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The prediction of woody productivity in the savanna biome, South Africa

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was present, failed to corroborate the presence of competition at those plots. Grundy *et al.* (1994) also found no relationship between interplant distance and combined RGR for *Julbernardia globifera*, but one did exist for *Brachystegia spiciformis*.

3. Exclusion of the smallest size classes

In most of the studies cited, as well as this study, the nearest-neighbour analysis is confined to established stems larger than a specified minimum, frequently 1 m tall. The smallest stems are excluded from the analysis. Yet it can be argued that it is the smallest stems that are most vulnerable to adverse abiotic and biotic factors as evident in the higher mortality rates of small stems relative to big stems (Sect. 3.4.6). Such factors, including competition from neighbours, may lead to the death of the newly recruited plant within one or two seasons after establishment (the equivalent of competitive exclusion), or restrict it to a small size with frequent shoot die-back (Milton 1987, Chidumayo 1992a, b) until a change in circumstances allows it grow though into a larger size class. Thus, perhaps the current application of nearest-neighbour studies to detect competition are at an incorrect resolution and should be focused on, or certainly include, the smallest individuals. A high stand density and proportion of small stems was important in differentiating sites with significant intra-specific competitive interactions.

4. Consideration of the nearest-neighbour only

The basic assumption of the nearest-neighbour approach is that the closer together two individuals are, the stronger the degree of competition between them. However, this need not necessarily be so since the assumption ignores the relative sizes of the two individuals, and other adjacent trees. Thus, a relatively large tree (***C***) in the vicinity of a small tree (***A***) could be expected to have a greater influence on that small tree (***A***) than another small tree that is closer (***B***) (Fig 6.3). The nearest neighbour pair is ***A*** and ***B***, but the strongest competitive effect is ***A*** and ***C***. It may well be that ***C***'s nearest neighbour is not ***A***, and therefore the competitive influence of ***C*** is never measured. This may be addressed by measuring more than one nearest-neighbour per point tree, for example the nearest tree in each 90 ° quadrant around the point tree.

Acceptance of the results of this study suggests that niche separation between species and within species

is generally greater than previously assumed. Alternatively, if competition is occurring, its impact is relatively low, both at the level of specific pairs of trees, as well as the community as a whole. It may occur on a spatial as well as a temporal dimension. It is necessary to obtain a predictive capacity in this regard, so that the role of competition can be determined for specific sites where previously it has been assumed that it played a significant role.

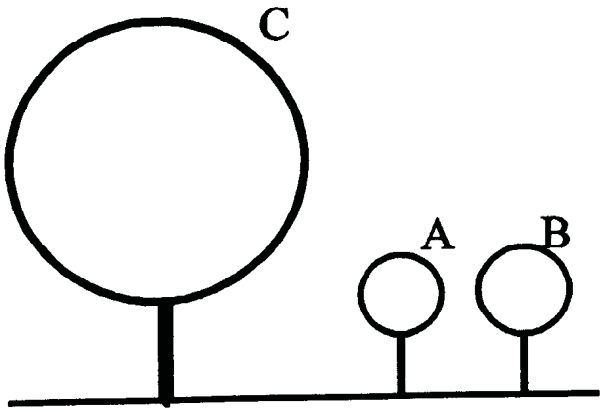


Figure 6.3. Nearest-neighbour analysis and spatial interpretation of competition (see text for details).

This conclusion is at odds with the finding that relative basal area increment is a negative function of the basal area of a stand (Chap. 3), i.e. basal area increment decreases with increasing stand basal area. The general interpretation of such a relationship is that it is a result of increasing competitive effects with increasing amount of vegetation. The results of this study question such an interpretation. If correct, then what alternative explanations may resolve the relationship between basal increment and basal area? Two possibilities exist. The first is that the inadequacies of nearest-neighbour methods, as discussed above, reduce the detection of competition, and therefore the conclusion of this study is incorrect. A second hypothesis is that the negative relationship between basal area increment and basal area is an artefact of the size class profile of the stand. Basal area increment decreases with increasing stem diameter. Stand basal area is disproportionately a function of large tree basal area rather than simply stem density. Thus, lower basal area increment manifest in stands with a high basal area may be due the relatively higher contribution of larger, slower growing stems, to the overall basal area. This appears to be the case for the biome plot data

(Chap. 3). The contribution of the basal area of all large stems (≥ 75.1 cm) to the total stand basal area (m^2/ha) increases with increasing stand basal area, summarised in the form:

$$\%\ \text{contribution of large stems to total basal area} = 1.16\,(\text{stand basal area}) + 12.56 \qquad (r^2 = 0.21;\ p < 0.005;\ n = 51)$$

Whilst the relationship is linear across the range of data used, it is anticipated that a sigmoid curve would be a better fit, attaining some asymptote above which the percentage contribution of large stems does not increase, even though stand basal area does.

WOODY PLANT PRODUCTIVITY:
THE ROLE OF COMMUNITY PHENOLOGY

7.1 INTRODUCTION

Community phenology provides clues as to the major abiotic and biotic variables that determine the seasonal development and senescence of plant tissues and organs. Since initiation and termination of growth phases represent the boundaries of periods of growth and productivity, an understanding of the triggers and controlling variables contribute to an understanding of plant productivity. As with many aspects of savanna dynamics (Scholes & Walker 1993) most past phenological research has focused on the herbaceous layer because of the clear correlation with rainfall patterns in tropical and semi-arid systems (Prins 1988).

It has been argued that low and variable precipitation is the primary driving variable of savanna dynamics (Noy-Meir 1973). This has been questioned by Scholes and Walker (1993), who suggest that the influence of precipitation is through its effect on nitrogen mineralisation, rather than plant growth directly through photosynthesis and transpiration. Whilst accepting that nitrogen mineralisation may be the proximate determinant, its effect is controlled through the presence or absence of plant available moisture. This is mirrored in the role of water stress on plant nutrient concentrations (Prins 1988). Plant available moisture is a function of the amount and timing of precipitation in combination with the effect of temperature on evaporative demand. At a gross scale rainfall is a coarse index of plant available moisture, and can therefore be regarded as the proximate determinant of savanna dynamics.

If this is correct it can be hypothesised that community phenology and productivity would vary along a gradient of soil moisture availability. This has been clearly demonstrated with respect to herbaceous communities (e.g. Sarmiento 1983, Prins 1988), but less so with respect to woody communities. Such soil moisture gradients can be manifest as a direct gradient in rainfall, or as a gradient in soil type from sands to clays, i.e. toplands and bottomlands. This study sought to investigate woody community phenology across both such gradients.

7.2 OBJECTIVES

The objectives of this section were to: (1) contrast community phenology along a rainfall gradient, and (2) contrast community phenology between different soil types.

7.3 METHODS

Within the first week of each month (from Sept 1993 to Sept 1994) phenology transects were performed at each of the three intensive study sites (Chap. 2). There were ten transects per reserve, five in toplands and five in bottomlands. Transects were in the same locality each month, but the starting point was not permanently marked, and hence the same trees were not necessarily inspected every month. Each transect consisted of fifteen points placed 15 m apart. At each point the nearest tree (> 1 m tall) within four 90° quadrants was inspected with respect to its phenological state (thus there were 60 trees per transect). However, to promote inclusion of the less abundant species, no more than two of the trees at each point could be of the same species. Therefore, if the species in the third quadrant was the same as that in the previous two, then the second nearest tree in that quadrant was considered. If that was also of the same species, then the third nearest was inspected, and so on. Each tree recorded was classified into one of three height classes; (1) < 2 m, (2) 2 - 4 m, and (3) > 4 m.

The phenological state of each tree was rated in the following categories:

1 - leaf initials/buds present
2 - leaves emerging from buds
3 - mature leaves present
4 - leaves senescing
5 - leafless
6 - reproductive buds/flowers present
7 - immature fruits present
8 - mature/dehiscing fruits present
9 - fruits from previous season present
10 - shoot elongation evident

Data were expressed as percentages and the mean per month (n=5; rainfall zone by slope position) summarised graphically. Percentage values underwent arcsine transformation prior to statistical analyses.

7.4 RESULTS

A clear seasonal phenological pattern was evident at each site, with differences between sites and catenal position evident for some categories (Fig 7.1).

7.4.1 Leaf buds/initials

These were evident for a two month period from mid September to mid November at all sites. The peak was in the second month of this period (except for toplands at the moist site), with a rapid decline by the first week of December. Leaf buds/initials were not recorded from December through to August. The peak was greatest at the intermediate site, followed by the moist site and lastly the arid site. The low value of the peak suggests that most of the initials are short-lived, and a monthly monitoring frequency was too long to record a full flush of initials including most of the trees.

7.4.2 Emergent leaves

Emergent leaves were concentrated into spring and early summer. The moist site, plus the toplands from the intermediate site peaked in November. The arid site and bottomlands from the intermediate site peaked a month later in December. The magnitude of the peak was greatest at the moist site, followed by the arid site, and least at the intermediate site. Generally, there were no, or very few trees with emergent leaves from January through to August.

7.4.3 Mature leaves

Mature leaves were present on a small proportion of trees at all sites throughout the year, indicating the evergreen species. During winter the proportion of trees with leaves was lower in the toplands, than the bottomlands. The same generally applied during summer also. The peak in mature leaves was from January through to May, except for the moist site which peaked a month earlier, and retained leaves a month longer. Except for the peak months, where most sites had approximately 100 % of trees with mature leaves, the

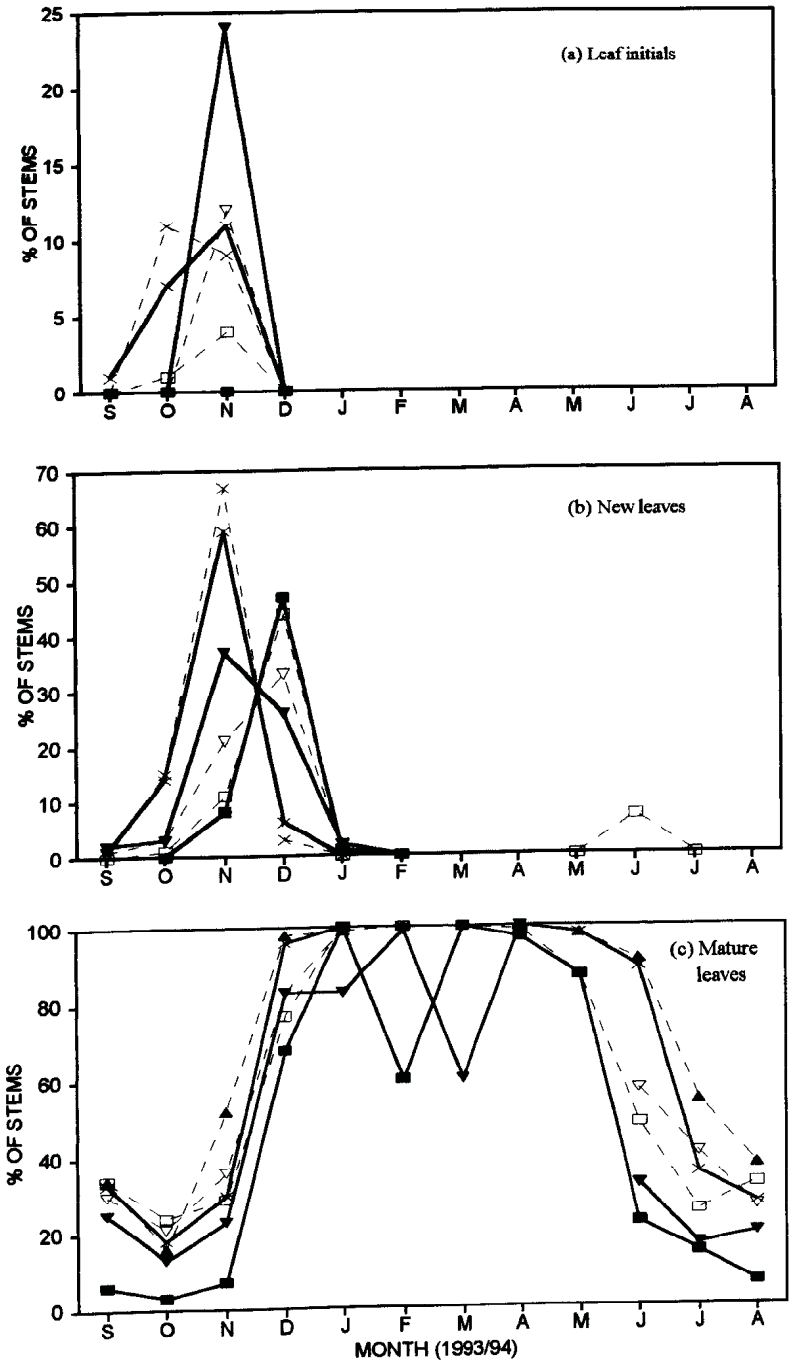
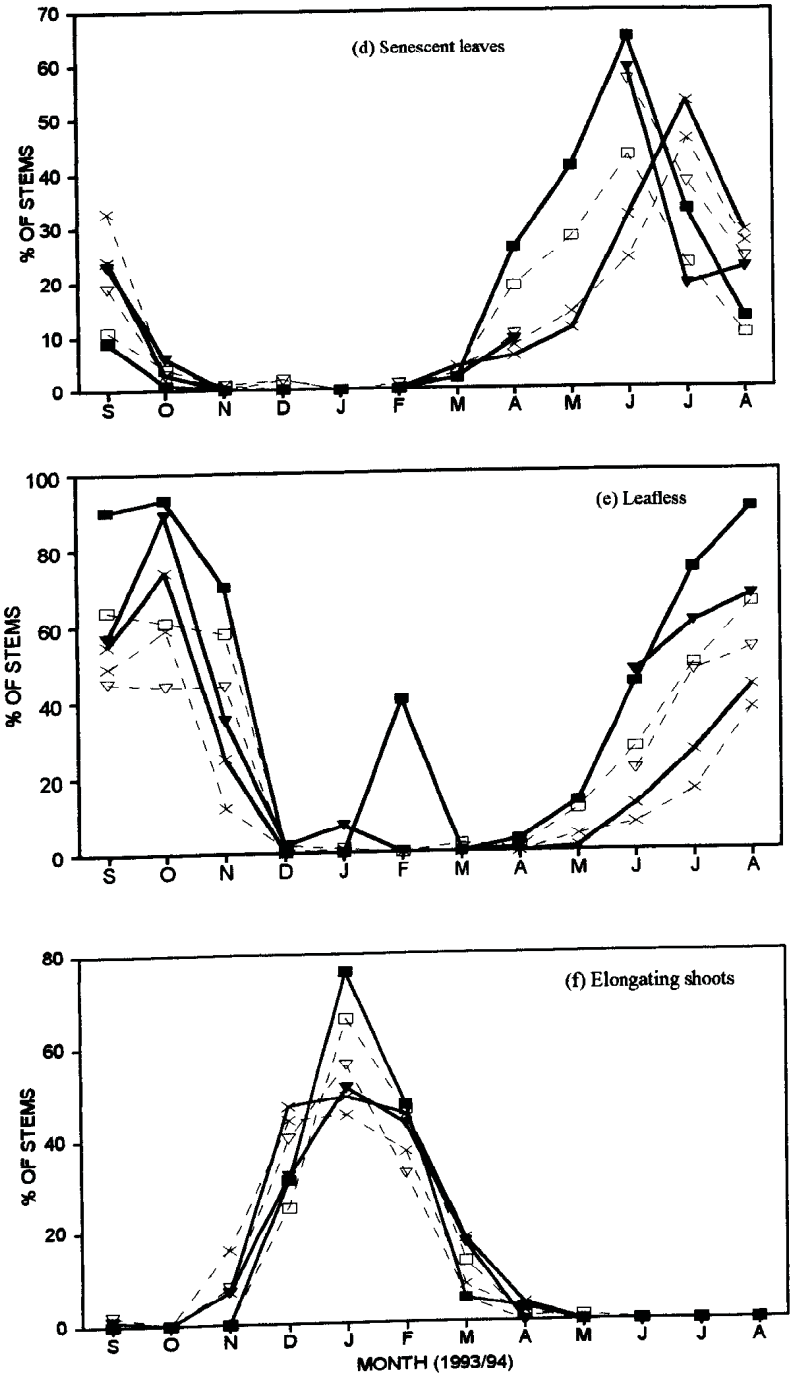
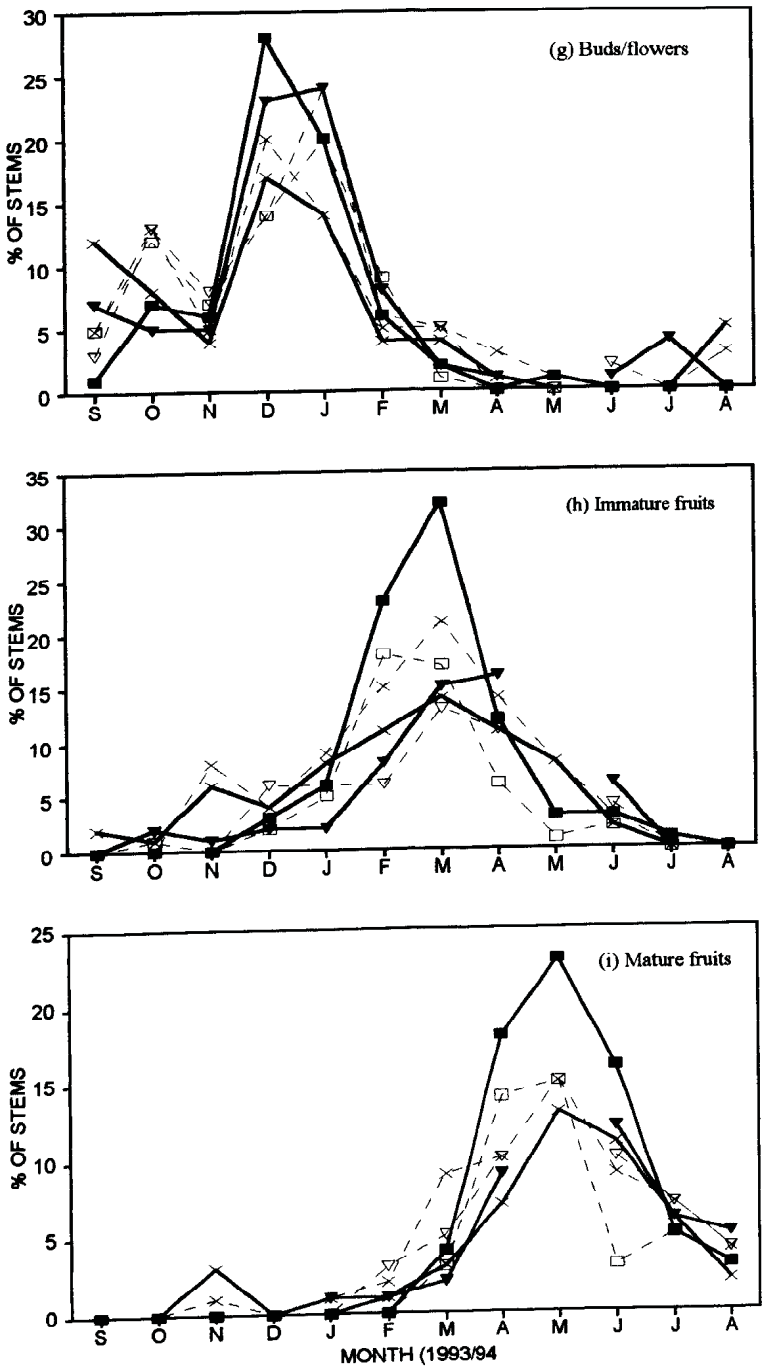


Fig 7.1 a - c. Phenophases at the arid (■/□), semi-arid (▼/▽) and mesic localities (X) on toplands (___) and bottomlands (------).



7.1 d - f. Phenophases at the arid (■/□), semi-arid (▼/▽) and mesic localities (X) on toplands (___) and bottomlands (------).



7.1 g - i. Phenophases at the arid (■/□), semi-arid (▼/▽) and mesic localities (X) on toplands (——) and bottomlands (------).

moist sites had a greater proportion of trees with mature leaves than the intermediate site, which in turn, had more than the dry site. There were anomalous drops in the proportion of trees with mature leaves from 100 % to approximately 60 % at the arid site (February) and intermediate site (April). This was correlated with a mid-season drought.

7.4.4 Shoot elongation

Shoot elongation was largely confined to the summer months, with a very concentrated peak in January. Top sites had a greater proportion of trees where shoot elongation was evident than bottomland sites at the arid and moist sites. The intermediate site was opposite; bottomlands had a greater proportion than toplands.

7.4.5 Buds and flowers

The presence of buds and flowers peaked in December and January with a rapid decline thereafter. There was no visible trend between rainfall zones or catenal position.

7.4.6 Immature fruits

Approximately two months after the appearance of buds and flowers, immature fruits become evident, peaking in March. Generally some fruits were evident throughout the year, but with lowest levels from July to October. At the moist site toplands had a lower proportion of trees with immature fruits during the peak months, than bottomlands. The reverse applied at the arid and intermediate sites.

7.4.7 Mature fruits

The presence of mature fruits peaked two months after the peak in immature fruits. Likewise, there were low levels of fruit throughout most of the year, as individual species came into season, but were lowest from

September through to December. There were no trends with respect to catenal position or rainfall zone.

7.4.8 Senescent leaves

A few trees with senescent leaves were recorded throughout the year, but were least from October through to March. At the arid and intermediate sites, the peak was in June, whereas the moist site indicated a peak one month later. Bottomland sites had a lower peak than topland sites.

7.4.9 Leafless

Mirroring that a small proportion of trees retain leaves throughout the year, so too, there is a small proportion of trees that are largely leafless even during the rainy season. However, the lowest levels are evident from December through to April/May. The peak was in September and October. The toplands always had a greater proportion of leafless trees than the bottomlands. Generally, the arid site had a greater proportion than the intermediate site, which had a greater proportion than the moist site. Bottomlands had a greater proportion of trees with leaves during winter, but a lower proportion of trees recorded with senescent leaves. Both of these were a result of the greater proportion of evergreen species such as *Euclea* species and *Cassine aethiopica* in bottomlands ($t=3.14$; d.f.=4; $p<0.03$;), as well as increased leaf retention by the deciduous species ($t=2.79$; d.f.=4; $p<0.05$) (Table 7.1).

Table 7.1. Proportion of evergreen and deciduous stems with mature leaves during winter (August 1994) at the arid site (% ± SE; n=5).

POSITION	EVERGREEN SPECIES		DECIDUOUS SPECIES	
	OCCURRENCE (%)	% WITH MATURE LEAVES	OCCURRENCE (%)	% WITH MATURE LEAVES
TOPLANDS	1.0 ± 0.7	100.0 ± 0	99.0 ± 0.7	4.7 ± 1.4
BOTTOMLANDS	19.3 ± 6.3	100.0 ± 0	80.7 ± 6.3	16.6 ± 4.0

7.4.10 Fruits from the previous season

Some fruits were retained from the previous season through to January of the following year, with very little thereafter. No trends were discernable.

7.5 DISCUSSION

As to be expected, a clear seasonal pattern was detected at all sites with respect to the different phenophases. However, of primary interest was whether or not the onset, duration and magnitude of individual phenophases was related to rainfall zone, or catenal position.

Rainfall zone appeared to influence the (1) onset and magnitude of leaf emergence, (2) the onset and duration of mature leaves, and (3) the proportion of leafless trees. Generally, the moist site demonstrated earlier leaf growth than the intermediate or arid sites. Emergent and mature leaves were recorded earlier, and in the case of mature leaves, retained longer. Overall there was a lower proportion of leafless trees at the moist site, followed by the intermediate site, followed by the arid site. The finding with respect to the earlier onset and longer duration of mature leaves at the moist site is particularly pertinent in that it suggests that the often greater productivity of sites in higher rainfall areas (Sect 3.5) may relate to the longer growing season, rather than the greater rainfall *per se*, as commented by Murphy & Lugo (1986).

Previous literature suggests that leaf initiation at the start of the growing season appears to be related more to changes in temperature than rainfall (Monasterio & Sarmiento 1976, Rutherford & Panagos 1982, Milton 1987, Steinke 1988), although day length has also been identified as a possible factor (van Rooyen *et al.* 1986a, Milton 1987). Indeed, the common phenomenon of savanna trees flushing prior to the start of the rainy season (Rutherford 1984, Fatubarin 1985, Milton 1987, Zietsman *et al.* 1989) suggests that rainfall is not the proximate trigger. Prins (1988) suggests otherwise, classifying woody shrubs into categories depending upon their phenological response to accumulated rainfall at the start of the rainy season in Lake Manyara National Park, Tanzania. The incidence of flowering and fruiting of arid zone *Acacias* is largely a function of soil moisture (Freidel *et al.* 1994). It is probable that there is a hierarchy

of trigger factors, each one coming into play only when the conditions for the preceding one have been met.

This study parallels the findings of Hoffman (1989) investigating community phenology in subtropical thicket and karroid shrublands along a rainfall gradient. Increasing aridity resulted in a concentration of phenological activity into a shorter period. This is possibly a response to a greater carryover of soil-moisture in higher rainfall regions than occurs at more arid sites (Scholes & Walker 1993). Teague (1987) recorded that *Acacia karroo* would initiate shoot growth whenever there was sufficient subsoil moisture. However, if the soil-moisture carryover was of sufficient quantity from the previous season, why then would leaf senescence occur at all, and why are there not frequent mid-winter growth events resulting from use of this carryover soil moisture? This reasoning again leads to the inclusion of some other variable, probably temperature, acting in conjunction with soil-moisture. For instance, a given temperature may act as a trigger. Whether or not leaf emergence occurs at this critical temperature depends upon the availability of sufficient carryover, or current season soil moisture, both of which are greater at sites of higher mean annual precipitation.

Differences with respect to catenal position were evident for (1) the proportion of trees in winter with mature leaves, and (2) the proportion of trees with senescent leaves. Bottomlands had a greater proportion of trees with leaves during winter, but a lower proportion of trees recorded with senescent leaves. Murphy & Lugo (1986) concluded that soil type was an important determinant of the degree of evergreenness of a community. On the other hand, Pierce and Cowling (1984) concluded that soil type had no influence on species phenology for species occurring across several soil types. However, the contrast of catenal position here does not relate solely to contrasting soil types but also to soil water dynamics. Bottomlands have a greater soil moisture status but reduced availability due to their higher clay content. It has been argued that the timing of leaf fall is related to reduction in soil-moisture indicating the onset of the dry season (Rutherford & Panagos 1982, van Rooyen *et al.* 1986b), and this may vary from year to year (Murphy & Lugo 1986). Menaut & Cesar (1979) suggest the same, noting that leaf fall is generally synchronous between different species in a given year, but the exact timing differs between years. At low rainfall regimes, available soil-moisture is greater in sands than clays during the limiting periods, i.e. at the start and cessation of the rainy season. This was not reflected in the data with respect to the onset and magnitude of leaf emergence or senescence. Bottomlands are also cooler due to catabatic flow during the night. It could be hypothesised that these temperature differences could also play a role in delaying leaf emergence and

hastening leaf fall at the start and end of the growing period respectively, as dictated by sufficient plant available moisture. This cannot be tested from the data at hand.

WOODY PLANT PRODUCTIVITY:
SEEDLING RECRUITMENT AND SURVIVAL

8.1 INTRODUCTION

With the high mortality rates of mature trees measured during this study (Sect. 3.4.6) woody plant basal area was declining in many plots, resulting in a net negative basal area increment for the stand. It was therefore likely that recruitment of new individuals is a key process in the maintenance of woodland structure and productivity.

Several studies have reported the importance of recruitment in the maintenance of woody community dynamics (Cleminson 1993, Jeltsch *et al.* 1996). Much work has been done at the species level, within the framework of species population dynamics studies, rather than approaching recruitment as an ecosystem process. Its role in other ecosystem processes such as succession, competition, bush-encroachment and productivity has been highlighted by a few key studies (e.g. Smith & Goodman 1987, Archer *et al.* 1988, Grundy *et al.* 1994). The contribution of seedling recruitment to increment in stand basal area is negligible by virtue of the small size of seedlings. But their relative growth rates are high. Initially, roots grow considerably faster than shoots.

Recruitment may be vegetative, via addition of more stems to an established plant, or sexual, through seed set, dispersal, germination and establishment. The fact that a large proportion of savanna trees are multi-stemmed attests to the importance of vegetative growth as a form of reproduction, and hence productivity. Seedling establishment is variable, requiring suitable conditions for seed production, seed survival and germination and establishment. Chidumayo (1993) found that seedling establishment accounted for approximately 65 % of regrowth in cleared savannas, and coppice growth constituted the rest. Scholes (1990b) found largely the opposite in a cleared mopane site.

8.2 OBJECTIVES

To determine: (1) the recruitment rate of new plants, i.e. seedlings across a range of sites, (2) the survival rate of established new individuals across a range of sites, and (3) the influence of site macro-climate and environment on recruitment and survival.

8.3 METHODS

In winter 1994 92 permanent quadrats were established at 23 of the 51 productivity plots (Chap. 3). At each locality four quadrats (2.5 m x 2.5 m) were distributed throughout the larger productivity plot. The positions of all stems less than 40 cm tall were mapped. Each quadrat was resurveyed in August 1995 and again in August 1996. Six quadrats could not be resurveyed in 1995 because of fire or some other major disturbance, and another was discarded in 1996. The height of seedlings was recorded in 1995 and 1996. Differences in seedling densities between the three years were assessed using the Wilcoxon Signed Rank Test. Associations between mean recruitment density and 17 site variables were explored through correlation analysis and stepwise linear regression.

8.4 RESULTS

Although there was an overall significant increase in the density of seedlings from 1994 to 1995 ($p<0.0001$), and again from 1995 to 1996, this was concentrated in a few quadrats, with the majority having no recruitment (Table 8.1). Similarly, what little mortality occurred (1994/5 - 1.9 %; 1995/6 - 12.7 %) was restricted to a minority of quadrats. The variance to mean ratio for recruitment was 1.5 - 2.3 and for mortality was 2.1 - 4.7.

Recruitment (density per quadrat) in 1994/95 was positively related to rainfall in the preceding season (1993/94) ($r^2 = 0.25$; $p<0.05$), rainfall in same season (1994/95) ($r^2 = 0.26$; $p<0.05$) and the total of the rainfall for both seasons ($r^2 = 0.35$; $p<0.005$). The higher the rainfall during the season, the greater the density of new seedlings (Fig 8.1). Survival was 100 % except at three localities and therefore appeared to be relatively independent of site and dynamic variables.

During the second year (1995/96) recruitment and survival were reduced. Recruitment was not correlated with any of the variables tested. On the other hand, survival, was positively correlated with the percentage sand at the site (r^2 =0.18; $p<0.05$). Additionally, survival and growth rate (increment in height) were strongly correlated with seedling height (Fig 8.2).

Table 8.1. Survival, mortality and recruitment of seedlings in permanent quadrats (2.5 m x 2.5 m) at 22 localities throughout the South African savanna biome. (Note: % frequency sums to > 100 % as some quadrats had both mortality and recruitment).

ATTRIBUTE	1994/95	1995/96
Survival	98.1 %	87.3 %
Mortality	1.9 %	12.7 %
Recruitment frequency (% of quads)	38.4 %	21.2 %
Mortality frequency (% of quads)	3.5 %	18.8 %
Quadrats without any recruitment or mortality (%)	59.3 %	65.9 %
Mean seedling density per quadrat	1994 - 1.85 1995 - 2.38 1996 - 2.45	
Mean recruitment per quadrat per year	0.64 plants	0.45 plants

8.5 DISCUSSION

Recruitment and mortality were both highly clumped phenomena, occurring only in the minority of quadrats. The short duration of the study precludes determination of whether this is primarily a result of extreme spatial variation resulting from the sampling design, temporal variation resulting from the need for certain triggers before recruitment occurs (e.g. sufficient rainfall), or both. The significant relationship with rainfall during the first year suggests temporal variation is an important factor, as indicted in other studies in savannas (O'Connor 1995) and other vegetation types (van Rooyen *et al.* 1984, Khan *et al.* 1986, de

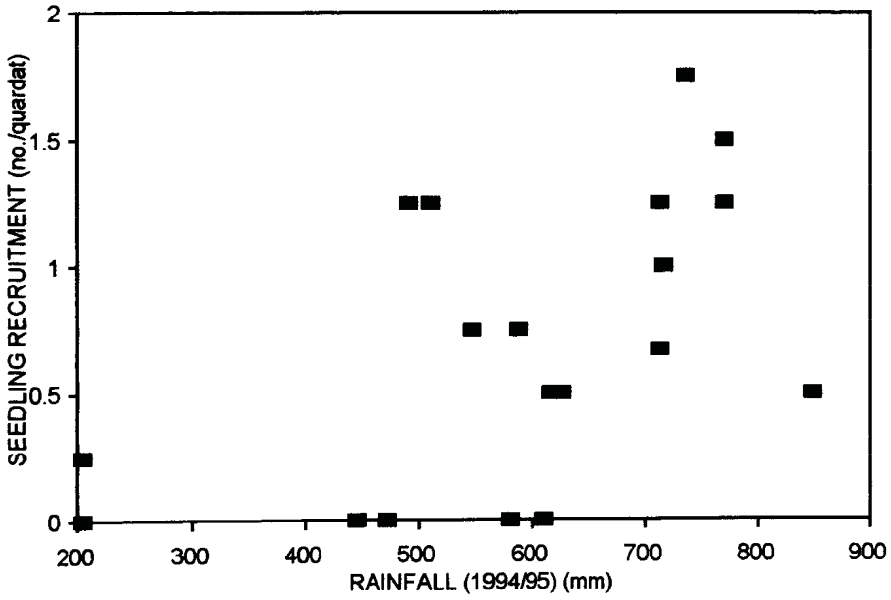


Figure 8.1. Seedling recruitment and rainfall (1994/95).

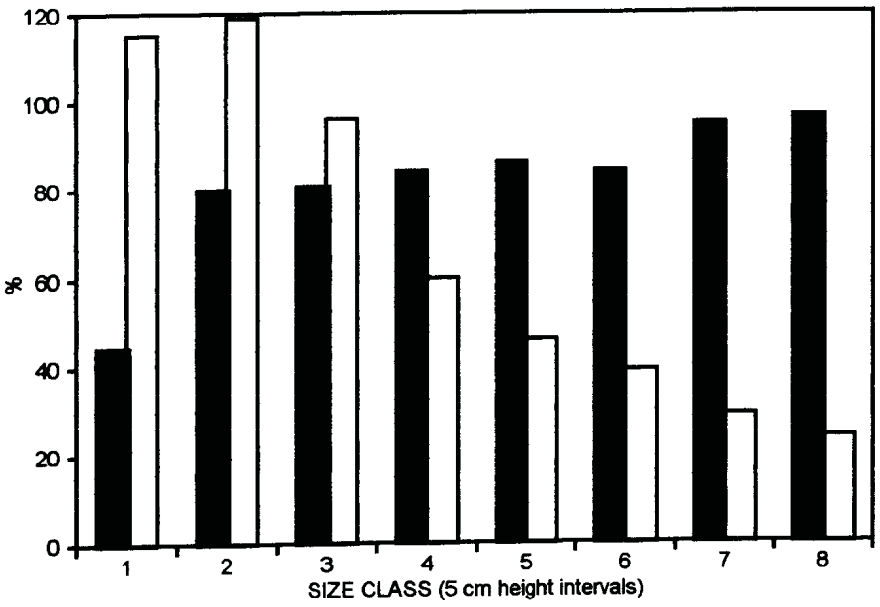


Figure 8.2. Seedling survival (■) and relative growth rate (□) relative to height size class.

Steven 1994, Johnson *et al.* 1994), although microsite characteristics may often override macroclimatic requirements (Midgley 1988, Borchert *et al.* 1989). If seasonal rainfall is truly a significant factor in savannas, it can be hypothesized that recruitment will be a less predictable occurrence with increasing aridity (e.g. Borchert *et al.* 1989). If the mortality rate of mature trees is the same in arid and moist savannas, then the lower density of plants common in arid environments may not simply be a reflection of increased competition for limited resources, but also of an inadequate frequency of conditions satisfactory for recruitment. Midgley (1988) argued that environmental factors were more important than competition in leading to mortality of fynbos Proteaceae.

The overall mean density of approximately 3 000 seedlings per hectare is almost four times greater than the maximum reported by Henderson (1979) (in Scholes & Walker 1983) at Nylsvley Nature Reserve, approximately ten times greater than densities recorded by Agnew & Waterman (1989) in an arid savanna in Kenya, and double that recorded by Hayashi (1992) for a mesic savanna in Kenya. This difference may be a result of differing definitions of what was considered a seedling and what was not. Similarly, differing definitions may be responsible for different estimates of seedling survival. This study followed the definition proposed by Johnson *et al.* (1994) that recruitment is the number of individuals that survive their first year of growth (summer and winter)(except the initial cohort marked in 1994 which could include individuals that although short, were probably greater than one year old). Relative to the 1.9 % mortality recorded in this study in 1994/95 and 12.7 % in 1995/96, Henderson (1979) (in Scholes & Walker 1983) reported an annual mortality of over 65 % for both *Terminalia sericea* and *Burkea africana* seedlings. Chidumayo (1992) recorded annual mortality rates of 22 % and 54 % for *Brachystegia spiciformis* and *Julbernardia paniculata*, respectively, but mortality of *Afzelia quanzensis* was only 12 % in the first year (Chidumayo 1992). Hart (1995), who monitored marked seedlings of two forest species for a 10 year period, recorded mortality rates of 51 - 86 % over that period. The low mortality recorded in this study may also relate to the timing of the survey. Being at the end of winter, only those stems that had become established during the rainy season and survived the onset of winter would have been marked in this study. Marking seedlings immediately after emergence, and before secure establishment, would result in a higher estimate of mortality rates (e.g. Chidumayo 1992, O'Connor 1995). O'Connor showed that mortality of *Acacia karroo* seedlings during their first growing season ranged from 35 % to > 90 % depending upon treatment, whilst mortality during the first winter period was only 15 %. The probability of survival during the first winter was strongly related to seedling size at the start of winter. This study also indicated that seedling survival is positively related to seedling size, as did Parker (1982).

Recruitment and survival during 1995/96 were less than in 1994/95. Nevertheless, in absolute numbers, recruitment was still greater than mortality, leading to a net increase in the density of seedlings. This was unanticipated, since all but one site experienced better rainfall during 1995/96 than 1994/95. Intersite comparison across a range of rainfalls demonstrates that recruitment is strongly correlated with rainfall, but intrasite dynamics (differences between seasons at the same site) do not conform to the same model. On the basis of this it is hypothesised that intrasite recruitment will be optimal during seasons of intermediate rainfall. The underlying reasoning being that good seasons of well above average rainfall do provide conditions suitable for recruitment, but these conditions are also conducive to improved herbaceous cover and growth. This leads to increased competition with newly germinated seedlings, as well as seedlings from previous seasons established in sub-optimal microsites (e.g. Brown & Archer 1989, McPherson 1993). Following this reasoning, it is possible to predict that during seasons of excessive rainfall, recruitment will be decreased, and mortality of seedlings from previous years will be increased. During years of good, but not high, rainfall a more equal competitive interaction will prevail between new and established seedlings and the herbaceous layer. This hypothesis requires testing across a range of species as seedling dynamics can be markedly species specific. For example *Acacia karroo* seedling establishment is relatively independent of grass competition (O' Connor 1995), whereas other species, including some *Acacias*, have been shown to be sensitive to such competition (Brown & Booysen 1967, Bush & van Auken 1990, Adams *et al.* 1992). A similar hypothesis was considered by Jeltsch *et al.* (1996) attempting to model the tree dynamics in an arid savanna. In cycles of good rainfall years, tree seedling establishment pulsed in the first good year only, and declined in subsequent consecutive good years due to competition from a vigorous herbaceous layer (Jeltsch *et al.* 1996).

Despite the absence of recruitment in most of the monitoring quadrats, there was a net increase of over 1 000 seedlings per hectare in the first year, and 110 in the second. Set against a mean loss of 64 ($\pm$ 15) mature individuals per hectare for the same period for the same plots (Sect. 3.4.6), recruitment is more than adequate. However, as recruitment is a highly episodic event (van Rooyen *et al.* 1984), then such excesses of recruitment over mortality are to be expected in the years that recruitment actually occurs. At the opposite extreme, Scholes (1990b) recorded recruitment of only four plants per hectare in bush-cleared areas of the Northern Province lowveld. Several studies in tropical forests have indicated that over short monitoring periods of only a few years, mortality is usually greater than recruitment (Felfili 1995). This also indicates that recruitment is largely an episodic event. Such overall dynamism with respect to seedling recruitment and mortality could well be the underlying basis for the patchy and dynamic nature of mature

woodlands, with shifting densities and species compositions (Lubke & Thatcher 1983). A stage structured model of coastal savanna dynamics in harvested areas indicated that seedling recruitment and mortality were the most important parameters in determining the outcome of the model (Cleminson 1993).

BIOMASS RELATIONSHIPS AND GROWTH RATIOS OF DOMINANT SPECIES

9.1 INTRODUCTION

In most instances in African savannas tree size does not equate to tree age (Kirkpatrick 1984). Irrespective, tree size itself is an important determinant of many attributes of savanna productivity and ecology. Relative productivity per tree declines with increasing tree size, as does the proportion of leaf production to wood production and stem mortality. Fruit production increases with tree size. So too does the overall impact of a given tree on its neighbouring environment with respect to extraction of water and nutrients, localised enrichment of sub-canopy habitat, and competition. Tree response to many potentially damaging factors, such as fire, browsing and chopping is also size-dependent (Pellew 1983).

Given the importance of size, especially through its influence on woody productivity, it is necessary that gross morphometric relationships for dominant species at specific sites are adequately explored. Few data exist for the Transvaal lowveld other than that of Scholes (1987) and Dayton (1978). Goodman (1990) provided substantial data from KwaZulu-Natal, and Rutherford (1979) for the Savanna Biome Study site at Nylsvley. In the absence of local data the relationships from Rutherford were used in other sections of this thesis. Recently Smit (1994) has provided extensive data and relationships pertaining to the production of the browse component, summarised into an accessible, management orientated model.

9.2 OBJECTIVES

This study sought to synthesise current knowledge of the biomass relationships of southern African woody plants, whilst at the same time providing locally based allometric relationships to underpin the extensive work on woody plant growth and management being undertaken in this study and others within the Transvaal lowveld.

9.3 METHODS

During February to April 1995, fifteen to eighteen stems of each of the dominant species at the arid (*Ormocarpum trichocarpum*), semi-arid site (*Acacia gerrardii*, *A. swazica*, *Combretum collinum*, *Dichrostachys cinerea*, *Terminalia sericea*), and moist site (*Faurea saligna*, *Pterocarpus angolensis*, *Parinari curatellifolia*) were selected. Dominant species in the area for which allometric relationships were already available were not included in this study (*Acacia nigrescens*, *Combretum apiculatum*, *Grewia bicolor*, *Sclerocarya birrea*). The basal circumference and crown diameter (long axis and short axis) were measured. Each tree was felled with a hand-saw as close to the ground as possible. Once felled, the height of the canopy base, total height, and height of the remaining stump were recorded. The fresh mass was determined in the field for the whole stem, leaves only, twigs (current season's growth), and wood. The leaves and twigs were stripped by hand. Subsamples of each component were oven-dried at 85^0 C for seven days to allow correction to dry mass. All masses reported are dry mass unless stated otherwise.

The mass data were $\log_{10}$ transformed. A range of models were tested as the best predictors of log(tree mass), including stem diameter, stem diameter^2, log (stem diameter), stem area, stem circumference, stem circumference^2, log(stem circumference), canopy area and tree height. Diameter and circumference provided equivalent relationships, and both provided consistently better models than tree height, canopy area or stem area. Given that stem circumference is easily measurable with a high degree of precision and does not require conversion for analysis, it, rather than stem diameter, was used as the independent variable. Given the log transformation of mass, a double log relationship consistently provided higher r^2 values than a single log relationship, except for *P. curatellifolia*. Analysis of residuals was used to detect significant outliers. After transformation no outliers were evident.

Leaf mass reflects a minimum estimate of annual leaf production when collected at the peak of the growing season. Wood mass is simply an estimate of standing crop because of the carryover from previous growing seasons. Wood production was determined from a combination of mean rate of change in basal area per stem size per species from the biome plot data (Chap. 3), and the allometric equations determined above. The ratio of annual wood to leaf production was then determined across a range of stem sizes for each species. This is not the best approach to derive such ratios because the leaf production and wood production were determined from separate trees, but it provides a useful foundation for interpretation of trends and patterns.

The term microphyll is used applied loosely to the four of the nine species that are fine leaved (*A. gerrardii*, *A. swazica*, *D. cinerea* and *O. trichocarpum*) relative to the remaining five species.

9.4 RESULTS

9.4.1 Total mass

Total mass (log transformed) was strongly related to stem circumference for all species ($p<0.0001$) (Table 9.1).

Table 9.1. Regression relationship per species between log(Dry mass) and stem circumference (cm).

SPECIES	log(DRY MASS) (kg)	r^2	log(FRESH MASS) (kg)	r^2
A. gerrardii	= 2.633 (log(circ)) - 2.580	0.99	= 2.628 (log(circ)) - 2.348	0.97
A. swazica	= 2.441 (log(circ)) - 2.423	0.94	= 2.396 (log(circ)) - 2.146	0.94
C. collinum	= 2.365 (log(circ)) - 2.319	0.98	= 2.362 (log(circ)) - 2.084	0.98
D. cinerea	= 2.521 (log(circ)) - 2.460	0.96	= 2.521 (log(circ)) - 2.243	0.96
F. saligna	= 2.606 (log(circ)) - 2.908	0.96	= 2.558 (log(circ)) - 2.550	0.97
O.trichocarpum	= 2.104 (log(circ)) - 2.116	0.95	= 2.157 (log(circ)) - 1.979	0.96
P. curatellifolia	= 0.033 (circ) - 0.360	0.95	= 0.033 (circ) - 0.004	0.95
P. angolensis	= 2.446 (log(circ)) - 2.545	0.97	= 2.414 (log(circ)) - 2.192	0.97
T. sericea	= 2.585 (log(circ)) - 2.612	0.98	= 2.608 (log(circ)) - 2.414	0.99

The moisture content differed between leaves, twigs and wood, but was reasonably consistent between species (Table 9.2).

Table 9.2. Dry mass as a percentage of fresh mass (mean ± SE).

SPECIES	N	WOOD	TWIGS	LEAVES
A. gerrardii	15	60.6 ± 0.5	57.2 ± 1.9	48.0 ± 1.5
A. swazica	15	61.6 ± 0.8	51.5 ± 2.1	45.9 ± 0.6
C. collinum	16	62.7 ± 1.4	46.5 ± 1.2	44.8 ± 1.4
D. cinerea	15	63.1 ± 0.6	56.5 ± 2.0	51.2 ± 1.6
F. saligna	16	54.1 ± 0.9	38.4 ± 0.8	38.3 ± 0.9
O. trichocarpum	18	66.0 ± 0.7	62.0 ± 3.2	45.5 ± 1.1
P. curatellifolia	15	42.9 ± 0.8	38.7 ± 1.4	42.0 ± 1.1
P. angolensis	16	51.0 ± 0.9	45.9 ± 1.6	42.3 ± 0.7
T. sericea	16	64.3 ± 1.0	40.1 ± 2.6	47.4 ± 1.9
Mean		58.5	48.5	45.0

9.4.2 Dry mass of wood

The total dry mass of wood was also strongly related to stem circumference, as was the mass of the stem, and mass of branches alone (Table 9.3).

The contribution of stem wood (below the first branch) to the total mass of wood varied significantly between species, from 18 % to 46 %, and was positively correlated with the maximum potential height per species using the function

$$sq\ root\ (\%\ of\ total\ wood\ in\ stem) = 0.0026(max.pot.\ height) + 4.048$$

(r^2 =0.48; n=9; $p < 0.05$). The percentage of the total dry mass contributed by wood increased with increasing stem size (all species pooled: r^2=0.11; $p<0.0001$; n=142).

Table 9.3. Regression relationships between wood mass (kg) components and stem circumference (cm).

SPECIES & MAX. POTENTIAL HT	log (DRY MASS) (kg)	r^2
A. gerrardii	Total wood = 2.692 (log(circ.)) - 2.699	0.99
(4.3 m)	Stem = 2.330 (log(circ.)) - 2.885	0.91
	Branch = 2.834 (log(circ.)) - 3.018	0.98
A. swazica	Total wood = 2.647(log(circ.)) - 2.703	0.94
(3.6 m)	Stem = 2.457 (log(circ.)) - 3.180	0.73
	Branch = 2.726 (log(circ.)) - 2.940	0.84
C. collinum	Total wood = 2.387 (log(circ.)) - 2.404	0.97
(8.1 m)	Stem = 2.052 (log(circ.)) - 2.481	0.86
	Branch = 2.582 (log(circ.)) - 2.883	0.94
D. cinerea	Total wood = 2.559 (log(circ.)) - 2.571	0.96
(3.1 m)	Stem = 2.363 (log(circ.)) - 3.205	0.73
	Branch = 2.641 (log(circ.)) - 2.756	0.95
F. saligna	Total wood = 2.701 (log(circ.)) - 3.102	0.96
(8.5 m)	Stem = 2.391 (log(circ.)) - 2.903	0.95
	Branch = 3.119 (log(circ.)) - 4.132	0.91
O. trichocarpum	Total wood = 2.119 (log(circ.)) - 2.151	0.95
(2.5 m)	Stem = 2.896 (log(circ.)) - 3.763	0.89
	Branch = 1.915 (log(circ.)) - 2.054	0.88
P. curatellifolia	Total wood = 2.665 (log(circ.)) - 3.092	0.92
(6.4 m)	Stem = 2.602 (log(circ.)) - 3.411	0.96
	Branch = 0.040(circ.) - 1.003	0.89
P. angolensis	Total wood = 2.443 (log(circ.)) - 2.575	0.96
(10.2 m)	Stem = 2.157(log(circ.)) - 2.482	0.92
	Branch = 0.027(circ.) - 0.271	0.92
T. sericea	Total wood = 2.687 log((circ.)) - 2.827	0.98
(8.4 m)	Stem = 2.590 (log(circ.)) - 3.391	0.81
	Branch = 2.762 (log(circ.)) - 3.054	0.97

9.4.3 Mass of twigs & leaves

The dry mass of leaves and twigs was also related to stem circumference, although the relationships were generally weaker than those for wood components (Table 9.4).

Table 9.4. Regression relationships between mass of leaves, mass of twigs and stem circumference.

SPECIES	log (DRY MASS) (kg)	r^2
A. gerrardii	Leaves = 2.075 (log((circ.)) - 2.983	0.95
	Twigs = 1.130 (log(circ.)) - 3.111	0.38
A. swazica	Leaves = 1.747 (log(circ.)) - 2.753	0.85
	Twigs = 0.440 (log(circ.)) - 2.486	0.17 n.s.
C. collinum	Leaves = 2.224 (log(circ.)) - 3.137	0.96
	Twigs = 2.155 (log(circ.)) - 4.096	0.96
D. cinerea	Leaves = 2.257 (log(circ.)) - 3.043	0.94
	Twigs = 2.014 (log(circ.)) - 4.004	0.87
F. saligna	Leaves = 1.834 (log(circ.)) - 2.900	0.89
	Twigs = 1.401(log(circ.)) - 2.971	0.70
O. trichocarpum	Leaves = 1.855 (log(circ.)) - 3.280	0.89
	Twigs = 1.093 (log(circ.)) - 3.625	0.39
P. curatellifolia	Leaves = 2.102 (log(circ.)) - 3.433	0.90
	Twigs = 2.083 (log(circ.)) - 4.160	0.90
P. angolensis	Leaves = 2.637 (log(circ.)) - 4.069	0.96
	Twigs = 2.674 (log(circ.)) - 5.151	0.93
T. sericea	Leaves = 2.022 (log(circ.)) 2.716	0.98
	Twigs = 1.594 (log(circ.)) - 3.313	0.82

There was a significantly greater ratio of leaf to twig mass for microphyllous than mesophyllous species ($F=25.5$; d.f=141; $p<0.0001$) (Fig 9.1).

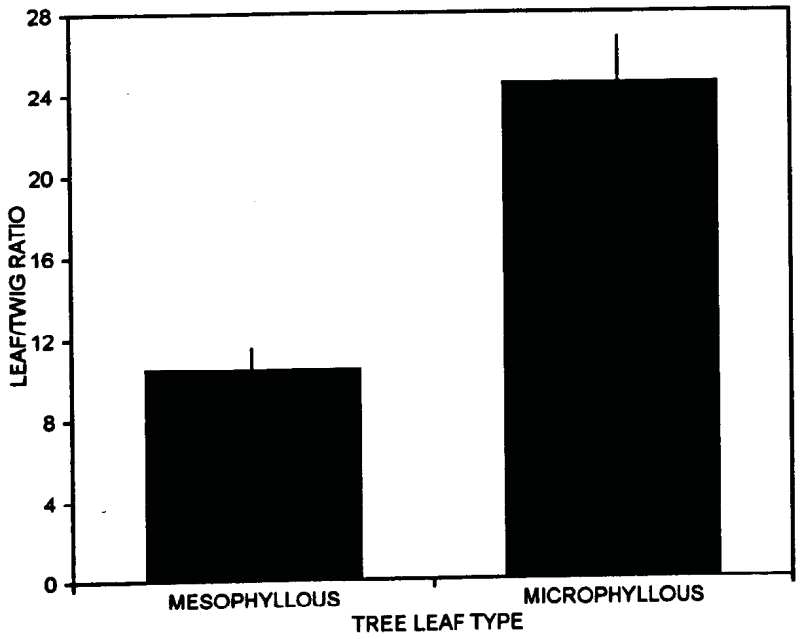


Figure 9.1 Leaf mass:twig mass ratio of mesophyllous and microphyllous species.

9.4.4 Ratio of wood to leaf production

Mean annual increment in basal area was negatively related to stem circumference for each species (Table 9.5). The magnitude of the intercept, which may be regarded as reflecting the inherent growth rate per species exhibited in the seedling stage prior to the effect of limiting factors (Bryant *et al.* 1991), did not differ between microphyllous and mesophyllous species, nor was there a trend relative to potential maximum height per species.

Using the equations in Tables 3, 4 and 5, general ratios of annual wood to leaf production were calculated (Table 9.6). A greater proportion of annual production is assigned to leaves for most species. The ratio declines with increasing stem size, except for *A. swazica*, where it increases. Wood production is greater than leaf production in the largest size classes only. The mean ratio is significantly higher for mesophyllous species than microphyllous species ($t=3.15$; $n=9$; $p<0.05$). It is also increases significantly ($r^2 = 0.53$; $n=9$; $p< 0.05$) with increasing maximum potential height per species:

$$log(wood{:}leaf\ production\ (20\ cm\ circ.)) = 0.00086(max.\ pot.\ ht)-0.32$$

Table 9.5. Regressions of mean relative change in basal area per stem circumference.

SPECIES	RELATIONSHIP (c=circum. (cm))
A. gerrardii	log(% BA change +1) = -0.0085c + 0.776
A. swazica	log(% BA change +1) = -0.7980c + 2.104
C. collinum	log(% BA change +1) = -0.0102c + 0.884
D. cinerea	log(% BA change +1) = -0.0132c + 0.998
F. saligna	log(% BA change +1) = -0.0113c + 0.992
O. trichocarpum	% BA change = -0.2450c + 7.960
P. curatellifolia	log(% BA change +1) = -0.0087c + 0.721
P. angolensis	log(% BA change +1) = -0.0062c + 1.085
T. sericea	log(% BA change +1) = -0.0132c + 1.170

Table 9.6. Leaf production as a proportion (%) of total aboveground production (leaf + wood) per stem.

SPECIES	STEM CIRCUMFERENCE (cm)				
	10	20	30	40	50
A. gerrardii	81	66	55	47	38
A. swazica	33	44	67	-	-
C. collinum	87	79	75	72	71
D. cinerea	64	38	33	29	25
F. saligna	85	75	68	63	60
O. trichocarpum	50	33	30	-	-
P. curatellifolia	87	77	69	63	57
P. angolensis	71	58	50	45	44
T. sericea	83	72	66	60	58
MEAN	71	60	57	54	50

9.5 DISCUSSION

Whilst time-consuming work, determination of biomass relationships with any of a series of morphometric variables usually yields highly significant results, especially after transformation of one or both sides of the equation. The most commonly used independent variable from a variety of vegetation types is stem diameter or stem circumference (Dayton 1978, Guy 1981, Brown *et al.* 1989, Scholes 1987, Scholes 1990b, Singh & Yadava 1991, Tietema 1993). Inclusion of tree height sometimes improves the relationship (Chidumayo 1988, Schacht *et al.* 1988, Brown *et al.* 1989), although not always (Brown *et al.* 1989). It is also a covariate with stem diameter. Crown diameter, area or volume have also been used as the predictor variable by some authors (Kelly & Walker 1977, Coughenour *et al.* 1990, Deshmukh 1992), but as with this study, generally yield weaker regression relationships than stem circumference (Coughenour *et al.* 1990), and become very variable in dense vegetation where crown size is constrained (Tietema 1993).

The significantly higher proportion of annual production assigned to leaves is at odds with the recent conclusion of Gandar (1994b) that wood production in savannas is generally three times greater than leaf production. The data presented by Gandar (1994b) are characterised by very low shoot masses, whilst wood mass and production are reasonably similar to this study. The proportions calculated here are of the same order of magnitude as those from the litterfall study (Chap. 11). Scholes & Walker (1993) report that leaf production is approximately 80 % greater than wood production. Menaut & Cesar (1982) provide data for a range of West African savannas also indicating higher leaf production, with ratios ranging from 3.6 to 7.3. Chidumayo found higher leaf than wood production in arid and mesic miombo (Chidumayo 1990, 1991). Singh & Yadava (1991) found a relatively equal division between leaf and wood production in a moist oak forest in India.

The microphyllous species were characterised by a higher leaf to wood production ratio, as well as a greater leaf to twig than the mesophyllous species. Both suggest reduced masses of leaves in microphyllous species. Thus, not only is leaf size reduced, so to is the absolute amount of leaves, in favour of twigs and wood. Thus, overall leaf area index will be low. This may lead to reduced growth, but this is likely to be compensated for by the higher leaf nitrogen.

Mean potential plant height appeared to be an acceptable index of the ratio of wood to leaf production and the proportion of total wood mass found in the stem. The greater the potential plant height, the greater the