that a positive relationship could be found, covariant with the relationship with MAR. Murphy & Lugo (1986) concluded that primary productivity of dry forests correlated well with rainfall, but other variables, including soil type, weaken the strength of the precipitation relationship.

Interpretation of the list of the significant variables suggests that growth at clayey sites is largely determined by the amount of woody vegetation present. Thereafter, the relative basal area increment on clays is a response to current season's rainfall. In contrast, absolute and relative growth rates on sands appear to be determined by moisture levels, including an element of the previous season's rainfall. Whigham *et al.* (1990) found a better correlation between annual basal area increment in Mexican dry forest and the sum of precipitation of the current and previous season, rather than either alone. Over the three year period of the study, moisture status was not a significant variable for sandy or clay sites as a subset of the larger data set, and differences between the two subsets disappeared, with only plot basal area being significant. This indicates that growth analysis should be pursued at a seasonal time-scale if the relationship with potential driving determinants is to be explored.

These data tend to refute the conclusion of Rutherford (1984) that production by the woody component is unrelated to rainfall except during a drought. The repeated identification of moisture related variables as the strongest, with the highest significance values, emphasizes the value of moisture availability in determining woody productivity. A linear relationship between MAR and mean absolute basal area increment (Fig 3.7) (*mean absolute growth = 0.00045(MAR) + 0.052*; $r^2 = 0.14$; $p < 0.05$; $n = 51$), and a curvilinear relationship between MAR and relative basal area increment (Fig 3.8) indicates that maximal productivity occurs at intermediate MAR, from 600 - 670 mm p.a..

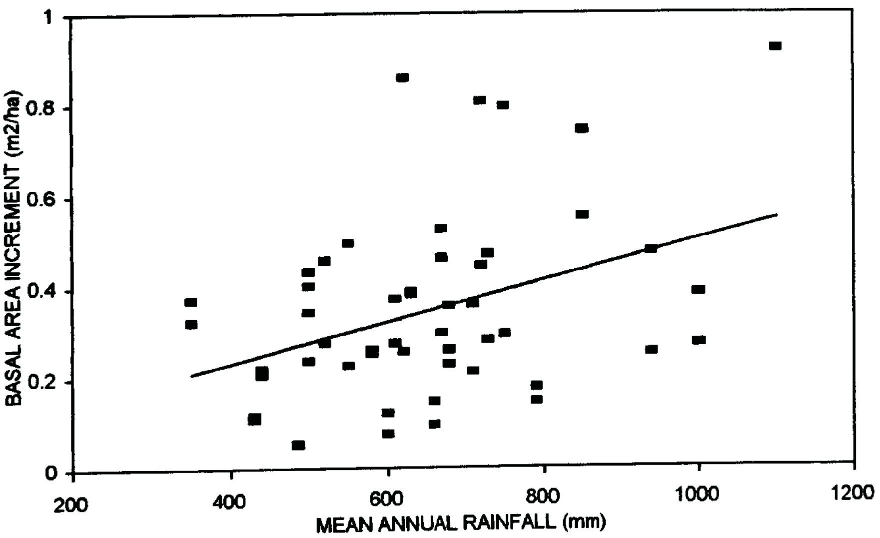

Figure 3.7. Mean absolute change in basal area relative to mean annual rainfall (51 sites).

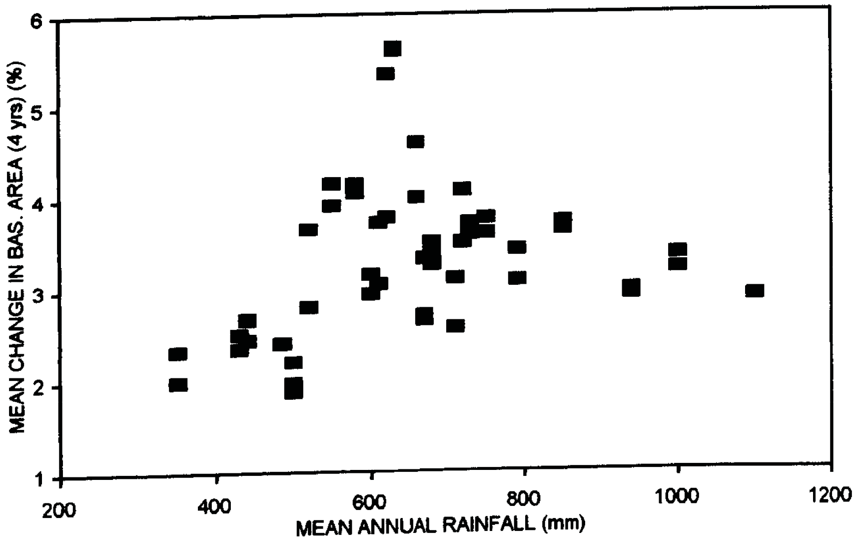

Fig 3.8. Mean relative change in basal area relative to mean annual rainfall (51 sites).

It must be noted that MAR is only a rough index of, and is not equivalent to, plant available water. The tapering of the slope at high rainfall occurs at approximately 3 % relative basal area increment. At the opposite rainfall extremes, the curvilinear relationship flattens out at 2.0 - 2.4 % annual basal area increment. This differential in basal area increment between high and low rainfalls suggests that growth at high rainfall is limited by a factor different to that which limits growth at low rainfall. It is hypothesised that limited moisture is the key factor at low MAR, and either limited nutrients (because of leaching) and/or competition (because of higher basal areas) is responsible for reduced relative growth at high MAR. It is noteworthy however, that this range of MAR is also that at which least mortality was recorded. The growth data have been corrected for mortality. Therefore, the combination of higher growth of surviving stems as well as lower mortality at intermediate MAR leads to greatest relative productivity. Murphy & Lugo (1986) commented that dry forest biomass was greatest at moist sites and diminished at dry and wet sites. Scholes (1990b) found a linear relationship between absolute basal area increment of *Colophospermum mopane* and rainfall during the same growing season ($y = 0.0012x$ rainfall - 0.08) at a single site. Taking the site with the longest monitoring records for this study (5 years; 3 plots at Wits Rural Facility) a linear relationship was also evident between seasonal rainfall and both the mean (n=3) absolute and relative basal area increment (Figure 3.9):

Absolute basal area increment (m^2/ha) = *0.000754 (rainfall)* (mm) - *0.253* ($r^2 = 0.94$; $p < 0.005$; $n = 5$)

Relative basal area increment (%) = *0.011 (rainfall)* (mm) - *3.206* ($r^2 = 0.93$; $p < 0.005$; $n = 5$)

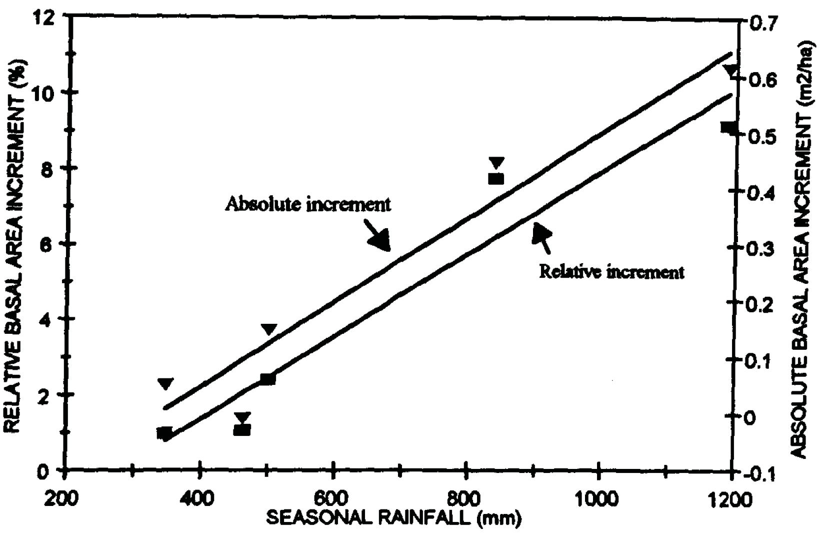

Figure 3.9. Relationship between rainfall and mean basal area increment (3 plots) at Wits Rural Facility (1991- 1996).

Competition has been mooted as a primary determinant of structure and productivity of the woody stratum (Smith & Walker 1983, Scholes 1990a, Scholes & Walker 1993). The competition index derived through nearest-neighbour analysis (Chap. 6) at each site was not identified as a significant variable. However, indices of vegetation abundance were; the strongest being basal area. There was a significant relationship between stand basal area and absolute basal area increment over the three year period (*basal area increment* = *0.103* $\sqrt{\textit{basal area}}$ + *0.0036*; $r^2 = 0.36$; $p < 0.00001$; $n = 51$) (Fig 3.10). The site with the highest basal area had strong leverage on the regression, although it was not a significant outlier. A significant relationship remained, even if that point was omitted (*basal area increment* = *0.095* $\sqrt{\textit{basal area}}$ + *0.036*; $r^2 = 0.24$; $p < 0.0005$; $n = 50$). There was also curvilinear relationship between relative basal area increment and stand basal area (Fig 3.11). From this it appears that competition becomes a factor at relatively low vegetation abundance, above 5 m^2/ha. Thereafter, increasing basal area leads to lower relative growth rates. Whilst the relative growth rate relationship was not statistically significant for either clays or sands alone, the decline in relative growth rate with increasing basal area was more rapid for sands than clays, but the intercept was greater. This implies greater growth rates on sands than clays at low basal areas (< ± 10 m^2/ha), and the reverse at high basal areas (> ± 22 m^2/ha), bearing in mind the covariance with rainfall. Chidumayo (1987) reported a linear relationship between stand basal area and aridity ratio (MAR/evapotranspiration) in Zambia.

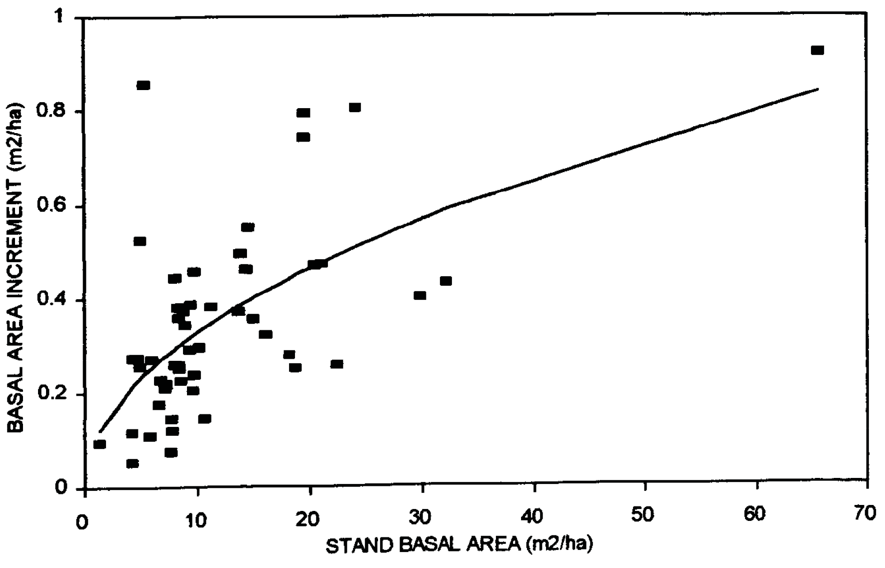

Figure 3.10. Mean absolute change in basal area (4 years) relative to stand basal area.

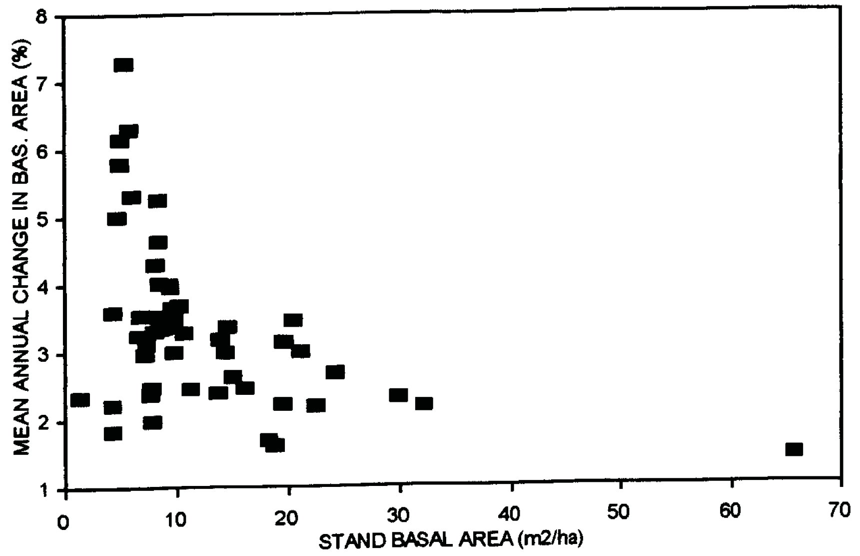

Figure 3.11. Mean relative change in basal area (4 years) relative to stand basal area.

The dependency of annual growth on certain site conditions confounds comparison of growth rates with other studies reported previously, since recorded rates are dependent on the MAR, basal area and soil type prevailing at each site. It will be some time before sufficient data points become available from an adequate range of sites factoring in these three site conditions, not to mention mean size-class distribution of the vegetation. Indeed, Childes (1984) went so far as to state that the high variability between even individual trees made a mockery of average growth rates as each stem had its own genetic potential and very specific microsite.

3.5.2 Mortality

In the absence of severe environmental stresses, such as drought or fire, the annual mortality rate was higher than anticipated. However, the (1) relative consistency of a value of greater than 3 % of stems and (2) the occurrence of some mortality in almost all plots on all sampling dates lends credibility to the high rate. It is to be expected that periods of stress will lead to a pulse of significantly higher mortality rates (eg fire effect, see Chap. 18).

There is little work in savannas against which to compare these data. Scholes (1985) measured mortality in three plots in an arid savanna following a drought. He measured negligible mortality in two of the plots and 4.5 % in the last. However, these data were not time-linked, being derived from a survey of the proportion of dead stems in the environment at a single time point. Lubke & Thatcher (1983) recorded marked increases and decreases in the density of key woody species at Nylsvley Nature Reserve from five repeated samples of marked areas between 1974 and 1982. The net decrease recorded in some instances must be due to pulsed mortality events. Non-fire related decreases of between 1.1 % and 13.1 % were recorded in short periods against an overall trend of increasing density during the eight year period.

A mean annual mortality of 4.4 % of stems recorded in this study provides a half-life of 15 years, indicating an extremely dynamic system. Sheil and May (1996) raised several cautions regarding the interpretation of mortality trends from permanent plots, the primary issue being that the age and size structure of the plot is not constant from year to year. Consequently, changes in mortality may be a reflection of the changing size class profile, but the interpretation is usually related to the originial data set only. Early on in the monitoring of such plots stems with an inherently higher probability of death (e.g. small stems) become eliminated from the permanent plot, thereby resulting in a spurious decrease in mortlity rates in subsequent years. It appears that the concerns of Sheil & May (1996) do not apply in this case because (1) the mortality rate increased across the monitoring period, not decreased as predicted by them, (2) the intervals between successive records were equal, and (3) the intervals were relatively short, namely one year. However, the logical framework of their argument remains, and therefore the half-life determination must be treated with caution the longer the monitoring continues.

In comparison, Condit *et al.* (1995) recorded mean mortality rates of approximately 3 % p.a. in a post-drought period, and 2 % p.a. thereafter in a Panamanian tropical forest. In their study it was demonstrated that mortality rate was highly variable between species and species guilds. This is consistent with other estimates of mean annual stem mortality in tropical forests, ranging from 2 % to 3 % (Lang & Knight 1983, Lieberman *et al.* 1985, Korning & Balslev 1994a, 1994b, Milton *et al.* 1994, Phillips *et al.* 1994, Felfili 1995), and up to 3.5 % in some instances (Felfili 1995). A review by Swaine *et al.* (1987) provided 16 estimates for lowland tropical forests ranging from 1 % to 2.2 %. Most of these studies excluded stems below a specified diameter, in all instances greater than the one that used in this study, therefore leading to lower estimates of mortality. All demonstrated that mortality was highly variable between species.

The absence of any predictor variables for mortality suggests that mortality is not a result of particular levels or extremes of the same variables determining growth. Thus, other factors such as natural senescence, disease and competition may be the key determinants of mortality. However, stress brought about by extremes in macro-climate or biotic factors may predispose stems to an increased likelihood of disease. This would result in pulsed mortality, as recorded in several plots during this study. Such pulsed events are probably significant in moulding structural and dynamic characteristics at individual sites (Murphy & Lugo 1986). The lowest mortality at intermediate MAR is noteworthy even if not statistically significant, and requires further investigation. It suggests that more arid and moist environments are more stressful. The underlying causes of such stress may be limited plant available moisture at arid extremes, and increased competition at moist extremes.

WOODY PLANT PRODUCTIVITY:

EXTENDING THE TIME FRAME USING DENSITOMETRY

4.1 INTRODUCTION

Determination of mean growth rates with an estimate of variability requires a time-series data set. This is usually achieved by one of three means. One is to mark a sample of trees, measure their size, and return at regular intervals to remeasure the size. The time period between successive measurements is an important determinant of the nature and quality of the conclusions that can be drawn. If the interval is greater than one growing season, data automatically reflect a mean rate, and not an annual rate (e.g. Kigomo 1994, Felfili 1995). This weakens any attempt to correlate growth rates (as a mean) against deterministic variables, and thereby extrapolate over longer time periods. This shortfall is addressed if successive sampling periods resonate with the frequency of growth events, usually annually (e.g. Whigham *et al.* 1990, this study). However, this approach requires monitoring for many years to derive acceptable confidence limits around the mean value.

An alternative approach is to determine mean growth rates from trees of known age if the year of establishment is known, either as date of natural recruitment or planting (e.g. Gourlay 1995). This is a relatively easy and quick method, but unfortunately there are insufficient instances where the date of establishment of a given individual is recorded in a relatively natural environment, and hence this method is not widely adopted.

The last approach has been to interpret growth events from anatomical characteristics. The most frequently used has been the enumeration of 'growth rings' to determine the age of a stem, and the width of the ring to determine instantaneous growth rate. It rests on the assumption that a single growth ring is produced every year. This has been widely adopted in temperate biomes, but until recently was found to be inadequate in semi-arid and arid environments. This was because identification of distinct rings was impossible in many species (Lilly 1977, Gourlay 1995). Secondly, growth events, reflected by the presence or absence of rings, are not necessarily related to a given year, but more to the amount and distribution of plant available moisture in a given growing season. Thus, in poor rainfall years, perhaps no ring is formed

(Wyant & Reid 1992). In years where there is a mid-season drought, two rings may be formed. The same may occur if there is a major defoliation event during the growing season (van Daalen *et al.* 1992). Of the 108 South African species surveyed by Lilly (1977) for dendrochronological potential only five were rated as promising, 37 were rated as possibly useful species but with some problems, and 66 were unsuitable. Similarly, of the eleven species investigated by Stahle *et al.* (1996) only one provided good results and another showed promise but required further investigation.

However, recently several researchers have undertaken growth ring analysis in semi-arid areas, and reported strong correlations between the identified rings and mean annual rainfall events for selected species (Prins & van der Jeugd 1992, Wyant & Reid 1992, Gourlay 1995). Of nineteen shrub species examined by Prins and van der Jeugd (1992), sixteen had good "countable" rings.

This study sought to attempt a similar growth ring analysis. However, if view of the difficulty in identifying rings in some species, or indistinct boundaries between rings, an alternative approach was adopted, using a densitometer, as reported by Kanowski (1985) and van Daalan *et al.* (1992).

4.2 OBJECTIVES

The objectives of this study were to: (1) Use densitometry to identify growth rings across a range of species, and (2) To test whether a correlation exists between the width of 'annual' growth rings and rainfall.

4.3 METHODS

In August 1995 3 - 5 stems were cut at each of 39 of the 51 sites around the biome (Chap. 3). Criteria for stem selection included (1) it was one of the dominant species at that site, (2) it should not be too large (to minimise the probably of uninterpretable dead heartwood in the centre), (3) it should have had a positive increment in basal area in each of the previous three years (therefore stems that had experienced shrinkage in one or more of the years were excluded), and (4) it should be reasonably symmetrical without wound scars. In total 171 stems were felled spanning 31 species.

Cut stems were placed in paper bags and air dried for ten weeks. The bags were changed at 2 - 3 weekly intervals. Five stems were discarded due to fungal growth.

In November 1995 a subsample (32 species; 30 sites; no replicate samples) was selected and analysed at the Division of Water, Environment and Forest Technology, CSIR, Pretoria using a gamma-ray densitometer. A radial cross-section was prepared, approximately 1 cm wide and 0.5 cm high. Densitometer readings were recorded from the bark to the pith every 0.5 mm. The gamma rays are emitted from an ammonium source, and narrowed into a 0.1 mm beam. The beam passes through a thin section (< 5 mm) of the sample and is detected by a Geiger counter. After sufficient measuring period, the stem section is advanced on a motorised stage by 0.5 mm, and another reading is taken. The operation of the densitometer and the data capture are computer controlled. The digital density values were portrayed as a simple line graph. Peaks in the line graph indicate a band of denser parenchyma ('terminal parenchyma' or 'boundary parenchyma'), equivalent to the delimitation of the traditional growth ring common in stem cross-sections in temperate species. These delimit the end of a single growth event. It is assumed that the wider the distance between two adjacent peaks, the greater the growth. The number of peaks correspond to the number of growth events, possibly annual rings.

Major peaks were identified on the trace by two people, and generally corresponded to the apex after several successive points indicated an increasing trend. Minor peaks were also indicated by myself, as smaller increments in the trace between major peaks, and usually corresponded to a single point of greater magnitude than the one preceding or succeeding it. The distance between successive minor and major peaks was determined. These were then calibrated, if possible, against the known radial increments of that stem for the previous three years (Chap. 3). The successive relative magnitude of the distance between the first three peaks of the trace had to match the relative magnitude in change in basal area of the stems for the previous three years for a stem to be accepted as a potential viable indicator of previous growth events. Of the original 32 species in the sample 18 were accepted as producing potentially viable traces, and the replicate samples of those species were then analysed.

Those samples where the magnitude of densitometer readings parallelled those of the actual stem measurements (Chap. 3) the width of each ring was correlated with (1) seasonal rainfall for that period, (2) rainfall of the preceding season, and (3) rainfall received in a period of three successive months with the highest total rainfall. These correlations assume that a ring is produced each year. The width of each ring was cross-checked between the replicate samples.

4.4 RESULTS

4.4.1 Species selection

Of the 76 samples analysed with the densitometer, 19 provided a good correlation with the field measurements of radial increment during the preceding three year (Table 4.1). However, the results within species tested with multiple samples were highly variable. Only one species, *Acacia nilotica,* provided a consistent match between the measurements of radial increment in the field and the densitometer analysis for most of the replicate samples.

4.4.2 Ring width in relation to rainfall

Ring width for each of the 19 'successful' traces was correlated with rainfall in the same season, and preceding season. Two produced a significant correlation with the rainfall of the same season, whilst 17 did not. No correlations were found with rainfall in the presumed preceding season.

Table 4.1. Species tested via densitometry analysis.

SPECIES	NO. OF SAMPLES	ACCEPTED	REJECTED
Acacia burkeii	1	0	1
Acacia caffra	4	1	3
Acacia exuvialis	2	0	2
Acacia gerrardii	1	0	1
Acacia grandicornuta	3	0	3
Acacia karroo	2	0	2
Acacia nilotica	10	7	3
Acacia robusta	2	1	1
Acacia tortilis	2	0	2
Bolosanthus speciosa	2	0	2
Burkea africana	1	0	1
Clerodendrum glabrum	2	0	2
Colophospermum mopane	2	0	2
Combretum apiculatum	2	0	2
Combretum collinum	2	1	1
Combretum molle	1	0	1
Combretum zeyheri	2	1	1
Dichrostachys cinerea	2	0	2
Dombeya rountifolia	5	2	3
Englerophytum magalismontanum	3	1	2
Euclea schimperi	3	1	2
Faurea saligna	1	0	1
Faurea speciosa	6	3	3
Heteropyxis natalensis	8	1	7
Parinari curatellifolia	3	1	2
Pterocarpus rotundifolius	1	0	1
Pterocelastrus echinatus	2	1	1
Rhus lancea	2	1	1
Strychnos madagascariensis	2	0	2
Szygium cordatum	2	1	1
Terminalia sericea	2	0	2

4.5 DISCUSSION

From the results it appears that densitometry is not a reliable approach towards growth ring analysis. *Acacia nilotica* was the only one of the 31 species examined for which a reasonable correlation was found between the measured radial increment in the field and that evident on the densitometer trace. Even then, 30 % of the samples examined for this species failed to provide a satisfactory correlation. Based on these results and the process of the densitometer analysis three sources of error can be identified.

(1) The start of the trace was frequently characterised by a short series of points with atypically high or low values (relative to the rest of the trace) (Fig. 4.1). This leads to problems regarding identification of where to start the correlation with the known field values, i.e. which is the first peak? The reason for this problem is not clear. One suggestion is that the atypical values are for the bark and not the stem wood. However, given that bark is usually less dense than the wood of the species from which it is derived, the error should always be a zone of lower density values if the bark had not been stripped. This does not explain the frequent problem of a zone of atypically high values.

(2) The resolution of the densitometer is inappropriate for some species. A good trace is characterised by a series of definable peaks, each well separated from the one preceding or succeeding it. A peak is defined by a series of points of successively increasing values, until some maximum, followed by a series of points with successively decreasing values. In many of the densitometer traces, peaks on troughs were defined by a single point, rather than a series of points. Thus, every alternate value is a peak separated by a trough.

(3) The main criterion for rejecting a given trace was that the trend in ring width defined by the densiotometer trace did not correlate with known growth rate from the yearly measurements in the field. For example, from the field results it was known that radial increment in year one was less than year two, but greater than year three, irrespective of actual values. The densitometer trace did not reproduce this pattern of relative growth rates between the three years of known growth rates. Thus, it appears that the distance between two peaks on the densitometer trace did not correlate to a known growth event. It is possible that more than one growth event occurred per season in response to the pattern of rainfall. Checking for this meant that very arbitrary decisions were made regarding lumping, or not, of successive peaks on the trace. Additionally, for traces with well defined, and well spaced peaks and troughs, this led

to unrealistically high values. Lastly, even when this was done, it still generally failed to produce the required correlation with the field growth measurements.

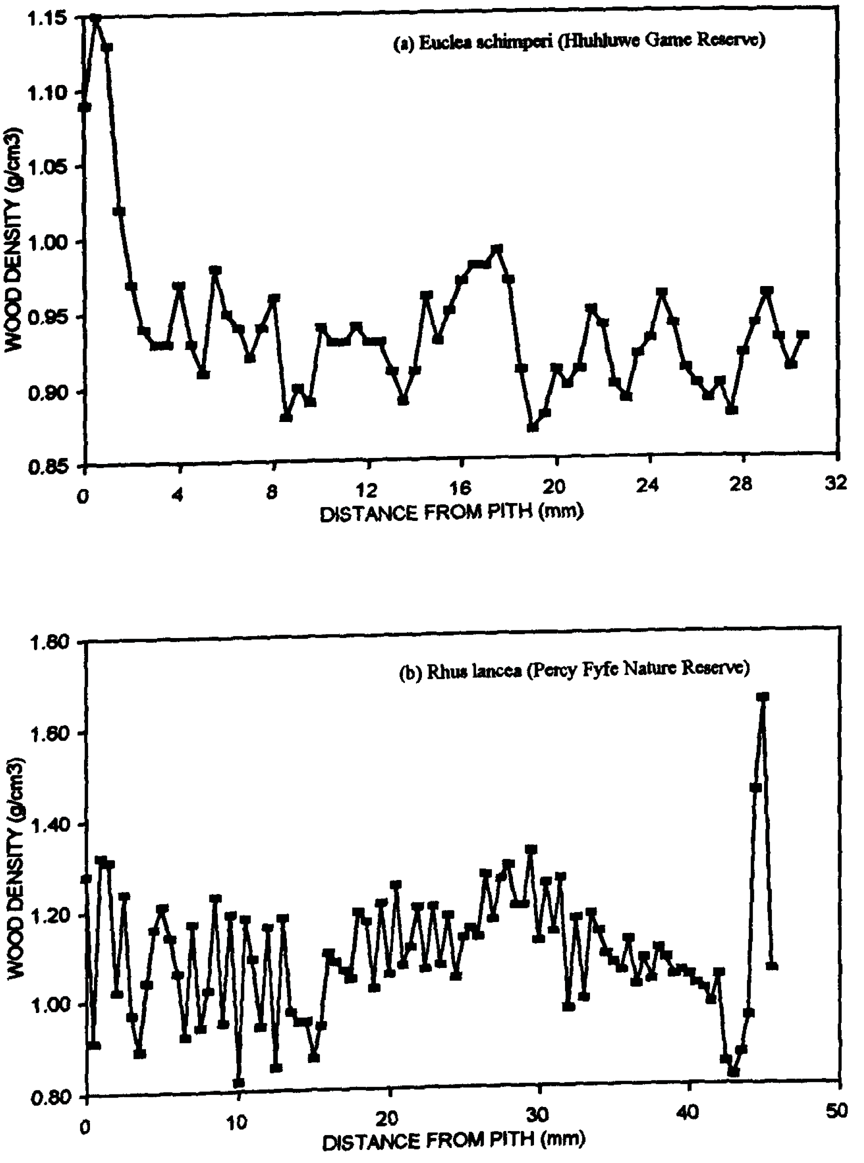

Figure 4.1. Examples of a (a) good and (b) poor trace (see text for details).

Having summed up the main problems with densitometry as a tool for growth analysis it must be noted that the failure may be in many instances due to the unreliable characteristics of the species examined rather than the method itself. This was controlled for by selecting stems that had experienced three successive years of positive changes in radius, but it is possible that the anatomy of the species selected was such that interpretation of growth events by densitometry or any other current method would also yield disappointing results. In other words, many species fail to produce identifiable rings. Van Daalen *et al.* (1992) identified some problems regarding the use of a densiotometer for the identification of growth rings, but argued the biggest problem was that many species did not have definable rings rather than the method of analysis. Of the twelve species in common between this study and that of Lilly (1977) he regarded only *Burkea africana* as a promising species for growth ring analysis. That said, he rated *Acacia tortilis* as one of the worst species of the 108 he examined, yet Wyant & Reid (1992) found *A. tortilis* (in Kenya) to have good rings for dendrochronological analysis. Was this due to geographical differences in species anatomy or methods used? Criteria of possible successful species need to be defined, as attempted by Lilly (1977). Stahle *et al.* (1996) suggest that members of the Rubiaceae in particular need further attention in terms of dendrochronological analysis.

WOODY PLANT PRODUCTIVITY: THE INFLUENCE OF WATER AND FERTILISATION

5.1 INTRODUCTION

Woody plant productivity in a variety of biomes has been variously correlated with aspects of plant available moisture, availability of specified soil nutrients and competition (Fowler 1986). These relationships have been derived from survey and monitoring studies of established stands in field studies, or of seedling growth in nursery experiments (Turner 1991). The first are compounded by influences of external variables beyond the control of the researcher, as well as a limited set of variables investigated against which correlations are sought and conclusions made. The second may not reflect the field situation pertaining to a mature tree or shrub.

This study was no exception, and woody basal area increment was found to have a higher correlation with MAR, soil type and stand basal area than any other variables (Sect. 3.4.3). As such this finding suffers from the methodological problems described above. Consequently, a controlled factorial experiment was designed to test the influence of elevated soil moisture and nutrient levels on the growth of selected woody species.

5.2 OBJECTIVE

The objective was to provide a controlled experiment to test the null hypothesis that available plant moisture and soil nutrients have no effect on woody plant growth.

5.3 METHODS

As an independent validation of the role of rainfall and soil nutrient status in determining woody productivity a factorial experiment was set up in mid-November 1993 at the arid, semi-arid and mesic intensive monitoring sites (Chap. 2) with three watering and three fertilisation levels. Watering treatments were (1) no additional water - rainfall only, (2) rainfall plus 20 % of the long-term mean annual rainfall at each reserve, respectively, and (3) rainfall plus 40 % long-term mean. Fertiliser additions of 2:3:2 organic fertiliser were (1) nil, (2) 20 kg/ha nitrogen and (3) 40 kg/ha nitrogen. These levels were selected in the knowledge that the annual nitrogen turnover at a typical South African savanna (at Nylsvley) is approximately 40 kg/ha (Scholes pers. comm.). Thus, there were nine treatments (3 x 3 factorial) at three localities.

At each locality two relatively common species were selected, one a legume, and the other a broad-leaved species (arid locality - *Dichrostachys cinerea* and *Combretum apiculatum*; semi-arid locality -*D. cinerea* and *Terminalia sericea*; mesic locality - *D. cinerea* and *Parinari curatellifolia*). A uniform stand of each species was subdivided into four blocks. Eighteen trees were randomly selected from each block and two replicates assigned to one of the nine treatments. Thus, there were eight replicates per treatment for each species in each reserve.

A 2 m^2 soil basin was constructed around each tree, including those not receiving additional water. Existing grass and other woody stems within the basin were not removed. Fertiliser was applied at the initial treatment only. Watering occurred once a month over six months. Each tree was labelled, and a line painted on at approximately 35 cm above the ground. The circumference of each stem was measured at this line. The height of each stem was also measured. The circumference was remeasured at the end of winter for the subsequent two years (i.e. Aug 1994 and Aug 1995).

Once shoot growth was initiated ten shoots per tree were selected (three height levels, three shoots 120° apart in the canopy at each height level, plus the terminal shoot on the tallest branch) and marked at the bud-scar. The length of each shoot was remeasured at the end of the growing season (May 1994). At the same time, foliar samples were collected from randomly selected trees receiving the different fertiliser levels, but with no additional water (three replicates per fertiliser level per species per reserve). The foliar samples were analysed for N, P and K.

It is assumed that although growth may be influenced by factors other than included in the experimental design, that the intensity of these other factors was equal throughout all the treatments, nor was it interactive with any treatment level, and thus the experimental results reflect the role of water and nutrients only.

The circumference data were converted to basal area, and growth expressed in terms of percentage increase or decrease in basal area. Replicate shoot length measurements were averaged per tree. After testing for normality values of percentage change in basal area were arcsine transformed. Data were analysed by multi-way ANOVA excluding species effects which were not of interest. An interaction term for water and fertiliser was included. Differences in means per treatment for significant factors were explored by means of LSD.

5.4 RESULTS

5.4.1 Effects of water and fertiliser

Both indices of growth, namely change in basal area and shoot length, responded in the same pattern. At the end of the first growing season there were significantly higher growth rates associated with increasing levels of fertiliser (F = 3.08; d.f. = 2; $p < 0.05$), but not water (F = 2.3; d.f. = 2). There was no significant interaction between these two factors (F = 0.94; d.f. = 4) (Table 5.1).

Table 5.1. ANOVA table for relative change in basal area for first growing season.

SOURCE	DF	SS	MS	F	P
Water	2	82.3	41.2	2.30	0.0997
Fertiliser	2	110.5	55.3	3.08	0.0458
Water * Fert.	4	67.1	16.8	0.94	0.4442
Reserve	2	7423.0	3711.5	206.90	0.0001
Replicate	15	102.4	6.8	0.38	0.9831
Error	406	7283.2	17.9		
Total	431	15068.6			

Comparison of means indicated that the highest fertiliser level was significantly different from the other two as indicted by shoot length, and only the no-fertiliser treatment in terms of change in basal area (Fig 5.1)

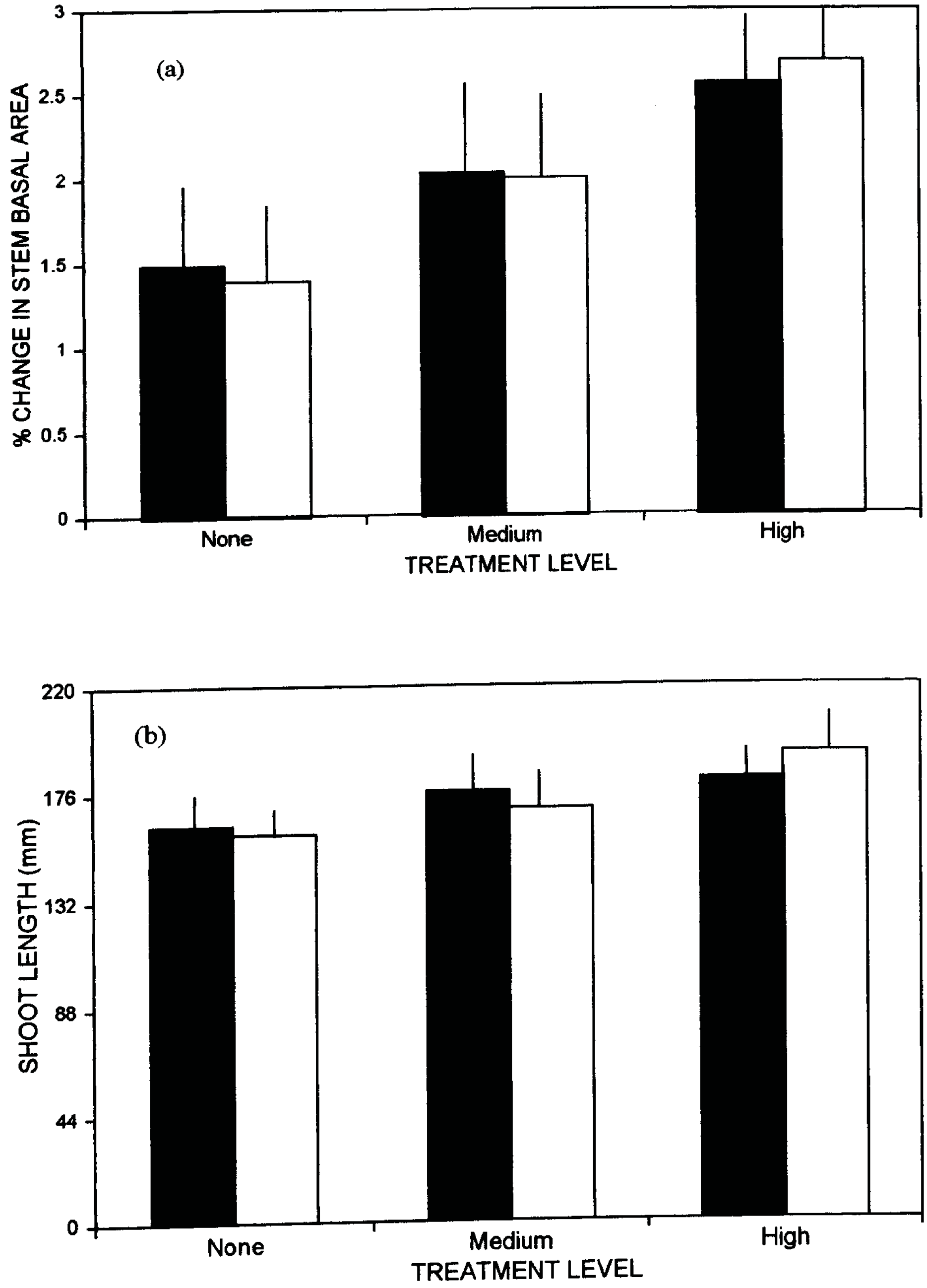

Figure 5.1. Influence of water and fertiliser on (a) relative basal area increment and (b) shoot length (■ - water; □ - fertiliser).

There was a trend of increasing increment in basal area and shoot length with increasing water application, although not significantly so (Fig 5.1). This suggests that a greater sample size may have resulted in a significant difference, and requires further investigation.

The highly significant term indicating different growth rates between the three reserves is problematic. Both basal area increment and shoot length were greatest at the semi-arid site and least at the moist site. The arid site was intermediate between these two. This result may be a reflection of the apparently higher relative productivity at intermediate rainfalls (Sect. 3.5.1), or may simply be a reflection of inherently higher growth rates of the species selected at the semi-arid site relative to the broad leaved species selected at the other two sites.

Neither fertiliser nor water exhibited significant effects for change in basal area for the second growth season. Indeed, there were no clear trends in the data relative to the treatment levels. Thus, it appears that there were no lag effects of either the water or fertiliser treatment.

5.4.2 Foliar analyses

There were no significant differences in foliar N, P or K related to fertiliser treatments. This suggests that growth was nutrient limited, and that the increased growth response resulting from fertiliser diluted the increased uptake of nutrients to the new limiting levels (Scholes pers. comm.). It is also possible that collection of foliar samples was too late in the season, and translocation from the leaves prior to abscission had already occurred, although leaf colouration stage is recommended for collection of foliar samples in temperate hardwoods (Lea *et al.* 1980). Analysis of samples collected at the start of the subsequent growing season may have addressed this possibility.

5.5 DISCUSSION

It is indicated by the results that increased soil nutrient levels lead to increased woody plant growth. The same is suggested for increased soil moisture. Whilst not surprising, these data are an independent validation of the results in Chapter 3, whilst simultaneously indicating that the relationship of woody productivity with soil type summarised from the biome plots may be a reflection of the influence of soil nutrients, rather than solely soil moisture as hypothesised. However, given the positive correlation between soil texture and soil moisture and nitrogen mineralisation, it is difficult to tease out the proximate correlate without additional empirical experimentation. Pastor *et al.* (1984) described a strong correlation between woody productivity and soil texture (% clay and silt) in a temperate forest, but also between nitrogen mineralisation rate and soil texture, and between woody productivity and nitrogen mineralisation. No relationship was evident with other indices of soil nutrient status.

The marked effect of increased soil nutrient status concurs with the findings of other studies using a laboratory or field survey approach. Turner (1991) showed that seedlings of two tropical forest species responded positively to fertilisation, increasing in height and girth. There was a species fertiliser interaction. Prins & van der Jeugd (1992) contrasted growth rates of several shrub species occurring on both eutrophic and dystrophic soils in Tanzania. The same species grew approximately 40 - 50 % faster on eutrophic soils than dystrophic soils. However, a similar conclusion was not evident from the data in this project. Comparison of toplands and bottomlands, and comparison of sites with high nitrogen and/or organic matter with sites having low values (Chap. 3), found no significant differences in growth rates. McNulty and Aber (1993) cite several studies of fertiliser addition on temperate species, all reporting higher growth rates until nitrogen saturation is attained (Aber 1992). Continued saturation may lead to a decrease in growth (Magill *et al.* 1997). Lea *et al.* (1980) demonstrated greatly enhanced foliar nutrient concentration following fertilisation of several species, as did Magill *et al.* (1997).

Despite the high levels of fertiliser addition, the growth enhancement lasted for a single growing season only. This suggests relatively rapid leaching, volatilisation, immobilisation or total uptake of the added nutrients. Leaching appears to be a relatively slow process in these savannas (Meredith 1987, Blackmore *et al.* 1990, Scholes & Walker 1993). Immobilisation will depend upon the magnitude of the cation and anion exchange capacity at each site (Kellman 1985), but loss of NO can be marked in arid savannas (Parsons *et al.* 1996, Scholes & Scholes 1997). Total uptake remains a possibility, again suggesting that growth without fertilisation is nutrient limited as suggested from the results of the foliar analysis. The effects of relatively high fertilisation additions during establishment of commercial plantations remain evident many years afterwards, with fertilised plots having a higher biomass (Rapp 1983). Whether or not this is a result of higher growth rates during the establishment phase, or that even the mature trees exhibit accelerated growth is unclear.

It is noteworthy that whilst a clear increase in growth was associated with fertilisation, the same did not apply with respect to watering. This conflicts with the large body of literature arguing that water is the primary limiting factor in savannas. Moreover, the effect of increased soil nutrient status is frequently dependent upon adequate plant available moisture (Scholes 1990a, Nambiar 1995)). Fowler (1986) surmised that with respect to herbaceous species fertilisation usually results in increased growth, but is commonly interactive with or dependent upon increased watering levels, especially in arid and semi-arid environments. Nambiar (1995) stated that water availability was the primary limiting factor of woody plant growth in Australian forests, even at high rainfall sites, relative to soil nutrients. Similarly, productivity of *Acacia koa* in Hawaii was found to be limited more by water than nutrient availability, even at relatively high MAR. The anomalous results from this study may be a consequence of the treatment levels selected for fertilisation and watering respectively, and the physical design of the experiment. The fertiliser treatments represented a 50 % and 100 % increase in anticipated background levels. The watering treatments were only 20 % and 40 % higher than the long-term MAR and well within the 95 % confidence limits around that mean. Water additions of the same relative magnitude as the fertiliser may well have resulted in watering producing a greater effect than fertilisation. Indeed, extrapolation of the data, assuming linearity and constant LSDs, indicates that watering additions of 30 % and 60 % greater than MAR would have resulted in a significant effects, again, well within confidence limits associated with the MAR. Lastly, the watering was spread over six months, whereas the fertiliser was applied in one application. Thus, the magnitude of each watering event, coupled with the lower total increase in water relative to fertiliser, may have been inadequate to lead to significantly increased growth, although a trend was evident.

WOODY PLANT PRODUCTIVITY:
THE PREVALENCE AND ROLE OF COMPETITION

6.1 INTRODUCTION

Competition between the woody and herbaceous components of savannas is frequently invoked as one of the major processes influencing the structure and function of African savannas (Knoop & Walker 1985, Skarpe 1992, Teague & Smit 1992, Scholes & Walker 1993). It has also been implied that competition between trees may be a significant determinant of woody community structure and productivity (Smith & Goodman 1986, Teague & Smit 1992, Scholes & Walker 1993).

The presence or absence of competitive interactions between woody plants across a range of biomes, including savannas, has been inferred from the spatial distribution of individuals within the community (e.g. Phillips & MacMahon 1981, Midgley & Watson 1992). The most common approach has been to use nearest-neighbour methods which assume that competitive interference between neighbouring plants, if present, will be manifest through a reduction in the size of one or both of the competing neighbours. In this way, if there is a significant correlation between the distance separating the two neighbouring plants and the sum of their sizes (canopy cover is the most frequently used variable), then competition is inferred (Pielou 1962).

In savannas, Smith and Walker (1983) analysed four bottomland sites and concluded that inter- and intra-specific competition played a role in spacing *Acacia* communities, but did not regulate broadleaved communities. Smith & Grant (1986) determined from nearest-neighbour analysis that intra-specific competition occurred within the two dominant broadleaf species at a single plot at Nylsvley; whilst Smith & Goodman (1986) demonstrated intra- and inter-specific competition in the spacing of two *Acacia* species at three sample sites. Intra-specific competition was also detected in this manner at three sites by Gutierrez & Fuentes (1979) for *A. caven* in Chile. Grundy *et al.* (1994) using the same approach detected intra-specific competition at three (out of five) sites for *Brachstegia spiciformis*, and two out of five sites for *Julbernardia globifera* at Marondera, Zimbabwe.

It is consistent from the above studies that intra- and inter-specific competition affects *Acacia* dominated communities, although from a relatively small number of plots (10 across all studies). Results for the broadleaved species or communities were inconclusive, and again, are based on a relatively small sample number.

In light of the inferred importance of competition, the small sample size of the above studies, and the inconclusive evidence resulting from broadleaved savannas, a study was undertaken to determine the prevalence of intra- and inter-specific competition in a variety of South African savanna communities, using nearest-neighbour methods.

6.2 OBJECTIVES

To determine the prevalence of intra- and inter-specific competition in South African savanna communities using nearest-neighbour methods.

6.3 METHODS

Between 30 and 40 nearest-neighbour pairs were measured at 45 of the 51 sites around the biome (Sect. 3.3). Stems less than 1 m tall were not considered. For each pairing the following were measured: (1) the distance between the point tree and its nearest neighbour, (2) the circumference of each tree, (3) the height of each tree, (4) the height of the canopy base, (5) the length of the long and short axis of each canopy.

The size of each canopy was then calculated from these dimensions, on an area and volume basis. The sum of the areas, and the sum of the volumes of the two neighbouring trees was then regressed against the distance between the two trees for all the pairs within that plot, following the approach of Pielou (1962). Intraspecific competition was considered for any plot where at least five of the nearest-neighbour pairings were between trees of the same species. Two of the sites were mono-specific sites dominated by a single *Acacia* species. These were assessed for intra-specific interactions only. Thus, sample size for analysis of inter-specific competition was 43 (11 *Acacia* dominated communities; 26 broadleaved communities; 6 mixed), and for intra-specific competition it was 31 (18 *Acacia* species; 12 broadleaved species; 1

microphyllous, non-*Acacia*).

The characteristics of sites exhibiting competition were examined relative to sites were competition was not identified through means of a t-test (assuming variances to be equal).

6.4 RESULTS

6.4.1 Inter-specific competition

Analysis using canopy area generally resulted in higher r^2 values than canopy volume. Only four of the 43 sites (9.3 %) indicated a significant relationship between summed canopy area and the distance between nearest neighbours. Two were *Acacia* dominated communities (18.2 % of *Acacia* sites) and two were broadleaved communities (7.7 %).

Comparison of the four sites where competition was inferred, relative to the rest suggested that soil texture was a key factor differentiating those sites in that they had almost double the amount of clay in the A-horizon, and significantly less sand (Table 6.1). Additionally, there were less species at those sites exhibiting competition, although the difference is not quite significant.

Table 6.1. Comparison of site attributes for sites with (n = 4) and without (n = 39) inter-specific competition.

VARIABLE	SITES WITH COMPETITION	SITES WITHOUT COMPETITION	T	p	d.f.
Competition index	0.507	0.056	6.27	< 0.0001	41
Clay (%)	35.7	19.3	2.38	< 0.05	41
Sand (%)	49.0	69.6	-2.41	< 0.05	41
No. of species	8.8	12.9	-1.77	$= 0.08$	41

6.4.2 Intra-specific competition

Again, canopy area usually resulted in higher r^2 values than canopy volume. Yet on a canopy area basis only six of the 31 inter-specific analyses showed a significant competitive effect, whereas using canopy volume, ten of the 31 analyses resulted in a significant correlation with nearest-neighbour distance. Of the ten sites indicating a significant correlation between the interplant distance of the dominant species and the summed canopy volume, seven were *Acacia* species (55.6 % of the *Acacia* species comparisons) and three were broadleaved species (21.4 % of the broadleaved species comparisons).

In terms of intra-specific competition, there were no abiotic site variables that differentiated the sites with competition from those without, although the competition sites were generally characterised by higher soil organic matter, clay and nitrogen mineralisation than the non-competitive sites. However, density, particularly small stems, was significantly greater in sites with competition relative to those without (Table 6.2).

Table 6.2. Comparison of site attributes for sites with (n = 6) and without (n = 25) intra-specific competition.

VARIABLE	SITES WITH COMPETITION	SITES WITHOUT COMPETITION	T	p	d.f.
Competition index	0.357	0.105	-2.67	< 0.05	29
Density (stems/ha)	2886.0	1427.1	-2.50	< 0.05	29
% of small stems	36.9	18.7	-3.06	< 0.005	29

6.5 DISCUSSION

From the above, evidence for competition (based on nearest-neighbour analysis) as a determinant of savanna woody community structure is not as prevalent as previously suggested. Intra-specific competition seems more prevalent than inter-specific competition (32 % and 9 % of sites, respectively). Additionally, competition was more prevalent in *Acacia* communities and within *Acacia* species than broadleaf communities or species. This is in general agreement with the previous studies.

The absence of detectable competition within most of the sites examined using this method is contrary to most previous studies in savannas, especially *Acacia* communities, and summaries from other biomes (Fowler 1986, Goldberg & Barton 1992). This result prompts analysis of why this may be so. An answer may lie in (1) analysis of what is different at those few sites that did indicate the presence of competition relative to the the sites that did not, or (2) examination of the method used.

In terms of site characteristics of sites exhibiting inter-specific competition the only difference found in this study was that competitive sites have significantly more clay and less sand than sites where competition was not inferred. There was also a suggestion of fewer species at competitive sites relative to non-competitive sites. This differentiation is attractive, but is not mutually exclusive. There were some sites where competition was not detected with a higher clay content than some of the sites where competition was inferred. Thus, no threshold level of soil clay could be identified above which inter-specific competition begins to assume a prominent role in community structure and function.

Differentiation of sites with and without intra-specific competition was achieved on the basis of stand density and the proportion of small stems. Stands with a high density and a relatively high proportion of small stems tended to have significant competitive interactions as measured through nearest-neighbour analysis. Once again though, this was not an exact categorisation, with several plots without intra-specific competition having higher densities than plots with competition. Thus, a high density appears to predispose a site to intra-specific competition, but does not demand it. Some other factor may be required once a high density has been achieved.

Overall, there were significant relationships between the inter-specific competition index (significant or not) and (1) the dominance index, and (2) the number of species at a site, summarised as:

$$\textit{Competition index} = 0.319(\textit{Dominance index}) + 0.00218 \qquad (r^2 = 0.11;\ p < 0.05;\ n = 45)$$

$$\textit{Competition index} = -0.0187\ (\textit{No. of species}) + 0.351 \qquad (r^2 = 0.19;\ p < 0.005;\ n = 45)$$

Although based on different measures, both these relationships indicate that competition increases with decreasing species number, suggesting a change from inter-specific to intra-specific competition, and that the latter plays a more prominent role than inter-specific competition. The greater the number of species, the less the dominance and the greater the niche separation within the community.

The method used here was the same as that used in previous studies where competition was inferred for most savanna woody communities. However, the low proportion of sites in this study, relative to previously published work, begs a critical analysis of the method, and whether or not it is more applicable in some situations than others. In this regard four potential problems exist.

1. Canopy area versus canopy volume

Canopy area has been the dependent variable most commonly used by previous authors. In this study, it generally provided higher r^2 values than canopy volume. However, is appears simplistic to measure tree canopy growth responses in the horizontal dimension only. It is well accepted that trees competing for light allocate more resources to increase vertical dimensions (so to reach the light sooner) than horizontal dimensions. There is no reason to doubt why the same should not apply for woody savanna communities. Thus, if two individuals compete it is hypothesised that a range of strategies may result, and especially in dense vegetation, increase in canopy height as opposed to canopy spread is probable.

The second problem with canopy spread alone is that species differ with respect to their inherent architecture. Some species are characterised by a spreading canopy, i.e. favouring horizontal growth (e.g. *Acacia sieberiana, Acacia tortilis, Pterocarpus angolensis*), whilst others are noted for their relatively tall and narrow growth from (e.g. *Faurea saligna, Pterocarpus rotundifolius*) (Fig 6.1). Therefore, attempts to detect inter-specific competition using nearest-neighbour analysis based on canopy area in communities where both types of species are present will be confounded by the influence of canopy architecture. This problem would not apply to analysis of intra-specific competition. Canopy volume accounts for both horizontal and vertical dimensions of the canopy and should therefore address the problems highlighted here.

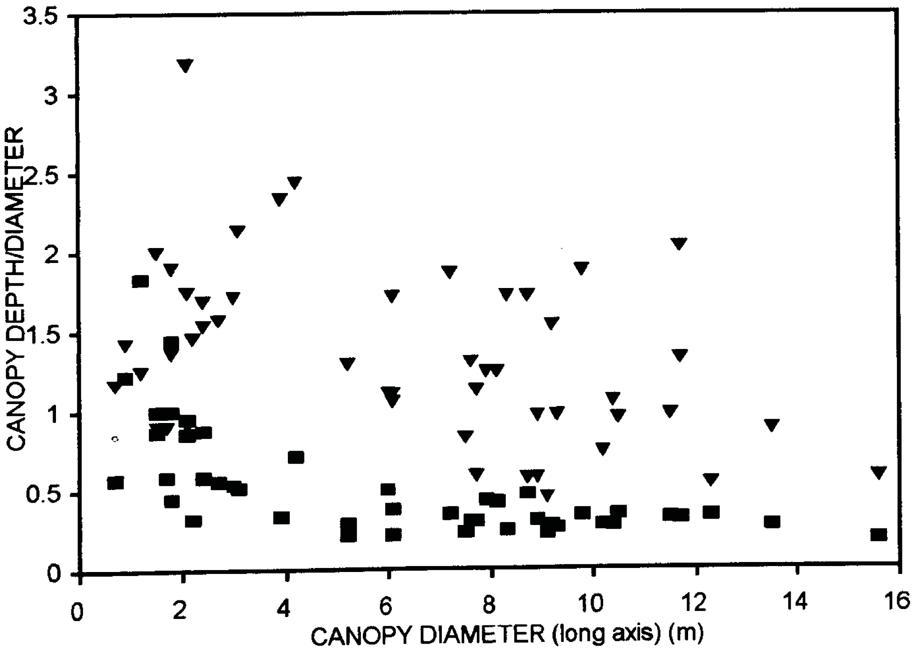

Figure 6.1. Canopy height:width ratio for two species with contrasting architecture (■ - *Pterocarpus angolensis*; ▼ - *Faurea saligna*).

2. No consideration of temporal dynamics

Nearest-neighbour analysis is based upon a snapshot of the current situation of the spatial arrangement of individuals in the community. It fails to interpret these within the context of the temporal dynamics of an inherently variable system. A typical example is provided in Fig 6.2. At time zero two large mature trees are present (*A* and *B*), and are far enough apart not to compete at the time of measurement (a number of years in the future, as they continue to grow, they may be competing). Sometime later on (time t1), another plant *C* is recruited into the space between *A* and *B*. Nearest-neighbour measurements now may well conclude that competition is present as the sum of canopy sizes of *A* and *C*, or *B* and *C*, is less than that between *A* and *B*. By chance, plant *C* is of a species that has an inherently faster growth rate than plants *A* or *B*. Remeasurement of the nearest-neighbour dimensions several years later (t2) may well provide a picture that leads to the interpretation that no competition is occurring. This example serves to illustrate that the determination of the presence or absence of competition through nearest-neighbour methods is highly dependent upon the snapshot of the potential pairings at that time only. Thus, it seems that recruitment and mortality will continually interfere with the nature of existing competitive or non-competitive nearest-neighbour interactions.

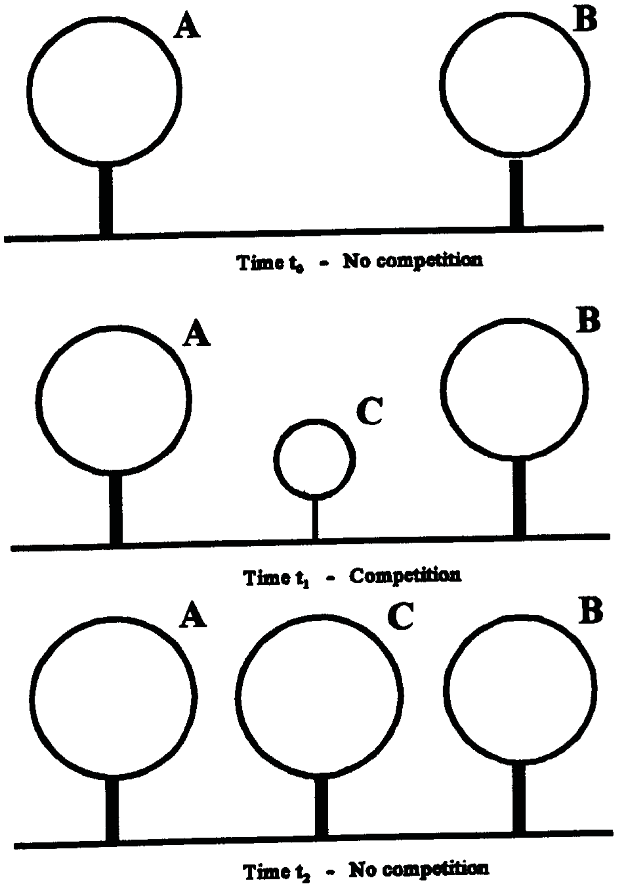

Figure 6.2. Schematic representation of the problems of nearest-neighbour analysis with temporal changes in competitive interactions (see text for details).

This problem may potentially be addressed by analysis of relative growth rates (RGR) between neighbouring trees, rather than canopy size. However, this too would have its problems, including (1) the time required to obtain an adequate measure of RGR, and (2) the fact that RGR is dependent on the size and species of the tree. Moreover, testing this hypothesis using growth rate data from the biome growth plots (Chap. 3) for those four plots where nearest-neighbour analysis suggested inter-specific competition