62 km. The east-west displacement is 16 km. Altitude at all these localities is approximately 550 m a.s.l.

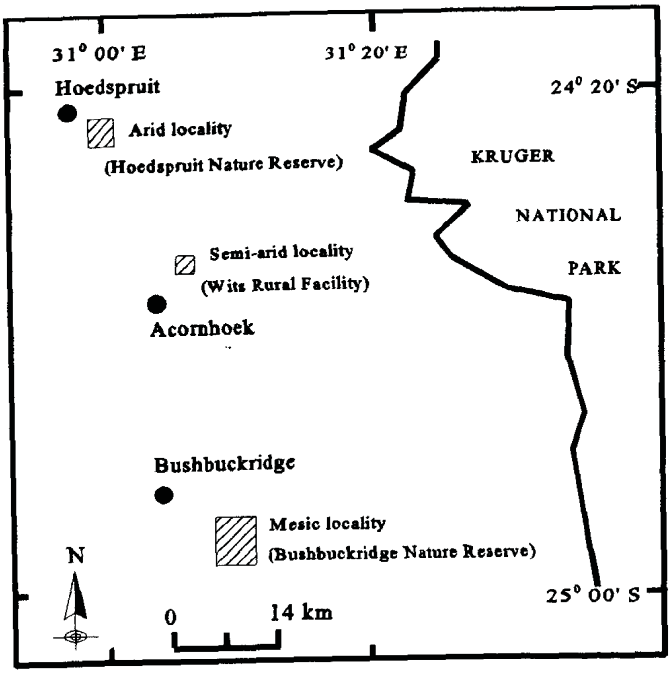

Figure 2.1. Location of intensive monitoring areas.

The arid locality is a 2 000 ha nature reserve surrounding the Hoedspruit (HNR) military airforce base. The semi-arid locality, at Wits Rural Facility (WRF) covers 350 ha and is managed as a tertiary education facility. The mesic locality is situated in the central lowland area of Bushbuckridge Nature Reserve (BNR). Bushbuckridge Nature Reserve is approximately 4 000 ha in extent, but only the central section is comparable to the other two localities with respect to geology and geomorphology, hence all work was limited to an easily definable 550 ha portion on the lowlands.

2.3.2 Geology and soils

All three localities are situated on weathered granites with doleritic intrusions reaching the surface in isolated places. Typical catenal sequences are evident at all three localities. Thus, upland soils are shallow, coarse-textured and dystrophic, whilst bottomland soils are deeper, finer-textured and more eutrophic.

2.3.3 Rainfall

Mean annual rainfall (MAR ± SE) is the primary variable differentiating the three localities, being 484 ± 32 mm (n = 27) at the arid site, 651 ± 123 mm (n = 28) at the semi-arid site, and > 870 mm at the mesic site (MAR at Injaka (2 km west, 780 m.a.s.l.) = 1161 ± 225 mm; n = 5)). At all localities rainfall is concentrated into the summer season from October to May. The length of the rainy season increases with increasing MAR. Rain is received largely in the form of convectional thundershowers, although periods of prolonged cyclonic showers do occur.

2.3.4 Vegetation

The three localities fall into Acocks' (1988) broad vegetation type of Tropical Bush and Savanna. More specifically, the arid locality is in Veldtype 11, Arid Lowveld, dominated by members of the Mimosaceae (especially *Acacia nigrescens*, *A. gerrardii*, *Albizia harveyii*, *Dichrostachys cinerea*), along with *Combretum apiculatum*, *Sclerocarya birrea*, *Ormocarpum trichocarpum* and *Grewia* species. Mean height of the canopy is 5 - 6 m.

The semi-arid locality is situated on the boundary between the Arid Lowveld and Lowveld Veldtypes. The woody stratum is dominated by Combretaceae species (including *Terminalia sericea*, *Combretum collinum*, *C. hereroense*), with *S. birrea* and *D. cinerea* also being significant contributors to the biomass. Mean canopy height is 6 - 7 m.

The mesic locality is situated on the boundary between the Lowveld Veldtype and Lowveld Sour Bushveld Veldtype, dominated by taller (8 - 9 m), more broadleaved species than the other two sites, namely *Pterocarpus angolensis*, *Faurea saligna*, *T. sericea*, *C. collinum*, *Parinari curatellifolia* and *Dombeya rotundifolia*, along with *S. birrea* and *D. cinerea*. More details of the vegetation at each locality are provided in Section 2.5.

2.3.5 Fauna

Biomass of indigenous fauna at the semi-arid and mesic localities is low. The arid locality has a range of indigenous ungulates, with a mean biomass of 34 kg/ha, dominated by giraffe (30.0 %), Burchell's zebra (12.5 %), blue wildebeest (10.5 %), impala (9.5 %) and waterbuck (8.9 %).

2.3.6 Land use

In precolonial times, the central lowveld was only sparsely inhabited due to the prevalence of tsetse fly and malaria (Shackleton *et al.* 1995a). However, with commercialisation of the lowlands for cattle production, as well as land purchases by large mining companies to reserve access to mineral rights, increased settlement occurred, both on crown lands, as well as private lands as labour tenants (Shackleton *et al.* 1995a). It is to be expected that the increasing settlement density had localised impacts on the fauna and flora, but not of significant magnitude. Relics of human settlements (pot sherds, grinding stones, grain pits, etc.) are to be found within each locality indicating past human occupation, but there appear to be no macro-environmental disturbances resulting from these.

After the turn of the century all three localities were subjected to cattle ranching up until the mid 1960 or 1970s. Wild ungulates were also present during this period, but without any active management. The arid locality was declared a military area in 1978, and a nature reserve established as a surrounding buffer zone. Wild ungulates were reintroduced, and the area is currently managed by the South African National Defense Force. The semi-arid site became a commercial game ranch in 1968, focusing on tourism. Stumps of large trees of commercially valuable species such as *Pterocarpus angolensis* and *Combretum imberbe* are evident at the semi-arid locality, and to a lesser extent, the mesic locality. Local inhabitants suggest that at the semi-arid locality these species were cut out to supply a furniture factory at GreenValley (A. Shabangu, pers. comm.). This may explain why the biomass per hectare at this locality is lower than at the arid locality (see Sect. 2.5.1). In 1988 most of it was converted to a research and education centre of the University of the Witwatersrand. There is little active management of the natural habitat other than a periodic block burn conditional on fuel-load. Wild ungulate biomass is low. The mesic locality was designated as a nature reserve in 1975 with partial control designated to the Gazankulu homeland government, and part control to the South African Development Trust. The reserve was not fenced and thus experienced continuous low levels of cattle grazing, and removal of resources (thatch, fuelwood, fruits, carving timber) by neighbouring inhabitants. The area was fenced in 1994, but resources are still removed by the surrounding communities, albeit illegally in the perspective of the current managers (the Mpumalanga Department of Environmental Affairs). The reserve is burnt every one or two years, intentionally or unintentionally.

2.4 METHODS

The woody vegetation at each study reserve was characterised by means of random transects; 95 at the arid locality, 30 at the semi-arid locality, and 52 at the mesic locality. Transect size was 5 m x 50 m at the arid and mesic localities, and 5 m x 80 m at the semi-arid locality. Transect size differed since the data for the semi-arid locality were taken from Shackleton (1993).

Within each transect the following variables were measured for each woody stem irrespective of whether the plant was multi- or single-stemmed: (1) height, (2) basal circumference at 5 cm above ground level, unless coincidental with the basal swelling, in which case the basal circumference just above the swelling was taken, (3) species. Heights less than two meters were measured using a tape. Heights greater than two meters, but less than 4,5 m were estimated visually to the nearest 10 cm. Heights greater than 4,5 m were determined via trigonometric conversion after measuring an angle to the top of the tree with an Abney level.

Total standing biomass was determined using regression equations of Rutherford (1979). Size class profiles were constructed using 5 cm increments in circumference (Shackleton 1993, Shackleton *et. al.* 1994).

Significant differences in most variables were assessed using one-way ANOVA. Subsequent pairwise comparisons on significant ANOVAs used the Least Significant Difference. Size class distribution profiles were compared using a Kolgomorov-Smironov test.

2.5 RESULTS

2.5.1 Woody structure

Overall there was a gradient of increasing woody density from the arid locality to the mesic locality, with the semi-arid locality being intermediate (Table 2.1). However, there were no significant differences between the arid and semi-arid localities with respect to density, biomass, basal area, volume and mean height. In several instances the mean for the semi-arid locality was less than that of the arid. This may be a result of the probable felling of the more valuable timber species at the semi-arid locality (Sect. 2.3.6). Inclusion of a few large specimens of *Pterocarpus angolensis* or *Combretum imberbe* would markedly increase the basal area and biomass at this reserve. The mesic locality was significantly more woody than either the arid or semi-arid localities for all variables considered.

2.5.2 Size class distribution

The size-class distribution profile at the mesic locality was significantly different to that at the arid and semi-arid localities ($S=0.45$; $p<0.0001$), having a greater proportion of stems in the smallest size class, and fewer stems in the intermediate size classes (Fig 2.2). The proportion of stems in the largest size classes were similar at all three sites. Although there was a tendency for the proportion of stems in a given size class at the semi-arid locality to be intermediate between the arid and mesic, the distribution profiles between the arid and semi-arid localities were not significantly different ($S= 0.06$; $p> 0.05$).

2.5.3 Proportion of regenerative stems (≤ 2 cm circumference)

The proportion of regenerative stems differed significantly between the three localities ($F=162.1$; $p < 0.0001$), being highest at the mesic locality, and least at the arid locality (Fig 2.3). Whilst there was a strong trend of an increasing proportion of regenerative stems with increasing rainfall, the difference between the arid and semi-arid localities was not significant.

Table 2.1. Woody community structural characteristics at the arid, semi-arid and mesic localities (± SE). (Note: transect size at the semi-arid locality was double that at the other two). (Unlike letters indicate significant differences between those sites; like letters indicate no significant difference).

ATTRIBUTE	LOCALITY			
	ARID (n = 95)	SEMI-ARID (n = 30)	MESIC (n = 52)	p
Density of all stems (no./ha)	5208 (235.1)	5583 (328.0)	21374 (1410.6)	<0.0001 **a a b**
Basal area (m^2/ha)	10.1 (0.61)	8.6 (0.90)	14.1 (0.93)	<0.0001 **a a b**
Biomass (t/ha)	23.1 (2.28)	18.9 (3.67)	41.3 (4.53)	<0.0001 **a a b**
Volume (m^3/ha)	52.2 (4.83)	43.5 (7.7)	94.8 (9.7)	<0.0001 **a a b**
Height of tallest stem/ transect (m)	6.61 (0.28)	6.69 (0.52)	8.91 (0.35)	<0.0001 **a a b**

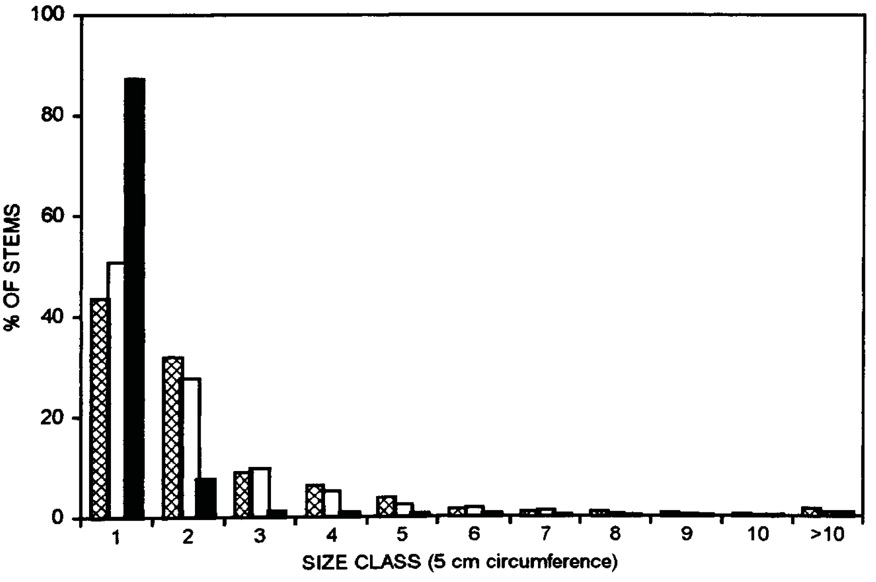

Figure 2.2. Size class profiles at the arid (☒), semi-arid (☐), and mesic (■) localities.

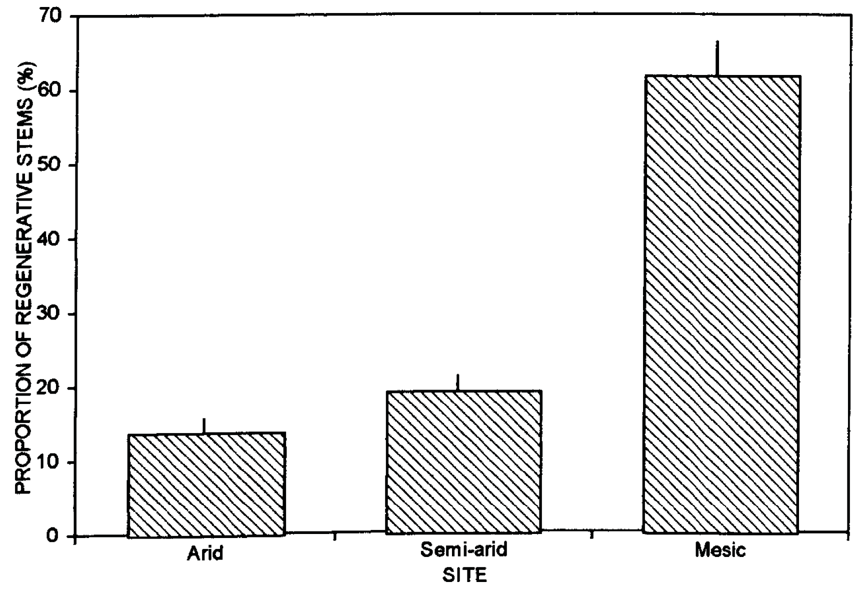

Figure 2.3. Proportion of regenerative stems at each locality.

2.5.4 Species composition

There were considerable dissimilarities in the species composition between the three localities (Table 2.2). There was a decreasing proportion of the biomass in spinescent species as well as members of the Mimosaceae with increasing rainfall ($p< 0.0001$) (Fig 2.4).

2.6 DISCUSSION

Witkowski & O'Connor (1996) commented that most phytosociological studies of southern African savannas have been at an inappropriate scale to analyse the effects of rainfall on savanna structure. Whilst the primary objective of this section was simply to describe for the reader the localities for several of the more intensive components of the overall study, it was possible to make some comparisons of woodland structure along the selected rainfall gradient.

Several changes were evident along the gradient of increasing rainfall, including increasing woody plant density, height of the canopy, number of species, density of regenerative stems and a greater proportion of stems in small size classes. The proportion of spinescent species decreased with increasing rainfall. A important question to consider in assessing the significance of these trends, as highlighted by Witkowski & O'Connor (1996), is the degree to which changes in structure are a response to environmental gradients rather than changing species composition. Their study indicated marked changes in community physiognomy along the primary environmental gradients (mainly edaphic) after species composition was accounted for.

At a superficial analytical level, the same is not apparent in the current study as species composition and type changes along the rainfall gradient. However, whilst an awareness of the question is relevant it may lead to spurious diversions. Community physiognomy is a function of community species composition, which in turn is a function of the interaction between primary and secondary determinants. Thus, physiognomy may be said to be a result of the same environmental determinants.

Table 2.2. The species contributing 2 % or more to either the density, biomass or basal area at each locality.

LOCALITY	SPECIES	DENSITY (stems/ ha)	%	BASAL AREA (m^2/ha)	%	BIOMASS (t/ha)	%
ARID	*Acacia exuvialis*	130.5	2.5	0.0467	0.5	0.0330	0.1
	Acacia nigrescens	133.1	2.6	1.2105	12.2	5.4071	23.5
	Albizia harveyii	130.5	2.5	0.8885	9.0	1.9619	8.5
	Combretum apiculatum	557.9	10.8	2.0580	20.8	3.6827	16.0
	Combretum hereroense	91.4	1.8	0.2419	2.4	0.4094	1.8
	Commiphera schimperii	172.6	3.3	0.0480	0.5	0.0140	0.1
	Dichrostachys cinerea	932.6	18.0	0.5795	5.9	0.4995	2.2
	Grewia bicolor	700.6	13.5	0.4671	4.7	0.3661	1.6
	Grewia flava	452.6	8.7	0.2479	2.5	0.1770	0.8
	Grewia flavescens	212.2	4.1	0.0442	0.5	0.0263	0.1
	Lannea stuhlmanniana	13.1	0.3	0.3065	3.1	0.9909	4.3
	Ormocarpum trichocarpum	409.3	7.9	0.2526	2.6	0.1853	0.8
	Peltophorum africanum	25.3	0.5	0.2297	2.3	0.4266	1.9
	Sclerocarya birrea	16.8	0.3	1.2705	12.8	4.6719	20.3
	Total	3978.5	76.8	7.8816	79.8	18.8517	82.0
SEMI-ARID	*Acacia swazica*	304.3	5.5	0.2270	2.6	0.1520	0.8
	Albizia harveyii	144.3	2.6	0.2976	3.5	0.4937	2.4
	Combretum collinum	292.5	5.3	1.0365	12.0	3.1796	15.7
	Dichrostachys cinerea	1227.5	22.0	0.9111	10.6	0.8625	4.3
	Diospyros mespiliformis	32.5	0.6	0.4469	5.2	1.6693	8.3
	Euclea natalensis	192.5	3.5	0.1100	1.3	0.0794	0.4
	Lonchocarpus capassa	41.8	0.7	0.5185	6.0	2.1373	10.6
	Maytenus senegalensis	215.0	3.9	0.0981	1.1	0.0579	0.3
	Sclerocarya birrea	107.5	1.9	1.3481	15.6	6.2233	30.7
	Strychnos madagascariensis	321.8	5.8	0.6669	7.7	1.4039	6.9
	Terminalia sericea	1116.8	20.1	1.4615	16.9	2.1353	10.6
	Total	3996.5	71.9	7.1222	82.5	18.4124	91.0
MESIC	*Annona senegalensis*	223.1	1.1	0.3710	2.6	0.3301	0.8
	Antidesma venosum	1113.1	5.2	0.4410	3.1	0.7116	1.7
	Combretum collinum	793.1	3.7	1.0533	7.5	3.0062	7.2
	Dichrostachys cinerea	2896.1	13.6	0.6890	4.9	0.5212	1.3
	Dombeya rotundifolia	1059.2	5.0	0.0726	0.5	0.0650	0.2
	Euclea natalensis	584.6	2.8	0.0246	0.2	0.0079	-
	Faurea saligna	2820.0	13.3	2.1931	15.6	8.9101	21.5
	Heteropyxis natalensis	559.2	2.6	0.2617	1.9	0.7557	1.8
	Ochna sp	659.2	3.1	0.0104	-	0.0022	-
	Parinari curatellifolia	1936.9	9.1	0.7747	5.5	1.4333	3.5
	Pavetta schumanianna	1131.5	5.3	0.0927	0.7	0.0628	0.2
	Pterocarpus angolensis	326.9	1.5	2.5744	18.3	9.2908	22.4
	Pterocarpus rotundifolius	596.9	2.8	0.3587	2.6	0.9252	2.2
	Sclerocarya birrea	37.7	0.2	1.2223	8.7	5.2268	12.6
	Strychnos madagascariensis	1793.1	8.4	0.5131	3.7	0.9922	2.4
	Terminalia sericea	1999.2	9.4	1.7832	12.7	5.6646	13.6
	Total	18530	87.1	12.4358	88.5	37.9057	91.4

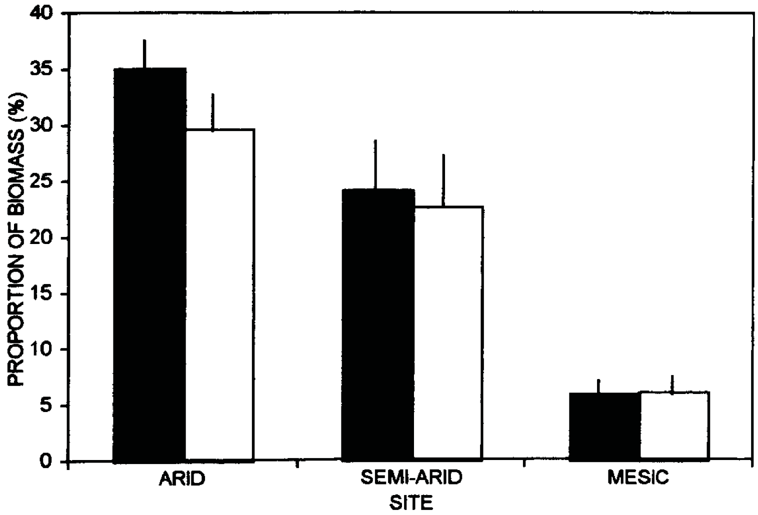

Figure 2.4. Proportion of spinescent species (□) and members of the *Mimosaceae* (■) at each locality.

These trends relative to rainfall conform to other studies contrasting vegetation in different rainfall zones (e.g. Whittaker 1975, Harrington *et al.* 1995, Frost 1996) as well as current understanding of savanna woody structure and dynamics (Scholes & Walker 1993). Frost (1996) provided regressions of stand basal area and stand biomass relative to MAR for miombo woodlands. Both had a positive relationship with rainfall. However, the regression relationships he provided did not match the data from this study ($p < 0.005$). A positive regression was evident between stand biomass and basal area and MAR for the productivity plots round the South African savanna biome recorded in this study (Chap. 3):

$$Biomass\ (\mathrm{t/ha}) = 0.10\ (MAR)\ (\mathrm{mm}) - 30.75 \qquad (r^2 = 0.12;\ p < 0.05;\ n = 51)$$

$$\sqrt{Basal\ area}\ (\mathrm{m^2/ha}) = 0.0023\ (MAR) - 1.812 \qquad (r^2 = 0.11;\ p < 0.01;\ n = 51)$$

No relationship was found between density and MAR by Frost (1996) for miombo woodlands, nor was one evident for the productivity plots of this study (Chap. 3), but a trend was apparent when comparing the three intensive study localities described here.

Floristically, the three localities are typical of the broader vegetation types of the region, each with subcomponents differentiated largely on the basis of rainfall and topo-edaphic gradients (e.g. Bredenkamp *et al.* 1983, Gertenbach 1983, Fraser *et al.* 1987, Witkowski & O'Connor 1996).

WOODY PLANT PRODUCTIVITY:
GROWTH AND DEATH (1992 - 1996) ACROSS A RANGE OF SITES

3.1 INTRODUCTION

The degree of uncertainty pertaining to woody productivity in southern African savannas has been highlighted (Chap. 1). Whilst Scholes & Walker (1993) suggest that one result of the sixteen year long Savanna Biome Project at Nylsvley was to focus more attention on the woody component of savannas, Smit *et al.* (1996) recently concluded that there remains only limited information on woody productivity and Frost (1996) stated that there have been "no complete studies of woody plant production in miombo woodland".

There are two key contributions that would enhance current understanding of woody productivity, and hence savanna structure and function. The first is more information regarding the spatial and temporal range in woody productivity. The second is some understanding of the causes of that spatial and temporal variability. This requires estimates of woody production at a range of sites, across all species at that site, and across a number of years. Growth ring measurements can be taken for individual stems to determine temporal variation, although well defined boundary parenchyma is relatively uncommon in savanna species (Lilly 1977). Moreover growth rings provide data for individual stems, which can provide an index of stand productivity, but extrapolation to the stand level is imprecise (Sect 1.5.3).

There is little published productivity data at the stand level spanning more than a single year. Good data exist for individual species including *Baikiaea plurijuga* and *Terminalia sericea* (Childes & Walker 1987), *Colophospermum mopane* (Scholes 1990b), *Brachyleana huillensis* (Kigomo 1994), *Acacia* species (Gourlay 1995), *Acacia tortilis* (Reid & Ellis 1995), *Pterocarpus angolensis* (Desmet *et al.* 1996) and a few studies that measured several species (Rutherford & Kelly 1978). Most of these studies established some relationship between species growth rate and rainfall.

Studies spanning more than one site are equally limited. Menaut & Cesar (1982) compared four sites along a topographic sequence grading from dense woodland savanna through to open shrub savanna. Productivity was highest in the densest stand (11.7 %) and decreased with declining woody density. Kelly & Walker

(1976) compared browse production from nine sites of similar abiotic characteristics but differing in intensity of use. Browse production was relatively independent of intensity of use, with a coefficient of variation of 31 %. Again, individual species studies provide some insight of dynamics at a stand level, but not stand productivity levels. Prins & van der Jeugd (1992) found markedly higher growth for all five species tested on eutrophic soils relative to the same species on dystrophic soils.

One theoretical constraint to comparative productivity studies at the community level is the inability to differentiate between site and species effects. Thus, differences in productivity between sites may be interpreted as more of a reflection of inherent differential growth rates between species (Lambers & Poorter 1992) rather than site characteristics. This may be a superfluous diversion. Different sites are characterised by different species, although there may be some generalist species in common. However, it is the specific site characteristics that impose the selective pressures that determine the species composition modified by past disturbance and management (Guach 1982, Bryant *et al.* 1983, Colely *et al.* 1985). Therefore, site quality is the primary determinant of community productivity (Vanclay 1991). Community biomass may also be more a reflection of substrate than floristic composition (Menaut & Cesar 1982, Mooney & Gulmon 1983).

3.2 OBJECTIVES

To determine: (1) the annual growth rate of a stand of savanna trees and shrubs from a range of sites, and (2) correlations between the growth rate and selected abiotic and biotic variables.

3.3 METHODS

In July/August 1992 47 plots were established at 24 localities around the South African savanna biome, including the three pilot plots established at Wits Rural Facility the previous year. The 1991/92 season was an extreme drought year throughout most of the South African savanna biome. In winter 1993, four more plots were added (at two localities), bringing the total to 51 plots (Fig. 3.1). Plots were of variable size depending on woody plant density. The sheer logistical constraints of determining all components of total woody productivity across numerous sites were overwhelming. Consequently, increase in basal area (often referred to as mean annual increment (MAI)) was used as an index, which could also be converted to biomass through allometric relationships.

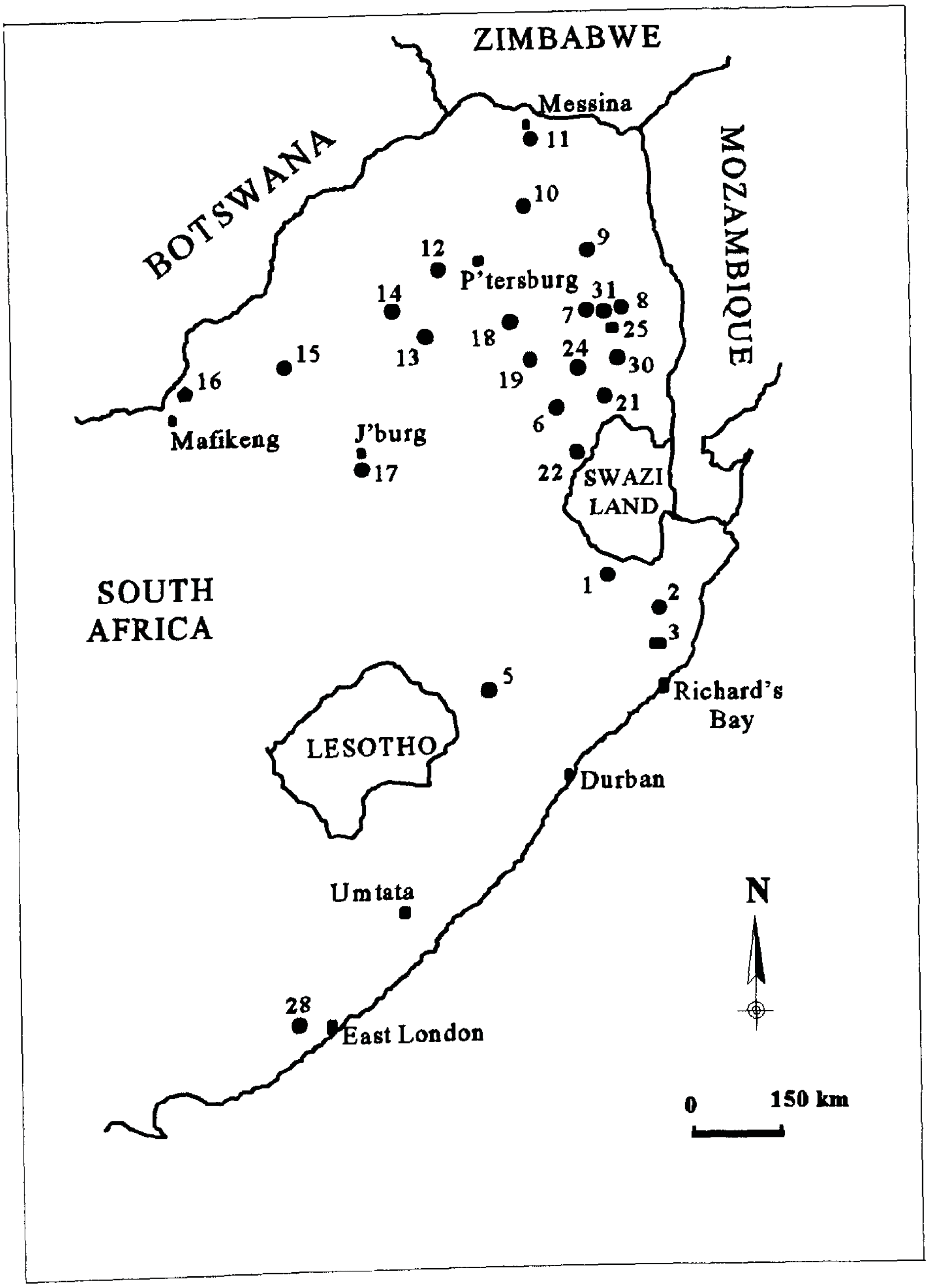

Figure 3.1. Distribution of study localities (2 plots per locality except number 3 & 25 (3 plots) and 16 (1 plot)).

At most localities two plots were established; one at the top of a slope and the other at the base to contrast the effects of soil type under uniform macro-climate. Between 125 and 286 stems of 75 cm or taller were marked per plot (less in the pilot plots). If the area was very shrubby, not all the smaller shrubs were marked. The total number of stems marked was 9 296, comprising 167 species. Each stem was marked at 30 cm above ground level with a strip of paint to ensure that repeated measurements were at exactly the same place. If this height coincided with the basal swelling or branching a lower height was taken. In the first year basal circumference and height were measured. If the height was greater than 4 m an Abney level was used to determine the angle from the top of the tree taken from a predetermined distance away from the tree. Height was then calculated through trigonometric conversion. In subsequent years only basal circumference was recorded as well as the status of each marked stem. Possible status included alive, dead, broken (main stem snapped at height above the recording height), smashed (main stem broken at a height below the recording height), cut, burnt, or lost which included stems that could not be relocated, stems where the paint line had disappeared and stems that were no longer recordable for some reason (e.g. two stems that had grown together). The proportion 'lost' per year ranged from zero to 0.2 %.

Several abiotic and biotic variables were recorded for each plot, including latitude, longitude, altitude, aspect, slope, landscape position, rockiness, mean long-term rainfall, rainfall per season (1 July - 30 June), deviation of seasonal rainfall from long-term mean, soil depth (total, A horizon and B horizon), species richness, dominance (Simpson's index), competition index (nearest-neighbour analysis), density of stems, mean basal area, biomass (using Rutherford's 1979 general allometric equation), proportion of stems < 10.1 cm basal circumference, mean height, herbaceous cover (yearly), and stocking rate. Soil samples (A and B horizons separately) were taken at five places throughout the plot, mixed, and analysed for texture (Bouyoucos hydrometer method), stones (%), pH (1 M KCl), organic matter (Walkley-Black), CEC (atomic absorption), Ca, Mg, Na, K, P (Ambic I extraction followed by AA spectroscopy), N (Keldjahl), nitrogen mineralisation (anerobic incubation), and extractable acidity.

Productivity was expressed in absolute increments in basal area per hectare (corrected for death). A strong relationship was found between basal area increment and basal area, therefore further analysis was done with relative growth rates expressed as the percentage increase in basal area, corrected for death during the intervening period. Correction for death was effected by deletion of dead stems from the data set for that year onwards. Thus, corrected values reflect the basal area change of living stems only (which may have grown, shrunk or remained the same size).

Forward linear stepwise regression was used to identify key variables associated with a predictive understanding of productivity. This was performed on basal area data for each year individually as well as the total growth between the first and last measurement periods. No analysis for 1995/96 was performed as more than 30 % of the managers/owners on whose land the plots are located failed to submit rainfall records for that season, despite repeated requests. Prior to this, the independent variables were subject to a correlation analysis to identify significantly correlated variables, one of each pair of which were then omitted from the regression analysis. This reduced the variables from 38 to 25. Plots with missing data for any of the variables were automatically dropped from the regression. Basal area was not included as a predictor variable in the analysis of relative growth rate. Appropriate transformations were completed on variables that were not normally distributed. Significant variables accounting for 10 % or less of the variance were not included in the final model. Due to the known significance of soil type as a determinant of savanna structure and function (Frost *et al.* 1986, Scholes & Walker 1993), and since it was identified as significant in the stepwise regression of all sites, a series of subset regressions were performed on sites of contrasting soil texture. All sites were ordered according to clay content. The top one-third of the data set was taken as a subset representing clay sites (> 25 % clay), and the bottom one-third of the data set was used to represent sandy sites (< 15 % clay). Because of the reduced sample size, the number of variables used in the subset stepwise regression also had to be reduced to at least one less than the number of plots included (Sokal & Rohlf 1981). Those non-significant variables contributing the least to the full stepwise regression were successively omitted until the maximum permissible number for the subset was attained.

Association between shrinkage of a given stem in year$_t$ and death of the same stem in year$_{t+1}$ was examined using a Chi-squared test. Expected values were determined using stems that did not shrink. The population half-life was calculated according to the manner of Felfili (1995), using the mean mortality rate.

3.4 RESULTS

3.4.1 Status of marked stems

Every year the greatest proportion of stems (60 % to 86 %) underwent a positive increment in basal circumference (Table 3.1). The percentage of stems that died was relatively high each year, ranging from 3.3 % to 5.6 %.

The sum total of positive and negative changes per stem for all the stems in a plot resulted in variable growth dynamics on a stand basis. In 1992/93 most plots experienced a net increase in basal area. This was reversed in the subsequent year. Over the four year period, approximately two thirds of the plots had a net increase in basal area (Table 3.2).

Table 3.1. The status of marked stems after each year (% of the total ± SE). (Other refers to the sum for stems that were smashed, burnt, cut or lost).

YEAR	GROWN	SHRUNK	SAME	DIED	OTHER
1992/93	67.3	15.3	13.2	3.6	0.6
(n=47)	(2.0)	(1.2)	(1.1)	(0.5)	
1993/94	60.0	24.6	9.9	5.0	0.5
(n=51)	(1.9)	(1.1)	(1.1)	(0.5)	
1994/95	72.2	13.7	8.2	5.6	0.3
(n=51)	(2.2)	(0.8)	(0.7)	(0.1)	
1995/96	85.8	5.8	4.9	3.3	0.2
(n=48)	(7.9)	(3.8)	(4.3)	(3.0)	
MEAN	71.3	14.9	9.1	4.4	0.5
(4 yrs)	(5.4)	(3.9)	(1.7)	(0.6)	

3.4.2 Absolute growth rates (corrected for death)

From 1992/93 to 1994/95 the range of mean basal area increment was relatively consistent, from 0.20 m^2/ha to 0.29 m^2/ha. In the last year (1995/96) it was 0.65 m^2 /ha. Several sites had negative changes in basal area for a given year even after correction for death. This was because a large proportion of stems shrunk during that year, but did not die. The basal area increment equated to an annual biomass change of 0.66 - 0.97 t/ha for the first three years and 2.19 t/ha for 1995/96.

Table 3.2. Net change in stand basal area on annual basis.

YEAR	% OF SITES WITH A NET INCREASE IN BASAL AREA	% OF SITES WITH A NET DECREASE IN BASAL AREA
1992/93 (n=47)	74	26
1993/94 (n=51)	33	67
1994/95 (n=51)	59	41
1995/96 (n=48)	96	4
MEAN (4 yrs)	66	34

3.4.3 Absolute growth rates and site variables

Stand basal area was the most consistent predictor variable of annual and mean growth rates (Table 3.3); the higher the basal area, the higher the absolute increment. Current season's rainfall was also identified as important for two of the three years analysed, as well as a negative relationship with the degree of deviation from MAR for the preceding year. Thus, the higher the current season's rainfall, the higher the absolute basal area increment, and the greater the negative deviation from MAR for the preceding season, the lower the basal area increment. Stand basal area was the only predictor of mean growth over the four year period. Forcing MAR into the stepwise regression for mean growth accounted for only an additional 17 % of the variance, even though the actual relationship with MAR alone was significant.

Consideration of clays and sands separately highlighted different variables via the stepwise regression (Table 3.4). Basal area increment at clay sites was generally a function of basal area of the site. A few other variables were also identified, but they were not consistent from year to year and did not account for much of the variation in the model. In contrast, stand basal area was not a significant variable related to basal area increment for sandy sites, except in 1994/95, but even then only as a secondary variable. On these sites moisture regime appeared to be the key variable determining growth.

Table 3.3. Forward stepwise regression results of absolute change in basal area against 25 site variables.

PERIOD	SIGNIFICANT VARIABLES (* = a negative relationship)	Cuml. r^2	p	RELATIONSHIP
1992/93	a. % Sand	0.259	< 0.00001	$= 0.008a - 0.005b - 0.509$
(n=40)	b. Deviation from MAR (1991/92) *	0.355	< 0.05	
1993/94	a. Rainfall (1993/94)	0.413	< 0.00001	$= 0.00089a + 0.015b - 0.025c - 0.0308$
(n=46)	b. Basal area	0.555	< 0.00001	
	c. Number of species *	0.604	< 0.01	
1994/95	a. Basal area	0.469	< 0.00001	$= 0.012a + 0.00067b - 0.0035c - 0.331$
(n=44)	b. Rainfall (1994/95)	0.648	< 0.00001	
	c. Deviation from MAR (1993/94) *	0.727	< 0.001	
4 yr mean (n=40)	a. Basal area	0.455	< 0.00001	$= 0.013a + 0.180$

Table 3.4. Forward stepwise regression results of absolute change in basal area for clay and sandy sites.

PERIOD	SIGNIFICANT VARIABLES (* = negative relationship) CLAY SITES (Clay > 25 %) (n=14)	 SANDY SITES (Clay < 15 %) (n=16)
1992/93	none significant	Deviation from MAR (1992/93)
1993/94	Deviation from MAR (1993/94) Basal area Aspect	Rainfall (1993/94)
1994/95	Basal area % Sand Number of species	Rainfall (1994/95) Basal area
3 yr mean	Basal area % of small stems (*)	MAR

3.4.4 Relative growth rates (corrected for death)

During the first three years, mean relative change in basal area was approximately 2.4 ± 0.2 %, ranging from 2.0 ± 0.5 % (1993/94) to 2.6 ± 0.4 % (1992/93). Because a few sites had high relative changes in basal area (> 7 %), these averages have been skewed; generally, more than 70 % of the sites had a relative basal area change of less than 3 % (Fig 3.2). In 1995/96 this pattern was totally reversed. The mean relative change in basal area was 6.4 ± 2.9 %, with 90 % of the sites having a change of greater than 3 %.

Relative basal area change is not solely a function of abiotic or biotic driving variables, but also the size-class distribution of the stems at a given site. The relative growth rate of small stems was greater than large stems (Fig 3.3). For example, stems less than 5 cm circumference had a mean change in basal area of 15 % (1994/95), whilst stems larger than 100 cm experienced a basal area change of approximately 2 %.

The mean change in biomass was slightly less than that for basal area, at 2.0 ± 0.3 % (1992/93), 1.8 ± 0.3 % (1993/95 and 2.2 ± 0.2 % (1994/95).

3.4.5 Relative growth rate and site variables

Annual relative growth rate was significantly related to variables associated with rainfall and soil type. The same did not apply with respect to mean relative growth rate over the three year period (Table 3.5).

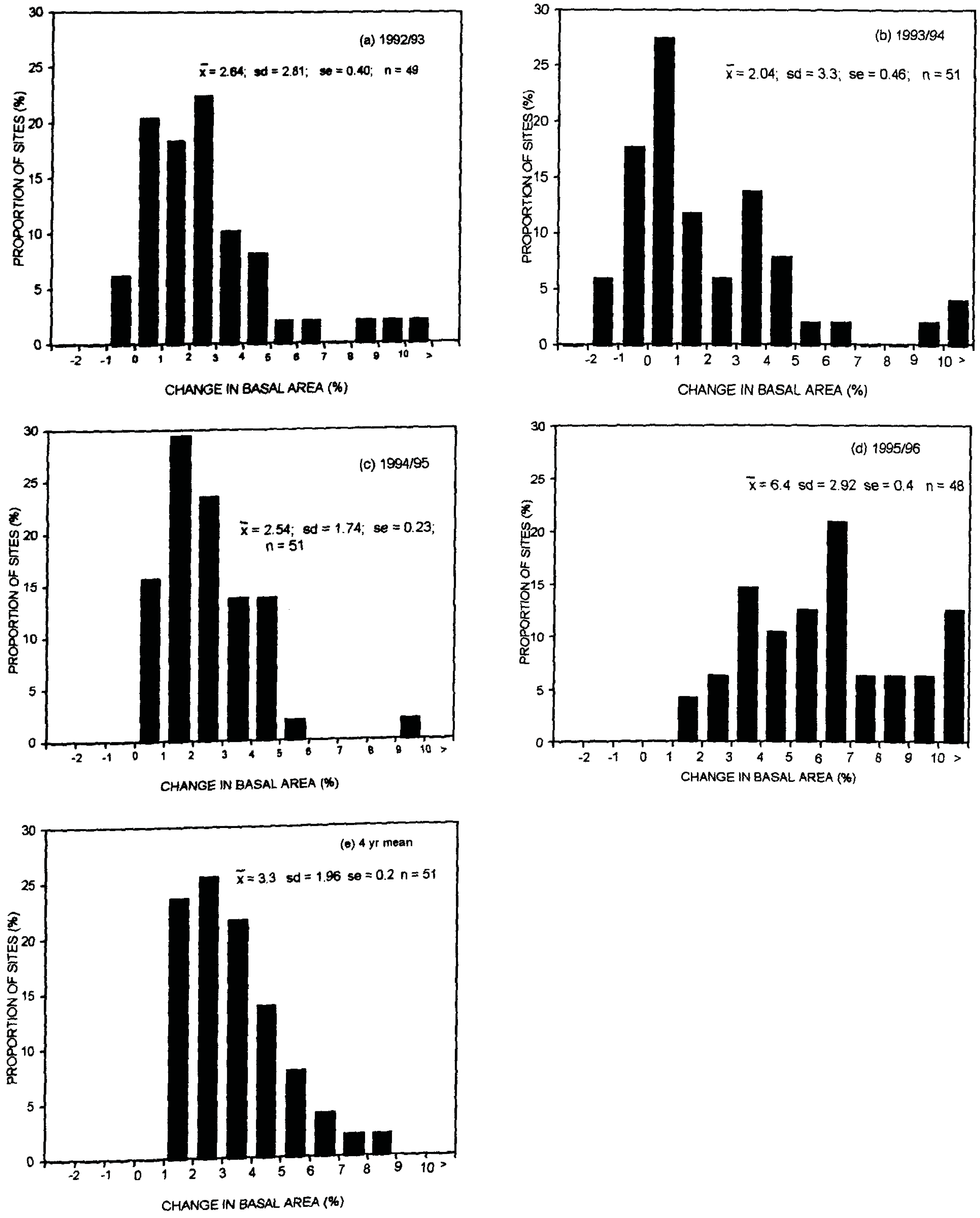

Figure 3.2. Annual relative change in basal area.

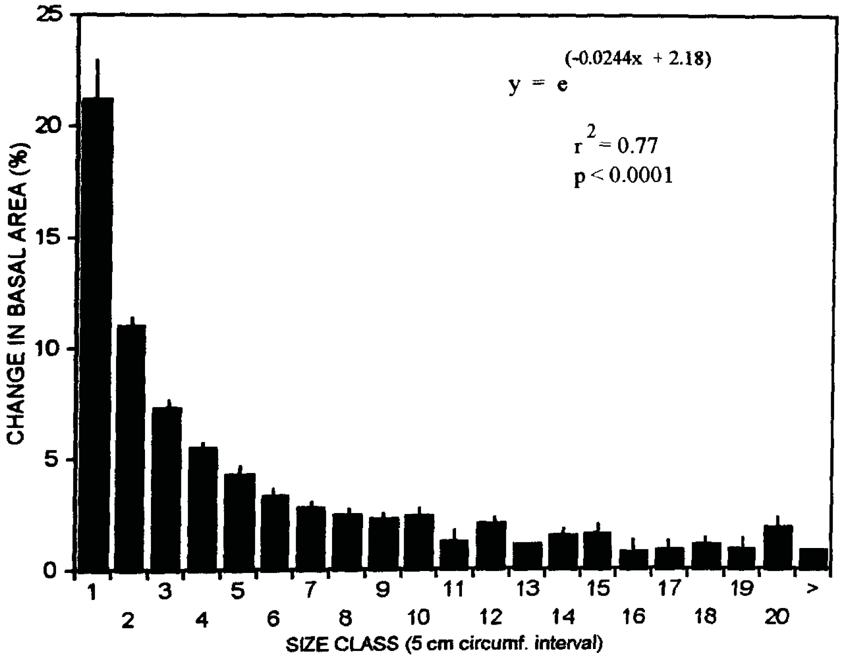

Figure 3.3. Stem basal area change relative to stem size (1994/95), data pooled from all sites.

Table 3.5. Forward stepwise regression results of relative change in basal area against 25 site variables.

PERIOD	SIGNIFICANT VARIABLES (* = a negative relationship)	r^2	p	RELATIONSHIP
1992/93 (n=40)	a. Deviation from MAR (1992/93)	0.212	< 0.05	= 0.069a + 0.057b - 1.27
	b. % Sand	0.290	< 0.05	
1993/94 (n=46)	a. Deviation from MAR (1993/94)	0.367	< 0.01	= 0.06a + 0.12b + 1.04
	b. % Silt	0.430	< 0.05	
1994/95 (n=44)	a. Rainfall (1994/95)	0.214	< 0.001	= 0.006a - 0.038b - 0.05c + 0.35
	b. Deviation from MAR (1993/94) *	0.336	< 0.001	
	c. No. of spp *	0.429	< 0.05	
3 yr mean (n=40)	- no significant variables			

3.4.6 Mortality rates

A significant proportion of stems died each year, ranging from 3.3 % to 5.6 % (Table 3.1). This excludes stems that were burnt, smashed or lost. It is highly probable that several stems classified as lost had actually died and the stump was no longer visible. Except for three plots in 1993/94, two in 1994/95, and four in 1995/96 some mortality was recorded in every plot on each sampling occasion.

As with growth, mortality was size-class dependent, being highest amongst small stems, and least amongst large stems (Fig 3.4).

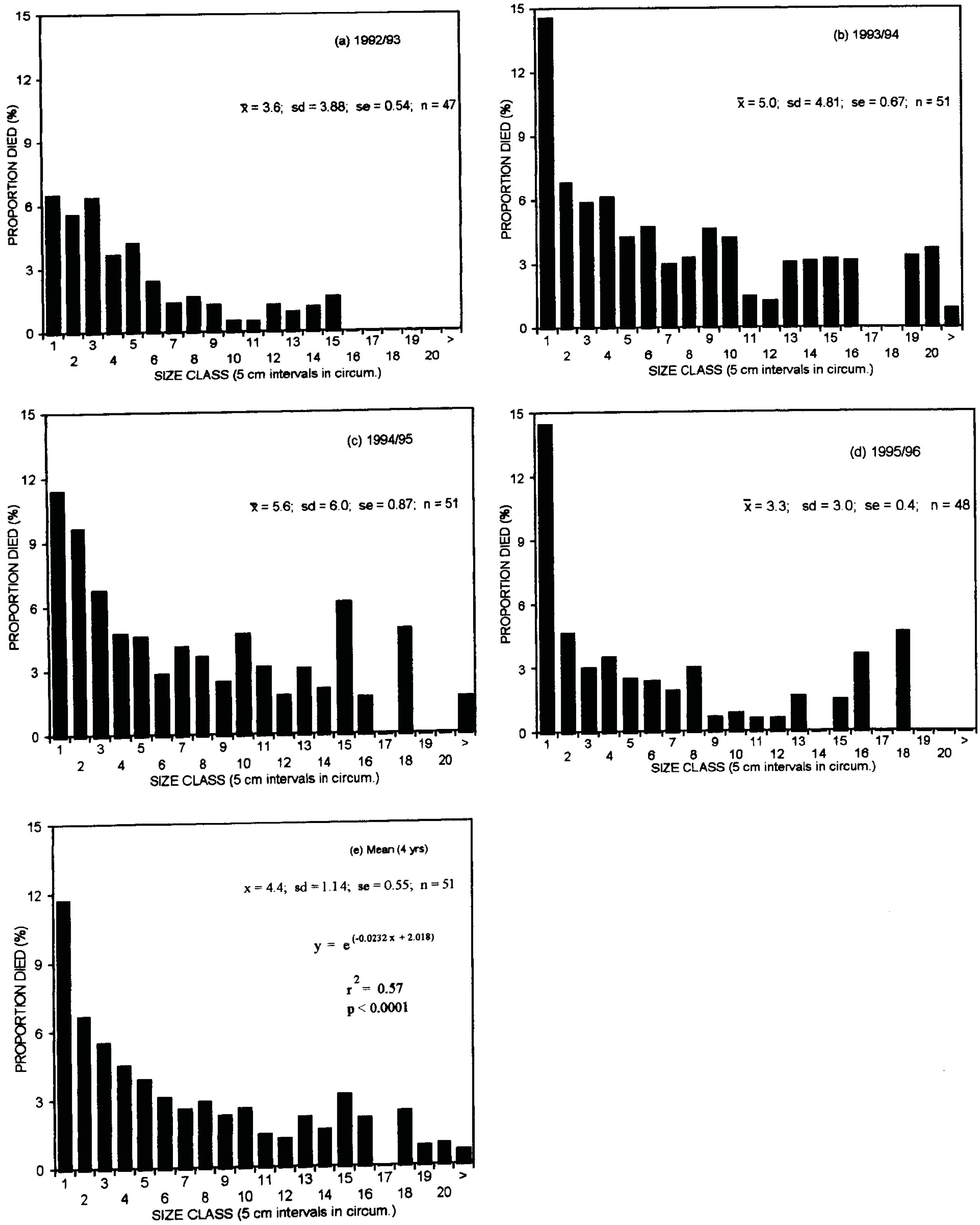

Figure 3.4. Annual stem mortality relative to stem size.

On a basal area basis the annual mortality was lower than on a density basis, with a mean for the four years of 2.3 % (1992/93 - 1.6 %, 1993/94 - 2.8 %, 1994/95 - 3.4 %, 1995/96 - 1.4 %). Corresponding figures for estimates of biomass mortality were 1.2 %, 2.2 %, 2.3 % and 1 % for the same four years, respectively.

Shrinkage of a given stem during one season significantly increased the probability that it would die during the subsequent season ($X^2 = 90.6$; d.f.=1; $p<0.0001$), although the absolute probability of death was low (Table 3.6). The greater the degree of shrinkage, the greater the risk of death in the subsequent year (Fig 3.5).

Table 3.6 The proportion of stems that shrunk during year$_{(t)}$ that died during the following year$_{(t+1)}$.

YEAR$_{(t)}$	PROPORTION OF STEMS THAT SHRUNK DURING YEAR$_{(t)}$ THAT DIED DURING YEAR$_{(t+1)}$	
	Observed	Expected
1992/93	0.106	0.037
1993/94	0.087	0.045
1994/95	0.062	0.023

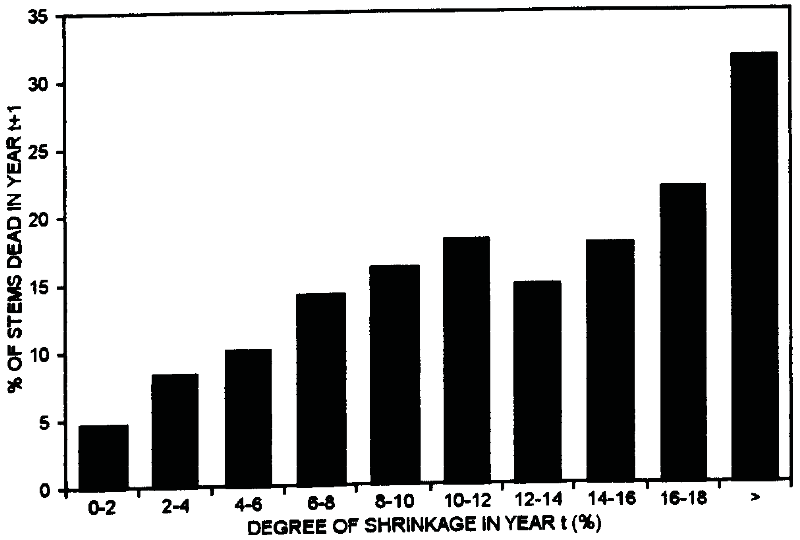

Figure 3.5. Relationship between the degree of stem shrinkage and mortality.

3.4.7 Relationship with site variables

No consistent patterns were detected between annual mortality and site variables. In 1993/94 a significant relationship was evident with deviation from MAR in the same year. In the subsequent season, a significant relationship was found with rainfall in 1993/94. Therefore, it appears that the prevailing conditions in 1993/94 had an impact on mortality during that year and the subsequent year. Over the three year period no predictor variables were identified. Despite this an almost bimodal pattern of mortality is evident when plotted against MAR (Fig 3.6) with a minor peak at 450 - 550 mm and a major peak at 680 - 880 mm, and reducing again at higher MAR. There is a trough with a cluster of sites between these two peaks.

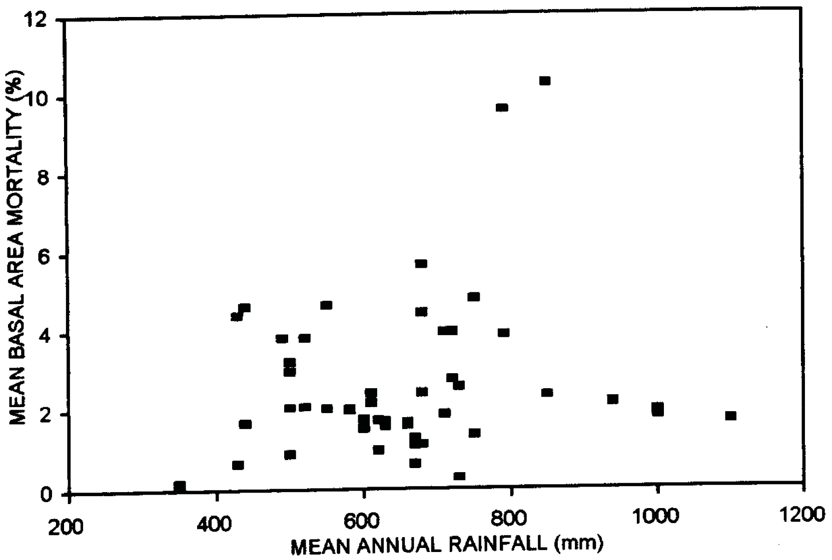

Figure 3.6. Stem mortality as a function of mean annual rainfall (2-point moving average).

3.5 DISCUSSION

3.5.1 Growth

The mean absolute basal area increment of 0.2 - 0.8 m^2/ha/yr , or a biomass increment of 0.7 - 2.1 t/ha/yr, is within the general range reported in the limited number of previous studies in savannas, albeit towards the upper end of the range (see Menaut & Cesar 1979, Chidumayo 1993, Frost 1996). Given that absolute basal area increment is strongly related to stand basal area, comparision of mean values between studies is not particularly informative because of the large variation in stand basal area from place to place which is then averaged out through reporting of mean values. The large number of samples in this study permits the derivation of summary relationships (Table 3.3) which should facilitate such comparision with future studies where stand basal area is reported. The applicability of the relationship across a range of woodland types requires to be tested.

A mean relative basal area increment of 3.4 % measured across all sites in this study is at the lower end of values reported previously for savannas. Gandar (1988) recorded a basal area increment of 5.7 % at two sites in KwaZulu-Natal. Of the seven studies recently summarised by Scholes & Walker (1993), only one falls within the range reported here, the rest are well above it. Why is this so? Some previous studies considered only a few selected species at a single site (e.g. Rutherford 1984, Knoop & Walker 1985, Childes & Walker 1987), and therefore do not represent productivity expected from all stems of all species in a specified area, i.e. productivity at community scale. Nearly all other studies were based on small samples in terms of stems marked (Rutherford & Kelly 1978, Knoop & Walker 1985), or range of sites (Malaisse *et al.* 1975) or were extrapolations from a series of indirect measurements (van Vegtan 1983), with each step encompassing a degree of error or variability that is ignored in the extrapolation.

The broader spectrum of sites and stems selected in this study results in higher values being averaged out with low values. Nevertheless, during the first three seasons, 70 % of the sites had relative growth rates of less than 3 %, a value that Rutherford (1978) suggested was a reasonable estimate of basal area increment after review of available data. In 95/96 most of the plots experienced relative growth rates well above 3 %. Three of the seven comparative studies listed by Scholes & Walker (1993) were done at or near Nylsvley Nature Reserve. It is noteworthy that the value for this study from the top plot at Nylsvley (4.1 %) was approximately the same as for these previous studies, but the value for the bottom plot (2.0 %) was lower. The bottom plot has a considerably higher basal area. This difference between two plots at a single reserve, one similar to previous estimates, and one substantially lower, demonstrates the value of having data from a range of sites. The full range of species is also important, as typified by the widely differing rates of basal area increment of two species at Nylsvley measured by Knoop & Walker (1985). From the same site and same period (1980/81), *Burkea africana* had a relative growth rate (basal area) of 3.9 % (n=7) and *Ochna pulchra* 32.0 % (n=11). Corresponding figures for 1981/82 were 1.9 % and 15.9 %. The significance of stem size is demonstrated from the data of Childes & Walker (1987), where saplings of *Terminalia sericea* had a mean annual relative basal area increment of 18.4 %, young trees, 8.4 %, and mature trees 2.7 %.

On a wider scale Menaut & Cesar (1979) recorded a mean annual biomass increment of 1.3 - 1.6 % from four savanna types of contrasting density in the Ivory Coast (MAR = 1 300 mm). Chidumayo's (1988) data from miombo regrowth sites in Zambia indicate a basal area increment of approximately 6 % p.a. in young stands with a small mean stem diameter (± 5 cm), and approximately 3 % p.a. in older sites with stems of approximately 10 - 11 cm diameter. The derived relationship indicates a decreasing mean annual increment with increasing mean stem diameter. In comparison, the relationships derived by Guy (1981) provide an annual biomass increment of 14.1 % for a stem of 5 cm diameter, and 7.1 % and 2.3 % for stems with a diameter of 10 cm and 30 cm, respectively. Reworking the data from Guy (1981) (assuming tree diameter to be the class mid-point) provides a plot based annual biomass increment of 1.0 % to 2.5 % (stems > 5.9 cm diameter). Chidumayo (1993) recorded a mean annual increment in stand biomass of 1.0 % and 12.6 % at two sites in Zambian miombo. Two other sites had mean negative growth rates which he attributed to cutting at one site and fire at the other. Basal area increments of five shrubs species ranged from 4.3 % p.a. to 7.6 % p.a. depending on soil type in northern Tanzania (Prins & van der Jeugd 1992). Hayashi (1992) recorded an annual basal area increment of *Commiphora africana* of 4.2 % in a moist savanna in Kenya. Agnew & Waterman (1989) recorded mean annual increments of several species ranging from 0 % to 1.6 % in an arid savanna in Kenya.

Data from other vegetation types suggest similar rates of basal area increment. Milton *et al.* (1994) recorded relative growth rates of 20 common species in a Panamanian lowland forest ranging from 0.8 % to 4.0 %. Korning & Baslev (1994a) reported plot based increments in basal area of an Amazonian tropical rain forest of 2.1 - 3.5 %. Sundriyal *et al.* (1994) reported a 4.7 % annual increment in woody biomass in a Himalayan sub-tropical forest, and Singh *et al.* (1994) reported biomass increment of 2.3 - 8.8 % p.a. for 20 forest types in the Himalayas. Basal area increment of *Brachylaena huillensis* in Kenyan semi-deciduous forests was approximately 1 - 1.5 % (Kigomo 1994).

Results from this study may be considered as minimum estimates for three reasons. (1) Stems less than 75 cm tall were not included. However, although smaller stems demonstrate higher growth rates, their contribution to the total basal area is low, and therefore so too is their effect on the plot growth rate, unless it is an atypically shrubby plot. (2) Recruitment of new stems is not included. The figures represent growth of existing stems. Area based estimates or repeated surveys on marked plots, but not marked stems (e.g. Guy 1981, Lubke & Thatcher 1983, van Vegten 1983), include recruitment and therefore can be expected to have higher values in the absence of some stress or disturbance resulting in significant mortality. The ommission of new recruits should not be too significant for the few seasons immediately after establishment of a permanent plot becuase their overall contribution to the basal area is negligible while they are small. The impact of their ommission will increase with time. (3) Most of the study sites experienced below average rainfall for the first three years of the study, and well-above average rainfall in the last year. A strong relationship between growth and rainfall was demonstrated. If the comparative studies quoted happened to cover a period of average or better rainfall, it could explain the higher growth rate values.

Shrinkage of stems is a common phenomenon in savannas (e.g. Childes & Walker 1987, Milton *et al.* 1994) and forests (Murphy & Lugo 1986), and is probably an indication that a stem is under stress from a range of possible causes, such as drought, disease, or competition. Swaine *et al.* (1987) demonstrated that repeated shrinkage over a few seasons generally resulted in death. Results from this study show that shrinkage over a single season leads to a higher probability of death in the subsequent season, and the higher the degree of shrinkage, the greater the probability of death.

The identification of indices of moisture status, soil texture and vegetation abundance as potential determinants of seasonal growth is not unexpected, since they conform with existing models of savanna structure and function for the woody layer (Huntley 1982, Frost *et al.* 1986, Teague & Smit 1992, Scholes & Walker 1993), and production dynamics for the herbaceous layer (Teague & Smit 1992). The effect of soil texture may relate to nutrient status (there being a positive correlation between clay content and cation exchange capacity ($r=0.392$; d.f.=48; $p<0.005$), but more likely to moisture relations through control of plant available moisture. Reanalysis of the data with only soil variables did not draw out any of the nutrient status variables for any season or the three year mean. Nor was there any difference in mean growth rate between high nutrient sites and low nutrient sites. Only soil texture, namely the proportion of sand and silt, were considered important contributors to relative growth rate in the first and second season respectively. However, Scholes & Walker (1993) argued that even the apparent relationship of herbaceous productivity with rainfall is, in reality, facilitated through the influence of rainfall on nitrogen mineralisation rates. Thus, soil nutrients are the driving force, which is mediated through adequate amounts and duration of soil moisture. This study has demonstrated that fertilisation leads to increased growth (see Chap. 5), corroborating the field study of Prins & van der Jeugd (1992) reporting higher growth rates of five indigenous shrubs on eutrophic soils than on dystrophic soils. Yet, in this study there was no discernable relationship between measured growth rates and potential nitrogen mineralisation rates. If seasonal mineralisation, as the product of mineralisation potential and number of rain days, was used, it is probable