major role of the grass and tree canopies in reducing evaporation from the soil surface is probably not through shading the soil surface, but through increasing the boundary layer resistance to the diffusion of moisture and heat. In this respect grasses, with a dense, low canopy are much more effective than trees, with a diffuse, high canopy. This hypothesis was not directly tested by the study. For modelling purposes the evaporation rate was assumed to be inversely proportional to the combined tree and grass canopy cover. Another factor which was not considered was the effect of surface litter on the evaporation rate, which is undoubtably important, but difficult to model.

In derived grasslands, shading, canopy diffusive resistance and surface litter are all increased above the levels in an uncleared savanna, provided that grazing and burning intensities are sufficiently low to allow a dense grass cover to develop. It is therefore anticipated that clearing of woodlands will decrease evaporation from the soil surface, thus increasing the water use efficiency (dry matter production per unit rainfall) of the system as a whole.

3.5.3 TRANSPIRATION

The measurement of transpiration for water balance purposes is technically difficult because most of the available techniques alter the plant environment and thus modify the transpiration rate (Slavik 1974). Furthermore, in order to obtain rates for an entire plant community, accurate measurements of the transpiration rate of each contributing species for all times of day and night and for all canopy aspects must be known. Since most measurements are made on a single leaf or portion thereof, the leaf area contribution of each species must also be known. Even with all this information, which is logistically almost impossible to obtain, the pitfalls of extrapolating from a small sample to an entire community are legion.

The approach of this study was twofold: estimate the transpiration rates by extrapolation from individual leaf rates; and compare these estimates with the results of a water-balance model based on the daily soil moisture readings. The partitioning of evapotranspiration into soil, tree and grass components could also be roughly estimated by comparison of soil moisture depletion in the root-free, grass only and trees plus grass profiles.

The leaf-based methods were used to determine the form of the dependence of transpiration rate on soil moisture conditions, as well as to reveal differences in the water use patterns of various species. Instantaneous transpiration rates were determined at two-hourly intervals throughout the day on eight occasions at each site. On several occasions measurements were taken throughout the night as well, to confirm that transpiration essentially ceased during the night. Sunlit leaves were used for all measurements. The total daily transpiration per gram of leaf tissue was calculated by integrating the area under the diurnal progression of transpiration rate. Examples of the daily course of transpiration rate under wet and dry soil conditions at each site are given in Figure 35 on page 110.

The cut-shoot weight loss technique (Slavik 1974) was selected for woody plants because of its simplicity and applicability to different leaf forms. Approximately 10 g of leaf and shoot material was cut from the parent plant and immediately weighed on a Ktron digital balance to the nearest 0.01 g. The sample was then replaced in its original position in the canopy and reweighed after five minutes. The mass difference was taken to be transpiration loss, and expressed per unit dry weight of leaf material per unit of time. The method was found to be unreliable for grasses.

Prior trials using time intervals between two and ten minutes showed a period of five minutes to be sufficient to show a measurable mass loss but insufficient to cause marked wilting of the sample. No sudden spurt of transpiration following severing of the shoot was noted (the "Ivanov effect"), but rates gradually declined over the ten minute period. The five minute standard was adopted for comparative purposes. Transpiration measurements were taken two- or three-hourly throughout

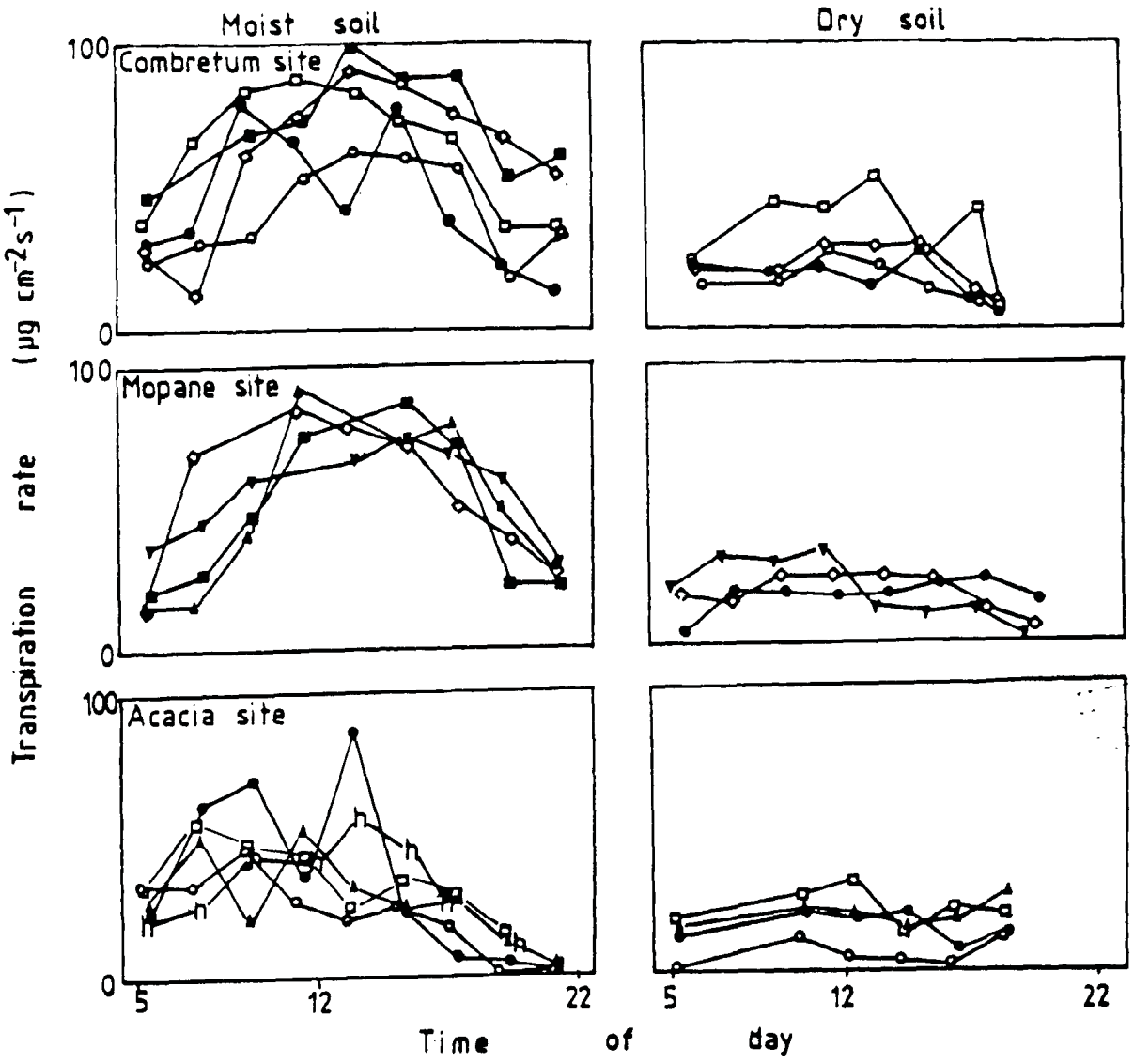

Figure 35. Daily course of transpiration rate: Combretum site ◇ =*Grewia bicolor*, □=*Sclerocarya birrea*, ○ =*Combretum apiculatum*, ● =*Schmidtia pappophoroides*, ■ =*Panicum maximum*; Mopane site ■ =*Colophospermum mopane*, ● =*Combretum apiculatum*, ▼ =*Digitaria eriantha*, ▲ =*Acacia nigrescens*; Acacia site ▲ =*Acacia nigrescens*, □ =*Sclerocarya birrea*, ● =*Panicum maximum*, h=*Heliotropium sp.*, ○=*Combretum apiculatum*.

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the day and night on one sample each of the five dominant woody plants at each site. The measurements were taken on numerous occasions to provide a range of soil moisture conditions, as measured by the soil moisture sensors in each site.

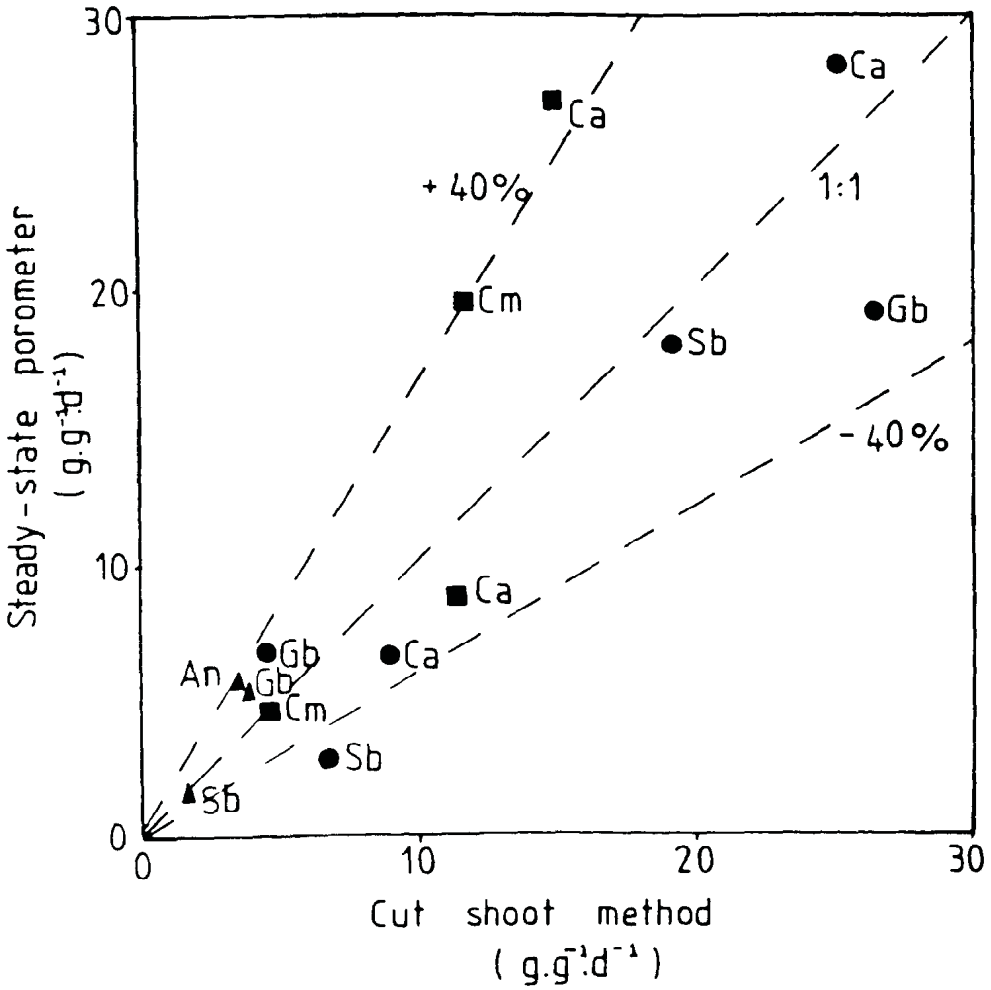

Figure 36. Correlation between porometry and the cut-shoot technique.: Gb=Grewia bicolor, Sb=Sclerocarya birrea, Ca=Combretum apiculatum, Cm=Colophospermum mopane, An=Acacia nigrescens.

Transpiration rate measurements were taken on several occasions on dominant tree and grass species using a LICOR LI-1600 steady-state porometer. A comparison between the daily transpiration calculated by the dry weight-based cut-shoot method and the leaf area-based porometer method was made using the specific leaf areas for each species involved

Table 3.7 Specific leaf areas (one side only) and canopy storage volume for the major species used in the study. Means and standard errors for 15 samples.

Species	Specific leaf area $dm^2.gDM^{-1}$	Canopy storage volume $ml H_2O.gDM^{-1}$
Acacia nigrescens	*1.11 (0.10)*	*0.49 (0.16)*
Grewia bicolor	*0.87 (0.09)*	*0.61 (0.12)*
Colophospermum mopane	*0.81 (0.08)*	*0.59 (0.16)*
Combretum apiculatum	*1.47 (0.12)*	*0.77 (0.40)*
Sclerocarya birrea	*0.43 (0.03)*	*1.09 (0.80)*
Bothriochloa radicans	*0.20 (0.11)*	
Digitaria eriantha	*0.71 (0.26)*	
Panicum coloratum	*0.53 (0.34)*	
Panicum maximum	*0.92 (0.44)*	
Sporobolus nitens	*0.41 (0.14)*	
Schmidtia pappophoroides	*0.33 (0.20)*	
Urochloa mosambicensis	*0.80 (0.27)*	

(Table 3.7). Porometry was performed on adaxial surfaces only. The porometer could not be used on narrow-leafed species. The comparison is presented in Figure 36. The estimates were in broad agreement for most species.

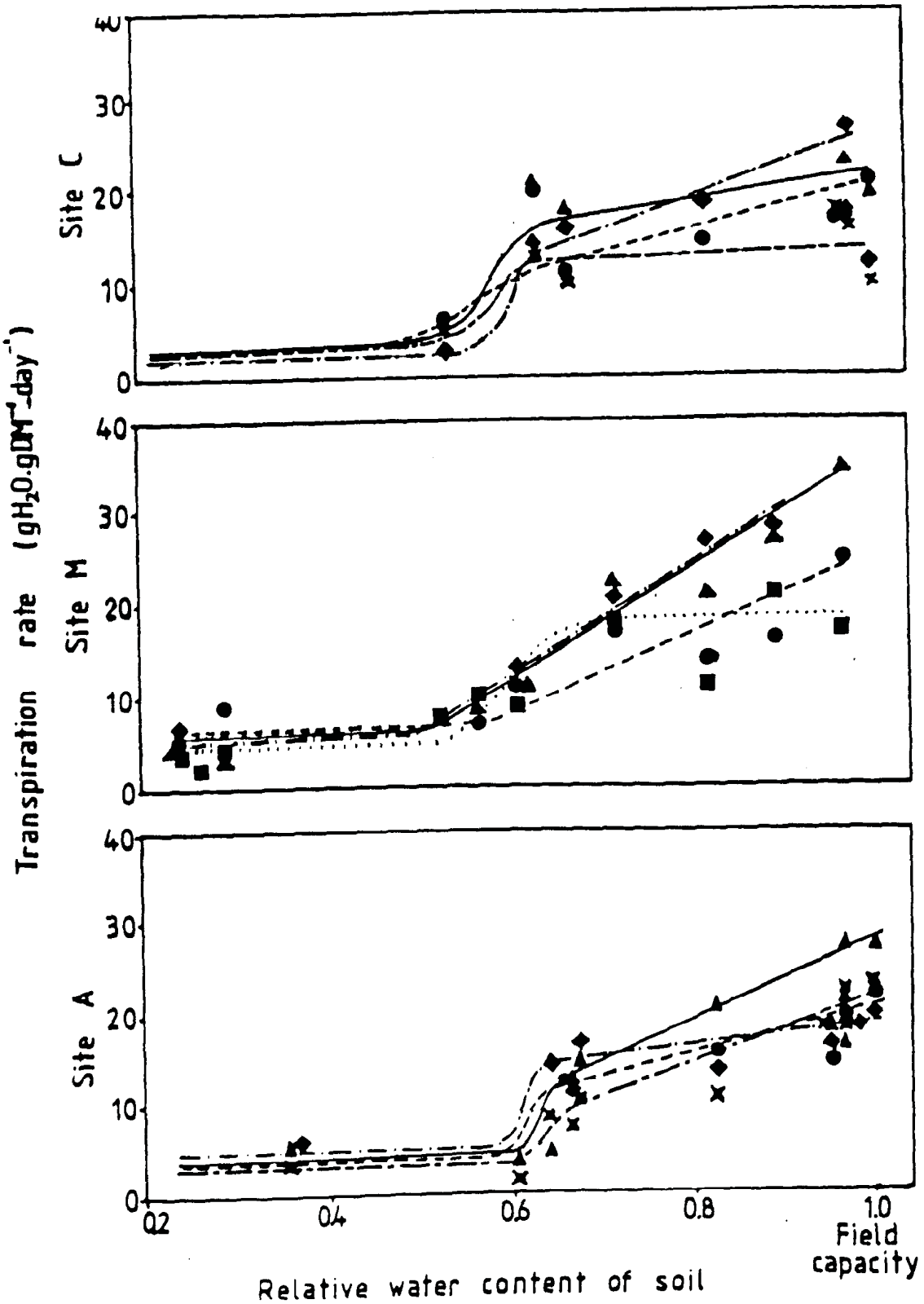

Figure 37. Relationship between daily transpiration and soil water potential: Soil moisture is weighted by root density in each layer. ▲=Acacia nigrescens, ◆=Grewia bicolor, ■=Colophospermum mopane, ●=Combretum apiculatum, x=Sclerocarya birrea.

Data from the cut-shoot method were used to calibrate the model because they were available for more species and a more complete range of soil moisture conditions. Daily transpiration was calculated as the area under the transpiration rate curve for a 24 hour period. Daily transpiration is plotted against an index of soil water availability in Figure 37 on page 113. Soil water availability was calculated by multiplying the relative water content (0=airdry, 1=field capacity) of each soil layer, as indicated by the mean soil moisture block reading, by the proportion of tree roots associated with that layer. The choice of a plausible function to express this relationship is not simple. Several forms have been suggested in the literature (Denmead & Shaw 1962). When the atmospheric demand is high, the transpiration rate is limited by the rate at which roots can extract water from the soil, which is in turn a function of the water potential gradient between the plant and soil, and the diffusive resistance in the soil and across the soil-root interface. Some workers (eg Feddes *et al* 1976) have therefore suggested a linear relationship between transpiration rate and soil water potential (ψ). As the soil dries, however, the cross sectional area of the diffusive pathway between soil and root declines as a function of the soil water content (θ) leading other workers to propose a linear dependence on relative water content (Hillel *et al* 1976), and yet others to use compound relationships of ψ and θ.

When the atmospheric moisture demand is low, then the transpiration rate tends to remain constant until the soil water potential falls to wilting point, when the transpiration rate drops abruptly. At intermediate atmospheric demand levels the relationship between soil moisture and transpiration rate can take on a variety of sigmoid forms. To avoid the introduction of arbitrary inflection points a complex curve was rejected for modelling purposes in favour of a simple one. Both trees and grasses were assumed to transpire at a maximum rate (E_{max}) until the relative soil moisture content (θ) fell below a given critical level (E_{crit}) whereafter the transpiration rate was a linear function of the difference between θ and the relative water content at wilting point (θ_{wilt}).

Transpiration rates of grasses (Table 3.8) were determined by repeatedly weighing pots in which grass tufts of known biomass were growing. Evaporation from the pots was suppressed by a 15mm mulch of 2mm di-

Table 3.8 Transpiration rates by *Panicum maximum* and *Schmidtia pappophoroides* measured by lysimetry over a two-week period (March 1985). Class A pan evaporation for the same period averaged 3.66 $mm.d^{-1}$. Data corrected for evaporation from the soil surface.

	Transpiration rate ($g.gDM^{-1}.d^{-1}$)			
	Panicum maximum		Schmidtia pappophoroides	
	Full sun	70% shade	Full sun	70% shade
Combretum site soil	7.81	9.35	3.47	4.22
Mopane site soil	7.68	5.17	7.72	4.65
Acacia site soil	7.36	7.14	1.73	(died)

ameter plastic spheres, and corrected for evaporation from the soil surface by reference to the mass loss from control pots having no grass tufts. For details of the pot sizes and weighing, see the section on "pot experiment" in chapter 4.

4.0 PRIMARY PRODUCTION AND PLANT DEMOGRAPHY

In the absence of other limiting factors, the dependence of primary production on water availability should be linear over the range of water limitation. Many such relationships between annual production and various indices of moisture (usually annual precipitation) have been published for the grass component of savannas (Walter 1939, Rosenzweig 1968, and Phillipson, 1975). A critique is given by Rutherford (1980).

This study seeks to construct a mechanistic model of the relationship between plant production and water availability. For this purpose the above studies are inadequate on two counts. As Bell (1982) has pointed out, the relationship is not independent of soil fertility (nor is it likely to be independent of soil physical factors). Thus the relationship is site specific and should be determined for each new case. Secondly, the causal relationship is between plant available water and production. Mean annual precipitation, potential evapotranspiration and even soil moisture status are at best crude estimators of this parameter because a significant portion of the water budget leaves the system through non-productive pathways such as runoff, evaporation from the soil surface, interception and deep leaching. The slope of the relationship between individual plant production and plant water use will be referred to in this study as plant water use efficiency (WUE, grams carbon fixed per gram water transpired), while the slope of the annual aboveground herbaceous layer production-annual rainfall regression will be referred to as the sward water use efficiency (WUE', $kg.ha^{-1}.mm^{-1}$).

Under conditions of equal and constant water availability and no nutrient deficiency, the competitive contest would be won by the plant with the highest water use efficiency. However water availability fluctuates and is not equally accessible to all plants. Plant water use efficiency is probably not constant over all levels of water availability. Furthermore, as Cohen (1970) has pointed out, a high water use efficiency can be selected for only under conditions of exclusive water use, or where the

adaptations favouring high WUE does not reduce the transpiration rate disproportionately. Where soil moisture is a resource common to several competitors, water conservation at the expense of water uptake is not rewarded. The interaction of a variable moisture availibility and a variety of water-use strategies provides opportunities for coexistence in semi-arid savannas (Westoby 1980).

Under conditions of extreme water stress, when water availability is practically nil, the competitive outcome is determined by neither water use efficiency nor transpiration rate but by the ability to survive until the next period of water availability, either by avoiding or by tolerating the drought. Thus drought mortality data are also relevant to understanding the co-existence of savanna species.

In this chapter the methods and results of determining grass production under conditions of known water use (see chapter three) are described. In order to construct a system water budget, the biomass contribution of each transpiring component must be known. In a monitoring programme it is desirable that the biomass be estimated non-destructively, which limits the methods applicable. They were further restricted by the low production levels during the first two years of the study.

An increase in grass production is the most conspicuous consequence of woody plant removal, and the one most commonly cited as a reason for bush clearing. Grass production was therefore used as the major criterion for comparing the treatment (cleared) and control (uncleared) plots.

Changes in grass production are attributable to four sources, which operate sequentially at different time scales. The immediate response to improved growth opportunities is enhanced performance by individual tillers. Within weeks, the number of tillers per tuft increases, and if the resource levels are sustained, the number of tufts per unit area rises. Finally, all the above changes result in a species composition shift in favour of those species which perform better under the new resource regime; which may result in a higher system water use efficiency. All four sources were monitored (at their appropriate time scales) during this study.

Bush clearing is usually accompanied by a change in herbaceous species composition, often in the direction of lower palatability. The herbaceous layer species composition was therefore determined before clearing, two years after clearing and three years after clearing. Grass species normally confined to the sub-canopy habitat would be expected to decline following bush clearing, to be replaced by those normally found between canopies. One species from each of these groups was selected in each site for an intensive study of tiller dynamics and water use efficiency. Sub-canopy grasses were not conspicuous at the Acacia site before clearing, so representatives of the tall-grass/short-grass mosaic which occurs there were chosen. Number of tillers per tuft was recorded during the first two seasons, and tufts per hectare during the third. Herbaceous standing crop was measured at peak during the first two seasons, and monthly during the third.

Production by trees was not monitored, but estimates of above-ground woody biomass and peak leaf biomass were made using allometric techniques.

4.1 WOODY-PLANT BIOMASS

One of the main determinants of the magnitude of the herbaceous response to bush clearing is the pre-clearing woody biomass. None of the published bush clearing trials in Southern and East Africa report the pre-clearing biomass, and most neglect to report even the woody plant density or basal area. Woody plant biomass can be divided into above- and below-ground portions, and the above-ground portion into wood and leaf biomass (Rutherford 1979). The below-ground biomass is extremely difficult to measure, is not available to above-ground herbivores, is only indirectlly related to below-ground competition (root length or root activity would be better indices) and remains in the ground after clearing. For these reasons it was not measured in this study.

The leaf biomass is directly related to the leaf surface area, which in turn directly controls the rate at which water is transpired and energy is fixed by photosynthesis. It is therefore regarded in this study as the principle index of the influence of woody plants on grasses. Furthermore it represents a food resource to browsing herbivores. Only a small proportion of the wood biomass (the soft terminal twigs) is available to browsers. The principle importance of the wood biomass to bush clearing is as a nutrient pool which may be removed during the clearing operation. In some areas it may represent an economic resource which can help to balance the cost of bush clearing.

The total leaf mass of an individual woody plant is strongly related to the cross-sectional area of the stem (Barnes, Lloyd & McNeill 1976, Dayton, 1978). This relationship was determined for each dominant species by completely stripping the leaves of at least fifteen plants at peak leaf biomass, drying and weighing the leaves and regressing the dry leaf masses against the stem basal areas. This was possible for all species except *Acacia nigrescens*, where the regression was established for secondary branches. The cross-sectional area of secondary branches was then allometrically related to the stem basal area and the leaf mass versus stem area relationship was substituted into this second relationship.

Allometric regressions were also established between above-ground woody biomass (corrected for moisture content) and stem basal area. Again in the case of *A. nigrescens* it was not possible to weigh the entire tree, so the wood volume was allometrically determined, and multiplied by the wood density. The regressions (Table 4.1) are in reasonable agreement with relationships published by other workers (McNeill & Barnes 1976, Dayton 1978).

In order to determine the pre-clearing aboveground woody biomass, the allometric relations for woody and leaf tissue were applied to the frequency distributions of stem diameters obtained during the initial survey (Figure 13 on page 58). The values obtained (Figure 38 on page 121) agree quite well with estimates from savannas elsewhere (Rutherford,

Table 4.1 Allometric relationships in woody plants. Equations given are not necessarily the best fit in each case, but are of the class of equations which provide the best fit in the general case.

1. Leaf dry mass (L(kg)) versus Stem basal diameter (D (cm))

General form: $L=aD^2+b$

	a	*b*	r^2
Colophospermum mopane	0.0067	0.0290	0.94
Combretum apiculatum	0.0109	0.0520	0.98
Sclerocarya birrea	0.0074	0.0038	0.79
Grewia bicolor	0.0066	0.0019	0.65
Acacia nigrescens	0.0184	-0.0120	0.96

2. Woody dry mass (W (kg)) versus Stem basal diameter (D (cm))

General form: $lnW=alnD+b$

	a	*b*	r^2
Colophospermum mopane	1.2780	-3.04	0.99
Combretum apiculatum	1.4015	-3.27	0.99
Sclerocarya birrea	1.3086	-3.52	0.99
Grewia bicolor	1.1024	-2.09	0.99
Acacia nigrescens	1.2723	-3.61	0.97

3. Bark surface area (B (cm^2)) versus Stem basal diameter (D (cm))

General form: $lnB=alnD+b$

	a	*b*	
Colophospermum mopane	0.778	5.0553	*Equations derived*
Combretum apiculatum	0.902	4.8138	*on the assumption*
Sclerocarya birrea	0.809	4.9170	*that stems take the*
Grewia bicolor	0.602	6.2417	*form of a cylinder.*
Acacia nigrescens	0.772	4.5675	

1978). They are on the low side due to the fact that the published data mostly come from slightly moister savannas. The Mopane site has the highest woody-plant biomass, mainly due to the large wood biomass. This site is a multi-stemmed thicket rather than a woodland like the other two sites. Kelly (1973) estimated the woody-plant biomass in *C. mopane* woodlands and thickets to be 8700-30800 $kg.ha^{-1}$, with the leaf biomass contributing 590-2120 $kg.ha^{-1}$. Kennan (1969a) gives the leaf biomass in *C. mopane* thicket as 1490 $kg.ha^{-1}$. The thicket growth-form overrides

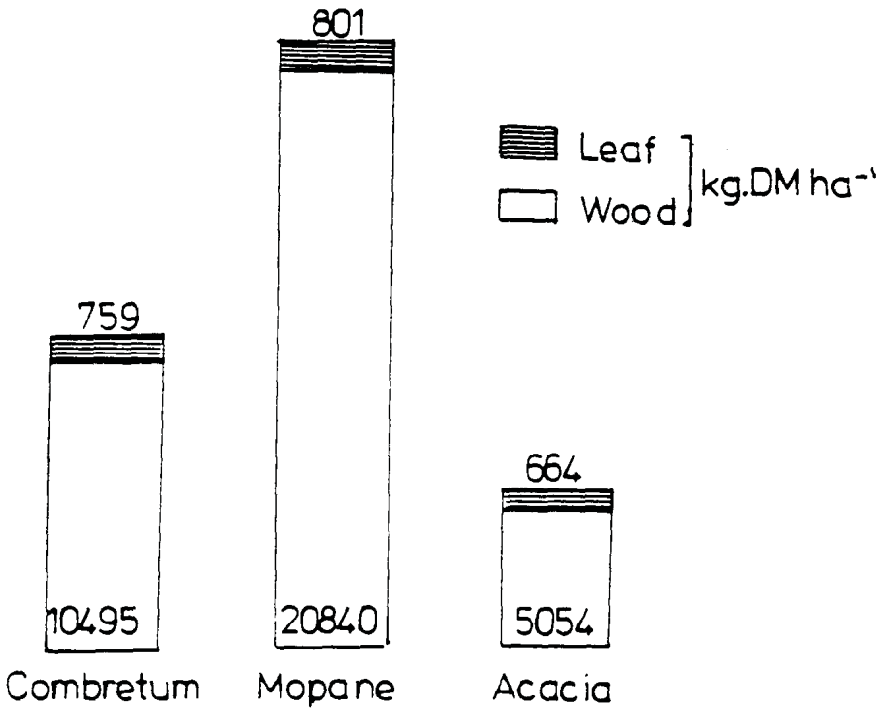

Figure 38. Pre-clearing aboveground standing crop of woody plants

the general tendency, as displayed by the Combretum and Acacia sites, for increasing woody biomass with decreasing clay content in the soil.

For all sites the standing crop of woody plants considerably exceeds the peak herbaceous standing crop, which is however of the same order as the tree leaf biomass alone.

For modelling purposes it was assumed that the woody-plant leaf biomass developed during the first three weeks following the commencement of the rainy season, and then remained constant until the soil dried out, at which stage leaf fall began in proportion to the water deficit. Thus more than one leaf flush per year could occur, as was observed following the intra-seasonal drought of 1983/4. During the drought years of 1981/2 and 1982/3 the assumption that woody-plant leaf biomass is independent of rainfall was incorrect for *C. mopane* coppice. During wet years the coppice

form of *C. mopane* bore a much higher leaf biomass per unit stem cross-section than the thicket form from which it was derived.

Rainfall interception by the stems of woody plants is partly dependent on the bark surface area of the plant. This was approximated for the dominant species by assuming that the form of a stem is cylindrical, and by using the wood density data published by van Wyk (1972) to calculate the stem volume from the stem mass. The regressions are presented in Table 4.1.

The specific leaf area for each species was determined by dividing the leaf area of a large number of leaf samples (as determined planimetry, i.e. one side of the leaf only) by the dry mass of the samples. The results are presented in Table 3.8. In the case of grasses, the specific leaf area is the leaf area divided by the mass of the entire tiller. The leaf area indices for the Combretum, Mopane and Acacia sites works out to 1.4, 0.6 and 0.7 respectively if only woody plants are considered, and up to about 1.5, 1.6 and 2.4 if grasses are included.

4.2 MONITORING OF HERBACEOUS PRODUCTION

The herbaceous layer species composition survey (dry-weight ranking method as modified by Barnes, Odendaal & Beukes 1982) done before clearing began was repeated in January 1984 and January 1985. The results, presented in Figure 39 on page 123 and Table 4.2, show a change to dominance by forbs on the cleared and uncleared plots of all sites. The change was most conspicuous on the Combretum and Mopane sites. Forbs were an insignificant proportion of the standing crop before the drought and were therefore not registered by the dry-weight- ranking technique. The overwhelming proliferation of forbs in 1984 also tended to conceal the differences between the control and cleared sites. O'Connor (1985) notes that the effects of climatic fluctuations tend to override the differences brought about by the bush clearing treatment.

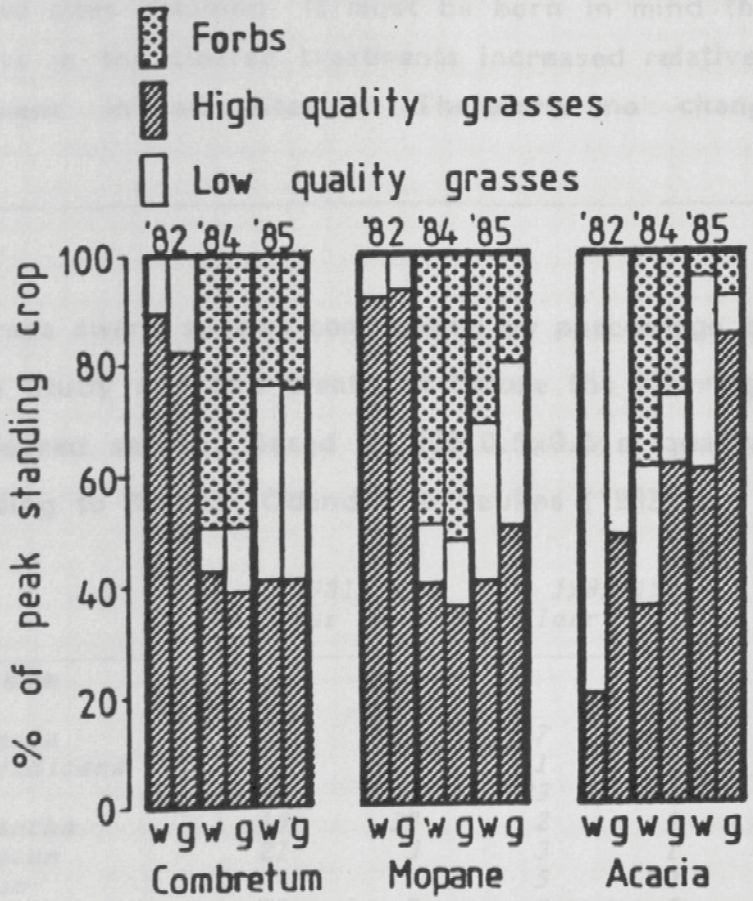

Figure 39. Herbaceous layer composition changes: % of the standing crop in March of each year. 1982 was the preclearing season.

Grass species were divided into two groups on the basis of a subjective assessment of their palatability. All *Panicum* species, *Urochloa mosambicensis* and *Digitaria eriantha* were considered to be of high quality, the rest low quality. The ratio of highly acceptable forage to poorly acceptable forage is nearly the same in the cleared and uncleared treatment on all except the Acacia site, where the cleared plot showed an increase in quality due to the proliferation of *Panicum maximum* and *Urochloa mosambicensis*. This site had a high quality sward in the un-

cleared treatment as well which showed a consistent quality increase over the period of the study, while sward quality in the uncleared treatment of the other two sites declined. It must be born in mind that the total herbage biomass in the cleared treatments increased relative to the uncleared treatment in all sites. Therefore no change in the

Table 4.2 Grass sward species composition by percentage bulk contribution in each study site and treatment before the clearing and during the second cleared season. Based on 100 0.5x0.5 m quadrats per plot ranked according to Barnes, Odendaal & Beukes (1982).

Species	*1981/1982*		*1983/1984*	
	Clear	*Control*	*Clear*	*Control*
1.Combretum site				
Aristida congesta	16	10	7	4
Bothriochloa radicans	1	-	1	3
Cyperaceae	4	3	23	28
Digitaria eriantha	18	39	2	1
Panicum coloratum	21	3	3	1
Panicum deustum	-	-	5	10
Panicum maximum	10	9	2	2
Schmidtia pappophoroides	12	9	4	1
Other grasses	2	-	4	1
Forbs	16	27	48	49
2.Mopane site				
Aristida congesta	7	8	6	7
Cyperaceae	28	29	16	24
Digitaria eriantha	48	45	14	8
Panicum maximum	5	6	1	1
Schmidtia pappophoroides	12	12	5	7
Other grasses	-	-	6	4
Forbs	-	-	52	49
3.Acacia site				
Aristida congesta	1	1	2	2
Bothriochloa radicans	50	76	5	14
Panicum coloratum	20	8	4	4
Urochloa mosambicensis	12	10	26	23
Panicum maximum	17	-	-	1
Other grasses	-	3	8	9
Panicum deustum	-	2	30	9
Forbs	-	-	25	38

palatable/unpalatable ratio nevertheless indicates an increase in the supply of palatable species. Similarly, the apparent decrease in the proportion of forbs between 1984 and 1985 is caused by an increase in the other categories. The forb biomass remained fairly constant, and observations in 1986 indicate that they persisted as a major component of the sward. The forb biomass in 1984 was dominated by *Heliotropium* sp, which was replaced by *Indigophora* sp. and *Sida* sp. in the subsequent years.

Standing crop estimates were obtained by clipping twenty 0.5x0.5m quadrats per treatment, separating the clippings into forb and grass components, drying and weighing. During the 1984/5 season standing crop estimates were made once a month for the duration of the wet season, and herbaceous layer production was calculated as the sum of the positive increments. Consumption by grazing was very low by comparison to herbage production during this and the 1983/4 season, following the large decrease in herbivore numbers due to drought mortality in November 1982 (Scholes 1985). Herbage production was too low during the 1982/3 and 1983/4 seasons to allow the sequential clipping method to be applied usefully. Herbage production in those years was equated to the peak herbaceous standing crop (March sample), since carry-over from the previous season was effectively zero. The peak aboveground herbaceous layer biomasses are given in Table 4.3, and annual herbaceous aboveground production (peak minus carryover from previous season) is plotted in relation to seasonal rainfall in Figure 40 on page 126. The data points marked Winter '84 refer to a second growth flush which occurred following unseasonal rainfall in that year. Total herbaceous layer production was greater on cleared than uncleared treatments at all sites. When grass production alone was considered, only the Mopane and Acacia sites showed a large increase. On the Combretum site the increase in herbaceous production on the cleared plot was almost entirely due to a proliferation of forbs, mostly unpalatable. The Acacia site showed an increase in both grasses and forbs.

Too few data points are available to allow a regression model to be fitted to the relation between herbaceous layer production and annual rainfall. The data from the two post-clearing seasons seem to follow the pattern

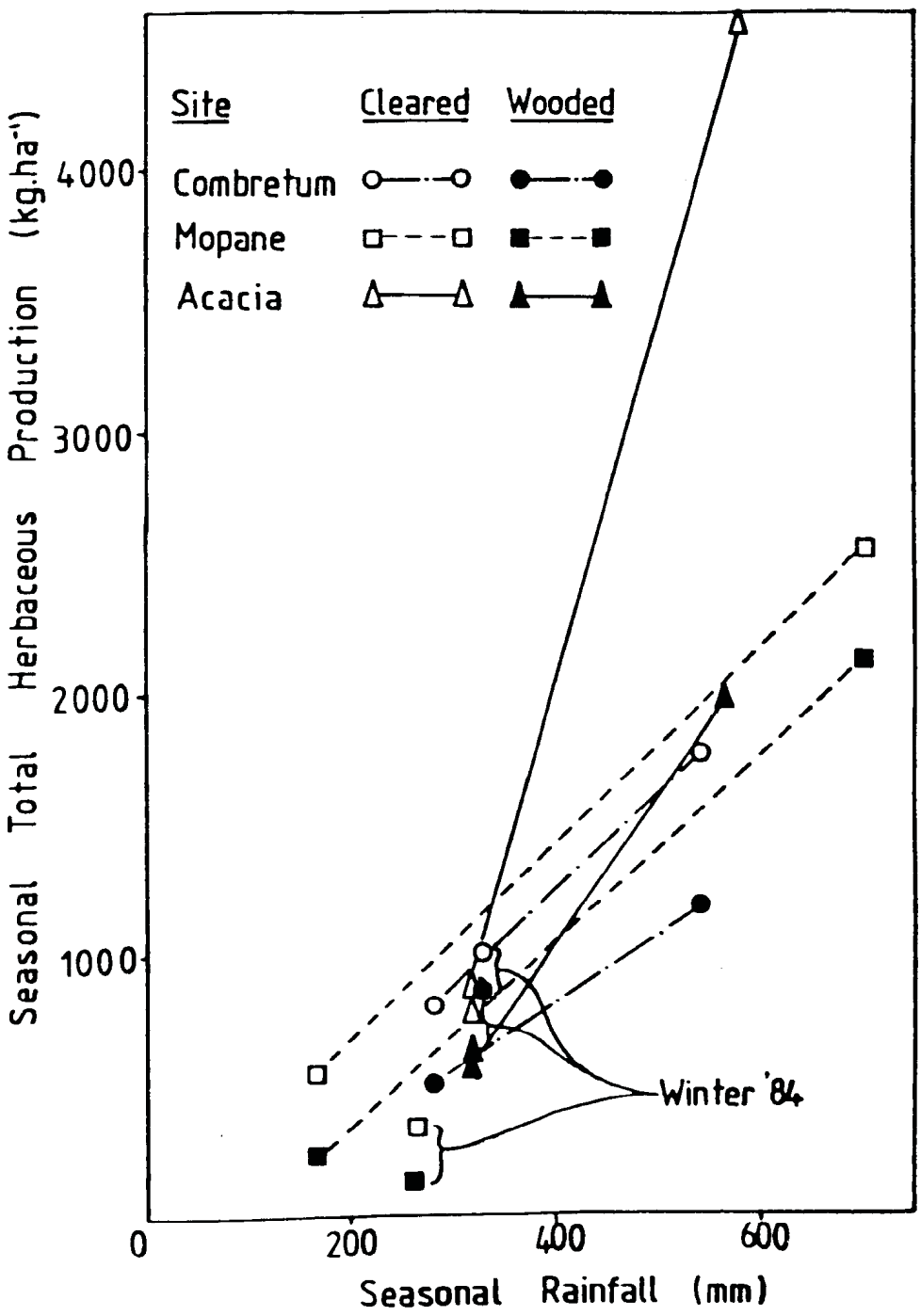

Figure 40. Herbaceous layer production related to rainfall: growing-season rainfall only. The sample is too small to apply regression analysis; lines are for clarity only.

of the Dye & Spear (1982) study, wherein the absolute increase in herbage production between cleared and uncleared treatments is relatively

Table 4.3 Peak herbaceous layer aboveground biomass ($kg.ha^{-1}$) for each growing season. The January 1982 records preceeded clearing. Drought conditions in 1983 prevented a meaningful measurement from being taken (biomass was effectively zero). Values in parentheses are standard errors for 20 samples.

	Grass		Forbs		Total	
	Control	Cleared	Control	Cleared	Control	Cleared
Combretum site						
Jan 1982	210	250	0	0	210	250
Jan 1984	240	260	258	550	498	810
Mar 1985	2091	2734	441	832	2533	3566
	(376)	(590)	(94)	(210)	(406)	(623)
Mopane site						
Jan 1982	914	669	0	0	914	669
Jan 1984	70	232	169	311	239	543
Mar 1985	1843	2748	634	676	2478	3425
	(216)	(187)	(230)	(264)	(442)	(467)
Acacia site						
Jan 1982	994	637	0	0	994	637
Jan 1984	460	705	131	175	591	880
Mar 1985	2969	6004	362	111	3347	6115
	(432)	(1005)	(143)	(100)	(429)	(885)

independent of the seasonal rainfall; in other words, the sward water use efficiency is unchanged, but the water supply is increased. The exception to this pattern is the Acacia site where the increase due to clearing is much greater in the 1984/5 season (c.550 mm effective rainfall) than in the 1983/4 season (c.320 mm). The species composition data (Table 4.2) show that the cleared treatment had a much higher proportion of of *P.maximum* and *Urochloa mosambicensis*. Both of these species have a relatively mesic distribution. It is suggested that their contribution raised the sward water use efficiency in the cleared treatment above that in the wooded treatment. The dense sward suppresses evaporation from the soil surface which further increases the WUE'.

The absolute increase in herbaceous layer production following clearing was 300-500 $kg.ha^{-1}$ (60-56%) in the Combretum site, 300-350 $kg.ha^{-1}$ (150-25%) in the Mopane site and 300-2500 $kg.ha^{-1}$ (120-80%)in the Acacia site. The expression of the bush-clearing response as a percentage increase in grass production is misleading, since the absolute increase is fairly constant between years, but the reference level (uncleared) is highly variable between both sites and years.

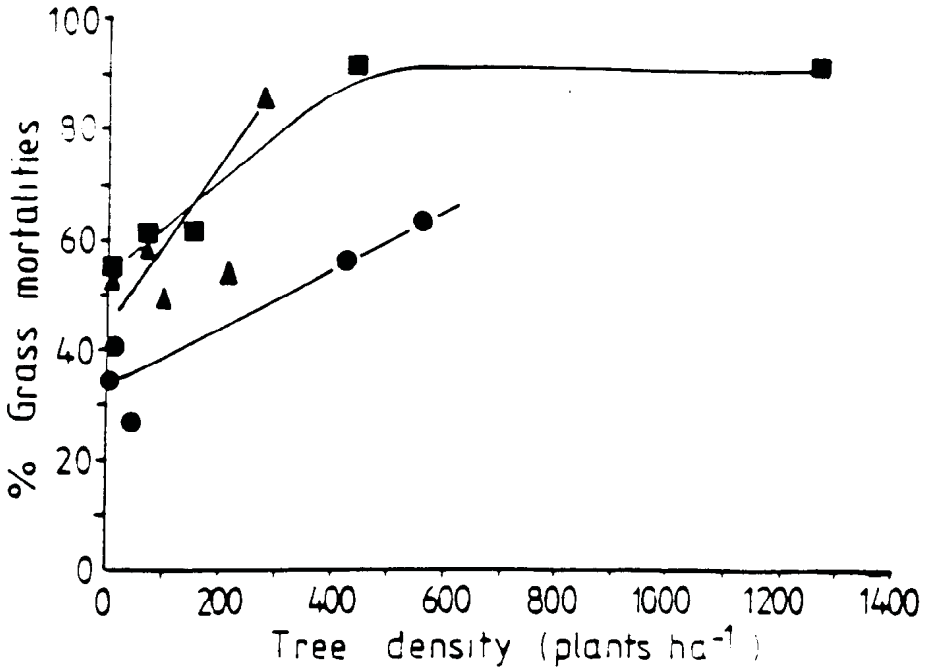

Figure 41. Influence of tree density on grass mortality: A=*A. nigrescens* woodland M=*C. Mopane* woodland O=*Combretum apiculatum* woodland. Curves fitted by eye.

A combination of high grazing pressure and drought during 1981/2 and 1982/3 reduced the grass standing crop to a level where its measurement was impractical and largely irrelevant, since the outcome of competition at this stage was determined not by which species produced the most but by which survived. Effort was therefore directed into determining grass mortality. The density of live and apparently dead grass tufts in relation to forb and tree density was determined by the point-centre-quarter method (Cottam & Curtis 1956) at five sites of differing tree density in each vegetation type. Twenty five points spaced 20 m apart were assessed at each site. A plotless method was chosen because of the order of magnitude differences between the densities of the components recorded. The influence of tree density on grass mortality in each vegetation type is illustrated in Figure 41. The presence of trees increased grass tuft mortality during a period of prolonged water stress. The effect was greatest on soils with a fine texture (the Acacia and Mopane sites)

and least on sandy soils (Combretum site), and was related to the tree density. There was relatively little tree mortality during the same period, and most of it could be ascribed to ring-barking by elephants (Scholes 1985). About 5% of the individuals in an extremely dense *Colophospermum mopane* thicket were killed by the drought, although many more showed some die-back followed by epicormic budding once the drought was over.

The intent was to monitor changes in grass standing crop non-destructively by the spectroreflectance method (Pearson, Miller & Tucker 1976). However during most of the study the green biomass was below the threshold for accurate measurement by this method. Low biomass and abundant forbs precluded the use of other indirect non-destructive methods such as the disc pasture meter (Bransby & Tainton, 1977). The marked tiller method of grass production estimation was therefore selected. One hundred and twenty eight individual tufts of each of the two dominant grass species in each plot were located within a grid system and marked with numbered metal tags. Every four weeks tiller length was measured from the ground to the extended tip of the highest leaf. During the 1982/3 season only the length of the tallest tiller per tuft was measured, but during the following season three individually marked tillers per tuft were measured, and the total number of tillers per tuft was recorded.

In order to assess grass production it was necessary to exclude grazing for a period. One quarter of the marked tillers were covered by a movable herbivore exclusion cage at any given time. The cage was moved to a new position once every four weeks. Additional tillers were marked to preserve the sample size when tillers died. A record was kept of tiller and tuft mortality, since sward productivity depends not only on production per tiller, but also on the number of tillers present. Cumulative tiller extension data are graphically presented in Figure 42 on page 130. Comparisons of tiller number between control and cleared treatments are given in Table 4.4. The experimental design is pseudoreplicated but not autocorrelated, since tillers were measured only during the period

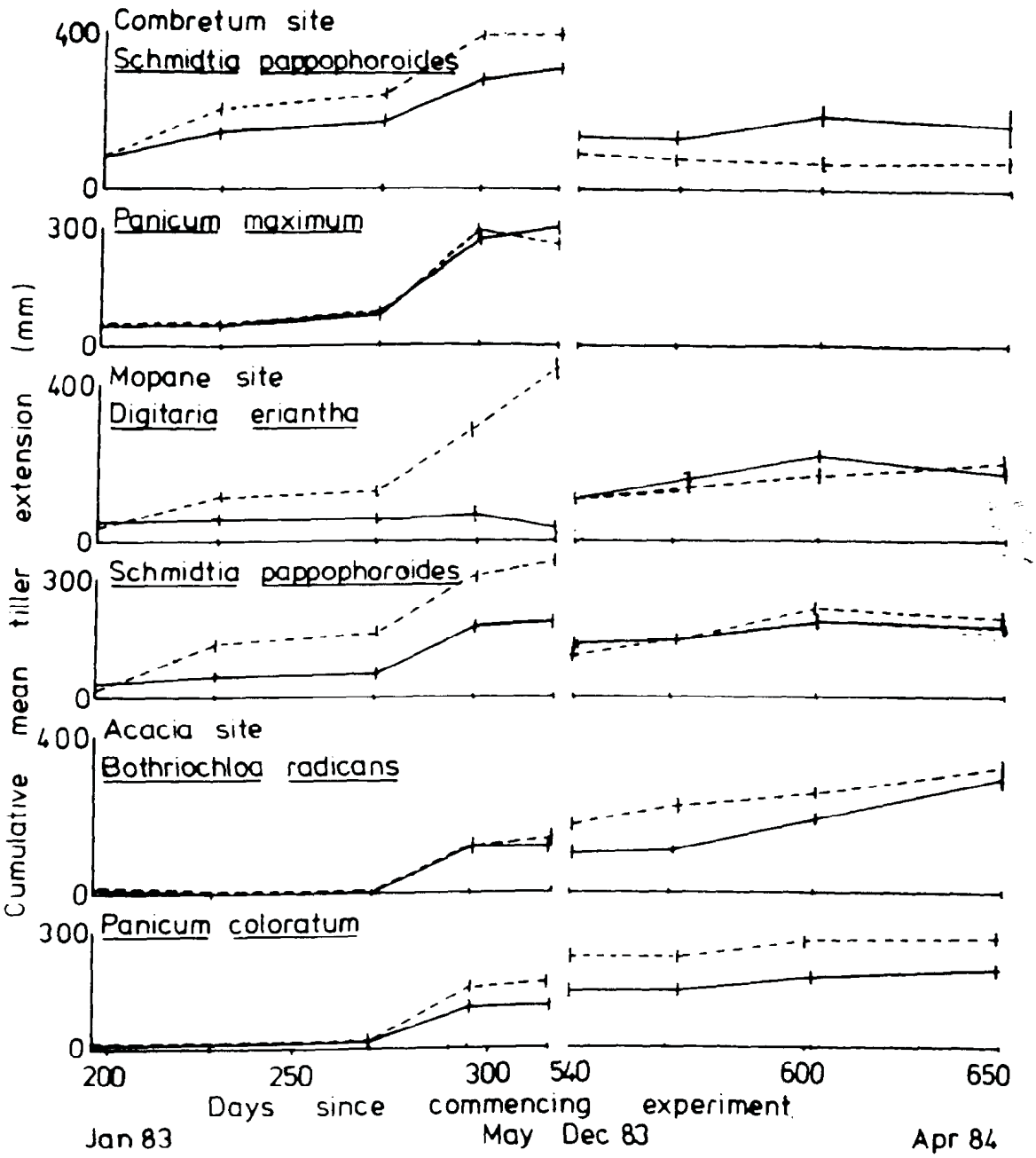

Figure 42. Cumulative tiller extension by site, species & treatment: broken lines are cleared treatments. solid lines wooded controls. Bars are standard errors.

Table 4.4 Mean number of tillers per tuft. Sample size is 64 in all cases but degrees of freedom for the t-tests may be less than 126 due to the assumption of unequal variances.

1.Combretum site

	Nov 1983		Dec 1983		Jan 1984		Feb 1984		Apr 1984	
Schmidtia pappophoroides	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	5.92	0.31	5.66	0.29	5.56	0.30	4.73	0.28	4.75	0.31
control	4.97	0.29	4.73	0.33	4.42	0.34	4.17	0.36	3.75	0.42
t-statistic	2.238	*	2.117	*	2.514	*	1.228		1.916	
Panicum maximum	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	5.95	0.31	5.56	0.30	5.58	0.31	4.88	0.26	4.67	0.31
control	9.12	0.69	9.42	0.64	8.04	0.59	10.64	0.96	12.14	1.03
t-statistic	-4.191	***	-5.461	***	-3.691	***	-5.791	***	-6.945	***

2.Mopane site

Schmidtia pappophoroides	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	11.72	0.71	12.51	0.66	10.77	0.58	10.50	0.67	12.63	0.71
control	9.98	0.66	11.17	0.64	11.67	0.66	10.66	0.74	11.81	0.77
t-statistic	1.795		1.458		-1.024		-0.160		0.783	
Digitaria eriantha	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	7.67	0.53	8.43	0.51	9.00	0.65	11.01	0.77	10.34	0.80
control	3.61	0.26	4.81	0.33	5.86	0.38	7.33	0.45	7.48	0.44
t-statistic	6.877	***	5.959	***	4.170	***	4.126	***	3.132	**

3.Acacia site

Bothriochloa radicans	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	7.06	0.55	15.72	0.83	17.11	0.84	15.92	0.82	13.13	0.70
control	6.34	0.38	15.06	0.98	14.09	0.90	15.23	0.96	14.23	0.75
t-statistic	1.077		0.514		2.453	*	0.547		-1.072	
Panicum coloratum	mean	se	mean	se	mean	se	mean	se	mean	se
cleared	9.75	0.81	13.22	0.87	11.78	0.82	12.48	0.82	12.83	1.04
control	8.39	0.57	10.25	0.72	8.47	0.58	10.91	0.68	10.63	0.68
t-statistic	1.373		2.630	**	3.296	**	1.474		1.771	

*=90, **=95, ***=99 % level of confidence

of herbivore exclusion, which occurred only once per tiller per season, on average.

Tiller length is an extremely sensitive indicator of tiller growth and can be directly related to tiller mass (Sharrow 1981), but is a rather poor measure of sward standing crop since it is very difficult to get unbiased

estimates for all species and tiller sizes in the sward. The marked tillers are not necessarily representative of the entire tiller population since only two species were studied. The species composition of the sward changed radically during the course of the study, both as a consequence of climatic events and of the clearing manipulation. Thus the chosen species were in some cases no longer dominant at the conclusion of the study.

The most rapid tiller growth occurred during the first month of the 1983/4 wet season. At the Combretum site *Schmidtia pappophoroides* grew markedly more on the cleared than uncleared site, but *Panicum maximum* slightly less. *Digitaria eriantha*, a species mostly associated with sub-canopy areas, also grew taller in the uncleared plot of the Mopane site towards the end of the season, and *Schmidtia pappophoroides* in the beginning of the season. At the Acacia site *Bothriochloa radicans* grew taller on the cleared site in the first two months of the season following clearing, but less in the third month. *Panicum coloratum* grew more on the cleared than uncleared treatment during the first month.

Differences in tiller number between treatments were more pronounced than differences in tiller length for most species, and persisted later in the season. The pattern at the Combretum site was the same as for tiller extension, with *S.pappophoroides* being favoured by clearing and *P. maximum* being disadvantaged. At the Mopane site, *S. pappophoroides* showed little difference between the plots, but *D. eriantha*, which showed less extension on the cleared treatment, nevertheless had consistently more tillers there. *B. radicans* showed little difference in tiller number between the treatments at the Acacia site, while *P. coloratum* had more tillers on the cleared plot during mid-season but by April the difference was small.

Three components of the grass production increase recorded as at the peak of the third post-clearing season are presented in Table 4.5. The fourth, change in sward water-use efficiency due to change in species composition, is a direct result of the changes in density and size of individual tillers. Mass per tiller (which is indexed by tiller length) increased more rapidly on the cleared than uncleared sites early in the first and second growing season (Table 4.3) but the difference was largely lost by the the third post-clearing season. The difference in tillers per

Table 4.5 The components of grass production increase, March 1985.

	Mass per tiller (g)		Tillers per tuft		Tufts per hectare	
	Cleared	Uncleared	Cleared	Uncleared	Cleared	Uncleared
Combretum site						
A. congesta	26.80	30.13	3.75	3.30	3.55	2.28
P. maximum	18.46	16.33	25.01	33.64	1.08	2.63
P. squarrosa	46.46	31.33	14.78	2.35	4.32	4.38
U. mosambic.	21.06	20.00	12.51	17.12 *	1.39	0.53
Other					5.10	7.68
Total					15.44	17.50
Mopane site						
A. congesta	46.2	42.06	6.61	4.98 **	3.46	8.88
E. rigidior	16.73	10.53	10.22	6.33 **	8.22	5.61
P. maximum	24.50	13.93 **	34.10	35.03	1.73	0.00
P. squarrosa	33.66	49.80 **	4.79	3.00 ***	3.89	5.61
S. pappoph.	19.60	18.86	6.15	4.94 *	9.95	9.35
U. mosambic.	29.46	24.46	16.42	14.77	0.43	1.87
Other					15.56	15.42
Total					43.24	46.74
Acacia site						
B. radicans	33.86	25.93	16.56	5.28 **	0.30	2.66
P. maximum	27.60	18.00 **	27.05	31.33	1.36	0.02
U. mosambic.	24.73	32.53	14.83	16.85	7.09	7.78
Other					6.33	10.01
Total					15.08	20.47

*=90, **=95, ***=99 % level of confidence

tuft persisted in the third season on the Mopane site, but less so on the other sites. The relative tardiness of this site in adjusting to the post-clearing environment is probably due to to the extremely low rainfall it received in 1982/3. In general the number of tufts per hectare decreased slightly (but not significantly) after clearing, while the performance per tuft had increased, largely due to increased tillering. The sub-canopy grass *P. maximum* increased in performance per tiller and decreased in tillers per tuft at all sites. The number of plants per hectare was lower on the cleared than uncleared treatment at the Combretum site, but higher at the Acacia site. Tuft density was measured in December 1984, using a plotless distance-based method (Diggle 1975, Cox 1976). One hundred points were systematically located within a one hectare area, using a wheel-point apparatus (Tidmarsh & Havenga 1955). The distance

from each point to the centre of the nearest grass tuft was recorded to a resolution of 10mm (d_x) and from the centre to the centre of the nearest neighbouring tuft (d_y) The total tuft density was estimated using the compound estimator of Cox (1976), which is corrected for non-random dispersion. These data were also used to test for evidence of competition in the sward. The results are presented in Table 4.7.

4.3 ROOT DISTRIBUTIONS

The distribution of roots in the soil profile is of critical importance to the Walter hypothesis. Strang (1969a) includes some observations of rooting depth in savannas and notes that while grasses have prolific roots in the surface horizons, they also have deeper roots. This was confirmed by Dye (1984) who showed that a significant portion of the water requirement of grass plants can be met by roots deeper than 0.5 m, and that rooting depth varies between grass species. Knoop (1982) showed that the hypothesis of exclusive access to deeper soil horizons by tree roots was false.

This study made no attempt to determine the productivity of underground plant parts, but the vertical distribution of grass and tree roots was estimated by the profile method (Bohm 1979). Two 1 m deep pits were dug in each treatment plot before clearing, one under a tree canopy and one in the open (thus four pits per site). One face of the pit was cut to the vertical, smoothed and washed to a depth of approximately 10 mm with a fine water spray. Care was taken to wash the entire profile evenly. A 0.5x1.0 m sheet of clear Perspex was fixed to the profile and covered with a thin sheet of clear acetate. Grass and tree roots, which were morphologically distinct down to about 0.5 mm diameter, were traced onto the acetate using different coloured pens.

The centimetres of root length for each root type (grass or tree) were summed horizontally in 5 cm deep bands to the depth of the profile. The

scoring was aided by the use of a 5x5 cm reticule ruled into 1x1 cm grid squares. A root occurring in a square was scored as one centimetre of root length, irrespective of root diameter. Root scores per type per 5 cm depth class were expressed as proportions of the total score for that root type over the entire profile to remove the bias introduced by unequal washing depth between profiles. These proportions are presented in Figure 43 on page 136.
The difference in proportions at each depth were tested for significance using the Mann-Whitney-Wilcoxon test for paired samples, since the root counts are non-normally distributed. Since many tests were performed, a few of the individual test results are likely to be spurious. The overall trends, however, are clear.

Grass plants have proportionately more of their roots in the surface horisons than tree roots do, and *vice versa* in the deeper soil layers. In between is a zone in which there is no significant difference between the grass and tree root distributions. This zone extends from 300mm to 500mm in the sandy site, 150 to 500mm in the sandy loam site and from 100 to 900mm in the clayey site. Therefore rooting depth differentiation is much clearer on soils with high infiltration rates and low water-holding capacity.

The total counts for grass roots greatly exceeded those for tree roots at all sites (Combretum site 3:1; Mopane site 2:1; Acacia site 6:1). This does not necessarily mean that grass root activity exceeded tree root activity by the same amount, since root density is only one of the factors influencing activity. Resource concentration, radial and axial root resistances, mycorrhizal infection and temporal factors also influence root uptake rates.

A depth of 350 mm, corresponding approximately to the transition between the A and B horizons in all sites, and corresponding also to the horizons used by other workers (Knoop 1982), was chosen as the lower limit of the topsoil. The proportions of each type of root occurring in the topsoil was used to test for differences in root distribution between treatment plots, sub-habitats within sites, and between sites (Table 4.6).

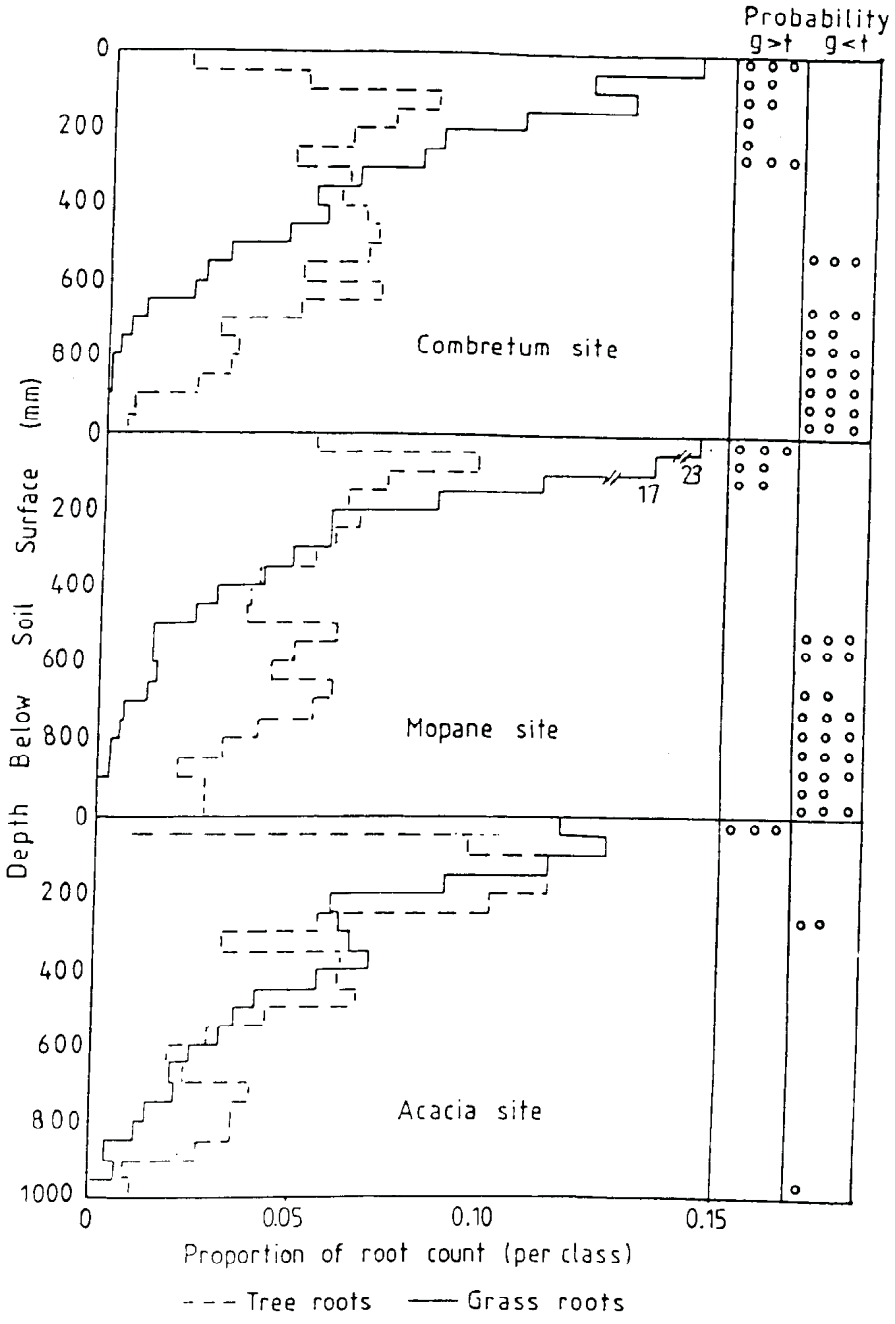

Figure 43. Root distributions: Proportions of the total count for each root type encountered at each depth. Significance levels o 90% oo-95% ooo-99%

Table 4.6. Tests of significance for differences in the proportions of grass and tree roots in the topsoil (< 350mm deep) between sites and subhabitats. O=between canopies, C=beneath canopy.

*=90% **=95% ***=99% significance level

Site	Acacia				Combretum				Mopane			
Root type	Grass		Woody		Grass		Woody		Grass		Woody	
Habitat	C	O	C	O	C	O	C	O	C	O	C	O
Code	a	b	c	d	e	f	g	h	i	j	k	l
Mean	55	73	51	69	76	74	72	69	77	85	70	81
sd	2.2	7.7	3.2	8.6	9.6	12.1	8.8	12.7	6.4	9.3	5.7	11.1
n	4	4	4	4	4	4	4	4	4	4	4	4
t-tests for	a-b		c-d		e-f		g-h		i-j		k-l	
Habitat												
|t|	4.607		3.916		0.259		0.387		1.377		1.876	
prob>|t|	.0147		.0196		.8049		.7135		.2240		.1275	
	*		*									
t-tests for	a-c		b-d		e-g		f-h		i-k		j-l	
Root types												
|t|	2.054		0.778		0.499		0.484		1.764		0.482	
prob>|t|	.0919		.4666		.6356		.6459		.1290		.6477	
t-tests for	a-e		b-f		a-i		b-j		e-i		f-j	
Sites (grass)												
|t|	4.216		0.035		6.615		1.904		0.260		1.474	
prob>|t|	.0209		.9736		.0039		.1074		.8043		.1945	
t-tests for	c-g		d-h		c-k		d-l		g-k		h-l	
Sites (trees)												
|t|	4.588		0.065		5.769		1.772		0.525		1.416	
prob>|t|	.0122		.9506		.0028		.1304		.6213		.2074	
	*				**							

Pooled habitat data

Root type	Grass	Woody	Grass	Woody	Grass	Woody
Code	A	B	C	D	E	F
mean	65	60	75	71	81	76
sd	11.2	11.3	10.1	10.2	8.5	7.6
n	8	8	8	8	8	8
t-tests for	A-B		C-D		E-F	
Root types						
|t|	0.754		0.734		1.166	
prob>|t|	.4634		.4750		.2640	
t-tests for	A-C	B-D	A-F	B-G	C-F	D-G
Sites						
|t|	1.963	2.033	3.402	2.880	1.364	0.898
prob>|t|	.0700	.0616	.0047	.0122	.1949	.3842
			**			

*=90% **=95% ***=99% significance level