proportion of total wood contained in the stem, and the greater the proportion of total production attributable to leaves.

The power of allometric relationships is vastly enhanced if a single suite of equations is applicable for more than one species for general estimates of standing woody biomass. At first glance at the data in Table 1 it appeared that this was unlikely. However, general relationships are evident if the smaller shrubby species (multi-stemmed species, generally less than 4 m maximum height) are considered independently from the taller tree species, summarised as:

$$\log(\text{tree dry mass}) = 2.397(\log(\text{circ.})) - 2.441 \qquad (r^2 = 0.94;\ p<0.00001;\ n = 94)$$

$$\log(\text{shrub dry mass}) = 2.320(\log(\text{circ.})) - 2.30 \qquad (r^2 = 0.94;\ p<0.00001;\ n = 48)$$

Since the same data from the individual species relationships were also used to determine the mean line, it is not possible to statistically test for significant differences or goodness-of-fit of the individual species lines against the mean line (Tietema 1993). However, with respect to trees, most of the relationship attributes for each species individually are well within one standard deviation of the mean line, except *A. gerrardii* where the slope deviates by slightly more than one standard deviation, and *P. angolensis* where the intercept is also slightly greater than one standard deviation less than the mean. Similarly, for shrubs, the slope and intercept of the individual species relationships were within one standard deviation of the mean, except the intercept for *A. swazica.*

In a similar fashion Tietema (1993) found that a single regression line ("combiline") adequately represented the biomass relationships of 14 tree species in Botswana. Independent validation of his combiline against species from other continents suggested that it was a robust relationship, with wide applicability for gross biomass studies. Unfortunately, it relates to fresh mass rather than dry mass. Conversion to dry mass using data from Table 9.2 allows comparison. Up to 60 cm circumference, the Tietema combiline results in markedly higher dry masses for a given circumference than the one derived here. Above 60 cm circumference the opposite applied. Chidumayo (1988) also derived a single line to estimate fuelwood volume from stem circumference for nine species in Zambia. He too found that separate lines were necessary for shrubby understorey species and larger trees. Scholes (1987) derived allometric relationships for five species from the Transvaal lowveld. Their fit against the summary line derived here is poor, as they provide a significantly higher mass than the combiline. The poor comparability of results from separate workers questions the general applicability of a single line for a defined region for gross biomass studies. Clearly, studies of the growth and biomass dynamics of a single species would be best accomplished with using an equation derived specifically for that species. Even for general biomass studies Tietema (1993) recommended that individual species relationships be used for the dominant species, and a summary line or combiline, for the lesser species. Dayton (1978) argued that one must expect a unique set of equations for individual species.

PRODUCTION OF UTILISABLE COMPONENTS:
DEADWOOD

10.1 INTRODUCTION

Deadwood is a key resource to most rural populations inhabiting savanna regions. Its most important use is for fuelwood, being favoured above the cutting of livewood (Shackleton & Prins 1992). It is also used for the manufacture of charcoal, construction timber, and attractive pieces are collected for the florist market. Frequently the localised high demand for deadwood cannot be met, and local communities resort to the harvesting of livewood to supply their needs (Grundy *et al.* 1993, Shackleton *et al.* 1994, Sundriyal, *et al.* 1994).

Despite this high demand, there is little understanding of the rate at which deadwood is produced, nor its potential value in savannas managed for other purposes and where access by rural harvesters is prohibited (Shackleton 1995, 1996). Similarly, there is inadequate understanding of the ecological role and value of deadwood as part of the biological system, other than generalised statements regarding its significance in nutrient cycles and provision of nesting sites for hole nesting bird species. These have been challenged by Shackleton (1994a, 1996).

Consequently, this study sought to obtain a gross estimate of the annual production of deadwood, and whether or not this was correlated with mean annual rainfall. It was conducted on a per unit area basis, since the large sample size required for a per individual stem basis was incompatible with the time and logistical constraints of this work. However, if a more complete, predictive understanding is the goal, a per stem basis study will be required.

10.2 OBJECTIVES

The objectives of this study were to determine: (1) the annual production of harvestable deadwood, and (2) if annual production of harvestable deadwood differed between rainfall zones.

10.3 METHODS

Plots of varying size (0.35 - 1.0 ha) and standing woody biomass were judgementally located in each of the three reserves of contrasting MAR. Local fuelwood harvesters were hired to clear all '*utilisable*' deadwood by hand from each plot at the end of winter (September) each year. The initial clearance was in 1992 at the semi-arid site (10 plots), and in 1993 for the mesic (9 plots) and arid (9 plots) localities. After collection the wood was made into bundles that were weighed with a spring balance to the nearest 100 g. These were totalled and results expressed on a per hectare basis. Moisture content was not determined but was low (< 10 %) since determinations were made at the end of the dry winter period.

The results are considered as underestimates of the actual annual production of total deadwood because not all deadwood was removed. Pieces that were too large to be removed by hand, too small to be have any purpose, too high or to hard to break off were left *in situ*.

In 1994 the circumference and height of all stems within each plot were measured, and biomass calculated from the allometric equations determined by Rutherford (1979). Differences between rainfall zones were tested using ANOVA. Annual production of deadwood was then related to standing biomass of each plot through linear regression.

10.4 RESULTS

The mean annual production of harvestable dead wood was relatively constant from year to year across the different rainfall zones and woody biomass levels (Table 10.1). The semi-arid locality had a lower production than the arid locality in 1993/94, and was not significantly different in 1994/95. This is probably a result of the lower mean standing biomass at the semi-arid locality for this particular study. There were no significant differences between rainfall zones for either 1993/94 ($F=2.32$; d.f. $=2$; $p>0.05$) nor 1994/95 ($F=1.04$; d.f.$=2$; $p>0.05$). In the last year, mean yield was higher at the mesic locality than either the arid or semi-arid localities ($F=3.91$; d.f. $=2$; $p<0.05$).

Table 10.1. Annual harvestable dead wood yield from the arid, semi-arid and mesic localities.

ATTRIBUTE		MESIC	SEMI-ARID	ARID
Mean Annual Rainfall		± 850 mm	670 mm	500 mm
No. of plots		9	10	9
Wodd harvesting history		Moderate	Negligible	Nil
Mean standing biomass of deadwood plots (t/ha ± SE)		25.3 (5.3)	14.4 (3.1)	17.7 (2.5)
Mass of dedwood at initial collection (kg/ha ± SE)		895.5 (116.7)	303.5 (61.2)	994.9 (139.3)
Deadwood production (kg/ha ± SE)	92/93	_	387.8 (85.5)	-
	93/94	438.0 (69.0)	270.4 (47.8)	380.3 (52.9)
	94/95	455.8 (62.3)	353.6 (55.4)	343.7 (63.2)
	95/96	211.7 (27.6)	259.8 (52.8)	590.1 (176.2)

Annual production per plot was strongly related ($p<0.0001$) to the standing biomass in each plot (Fig. 10.1) across the entire sample. The interannual yield for individual plots varied by as much as 500 %, suggesting that the plot size was too small. However, the overall relationship was relatively constant between the years when averaged across large number of plots:

*Annual production of harvestable deadwood (kg/ha) = k * Standing biomass (t/ha)*

Where k (1993/94) = 16.7 ($r^2 = 0.87$; $p<0.00001$)
(1994/95) = 17.1 ($r^2 = 0.81$; $p<0.00001$)
(1995/96) = 17.7 ($r^2 = 0.56$; $p<0.0001$)

For ease of calculation a constant of 17.0 is used in further calculations. The slope coefficient from the smaller data set from the semi-arid locality alone for 1992/93 was 21.1 (r^2= 0.65; $p<0.005$; n=10), not significantly different from the 17.0 derived for the larger data set in subsequent years.

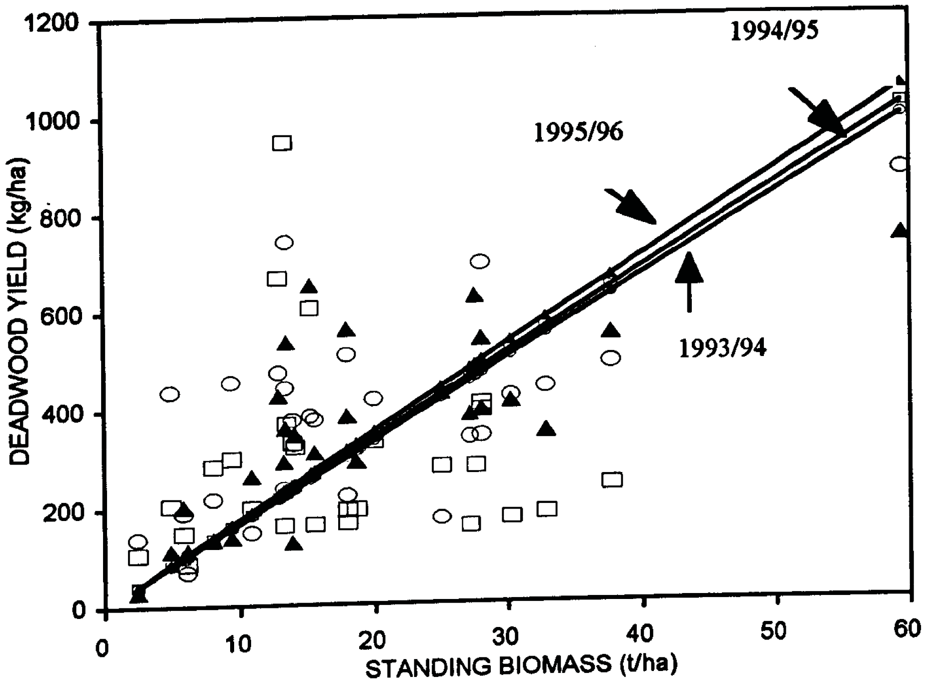

Figure 10.1. Annual harvestable deadwood yield relative to stand biomass (▲ - 1993/94; ○ - 1994/95; □ - 1995/96).

10.5 DISCUSSION

Dead wood is a result of total mortality of individual stems, as well the partial mortality of other stems, as a single, or a few branches. Despite a variable environment, deadwood production was relatively constant from year to year at a large spatial scale. This suggests that production of dead wood is controlled by factors other than those influencing productivity of living stems, for example, fungal or microbial attack, insect infestation, wind damage or browser damage. This is corroborated by the absence of any correlation between site variables and mortality (Sect. 3.4.6).

Deadwood production of 1.7 % of standing biomass is less than the rate of production of living tissue (Sect. 3.4.5), resulting in a net accumulation of standing woody biomass. However, the harvesting method, i.e. by hand, precludes a certain proportion of the annual production of dead wood from being collected. Thus, pieces of wood that were to high to reach, too strong to break off, too big to carry, too small to be useful for fuelwood purposes were left *in situ*. Hence, deadwood productivity is somewhat higher than determined. Additionally, a proportion has also been `lost' through comminution and decomposition between the sampling periods, although wood decays relatively slowly. Woody plant leaf litter lost 11 - 26 % of its mass per year at Nylsvley, depending upon species (Scholes & Walker 1993). Therefore, it can be assumed that losses from large deadwood pieces would be in the order of 2 - 3 % per annum, possibly slightly higher in areas with high termite activity, but insufficient to alter the general findings of this study.

Comparative figures are not available. Deadwood production calculated as whole tree mortality from the marked plots throughout the biome (Sect. 3.4.6) was 1.2 ± 0.32 % in 1992/93, 2.2 ± 0.6 % in 1993/94 and 2.3 ± 0.5 % in 1994/95. This estimate includes pieces that would have been regarded as too big to remove in terms of this study, but excludes production of dead branches from otherwise healthy trees. Therefore, it appears that an annual rate of deadwood production of 1.5 - 2.0 % of standing biomass seems realistic from the data at hand.

A key implication of the apparent constant supply rate is the predicability for management purposes at a community scale. More specifically, the possibility for sustainable harvesting of the deadwood component for a variety of purposes, such as fuelwood, curio pieces, florist decorations, charcoal production, and the like (Shackleton 1996). The ecological consequences of deadwood harvesting are unknown. However, ensuring that harvesting is by hand would go a long way to ensure that some deadwood remains *in situ* to serve its broader ecological functions, such a nesting sites for certain bird species, micro-habitats for small vertebrates and invertebrates, nutrient recycling, micro-sites for seed germination, etc. Comparison of areas subject to unsustainable harvesting of wood (i.e. extraction of live and dead wood at rates greater than annual productivity leading to a declining standing woody biomass) relative to protected areas have detected little change in system attributes other than a declining biomass (Chidumayo 1993, Shackleton 1993, Shackleton 1994b). Du Plessis (1995) documented a possible decline in hole-nesting birds in areas subject to intense wood harvesting, i.e. including live stems.

PRODUCTION OF USEABLE COMPONENTS:
LITTER

11.1 INTRODUCTION

Quantification of annual litter production is a useful indicator of leaf production, the quantity of material potentially recycled, and the availability of dry season forage for browsers, or mulch for arable plots. Whilst its value regarding the first two has been appreciated for some time by systems ecologists (e.g. Malaisse *et al.* 1975), the role of the last two has been underestimated. For example Nyathi and Campbell (1993) reported that all respondents from a survey across twelve villages in Masvingo Province, Zimbabwe, reported collecting and using litter on arable plots, whilst in the study area of this study local Tsonga herdsman report that cattle are able to survive the dry winter months because of the presence of woody plant leaf litter early in the dry season (A. Shabangu, pers comm.).

Despite multiple values from the estimation of litter production, the current data for southern African savannas is relatively scanty (Frost 1996). Whilst good estimates are available from a few authors (Morris *et al.* 1982, Scholes & Walker 1993) the low number of sites limit the ability to determine relationships with site variables such as rainfall or biomass for a predictive understanding at a wider scale.

Within the broader framework of the entire study to provide the basis for a predictive understanding of woody productivity in general, an estimation of the production of litter from a range of sites was considered necessary. Specifically, two hypotheses were tested: (1) total annual litter production will be positively related to standing biomass of the site, and (2) litterfall will commence earlier in the year at more arid localities relative to mesic localities.

11.2 OBJECTIVES

The objectives were to: (1) determine the amount and seasonal pattern of woody species litterfall from a range of sites, and (2) investigate whether the amount or seasonal pattern differs according to rainfall zone, and woody standing crop.

11.3 METHODS

Litterfall was quantified by means of litter traps in each reserve at three topland and three bottomland sites. The sites were randomly selected from the five sites per locality monitored for the phenological study (Chap. 7). At each site 50 litter traps were systematically arranged in a 6 m x 6 m grid in five rows of ten traps (describing a grid of 54 m x 24 m). The number of traps per site decreased throughout the study because of trampling by large ungulates, breakages and theft. Initially such losses were replaced, but as they became too numerous this was no longer possible. Traps were 21.9 cm in diameter, with the mouth approximately 75 cm above the ground. A stone was placed in the trap to minimise wind disturbance. After being set up on the last two days of November 1993, traps were emptied monthly during the first three days of every subsequent month until November 1995. The contents were oven-dried at 65°C for at least 72 hours and then weighed to the nearest 0.001 g. Prior to weighing, the contents of ten randomly selected traps from each site were sorted into litter categories; leaf, flower, fruit, twig and bark, which were weighed individually.

During 1994/95 a plot was described around the periphery of the litter trap grid, 2.5 m from the outer square of traps, and including the entire grid area. The height and circumference (35 cm above the ground) of all stems taller than 0.5 m within this plot were measured. From these data the biomass of the plot was determined using the allometric equations derived by Rutherford (1979).

A fire in June 1994 at the mesic locality destroyed all the litter traps at that locality. These were replaced, but no data were available for June and July. Another fire at the same locality in September 1995 destroyed the litter traps again. They were not replaced. To allow comparison of litter yield with the arid and semi-arid localities the missing data were estimated after extrapolation from (1) the actual yield measured during the months with traps, and (2) the monthly distribution of litterfall at each of the sites.

Data were tested for normality and appropriate transformations made as necessary. Linear regression was used to explore the relationship between annual litterfall and woody basal area and biomass per plot. Significant outliers were omitted. One-way ANOVA was performed to test differences in the annual litterfall per unit standing biomass. A paired t-test was applied to assess differences in the proportion of litterfall in peak months in plots at the top of the catena relative to those at the base. A 3-way ANOVA was used to assess differences in the composition of the litter (% leaves, % twigs, etc. (arcsine transformed)) relative to rainfall zone, slope position and year of collection.

11.4 RESULTS

Two-thirds, or more, of total annual litterfall was concentrated into a period of 3 - 4 months at each locality (Fig 11.1), although in the second year, the seasonal peak was interrupted by a decrease in litterfall at all three localities. The dry season months of April, May and June were commonly the peak months, but the distinct decrease in the second year resulted in an extension of the litterfall period through July and into August.

Total annual litterfall ranged from 90 - 360 g/m^2 from different plots at the three localities. At the mesic locality, litterfall was less in the second year than the first, which was also evident for four of the six plots at the semi-arid locality. This was not apparent at the arid locality. There was no consistent trend resulting from comparison of plots from the top and bottom of catenas in terms of absolute amounts of litter falling, but it did appear that the peak in litterfall was more concentrated at the top plots, resulting in a greater proportion of the yearly litterfall input during the peak period (Table 1) ($t=2.1$; d.f.$=17$; $p=0.05$). This was most pronounced during the first year, and at the arid locality.

Table 11.1. Proportion (%) of annual litterfall during the four months with the highest input.

Rainfall zone	Catenal position	Proportion (%) of annual litterfall input during defined peak period	
		1993/94	1994/95
Arid	Top	79.9	69.8
	Bottom	66.5	63.2
Semi-arid	Top	76.7	75.8
	Bottom	67.8	77.9
Mesic	Top	77.5	74.0
	Bottom	73.0	72.2

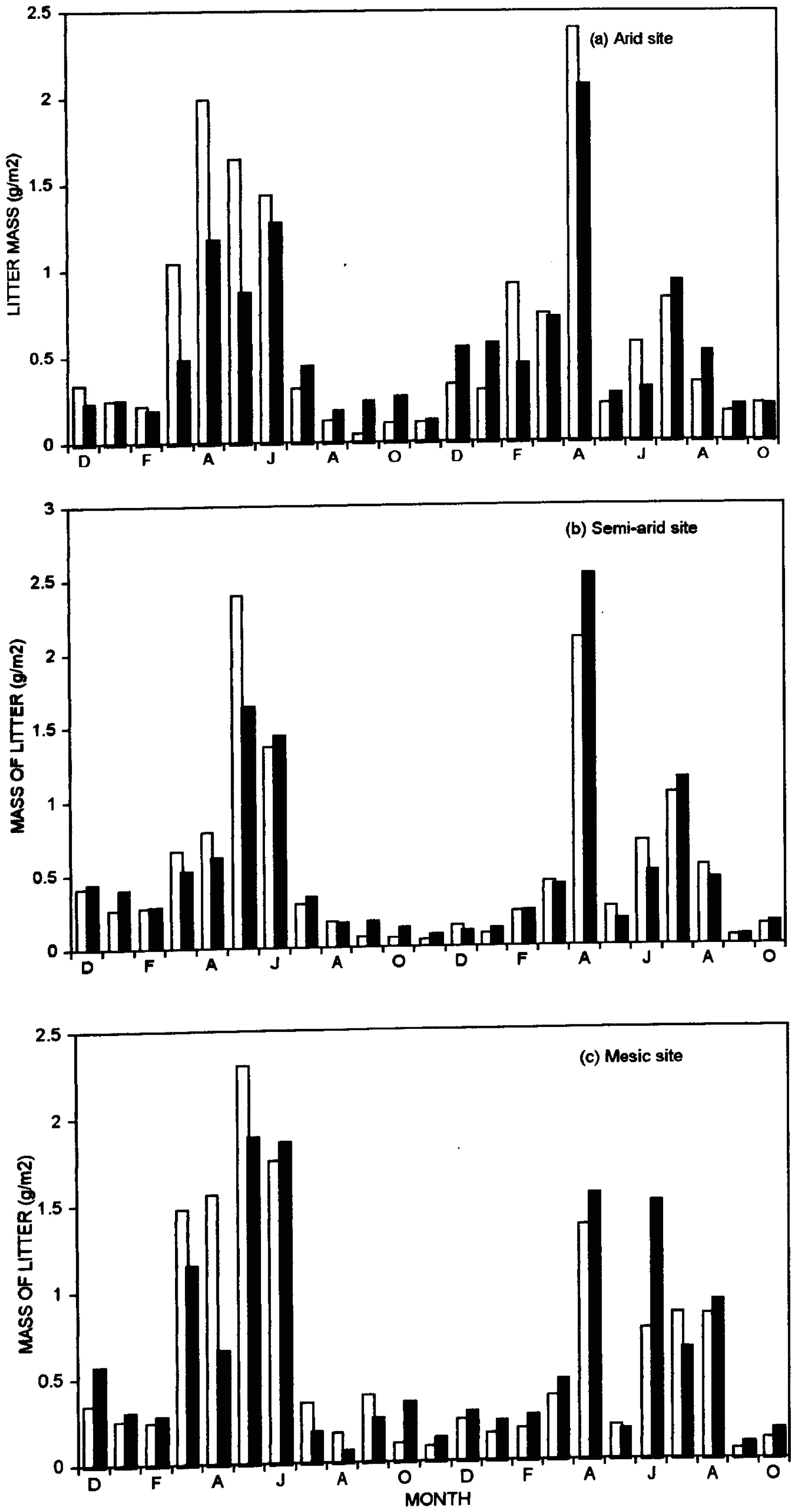

Figure 11.1. Litterfall at the arid, semi-arid and mesic localities (☐ - toplands; ■ - bottomlands). (Values for the mesic site for June & July 1994, and September - November 1995 are estimated value - see methods).

A significant proportion of the variation between plots was due to the varying standing woody biomass at each plot, summarised as:

1st yr annual litterfall (g/m^2) = *7.31(basal area)* (m^2/ha) + *109.0* (p<0.05; r^2 = 0.33; n=18)

2nd yr annual litterfall (g/m^2) = *3.75(basal area)* (m^2/ha) + *120.6* (p<0.05; r^2 = 0.29; n=16)

At a low plot biomass (< 20 t/ha) the difference in the predicted litterfall from year one to year two is insignificant. At high plot biomass (40 - 50 t/ha) the relationship for year two provides a value of 20 - 23 % less than the relationship for year one.

Despite the linear relationship with woody standing biomass, the quantity of litterfall per unit standing biomass differed significantly between the rainfall zones in the first year (F= 9.11; d.f.=17; p< 0.005) and the second year (F=4.07; d.f.= 17; p< 0.05). In each year the semi-arid locality had a significantly higher yield per unit biomass than either the arid or mesic localities (Fig 11.2), which were not significantly different from one another.

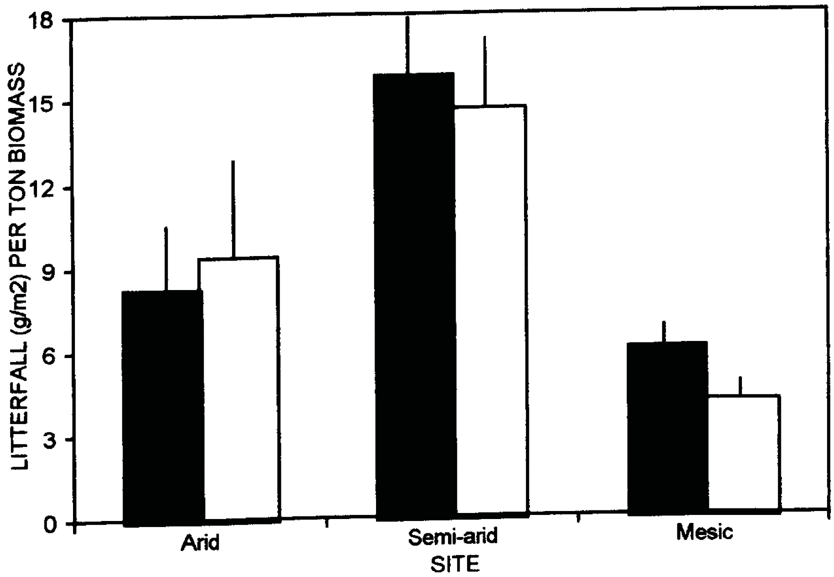

Figure 11.2. Litter yield per standing biomass (■ - 1st year; □ - 2 nd year).

The composition of the litterfall was relatively uniform across the aridity gradient and slope position (Table 11.2). However, there was a significant increase in the proportion of leaves in the second year relative to the first (F=37.1; d.f.=1 35; $p < 0.0001$). This was accompanied by a decrease in the proportion of all other components, except bark, which lacked a consistent trend between the two years. Although the proportion of leaves increased in the second year, the absolute amounts did not. However, the absolute amounts of twigs decreased in the second year (F=15.3; d.f. =1 35; $p<0.0005$), resulting in a significantly higher leaf:twig ratio.

11.5 DISCUSSION

At 90 - 360 g/m^2 the absolute amount of litterfall was comparable to that of other southern African savannas. For example, Morris *et al.* (1982) reported litterfall at Nylsvley of 170 g/m^2 and 179 g/m^2 during 1977 and 1978, respectively. Scholes & Walker (1993) report a five year mean at Nylsvley of 175.8 g m^{-2}. Malaisse *et al.* (1975) recorded a five year mean of 290 g/m^2 (range = 250 - 340) at a moist site (MAR = 1 270 mm) in Zaire. In West Africa, Collins (1977) reported leaffall as 239 g/m^2 (MAR = 1 175 mm). Frost (1996) provides data from three miombo sites with a range from 262 - 426 g/m^2.

Litterfall occurred throughout the year, but with strong seasonal patterns. The peak period of litterfall in this study was slightly earlier in the year than described in other studies, although also concentrated into the dry season. At Nylsvley, it was June, July, August and into September (Morris *et al.* 1982). Peak fruitfall was September to November. The Zairean study of Malaisse *et al.* (1975) recorded peak litterfall during August and September. Most forest ecosystems are also characterised by an inverse relationship between the proportion of the total annual rainfall in a given month and the proportion of annual litterfall in that month (Cooper 1982, Whigham *et al.* 1990, Pant & Tiwari 1992, Alvaez-Sanchez & Sada 1993).

With a minimum of 80 %, it appears that a greater proportion of the litter was leaf litter relative to most published data. The Nylsvley work showed that approximately 77 % of litterfall was leaf litter, 16 % twigs and bark and 7 % fruits and seed. Malaisse *et al.* (1975) reported 74 % of litterfall was leaf litter. Comparable figures from moist west African savannas were 77 % (John 1973) and 63 % (Collins 1977). Frost (1996) provided values for three sites in miombo with range from 67 - 95 %. Values for forest ecosystems correspond well with those published previously from savannas; for example, Indian oak forests - 78 % (Pant & Tiwari 1992); Mexican tropical rainforest - 68 % (Alvarez-Sanchez & Sada 1993) and approximately 85 % in Mexican dry forests (Whigham *et al.* 1990).

Table 11.2. Composition (% ± SE) of the litterfall.

Rainfall zone	Slope position	Year	Leaves	Twigs	Bark	Flowers	Fruit
Arid	Top	1993/94	89.1 (1.23)	4.4 (0.27)	1.4 (0.38)	1.6 (0.23)	3.5 (2.0)
		1994/95	94.6 (1.94)	1.9 (0.54)	3.0 (1.64)	0	0.6 (0.6)
	Bottom	1993/94	84.7 (0.64)	5.2 (0.19)	1.1 (0.48)	4.2 (0.49)	4.9 (0.69)
		1994/95	89.6 (3.35)	4.7 (1.39)	0.6 (0.52)	0.4 (0.21)	4.7 (2.48)
Semi-arid	Top	1993/94	88.1 (2.31)	5.3 (0.73)	1.2 (0.4)	2.5 (0.7)	2.8 (0.77)
		1994/95	96.3 (0.78)	1.7 (0.42)	1.7 (1.21)	0	0.4 (0.22)
	Bottom	1993/94	87.9 (3.06)	6.7 (2.29)	0.9 (0.58)	2.4 (1.11)	2.1 (0.84)
		1994/95	95.7 (0.77)	2.3 (0.23)	0.7 (0.43)	0.3 (0.3)	1.0 (0.49)
Mesic	Top	1993/94	80.7 (4.64)	5.6 (0.95)	4.0 (1.57)	6.1 (2.91)	3.7 (1.22)
		1994/95	94.3 (1.22)	2.8 (1.70)	1.9 (0.15)	0.3 (0.3)	0.7 (0.56)
	Bottom	1993/94	83.9 (3.40)	6.1 (1.76)	1.9 (0.82)	4.9 (0.35)	3.2 (1.49)
		1994/95	96.4 (0.96)	3.1 (0.95)	0.4 (0.1)	0	0.1 (0.1)

The only difference in the amount and dynamics of litterfall between toplands and bottomlands was the greater concentration of litterfall at toplands into a shorter period of the year. This phenomenon is also reported to occur with increasing aridity. John (1973) found no differences in litterfall dynamics on two different soils along a catena, one well drained and one not.

The greatest litter production per unit standing biomass was at intermediate rainfall. Collins (1977) found a strong positive linear correlation between rainfall and litterfall, but did not assess it relative to stand biomass. However, Madge (1965) failed to detect any relationship with total annual rainfall, and Whigham *et al.* (1990) reported a significant decrease in leaffall with increasing rainfall over several years at a single site. It is probable that seasonal distribution of the rainfall may be a critical factor in determining the strength of any relationship between litterfall and mean annual rainfall (Collins 1977). The greater litterfall per unit biomass at the intermediate locality correlates with the greater basal area increment recorded at these sites (Chap. 3). Thus, it is hypothesised that the relationship between rainfall and litter is manifest through the control of water balance on total productivity, rather than on litterfall directly. The increasing seasonality of litterfall with increasing aridity has been recorded previously (Collins 1977), as has been the early onset of the peak period of litterfall following a rainy season with less than normal rainfall (Whigham *et al.* 1990).

In the face of little consistency regarding the relationship between litterfall and rainfall, the strong relationship with basal area or biomass may be a more useful basis for developing predictive capacity. Cooper (1982) also reported a positive linear relationship for xeromorphic woodland and scrub.

Litterfall data need to be corrected for the loss due to herbivory of living or dead leaves whilst on the plant if the data are to be used as an estimate of annual production. Scholes & Walker (1993) summarised that approximately 18 g/m^2 is lost through herbivory at Nylsvley where the five year mean annual litterfall was 175.8 g/m^2, i.e. approximately 13 % of leaffall, and 10 % of total litterfall. None of the data reported for here, or from comparative studies have been corrected for potential losses to herbivory.

PRODUCTION OF USEABLE COMPONENTS:
FRUIT

12.1 INTRODUCTION

Wild fruits are an important component of the diets of rural communities throughout Africa (Fleuret 1979, Cunningham 1988, Campbell 1987, Shackleton *et al.* in press). This is apparent on both a subsistence and a commercial scale. At a subsistence level, indigenous fruits are significant in the diets of children, ensuring an adequate nutritional intake of certain essential nutrients and vitamins. Many communities also recognise the value of indigenous fruits in providing supplementary food during times of drought when agricultural crops fail (Campbell 1980, Zinyama *et al.* 1990). Key fruits are dried and stored for use during winter (Bradley & Dewees 1993, Dzerefos *et al.* 1995). On a commercial level, the collection of fruits represents a source of income for many families, either supplementary to other income, or being the only source of income. Currently most trade is in fleshy fruits and occurs within the local community, or between adjacent communities. There is potential for this to be developed further through the processing and decoration of dry fruits for sale at tourist markets and in the florist trade. Thus, development of a reliable internal and external trade in fruits may be one vehicle to boost rural economies (Taylor & Moss 1983, Shackleton 1996). A range of browsers species also make use of fruits, (Miller 1994, Reid & Ellis 1995).

At the same time, fruit production is a central element in the productivity of woody savanna species and other vegetation types. It requires significant allocation of carbon and nutrient resources (Ernst & Tolsma 1989), hence, usually being delayed until a tree attains a certain size. In terms of total above-ground woody productivity, fruit production is probably low (< 3,5 %) (Scholes & Walker 1993), but it represents the ability of the reproductive cohorts to disperse and regenerate. It is also a significant resource within the food chain with numerous insect, bird and animal species exploiting fruits (e.g. Miller 1994).

12.2 OBJECTIVES

The following key questions were considered:

1. What is the proportion of stems of selected species that fruit in a given season?
2. At what stem size do selected species begin to fruit?
3. Is there a relationship between stem size and mass of fruit produced?
4. What is the relationship between rainfall and fruit production?

12.3 METHODS

The dominant species (biomass or density) were selected at each of the three intensive study localities. At the time of peak fruiting for each species, three transects were assessed to determine the proportion of stems with or without fruit in a range of stem size-classes. There were 20 size classes defined as 5 cm increments in basal circumference, up to 100 cm. The last size class comprised stems greater than 100 cm. Transect length and width was variable, dependent upon the density of stems of the species in question. For each size class up to a basal circumference of 20 cm at least 25 stems were examined for the presence of fruits, irrespective of quantity or stage of maturity. For stems in the remaining size-classes, a minimum of 10 stems were inspected. Data collection ceased for a given transect once 100 % of stems in three consecutive size classes had fruit. It was assumed that all stems larger than this recorded threshold at which all stems had fruit, also had fruits. At the moist locality this was repeated for the same species in burnt areas where possible.

For most species data were collected in 1993/94 and 1994/95. However, the location of individual transects was not the same in each year and hence they can be regarded as independent samples.

For selected species allometric relationships were determined for the quantity of fruit produced relative to stem size. Fruit was stripped by hand from a range of stem sizes and weighed fresh. A subsample was then oven-dried for 5 days at 75oC and weighed. Stem size attributes measured were basal circumference at 35 cm above ground level (all stems included if multiple stems), height, and crown diameter (long and short axis). For large species, individual trees were marked, and fruit collected from underneath the tree at regular intervals throughout the fruiting period. Fruit were counted, and a representative sample of undamaged fruit was oven-dried for 5 days at 75°C.

An arcsine transformation was applied to the percentage data. Differences in size class profiles were analysed using a Kolmogorov-Smirnov test. Correlation coefficients were used to investigate the relationship between maximum size of a given species at each locality and (1) the smallest size class at which fruiting commenced per species (averaged for 1994 and 1995), and (2) the smallest size class at which all stems in the size class fruited (averaged for 1994 and 1995). The maximum potential size class of a species was determined from the vegetation survey results for each reserve (Chap. 2), and was taken as the mean of the three largest stems recorded for that species.

12.4 RESULTS

12.4.1 Fruit production profiles

The fruit production - size class profile differed between species, years and rainfall zones (Fig 12.1). Interannual differences were evident not only in the quantity of fruit produced, but also the size classes at which fruiting occurred. Of the 12 species observed over two fruiting seasons, a shift to larger stems was observed in the profile in 1995 relative to 1994 for six of them (*A. gerrardii*, *C. apiculatum*, *C. collinum*, *C. hereroense*, *P. curatellifolia* and *P. angolensis*). Thus, the smallest size class in which fruiting occurred was delayed in 1995, as was the size class at which 100 % presence was recorded. Consequently, there was a reduced range of size classes with fruits in 1995 relative to 1994. *Acacia gerrardii* did not produce any fruit in 1995. In contrast, *D. cinerea* indicated a shift in the opposite direction, such that fruiting was better in 1995 than 1994. There was no trend regarding yearly differences in the remaining species

Site differences were evident with species profiles. For example, comparison of profiles of *A. gerrardii*, *A. harveyii* and *C. hereroense* recorded at both the arid and semi-arid localities indicated a shift to larger stems for the arid locality. Thus, at the arid locality, fruiting was initiated at larger size classes than at the semi-arid locality; 100 % frequency was attained at larger size classes too, and in some instances the range of size classes between initial and maximal production was also greater. Comparison of the semi-arid and mesic localities, as represented by *C. collinum*, *D. cinerea* and *T. sericea* indicated a similar moisture affect for *C. collinum* and *D. cinerea*, i.e. the profile from the drier locality being to the right of the moister locality. There were no differences in the profile of *T. sericea*.

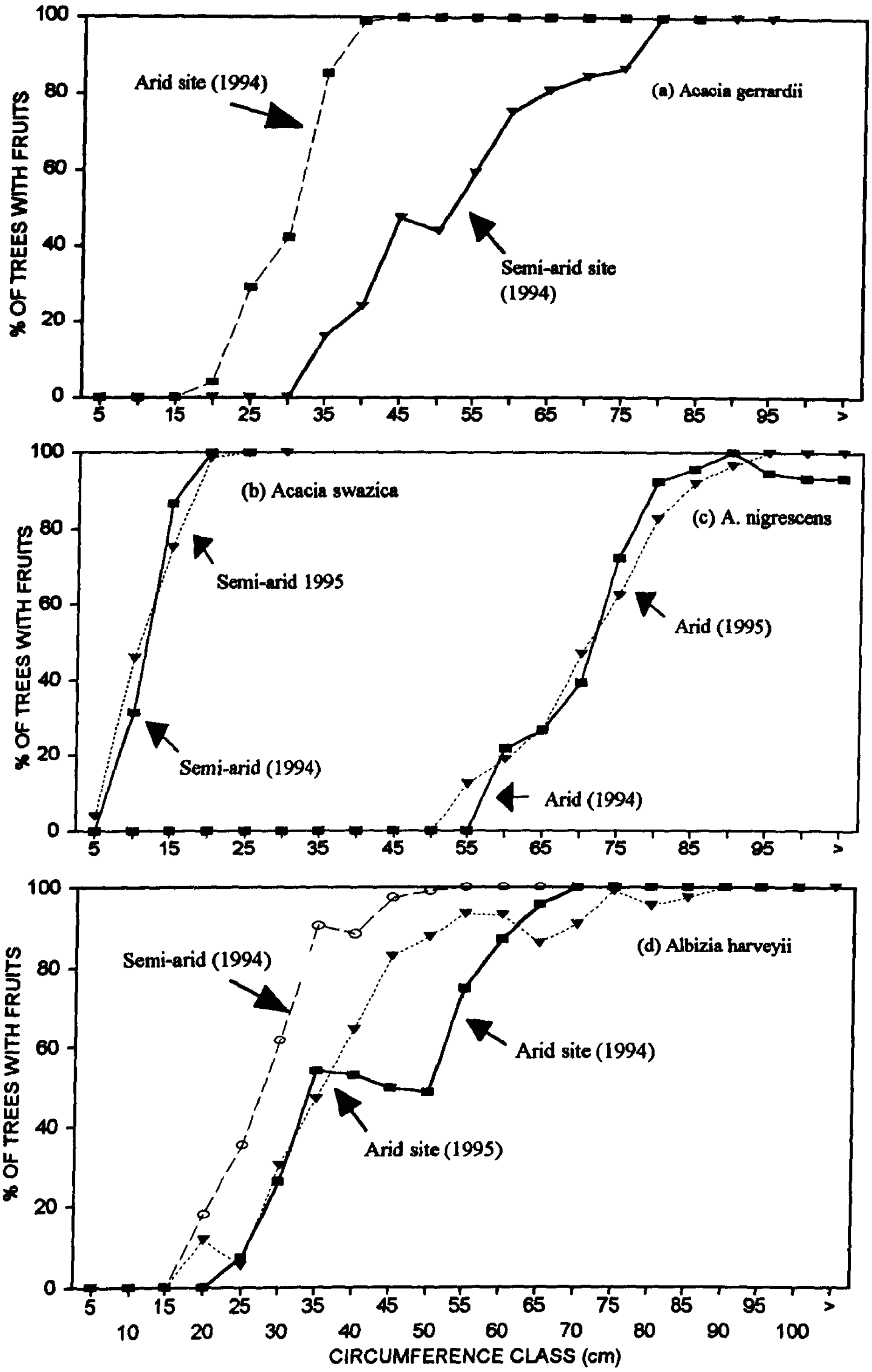

Fig 12.1a - d. Fruit presence profiles.

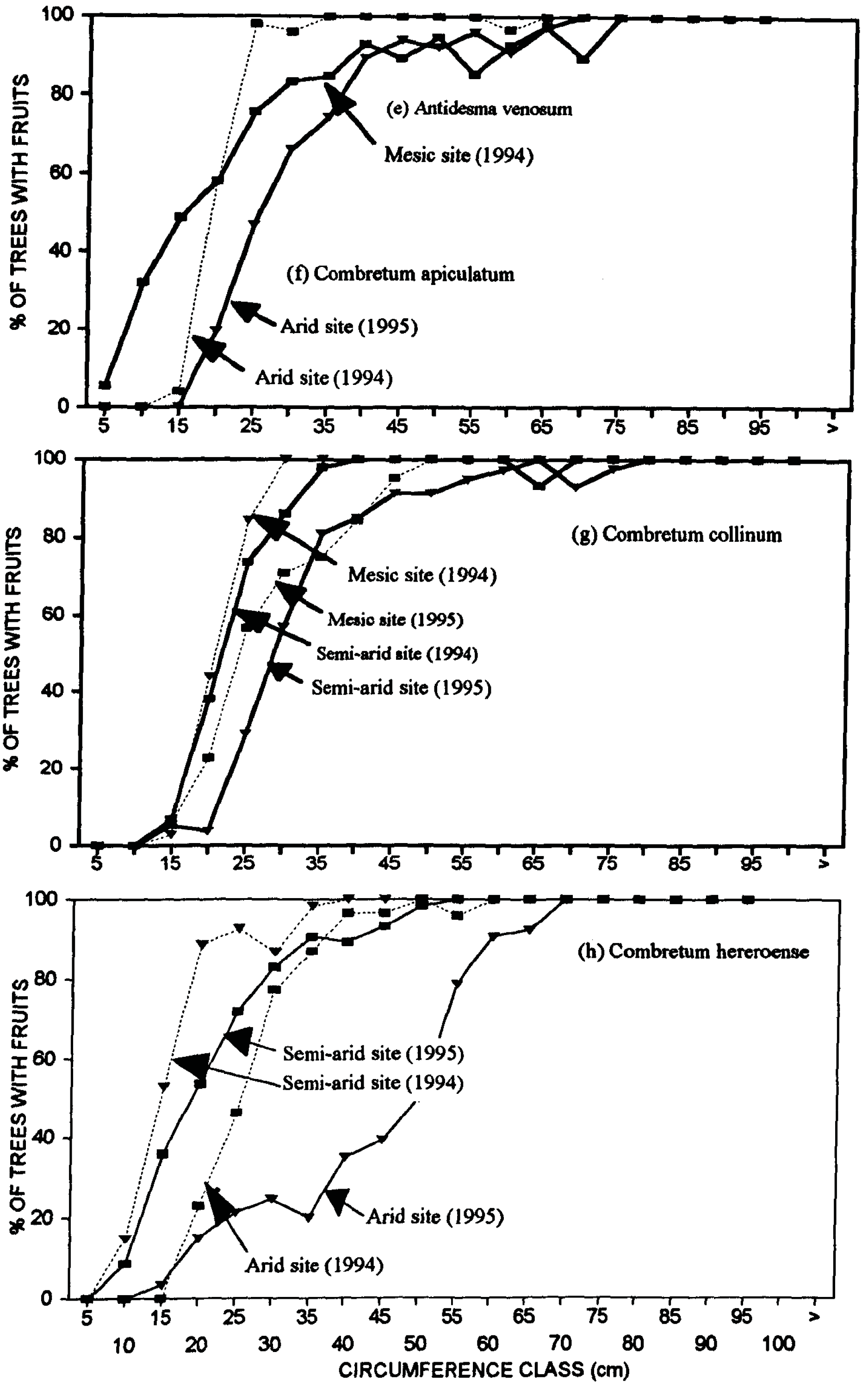

Figure12.1e - h. Fruit presence profiles.

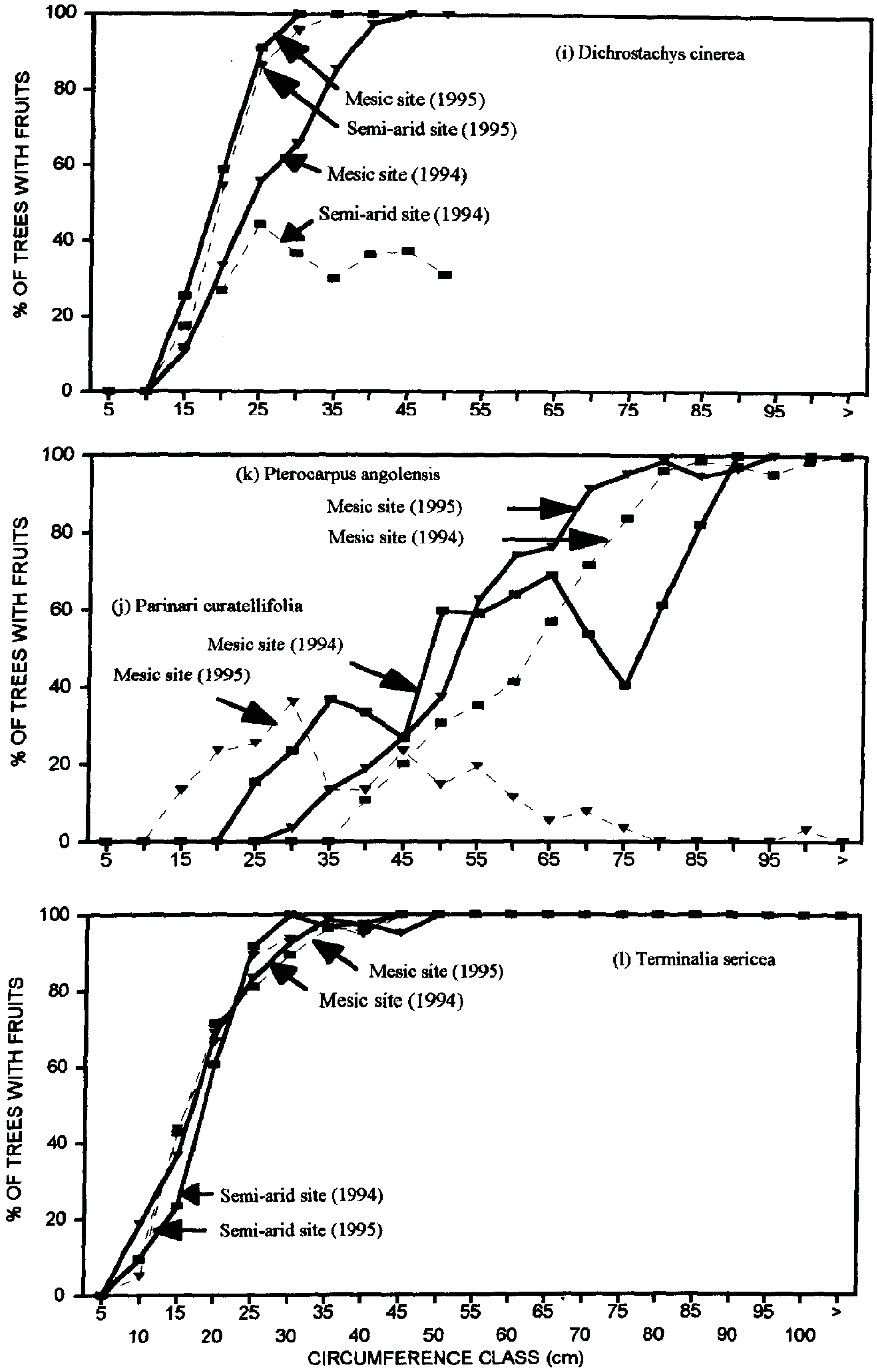

Figure 12.1 i - l. Fruit presence profiles.

12.4.2 Size class of first and maximal fruiting

There was a strong relationship between the potential maximum stem size per species per locality and (1) the smallest size class at which fruiting was observed ($r=0.91$; d.f.=14; $p<0.0001$), and (2) the smallest size class in which all stems recorded had fruits ($r=0.97$; d.f.=14; $p<0.0001$). In each instance, the larger the potential maximum stem size, the larger the size class at which fruiting was initiated, and the larger the size class at which all stems fruited (Fig 12.2). Generally, fruiting commenced at a size class approximately 1/5 of the maximum potential size for each species, and full fruiting (100 % of stems per size class) at approximately 2/3 of the maximum potential size class.

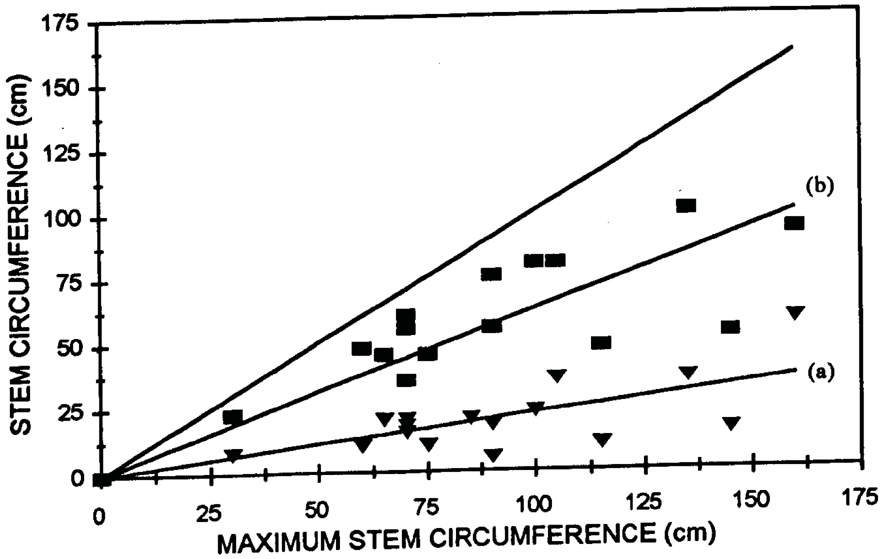

Figure 12.2. Stem size at which (a) first fruiting, and (b) 100 % fruiting occurs relative to maximum potential stem size.

12.4.3 Allometry

Total mass of fruit differed between species, sites and individual trees (Table 12.1). There was a strong relationship with tree size; the larger the tree of a given species, the greater the mass of fruit produced. Fruit

Table 12.1. Summary relationships between dry fruit mass (g) per species per year and tree dimension (LA = long axis; SA = short axis; BA = basal area; HT = height).

SPECIES	SITE	SEASON	RELATIONSHIP (Dry mass(g) = ...)	r^2	n	p
Acacia gerrardii	Semi-arid	93/94	= 607(LA) - 1963	0.77	22	< 0.0001
		94/95	No fruit			
Antidesma venosum	Moist	93/94	= 481(logBA) - 558	0.58	29	< 0.0001
		94/95	No fruit			
Combretum apiculatum	Arid	93/94	= 1694(logHT) - 658	0.36	22	< 0.005
		94/95	Minimal fruit			
Combretum collinum	Semi-arid	93/94	Freshmass = 557(SA)-544	0.70	20	< 0.0001
		94/95	Freshmass = 1.86(BA) -22	0.81	21	< 0.0001
	Moist	93/94	= 3.65(BA) + 413	0.82	24	< 0.0001
		94/95	= 3.18(BA) + 485	0.88	21	< 0.0001
Dichrostachys cinerea	Semi-arid	93/94	= 8.76(BA) - 78	0.88	22	< 0.0001
		94/95	= 7.11(BA) - 44	0.89	20	< 0.0001
	Moist	93/94	= 7.88(BA) - 70	0.88	22	< 0.0001
		94/95	= 7.62(BA) - 9	0.84	20	< 0.0001
Grewia bicolor	Arid	93/94	= 5.32(BA) + 131	0.58	20	< 0.0001
		94/95	Minimal fruit			
Grewia hexamita	Arid	93/94	= 788(SA) - 1332	0.68	20	< 0.0001
		94/95	No fruit			
Sclerocarya birrea	Arid	93/94	log(drymass) = 0.00036(BA) + 3.12	0.14	30	< 0.05
		94/95	Minimal fruit			
	Semi-arid	93/94	= 12.1(BA) - 4513	0.36	22	< 0.05
		94/95	= Minimal fruit			
	Moist	93/94	= 6.48(BA) + 994	0.46	12	< 0.05
		94/95	Minimal fruit			
Strychnos spinosa	Semi-arid	93/94	No fruit			
		94/95	Freshmass = 1035(HT) - 2873	0.43	20	< 0.005
	Moist	93/94	No fruit			
		94/95	Freshmass = 3803(HT) - 20000	0.15	32	< 0.05
Terminalia sericea	Semi-arid	93/94	= 3.94(BA) - 8.28	0.48	27	< 0.0001
		94/95	= 4.10(BA) - 0.584	0.86	21	< 0.0001
	Moist	93/94	= 116.7(HT) - 216	0.14	23	n.s
		94/95	= 1.28(BA) + 222.8	0.79	22	< 0.0001

production in 1994/95 was reduced relative to 1993/94 for most species, except *D. cinerea*.

Using the above relationships in combination with the size class profile of individual species in one third of the vegetation transects at the arid, semi-arid and mesic localities (Chap. 2) it was possible to determine total fruit production per unit area per standing biomass (Table 12.2).

However, the above relationships represent a minimum estimate because fruit production was not assessed for all species. Extrapolation of these data indicate that fruit production for all species would be 1.5 to 2.0 % of biomass per year (Table 12.3). Fruit production appears to be inversely related to rainfall regime, but the gross extrapolations derived here preclude any hypothesis testing from this trend.

Table 12.2. Relationship between fruit production (dry mass) for species studied and transect total basal area and biomass.

LOCALITY	RELATIONSHIP (Fruit dry mass (kg/ha) =	r^2	n	p
Arid	= 26.1 (Basal area)	0.73	31	< 0.0001
	= 8.7 (Biomass)	0.68	31	< 0.0001
Semi-arid	= 22.8 (Basal area)	0.54	10	< 0.01
	= 8.9 (Biomass)	0.45	10	< 0.05
Moist	= 20.4 (Basal area)	0.70	17	< 0.0001
	= 5.2 (Biomass)	0.51	17	< 0.001

Table 12.3. Estimated total fruit production (kg/ha/yr) for all species.

MEASURE	LOCALITY	FRUIT DRY MASS PRODUCTION CONSTANT	% OF SPECIES INCLUDED	ESTIMATED PRODUCTION CONSTANT FOR ALL SPECIES
Basal area	Arid	26.1 kg/m^2/ha/yr	43	60.7 kg/m^2/ha/yr
	Semi-arid	22.8 kg/m^2/ha/yr	55	41.5 kg/m^2/ha/yr
	Moist	20.4 kg/m^2/ha/yr	37	55.1 kg/m^2/ha/yr
Biomass	Arid	8.7 kg/t/ha/yr	41	21.2 kg/t/ha/yr
	Semi-arid	8.9 kg/t/ha/yr	61	14.6 kg/t/ha/yr
	Moist	5.2 kg/t/ha/yr	36	14.4 kg/t/ha/yr

12.5 DISCUSSION

Amongst the twelve species there appears to be three distinct patterns of fruit production profile relative to stem size class:

(1) Deterministic pattern represented by species that show a very steep and rapid, almost linear curve from zero fruit production to full fruit production, for example *A. gerrardii*, *A. swazica*, *C. apiculatum* (1994), *C. collinum* (1994), *C. hereroense* (1994), *D. cinerea* (except 1994 at semi-arid site) and *T. sericea*.

(2) An incremental pattern refers to those species with a distinctly sigmoid profile, with the rate of increase being relatively shallow, and spread out over several size classes, including *A. harveyii*, *A. venosum*, *C. apiculatum* (1995), *C. collinum* (1995), *C. hereroense* (1995) and *P. angolensis*.

(3) Opportunistic describes those species where fruit production was relatively unpredictable from one size class to the next, and rarely attaining 100 %, represented by *P. curatellifolia* and *D. cinerea* at the semi-arid site in 1994.

There were considerable interannual differences in production profiles for several of the species. Such interannual differences in fruit production of savanna trees are well recorded (Chidumayo 1993), but the trigger mechanisms and scale of operation are little understood. The variability has four sources;

(1) The proportion of trees that set fruit. The degree of interannual variation is probably greatest here, thereby having the greatest influence of total fruit mass per unit standing biomass. Similar to the findings of this study, Chidumayo (1993) found that fruiting percentage ranged from 0 % to over 70 % within a species between successive years. He attributed fruiting failure to a lack of flowering or flower abortion.

(2) The number of fruits per tree. This may show considerable variation (Chidumayo 1993, Tybirk 1993) and is a function of tree size as well prevailing climatic conditions controlling flowers and seed set.

(3) The individual fruit size. Chidumayo (1993) found no difference in individual fruit size between years. This is contrary to the findings of this study (unpublished data). It is possible that size varies little in small dehiscent fruits or seeds, such *Acacia* species, but more widely in larger fleshy fruits such as *Strychnos* or *Sclerocarya*.

(4) The proportion lost through pre-dispersal predation or browsing varies from year to year (Chidumayo 1993), as well as from tree to tree (Ernst *et al.* 1989, Miller 1994). Up to 90 % of seed maybe predated (Miller 1994). Differences between years must be related to the dynamics of the predator, but also possibly the actual amount of fruit production. Masting species commonly experience lower rates of predation than non-masting species (Miller 1994).

Overall it appears that burning had little effect on the proportion of stems that bore fruits in a given size class. However, since burning effects on stem survival are most apparent at the smaller size classes (Chap. 17), it can be hypothesized that the same should be apparent with respect to fruiting, i.e. the effect of burning on fruit production should be most apparent on smaller stems. Thus, for species that do not fruit until the stem is of a relatively large size, fire should have no impact. This was the case with *P. angolensis*. But for smaller species, there was a trend for the smallest size class with fruits to be set back by a size class in burnt areas. Or, if the same size class, then the proportion of stems fruiting in this initial size class was reduced in burnt areas relative to unburnt areas. This trend was not consistent and requires further investigation.

The absolute production estimate of 1.5 - 2.0 % per unit standing biomass is higher than previous studies, and the litterfall section of this study (Chap. 11). For example, Scholes & Walker (1993) report an annual productivity of fruit and flowers based on a litterfall study of 10 g/m^2 at Nylsvley, or the approximate equivalent of 0.6 % given a standing biomass of 16.7 t/ha. The litterfall section of this study provides an approximate figure derived from means across all the plots of 0.7 % or less. Malaisse *et al.* (1975) documented an annual fruit litterfall of 160 kg/ha in miombo (equivalent of 0.5 % if assume a standing biomass of 30 t/ha). In temperate biomes, Nihlgard (1972) found annual fruit production to be 0.3 % of standing biomass in beech forests, and 0.1 % in spruce forests, whereas Singh & Yadava (1991) found fruit production to be 0.3 % of stand biomass in a wet temperate mixed forest in India.

Fruit production per unit standing biomass was inversely related to mean annual rainfall. This may suggest that vegetative reproduction is more prevalent at moist sites than arid sites. This is corroborated by the higher proportion of small, regenerative stems at the mesic site (Sect. 2.5.3). However, given that fruit production was not determined for some of the dominant species (in terms of biomass) at the moist locality, but all dominants were included at the other two localities, this extrapolation needs to be verified with further work.

COMMUNITY LEVEL IMPACTS OF WOOD HARVESTING ON WOODY PRODUCTIVITY: A REVIEW

13.1 INTRODUCTION

Access to fuelwood and construction timber in indigenous forests and savannas is one of the primary basic needs of rural communities throughout the developing world (Goodman 1987). Southern and South Africa are no different, where over 75 % of rural populations are still reliant upon fuelwood for most of their energy needs (Gielink 1991). In the Mpumalanga lowveld over 95 % of rural households use fuelwood to a greater or lesser degree. Over 70 % of homesteads contain some indigenous timber in the walls or roofs of buildings and/or kraals and fences (Banks *et al.* 1996).

Negative impacts of wood collection from forests and savannas are conjured up in the word `deforestation', often with considerable emotive effect in the mass media and popular literature. The observation that rural people harvest wood identifies them as the culprit of all the negative images associated with deforestation. The reasons for the wood removal are rarely considered, the real ecological effects are never debated, and the remedies applied are therefore frequently inappropriate. The understanding that clearance for arable production is the primary cause of 'deforestation' (Chidumayo 1987, Goodman 1987, Grundy *et al.* 1993) does not appear in the popular literature.

The broader aims of this study have been to assess the production potential of savannas. In doing so it will aid attempts to derive sustainable harvesting levels for a variety of woody products. The act of harvesting constitutes an active management process, which in itself may have impacts on woody productivity. Some discussion of the impacts of harvesting on woody production is therefore appropriate. This chapter attempts to do this at the stand level. Chapters 14, 15 and 16 consider the impact of harvesting at the plant level.

This chapter is a review. It is hypothesised that the impacts of harvesting are a function of harvesting intensity, frequency and duration. Unfortunately, there is little literature regarding stand level impacts recorded from controlled trials contrasting the intensity, frequency and duration of harvesting. This has been done at the level of an individual tree for a few species (e.g. Milton 1988), but scaling up presents some problems. Therefore, much of the review will simply refer to harvesting, irrespective of intensity, frequency or duration. In some instances the levels may be qualified. It is assumed that the impacts of low intensity harvesting over a long period will be similar to a higher intensity over a short duration, but this requires empirical testing. The first scenario is typified by small, established rural settlements, extracting a variety of products such as fuelwood, construction timber, medicines, fruits, and browse on a continuous basis. Initially extraction rates were sustainable, but as human population density increases sustainability is lost and there is a slow, but progressive change in woodland structure and function. High intensity, short duration impacts result from large migrations of people within short periods, such as movements of refugees (Biswas & Tortajada-Quiroz 1996), government enforced translocations (Grossman & Gandar 1989, Wilson 1991), or clear-felling for charcoal production (Chidumayo 1987, 1993).

Harvesting is also a common management action on commercial farms, largely as a mechanism to control bush-encroachment. More literature exists around this topic (see review by Smit *et al.* 1996). However, most is not directly applicable to addressing the question of the impacts of harvesting on community structure and productivity, because (1) cut stems are usually treated chemically to prevent regrowth, and (2) community structure immediately after harvesting is the direct goal of the harvesting operation. Thus, the intensity of clearing is defined beforehand, so too are the size classes of stems to be removed and stems to remain.

13.2 IMPACTS ON WOODY COMMUNITY STRUCTURE

Woody communities subjected to harvesting are usually characterised by a change in overall community structure to a greater or lesser degree. Typically, there is a reduction in most structural attributes including mean stem size, mean stem height, basal area, biomass, and range of stem sizes represented relative to unharvested sites (Childes & Walker 1987, Shackleton 1993, Grundy *et al.* 1993, McGregor 1994, Shackleton *et al.* 1994, Murali *et al.* 1996). Density may be higher or lower than unharvested sites depending on the degree of coppice regrowth. If significant coppicing, then density may increase (Strang 1974, Chidumayo 1993), similar to the effects of frequent burning (Chap. 17). If harvesting is particularly severe or is in conjunction with marked browsing by animals (livestock or game) density is usually reduced as well. The alteration of the size class profile also shows different patterns, presumably in relation to harvesting intensity or duration. Fuelwood harvesters actively select stems of particular size classes and species (Shackleton 1993, McGregor 1994, Shackleton *et al.* 1994). Harvested communities frequently