is related to the mesic and moist broadleafed 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 report is largely limited to presentation of data which are important for the needs of the other researchers currently active in the project. Detailed consideration of methods, choice of biomass relations and particular practical problems encountered form the subject of a separate paper (Rutherford in prep).

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 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 thus 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 severe damage to shoot growth points occurs after fire such as may be expected to occur within the fire cycle as it exists 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 thus 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*).

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 analyzed 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 thus 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. Here more detail must be given of the very different approach that was needed in the estimation of its biomass. 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 Grewia 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 Grewia individuals stratified upon their different modes of growth and die-back. Mean mass ratios were then applied to each of these different forms. Four distinct and easily recognised growth mode forms were taken and each divided into shrub-sized and tree-sized individuals as with the other species. The four types were defined as follows :

- Type 1 : Only current season's growth produced from base of individuals. All older stems dead.

- Type 2 : All older stems dead but with basal growth markedly less vigorous than in Type 1 (less than 4 mm in stem diameter).

- Type 3 : Vigorous basal shoots as in Type 1 but with older upper parts alive, that is with terminal current growth not limited to basal growth.

- Type 4 : Older upper parts live but with less vigorous basal growth.

Thus in summary :

	Older upper parts live	Older parts dead
Vigorous current basal growth	Type 4	Type 1
Reduced current basal growth	Type 3	Type 2

The mean total mass was determined for each mass category for each type of tree- and shrub-sized individual. In each of the belt transects the following frequency of types was found :

	Type 1	Type 2	Type 3	Type 4
Belt transect A	45	4	43	7
Belt transect B	62	10	2	26
Belt transect C	66	0	3	32
Belt transect D	98	0	2	0
Belt transect E	98	2	0	0

It was clear during sampling that Types 1 and 2 often predominated in open exposed areas that were characterized by presence of large numbers of Grewia individuals whereas types 3 and 4 occurred in the shade of a larger tree.

RESULTS AND CONCLUSIONS

Major results are tabulated in Table 1.

Relative contribution of mass categories

For the whole study area the following broad breakdown of biomass types was found 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

This shows a far greater proportion of terminal growth for shrubs than for trees. The values in brackets are for all species omitting *Grewia* as a percentage of total biomass of the non-*Grewia* group. It is particularly for current twig biomass of shrubs that exclusion of *Grewia* greatly reduced the relative contribution of this category. The other biomass categories are little affected by inclusion or exclusion of *Grewia*. However, in the dead wood mass category, it is important to differentiate between relative contributions with and without *Grewia*. Dead wood mass as a percentage of total mass was found to be :

	Trees and shrubs	Trees	Shrubs
Percentage dead wood mass	10,3 (5,2)	7,5 (5,2)	27,1 (5,0)

Here, again, it is particularly the shrub-sized individuals where the exclusion of *Grewia* causes a very large decrease in the relative contribution of dead wood mass. That *Grewia* 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 together since the large scale die-off of older parts only allows for new self-supported shoot growth from ground level. It should be noted that data from the start of the 1977 growth season has shown much less die-off of older parts and a subsequent reduced amount of current twig growth. It may be postulated, therefore, that the Grewia population progresses through a cycle of possibly several years in which the relative amounts of particularly growth Types 1 and 4 change considerably.

An example of a fairly typical breakdown of biomass categories in a particular species is provided by Burkea :

	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%

For those species in which stem wood biomass and branch wood biomass were measured separately, that is in Burkea, Ochna and Terminalia 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 to 1,37 times in Ochna. This appears to show that the definition of branch wood, as applied in this work, gives reasonably consistent results.

Four species (Figure 1) account for 81,9% of shoot mass or terminal production. A major contribution of 93,8% to dead wood mass is made by the same four species. Although Burkea comprises more than half the total biomass, its productivity (terminal) is only about one third of the total. Conversely, the percentage contribution of Ochna to total terminal production is about twice that of its percentage contribution to total biomass while Grewia's productivity rank position of 4 (Figure 1) drops to 10 relative to total biomass (Figure 2).

Dead wood is also the only mass category where only three species account for more than 90% of the total amount. The mass of dead wood as a percentage of total mass is 79,3% for Grewia, 10,5% for Terminalia and 5,6% for Burkea. The other separately considered species vary between 1,6 and 4,9%. Three of the four species with the greatest terminal growth capacity also have the highest percentage of dead wood mass. Leaf mass and leaf area differences between species follow the pattern of differences in shoot mass (Figure 1), with the clear exception of Grewia.

Tree/shrub ratios

Differences in the ratio between mass categories for trees and shrubs in different species can only be made for those species for which actual field data was gathered and discussion here is further limited to the first seven ranking species for shoot mass (Figure 1).

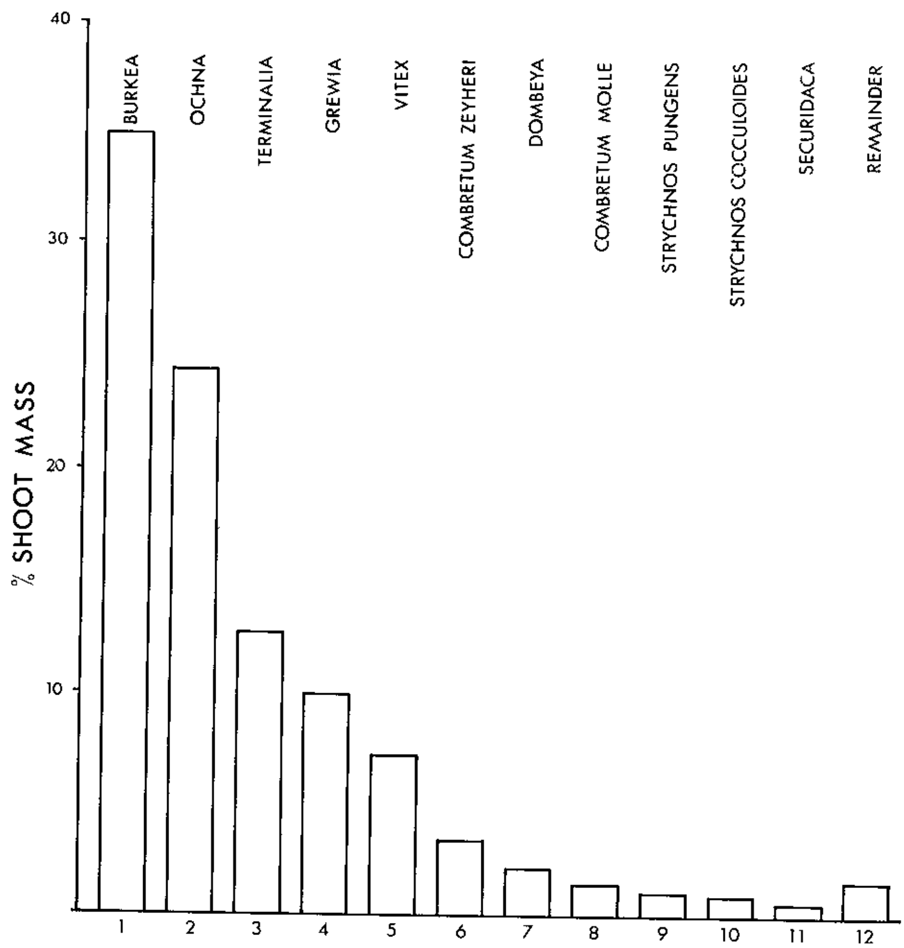
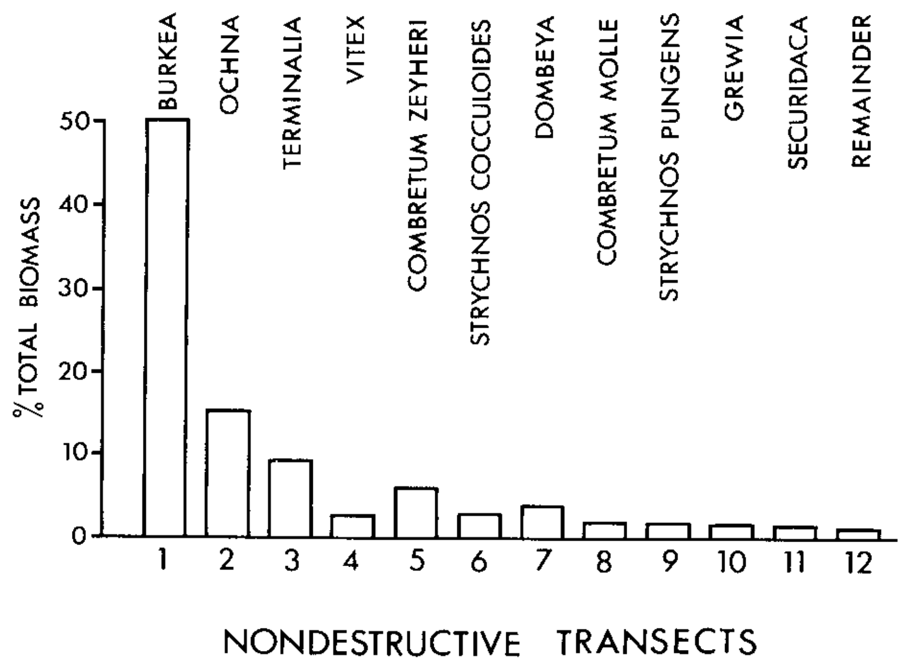


Figure 1. Relative contribution of different species to total shoot mass.

Three species stand out in all biomass categories of tree/shrub ratios. These are the two species with consistently high ratios, particularly Combretum zeyheri and to a somewhat lesser extent Dombeya rotundifolia, and the species with consistently low ratios, Grewia flavescens. These extreme situations merely reflect largely tree-sized populations on the one hand and largely shrub-sized populations on the other. However, in the remaining four species (which includes the top ranking three species) populations are less extreme in size distribution and merit further discussion.

The four species populations may be expected to have increasing tree/shrub ratios with decreasing shrubby growth forms, that is first Ochna then Vitex, Terminalia and finally Burkea; This ascending sequence is confirmed for ratios of leaf biomass where the values are respectively 0,34; 6,59; 10,04 and 10,12. Thus there is up to about ten times more leaf biomass on tree-sized individuals than on shrub-sized individuals. For twig mass the respective ratios are 0,22; 5,99; 9,76 and 7,63. That the ratio for Terminalia is greater than that for Burkea agrees with the more vigorous twig growth on young Burkea individuals



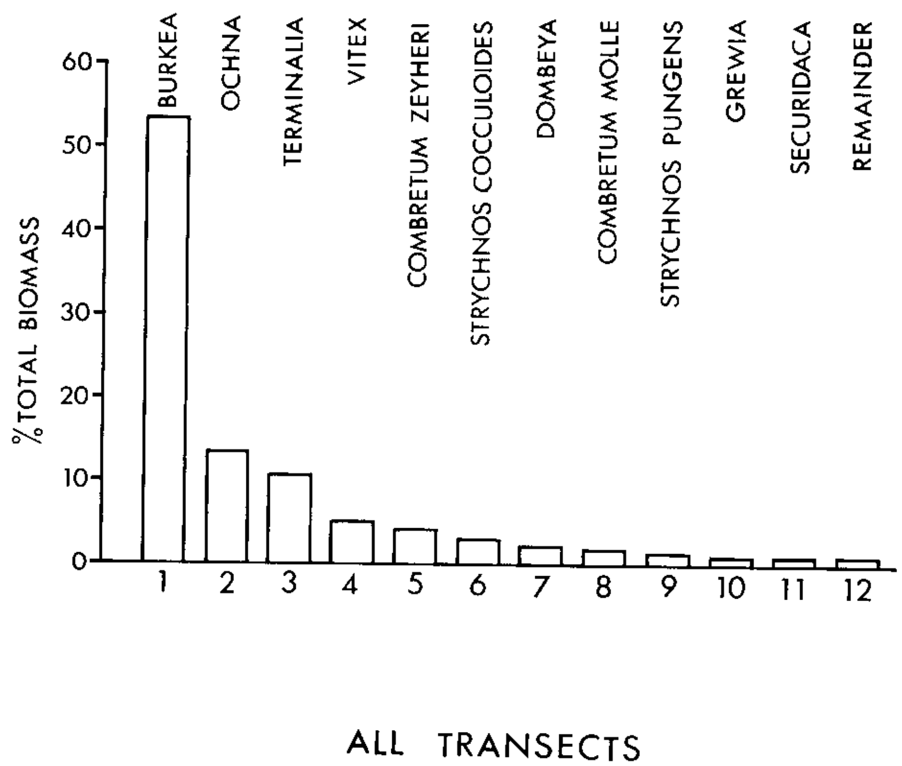


Figure 2. Relative distribution of total biomass for different species of the non-destructive transects and for all transects.

whereas on *Terminalia*, twig growth is not as strongly dependent upon age. For total biomass the respective ratios are 0,47; 10,09; 15,98 and 44,9. The greater range of ratios here reflects the increased needs for structural material in tree-sized individuals but also shows that particularly *Burkea* has a disproportionately large amount of this structural material relative to the other species.

For dead wood mass, the ratio of tree- to shrub-sized individuals was least for *Ochna* (1,25) but both *Burkea* (8,15) and *Vitex* (13,20) were distinctly less than *Terminalia* (21,90). The position of *Terminalia* here corresponds with it having the highest percentage of dead wood relative to all other species except *Grewia*. In *Ochna*, the only mass category which occurred more in trees than in shrubs was the dead wood mass which conforms to the expected higher incidence of dead material on larger and older individuals. Without *Grewia* there was about nine times more dead wood on trees than on shrubs but with *Grewia* included it was less than twice as much.

Comparing respective species tree/shrub biomass ratios, for each of the four species the ratio is smallest for twig biomass, intermediate for leaf biomass and greatest for total biomass. It appears therefore that size of plant affects total biomass to a greater extent than it does twig biomass.

Variation within the study site

One of the important differences between the five sample transects of the study area is the mode of biomass production in *Grewia*. In Figure 3 the ratios of shoot mass between the two main growth types are provided and change from 1,28 in transect A to infinity in transect E. The natural grouping of *Grewia* types corresponds closely to the division between destructive (D, E) and non-destructive (A, B, C) transects, with the former area being almost exclusively of Type 1. This virtual total dependence upon new shoots from ground level may be related to the probably higher frequency of fire in this area referred to before.

The presence of different *Grewia* types also changes the pattern of dead wood mass distribution per transect (Figure 4). Without *Grewia* the dead wood mass is roughly proportional to total mass which decreases towards the central part of the study area. It is particularly in transect B that *Grewia* makes a disproportional contribution to total dead wood mass.

There are relatively large differences in woody species leaf area index (LAI) from one transect to another (Figure 5) where LAI is up to, in transect A 177% greater than in transect C.

Species rank position relative to total mass in the non-destructive transects compared to the means for the five transects shows differences in the relative positions of *Vitex* and *Dombeya* (Figure 2). When only the non-destructive transects are considered *Dombeya* assumes greater importance.

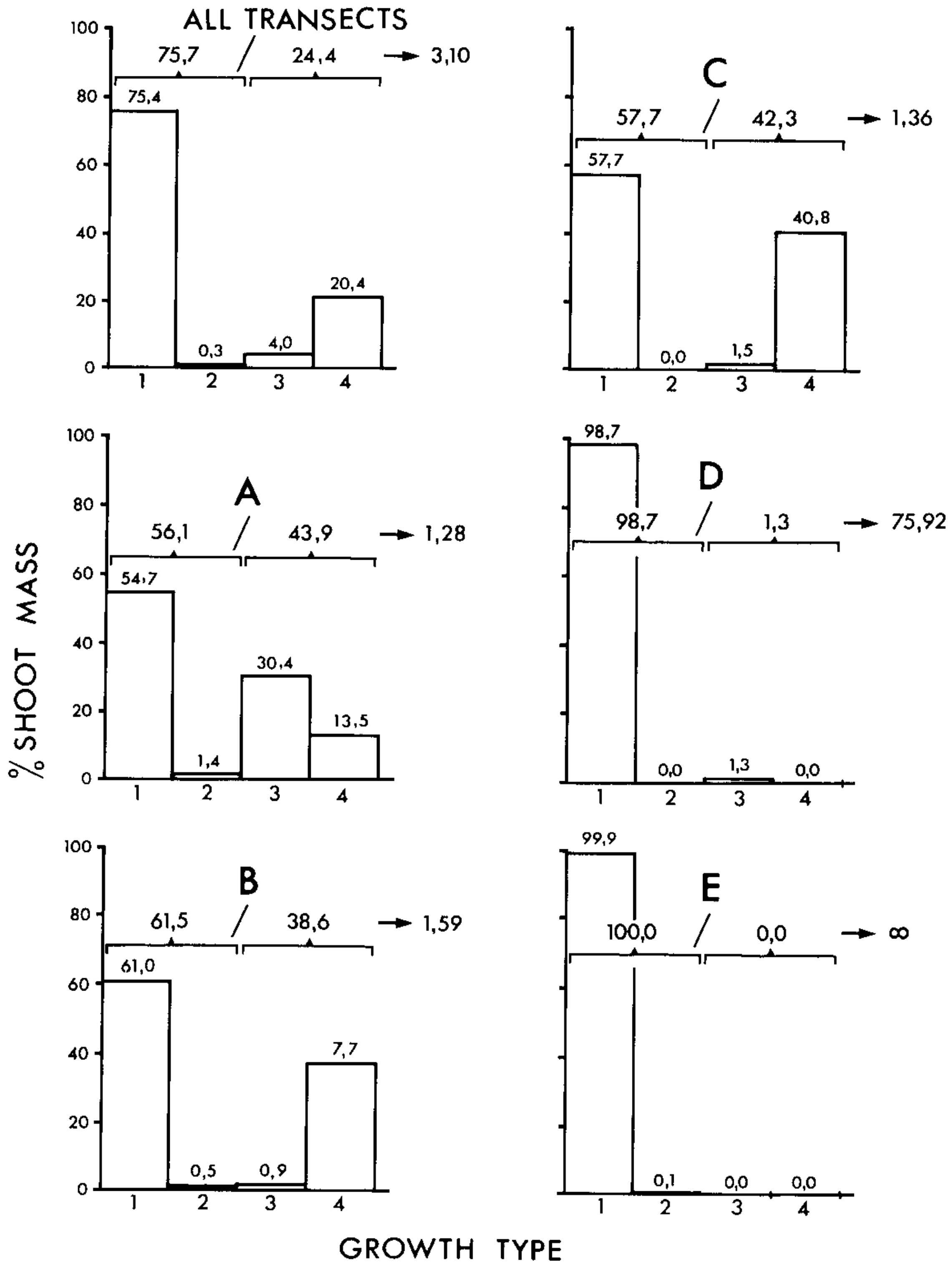


Figure 3. Relative contribution of shoot mass for different growth types of *Grewia flavescens* in each transect.

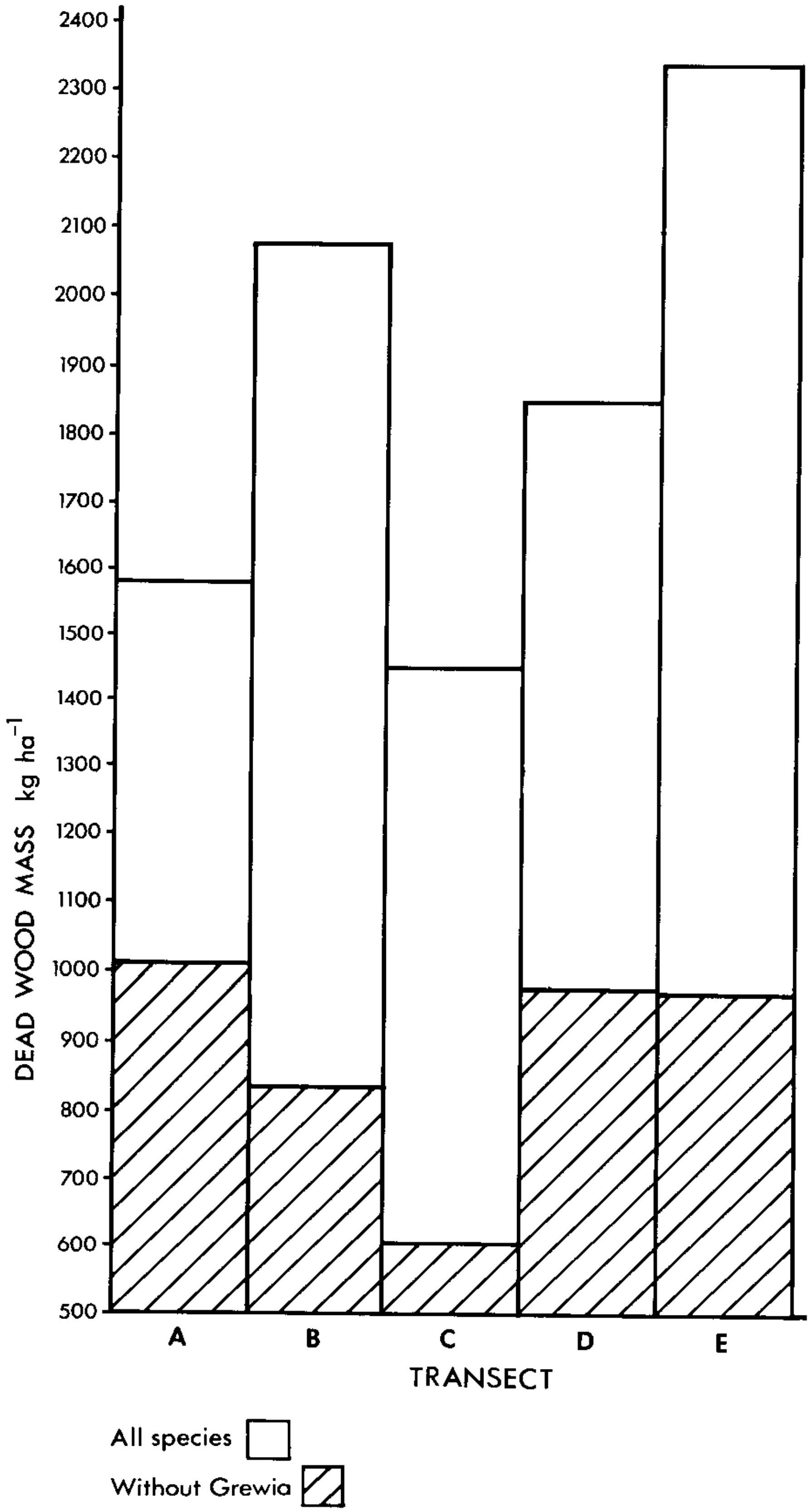


Figure 4. Relative contribution of mass of dead wood for all species and for all species except Grewia in each transect.

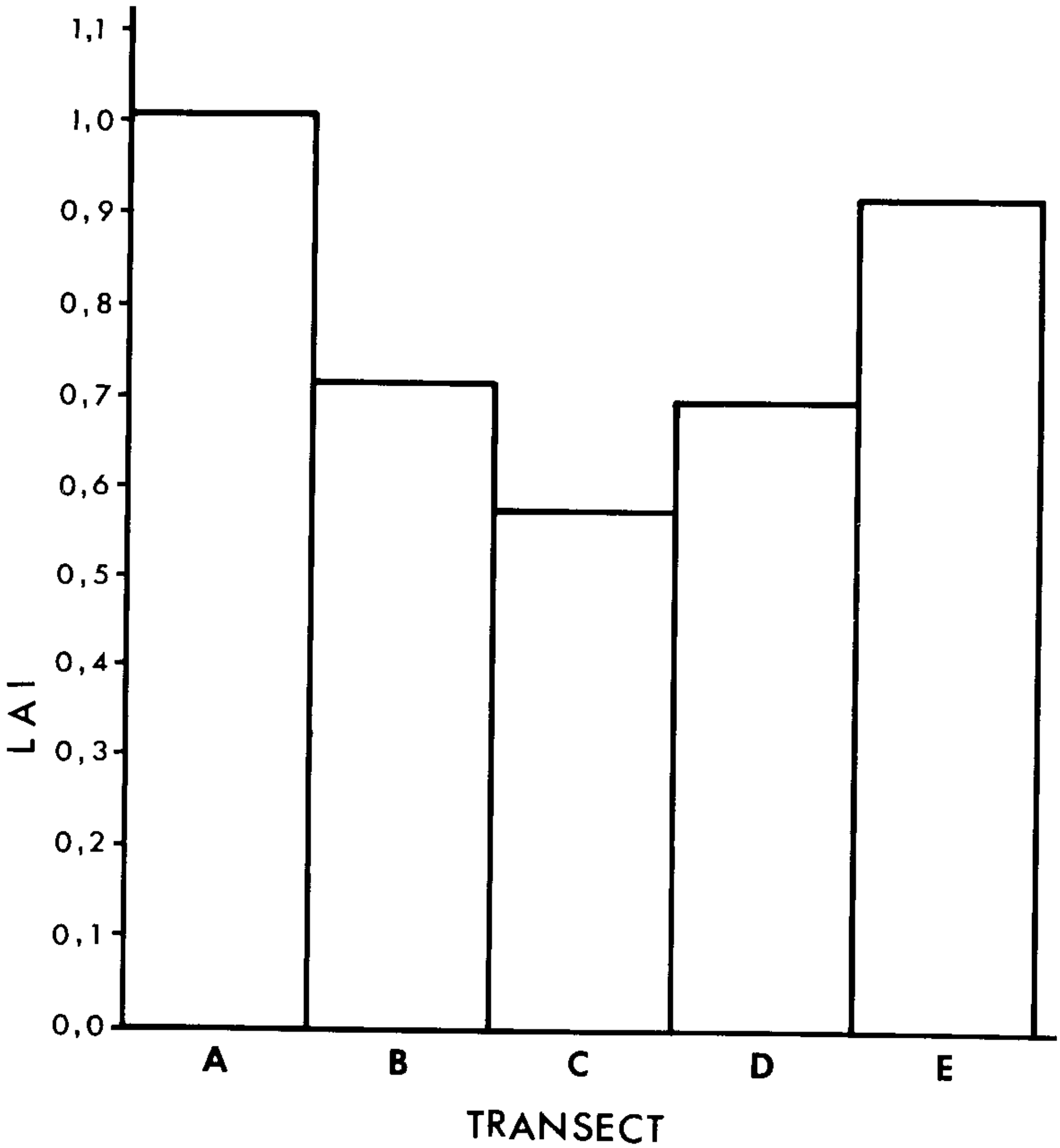


Figure 5. Leaf area indices for each transect.

The estimate of those species for which no direct field data was obtained is of importance to the consideration of totals of a particular category per hectare. It is interesting to note that the species considered separately account for virtually 100% of the total in transect C although over 3% of the total fell into the "remainder" group in transect E (Figure 6).

No clear pattern appears to exist in the ratio between tree and shrub biomass between different transects. In Burkea, for example, the tree/shrub ratio for leaf biomass varies from 6,63 in transect E to 18,46 in transect C. This erratic pattern possibly reflects very patchy past treatment and management within the study area.

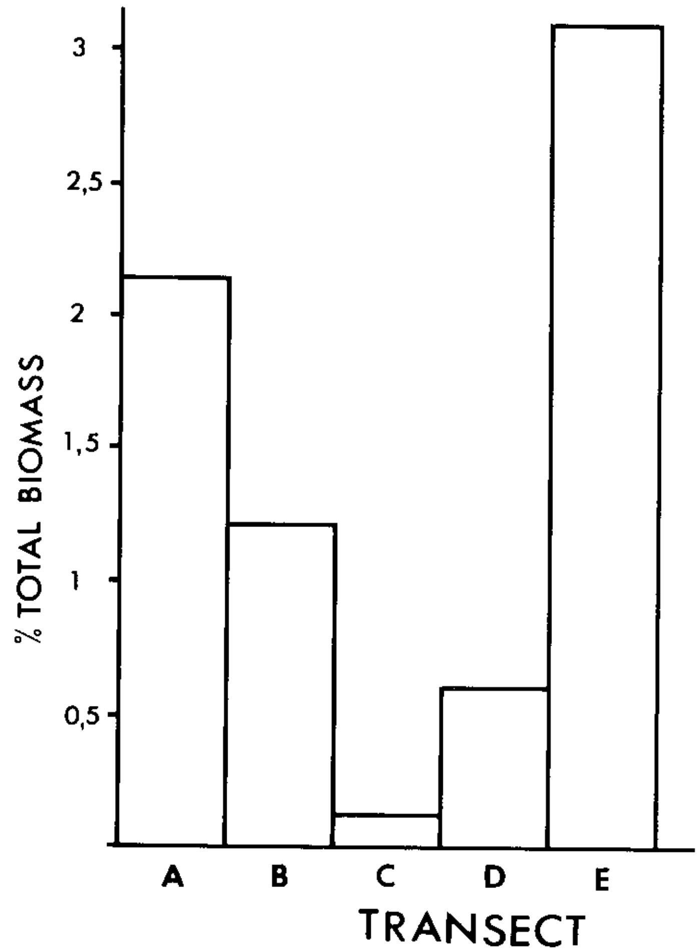


Figure 6. Relative contribution of total biomass for "remainder group" of species for each transect.

There are some major differences in distribution of the total biomass of some species from transect to transect, for example, that of Combretum zeyheri is very irregularly distributed and there is a large difference between the two parts of the destructive area for that of Ochna.

Biomass of the Nylsvley savanna compared to other southern African savannas

The mean woody species basal (at 20 cm above ground) area (excepting Grewia) 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 somewhat lower than the 8 m^2 ha^{-1} quoted for a long protected savanna woodland with Burkea dominant in north-eastern South West Africa (Rutherford 1978) and the 8,5 m^2 ha^{-1}, in a Burkea dominated community about 7 km from the Nylsvley study area, that had been protected from fire for several decades (Rutherford and 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 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 (in press) found that the biomass of Combretum apiculatum and Combretum 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 and 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 Rhodesia. 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 2 for comparison of the Nylsvley site with the South West African site (Rutherford 1975) and the Rhodesian site (Kelly and Walker 1976). The Rhodesian Colophospermum 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 and 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 Rhodesian Colophospermum 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 and Walker (1976) obtained an average shoot production of 1 506 kg ha^{-1} $season^{-1}$ which is eight percent of the mean total biomass. This proportion is identical to that found for the Nylsvley site where shoot production was also eight percent of total biomass. For the two dominant woody species in the abovementioned Combretum apiculatum and Combretum zeyheri savanna community, Dayton (in press) found shoot production to constitute nine percent of the total biomass. On Nylsvley, the terminal shoot production by the woody species was greater than for example, the peak season herbaceous layer biomass of 1 022 kg ha^{-1} determined on Nylsvley by Grunow in 1975/76 (Huntley 1977). However, shoot production of the shrub-sized individuals was less than half of this herbaceous layer biomass. For the Rhodesian Colophospermum mopane sites (Kelly and Walker 1976), mean herbaceous production (1 590 kg ha^{-1}) in an above average rainfall season was slightly greater (106%) than the woody plant shoot production for the same season.

The leaf area index of 0,783 for the woody species is certainly low compared to that of many other vegetation types and even with the addition of the herbaceous layer's LAI, total LAI will probably still be relatively low. Only in transect A does the woody species' LAI just exceed a value of 1. Lieth (1975) indicated a LAI of 1 as the lowest limit for a tropical grassland and states that a wide variety of deciduous communities have leaf area indices of 3 to 6. Leaf area index data from the present study show that the mean LAI of 0,6097 for the whole study area for the *Burkea africana*, *Ochna pulchra* and *Terminalia sericea* group is slightly lower than a previous Nylsvley estimate of 0,764 in which the enumeration survey sample size was less than one tenth that used in the present study (Tew and Cresswell quoted in Huntley 1977). The greatest difference between the two Nylsvley leaf area estimates is for *Terminalia sericea* where the present study indicates LAI to be less than half that found in the earlier study.

The 882 kg ha^{-1} of dead wood (excluding *Grewia*) is less than the annual terminal production but with *Grewia* included, the dead wood mass of 1 859 kg ha^{-1} greatly exceeds annual terminal production. Data on amounts of dead wood mass in other related savanna ecosystems appear to be lacking.

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APPENDIX 1

Prediction equations (Statistical variation not obtainable for arithmetically and algebraic equation combinations used for rarer species).

Key :

Y = Total biomass (kg)
P = Branch wood biomass (kg)
Q = Current twig biomass (kg)
L = Leaf biomass (kg)
A = Leaf area (m^2)
D = Dead wood mass (kg)
SLA = Specific leaf area (cm^2/g)
x = ln (stem diameter)^2. height (cm)
z = stem diameter (cm)
r = correlation coefficient
\+ Significant at P = 0,05
++ Significant at P = 0,01
+++ Significant at P = 0,001
$CI_{0,05}$ = Confidence Interval at P = 0,05
S_x = Standard error

<u>Burkea africana</u>

ln Y = -10,5573 + 1,2018 x	r = 0,993 +++
ln P = - 9,9895 + 1,0652 x	r = 0,985 +++
ln Q = -10,2934 + 0,7947 x	r = 0,985 +++
ln L = - 9,2845 + 0,8596 x	r = 0,987 +++
A = 7,136L	$CI_{0,05}$ = 0,1602 or ± 2,2%; S_x = 0,081
ln D = - 8,4120 + 0,8093 x	r = 0,922 +++

<u>Ochna pulchra</u>

ln Y = - 7,829 + 0,967 x	r = 0,989 +++
ln P = - 7,3749 + 0,8003 x	r = 0,944 +++
ln Q = $-20,6788e^{-0,2114}$ x	r = 0,923 +++
ln L = - 8,08375 + 0,76934 x	r = 0,980 +++
SLA = 87,4525 $z^{-0,0715}$	r = 0,7711 +++
ln D = $0,00000199e^{1,1093x}$	r = 0,919 +++

<u>Terminalia sericea</u>

ln Y = - 8,1124 + 1,0084 x	r = 0,988 +++
ln P = - 6,8060 + 0,7845 x	r = 0,952 +++
ln Q = -11,1603 + 0,8169 x	r = 0,963 +++
ln L = - 8,5338 + 0,8338 x	r = 0,962 +++
A = 6,115 L	$CI_{0,05}$ = ± 0,055 or ± 0,9%; S_x = 0,028
ln D = -11,6215 + 1,1274 x	r = 0,965 +++

Strychnos pungens

$\ln Y = -7,9002 + 1,0116\ x$ $r = 0,982$ +++
$\ln P = -8,1079 + 0,9607\ x$ $r = 0,977$ +++
$\ln Q = -11,4031 + 0,7650\ x$ $r = 0,977$ +++
$\ln L = -7,1022 + 0,6501\ x$ $r = 0,978$ +++
$\ln SLA = 5,3693\ x^{-0,1287}$ $r = 0,894$ +++
$\ln D = -11,5634 + 1,0249\ x$ $r = 0,904$ +++

Vitex rehmannii

$\ln Y = 0,5\ ((-8,1124 + 1,0084\ x) + (-7,9002 + 1,0116\ x))$
$\ln Q = -9,9334 + 0,7947\ x$
$\ln L = -8,5338 + 0,8338\ x$
$A = 7,2\ L$
$\ln D = 0,00000199e^{1,1093\ x}$

Combretum zeyheri

$\ln Y = -10,3373 + 1,2018\ x$
$\ln Q = -9,4834 + 0,7947\ x$
$\ln L = -8,9045 + 0,8596\ x$
$A = 7,3\ L$
$\ln D = -11,2734 + 1,0249\ x$

Dombeya rotundifolia

$\ln Y = -10,7873 + 1,2018\ x$
$\ln Q = -9,5734 + 0,7947\ x$
$\ln L = -9,2845 + 0,8596\ x$
$A = 6,9L$
$\ln D = 0,00000199e^{1,1093x}$

Securidaca longipedunculata

$\ln Y = -7,829 + 0,967\ x$
$\ln Q$ = same as combined species
$\ln L = 0,5\ ((-7,1022 + 0,6501\ x) + (-9,2845 + 0,8596\ x)) - 0,77$
$A = 7,3\ L$
$\ln D = 0,00000119e^{1,1093x}$

Combined species

$\ln Y = -8,5997 + 1,0472\ x$
$\ln Q = 0,25\ ((-20,6788e^{-0,2114x}) + (-10,2934 + 0,7947\ x) + (-11,1603 + 0,8169\ x) + (-11,4031 + 0,7650\ x))$
$\ln L = -8,2511 + 0,7782\ x$
$A = 6,4\ L$
$\ln D = -11,1810 + 1,0177\ x$

Table 1+. Mass and leaf area data per unit ground area for different woody plant components.

Transect	Species	Size Class	Biomass kg ha^{-1} Total	Stem Wood	Branch Wood	Current twig	Leaf	Dead Wood Mass $kgha^{-1}$	Leaf Area m^2ha^{-1}
A	Burkea africana	Tree	9815	6507	2847	63	398	500	2840
		Shrub	143	33	77	6	27	42	192
		Total	9957	6540	2924	69	425	542	3032
	Ochna pulchra	Tree	1210	832	275	8	95	33	690
		Shrub	2546	932	1117	62	435	38	3480
		Total	3753	1764	1392	70	530	71	4170
	Terminalia sericea	Tree	1912	1229	512	10	161	238	984
		Shrub	22	4	14	0	4	2	22
		Total	1932	1232	525	10	164	240	1006
	Grewia flavescens	Tree	141	112		16	13	274	91
		Shrub	135	95		22	18	291	129
		Total	275	206		38	32	566	220
	Vitex rehmannii	Tree	245	215		4	26	4	188
		Shrub	20	16		1	3	0	21
		Total	265	231		5	29	4	209
	Combretum zeyheri	Tree	2063	1922		28	113	85	827
		Shrub	2	0		1	1	0	9
		Total	2066	1922		29	115	86	836
	Dombeya rotundifolia	Tree	512	472		10	30	15	208
		Shrub	9	6		1	2	0	13
		Total	521	478		11	32	16	222
	Combretum molle	Tree	261	243		4	14	11	102
		Shrub	–	–		–	–	–	–
		Total	260	243		4	14	11	102

Transect	Species	Size Class	Biomass kg ha^{-1} Total	Stem Wood	Branch Wood	Current twig	Leaf	Dead Wood Mass $kgha^{-1}$	Leaf Area m^2ha^{-1}
	Strychnos pungens	Tree Shrub Total	67 58 126	63 51 114		0 0 0	4 7 11	2 2 4	23 42 65
	Strychnos cocculoides	Tree Shrub Total	190 10 200	185 8 194		0 0 0	5 2 7	10 1 10	22 11 34
	Securidaca longipedun-culata	Tree Shrub Total	234 1 235	228 1 228		1 0 1	5 0 5	8 0 8	37 1 37
	Remaining species	Tree Shrub Total	412 17 430	388 14 403		2 0 2	22 3 25	22 2 23	141 21 162
	All species	Tree Shrub Total	17062 2963 20022	16029 2368 18397		146 93 239	887 502 1388	1202 378 1580	6153 3941 10094
B	Burkea africana	Tree Shrub Total	7045 141 7185	4608 38 4646	2087 74 2160	48 5 54	302 24 326	382 38 420	2151 174 2326
	Ochna pulchra	Tree Shrub Total	1699 927 2625	1192 356 1547	370 396 766	10 22 32	127 153 280	48 14 62	912 1219 2131
	Terminalia sericea	Tree Shrub Total	1664 81 1744	1062 26 1087	452 42 495	8 1 9	142 12 154	202 7 209	870 70 941
	Grewia flavescens	Tree Shrub Total	115 278 393	73 137 210		29 86 115	13 55 68	383 860 1242	91 383 474

Transect	Species	Size Class	Biomass kg ha^{-1} Total	Stem Wood	Branch Wood	Current twig	Leaf	Dead Wood Mass $kgha^{-1}$	Leaf Area m^2ha^{-1}
	Vitex rehmannii	Tree Shrub Total	274 1 274	246 1 247		4 0 4	24 0 24	5 0 5	171 1 172
	Combretum zeyheri	Tree Shrub Total	- - -	- - -		- - -	- - -	- - -	- - -
	Dombeya rotundifolia	Tree Shrub Total	1380 0 1380	1280 0 1280		25 0 25	75 0 75	40 0 40	517 0 517
	Combretum molle	Tree Shrub Total	791 - 791	755 - 755		7 - 7	29 - 29	24 - 24	209 - 209
	Strychnos pungens	Tree Shrub Total	828 74 902	808 63 870		1 0 1	19 11 30	25 2 27	96 74 170
	Strychnos cocculoides	Tree Shrub Total	656 - 656	637 - 637		1 - 1	18 - 18	34 - 34	87 - 87
	Securidaca longipedunculata	Tree Shrub Total	176 11 186	170 10 180		1 0 1	5 1 5	5 0 5	33 4 37
	Remaining species	Tree Shrub Total	142 56 198	130 45 175		1 1 2	11 10 21	7 4 11	74 63 137
	All species	Tree Shrub Total	14767 1568 16335	13868 1187 15055		135 115 250	764 266 1030	1155 925 2079	5211 1989 7200

Transect	Species	Size Class	Biomass kg ha^{-1} Total	Stem Wood	Branch Wood	Current twig	Leaf	Dead Wood Mass kgha^{-1}	Leaf Area m^{2}ha^{-1}
C	Burkea africana	Tree	7457	4921	2185	48	303	378	2161
		Shrub	74	15	42	4	16	27	117
		Total	7531	4936	2227	51	319	404	2278
	Ochna pulchra	Tree	459	300	115	4	40	11	296
		Shrub	718	236	335	14	133	11	1083
		Total	1178	536	450	18	174	22	1380
	Terminalia sericea	Tree	546	338	157	3	48	66	297
		Shrub	291	100	148	3	40	25	247
		Total	834	437	305	5	89	91	544
	Grewia flavescens	Tree	112	74		26	12	298	86
		Shrub	212	110		62	40	546	281
		Total	323	184		87	52	845	367
	Vitex rehmannii	Tree	466	405		9	52	7	376
		Shrub	286	236		8	42	4	304
		Total	752	641		17	94	11	680
	Combretum zeyheri	Tree	1076	1024		10	42	38	307
		Shrub	-	-		-	-	-	-
		Total	1076	1024		10	42	38	307
	Dombeya rotundifolia	Tree	-	-		-	-	-	-
		Shrub	-	-		-	-	-	-
		Total	-	-		-	-	-	-
	Combretum molle	Tree	4	3		0	1	0	5
		Shrub	-	-		-	-	-	-
		Total	4	3		0	1	0	5
	Strychnos pungens	Tree	27	25		0	2	1	8
		Shrub	9	8		0	1	0	8
		Total	36	33		0	3	1	16

Transect	Species	Size Class	Biomass kg ha^{-1} Total	Stem Wood	Branch Wood	Current twig	Leaf	Dead Wood Mass $kgha^{-1}$	Leaf Area m^2ha^{-1}
	Strychnos cocculoides	Tree Shrub Total	413 - 413	402 - 402		1 - 1	10 - 10	21 - 21	46 - 46
	Securidaca longipedunculata	Tree Shrub Total	480 - 480	468 - 468		2 - 2	10 - 10	16 - 16	70 - 70
	Remaining species	Tree Shrub Total	0 15 15	0 11 11		0 0 0	0 4 4	0 1 1	1 22 23
	All species	Tree Shrub Total	11040 1605 12647	10418 1240 11658		102 90 192	520 277 797	836 614 1450	3652 2063 5715
D	Burkea africana	Tree Shrub Total	8748 254 8989	5576 55 5631	2682 136 2818	70 11 81	420 52 472	545 84 629	2996 371 3366
	Ochna pulchra	Tree Shrub Total	255 330 586	161 105 267	67 156 223	3 8 11	24 61 85	6 5 11	179 497 675
	Terminalia sericea	Tree Shrub Total	2148 5 2151	1296 0 1296	643 4 647	12 0 12	197 1 198	253 0 253	1205 6 1211
	Grewia flavescens	Tree Shrub Total	36 86 121	7 5 12		23 53 76	6 28 34	315 557 872	41 194 235
	Vitex rehmannii	Tree Shrub Total	1916 8 1925	1718 7 1725		28 0 28	170 1 172	33 0 33	1227 9 1236

Trans-ect	Species	Size Class	Biomass kg ha^{-1} Total	Stem Wood	Branch Wood	Cur-rent twig	Leaf	Dead Wood Mass $kgha^{-1}$	Leaf Area m^2ha^{-1}
	Combretum zeyheri	Tree Shrub Total	- - -		- - -	- - -	- - -	- - -	- - -
	Dombeya rotundifolia	Tree Shrub Total	- - -		- - -	- - -	- - -	- - -	- - -
	Combretum molle	Tree Shrub Total	- - -		- - -	- - -	- - -	- - -	- - -
	Strychnos pungens	Tree Shrub Total	40 - 40		37 - 37	0 - 0	3 - 3	1 - 1	15 - 15
	Strychnos cocculoides	Tree Shrub Total	872 - 872		848 - 848	1 - 1	23 - 23	45 - 45	109 - 109
	Securidaca longipedun-culata	Tree Shrub Total	13 - 13		13 - 13	0 - 0	0 - 0	0 - 0	3 - 3
	Remaining species	Tree Shrub Total	41 51 90		35 41 76	0 1 1	4 9 13	2 3 5	25 59 84
	All species	Tree Shrub Total	14065 736 14800		13081 510 13591	137 74 210	847 152 999	1201 649 1850	5798 1135 6933
E	Burkea africana	Tree Shrub Total	9414 349 9761	6190 95 6284	2762 181 2943	64 13 77	398 60 458	505 93 597	2838 428 3266

Transect	Species	Size Class	Biomass kg ha^{-1} Total	Stem Wood	Branch Wood	Current twig	Leaf	Dead Wood Mass $kgha^{-1}$	Leaf Area m^2ha^{-1}
	Ochna pulchra	Tree	810	501	221	9	79	19	585
		Shrub	1726	618	767	42	299	26	2387
		Total	2533	1119	987	51	378	45	2972
	Terminalia sericea	Tree	1881	1112	581	11	177	215	1086
		Shrub	118	44	57	1	16	11	97
		Total	1999	1156	638	12	193	225	1183
	Grewia flavescens	Tree	53	0		43	10	595	70
		Shrub	109	0		72	37	766	261
		Total	162	0		115	47	1361	330
	Vitex rehmannii	Tree	804	708		14	82	13	586
		Shrub	52	44		1	7	1	52
		Total	857	753		15	89	14	638
	Combretum zeyheri	Tree	315	286		6	23	15	170
		Shrub	-	-		-	-	-	-
		Total	315	286		6	23	15	170
	Dombeya rotundifolia	Tree	-	-		-	-	-	-
		Shrub	-	-		-	-	-	-
		Total	-	-		-	-	-	-
	Combretum molle	Tree	702	667		7	28	24	202
		Shrub	7	4		1	2	1	18
		Total	708	671		7	30	25	220
	Strychnos pungens	Tree	409	393		1	14	12	73
		Shrub	50	43		0	7	2	43
		Total	459	437		1	21	14	116
	Strychnos cocculoides	Tree	96	92		0	4	5	21
		Shrub	-	-		-	-	-	-
		Total	96	92		0	4	5	21

Transect	Species	Size Class	Biomass kg ha^{-1} Total	Stem Wood	Branch Wood	Current twig	Leaf	Dead Wood Mass kgha^{-1}	Leaf Area m^{2}ha^{-1}
	Securidaca longipedunculata	Tree	121	117		1	3	3	24
		Shrub	-	-		-	-	-	-
		Total	121	117		1	3	3	24
	Remaining species	Tree	472	440		3	29	25	187
		Shrub	73	62		1	9	5	60
		Total	545	503		4	39	30	247
	All species	Tree	15073	14069		157	847	1431	5841
		Shrub	2483	1915		131	438	903	3346
		Total	17555	15984		288	1285	2334	9187
A B C D and E	Burkea africana	Tree	8495	5560	2512	59	364	462	2597
		Shrub	193	47	102	8	36	57	257
		Total	8687	5607	2614	66	400	519	2854
	Ochna pulchra	Tree	887	597	210	7	73	23	532
		Shrub	1250	450	554	30	216	19	1733
		Total	2136	1047	764	36	289	42	2266
	Terminalia sericea	Tree	1631	1007	470	9	145	195	889
		Shrub	104	35	53	1	15	9	88
		Total	1734	1042	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

Transect	Species	Size Class	Biomass kg ha^{-1}: Total	Biomass: Stem Wood / Branch Wood	Biomass: Current twig	Biomass: Leaf	Dead Wood Mass $kgha^{-1}$	Leaf Area m^2ha^{-1}
	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	14402	13493	135	773	1165	5331
		Shrub	1872	1444	101	327	694	2495
		Total	16273	14937	236	1100	1859	7826

\+ 0 signifies a positive amount less than 0,5 and
\- indicates absence of a category.

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.

Table 2. Comparison of species relative contributions to total woody plant biomass for selected southern African savanna communities.

Nylsvley *Burkea africana* community (all transects)			Nylsvley *Burkea africana* community (Transect A)			South West African *Burkea africana* community			A Rhodesian *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	Colophospermum 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 psidioides	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

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