ECOPHYSIOLOGY OF INDIGENOUS TREES IN AGROFORESTRY SYSTEMS IN THE SEMI-ARID TROPICS

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DECLARATION

This thesis has been composed by myself from the results of my own work, except where stated otherwise, and has not been submitted in any previous application for a degree.

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January, 2000

ACKNOWLEDGEMENTS

The pages that follow and the work behind them were achieved through the efforts of many people. My greatest appreciation is to Colin Black for efficient supervision, careful reading of drafts and all round support. My sincere thanks to Chin Ong for supervisory support and inspiration in Kenya and Paul Jarvis for a desk in Edinburgh during the final stages of writing up.

My sincere thanks to the staff at the Machakos field station, especially Anthony Mwasa, Bernard Mbulu, Raphael Maweu, Peter Ochieng, Mike Maringa, Muthoka Mailu and Peter Kurira. Many thanks to Adrian Muxworthy for assistance with the canopy algebra and geometry, Peter Levy for assorted advice and Andreas Ibrom of Göttingen University for an introduction to modelling. I am much obliged to Rick Coe of ICRAF and Tony Hunter of Biometrics and Statistics Scotland for statistical advice and to Ahmed Khan, Jamie Lott, Mark Smith and Nick Jackson for support in Kenya. For miscellaneous suport and information I also thank Marie Lucas, Ross Reynolds, Michael Jackson and Jackie Humphries.

As well as the individuals involved I would like to thank the Natural Environment Research Council and The International Centre for Research in Agroforestry for funding and support and The Republic of Kenya for hosting my research. My time in Machakos was greatly enriched by the friendship of Ras Michael Kyalo Mbathi and the Domumba Rastas: Shamboki, Ndino, Dick, Felix, and Pedro; we will meet again. And finally I express my deepest appreciation to Odarac for unfaltering support to the end.

CONTENTS

ABSTRACT

Increasing demand for timber, fuelwood and other forest products has outstripped production in many areas of the semi-arid tropics, leading to deforestation and land degradation resulting from erosion and nutrient depletion. Agroforestry offers the potential to provide forest products, improve productivity and reduce soil erosion and environmental degradation. However, as previous reports have shown that competition between trees and crops for water in semi-arid areas adversely affects crop yields, attention has turned towards studies of the existing practice of boundary planting, where low tree planting densities and the associated benefits of land demarcation and soil stabilisation increase the viability of incorporating trees into crop land. The aim is to select and manage tree species in ways that limit their negative effect on crop yields and improve the overall value of the system.

The present study was carried out at Machakos (1° 33′ S, 37° 14′ E, altitude 1660 m) in the Kenyan highlands, where the bi-modal annual rainfall of c. 740 mm is divided approximately equally between two rainy seasons (short rains, October-February, long rains, March-July). The experiment was set up in April 1993 to examine the influence of tree/crop interactions on system productivity. Each 18 x 18 m plot, except for the sole crop plots, contained a central row of trees planted at a 1 m spacing. Four overstorey agroforestry treatments were examined between March 1996 and March 1998; these included two indigenous species, *Croton megalocarpus* and *Melia volkensii*, and two exotic species from Central America, *Senna spectabilis* and *Gliricidia sepium*. Beans (*Phaseolus vulgaris*) and maize (*Zea mays*) were grown during the short and long rains respectively.

M. volkensii and *S. spectabilis* exhibited similar leafing phenology patterns, losing almost all leaf cover during the long dry season (July-October) and flushing before the ensuing rains. During the short dry season, *S. spectabilis* lost few leaves, whilst *M. volkensii* lost some leaves before flushing prior to the onset of the long rains. *M. volkensii* lost a large proportion of its leaf cover during the 1997/98 short rains due to the unusually high soil moisture content. *C. megalocarpus*, although predominantly evergreen, lost a large proportion of its leaves during dry periods, whereas leaf area increased rapidly under wetter conditions. *G. sepium* had one annual period of low leaf cover during the long dry season and did not regain full leaf cover until mid- way through the short rains.

The three-dimensional model of canopy photosynthesis and transpiration, MAESTRA, was parameterised for *C. megalocarpus* and *M. volkensii* using existing models to describe the response of photosynthesis to light and temperature and stomatal responses to light and vapour pressure deficit. The photosynthesis model fitted the experimental data well, but stomatal conductance in *C. megalocarpus*, although showing responses to light and vapour pressure deficit, was not closely correlated with ambient environmental conditions. *M. volkensii* had higher leaf area than *C. megalocarpus* for most of the 18 month simulation period, comprising three rainy and three dry seasons; modelled assimilation for this period was 49 % greater in *M. volkensii*, while canopy water use efficiency and transpiration were respectively 35 and 11 % higher. These differences accounted for the more rapid growth rate and greater competition with adjacent crops associated with *M. volkensii* relative to *C. megalocarpus*.

Above-ground woody biomass production was greatest in *M. volkensii*, followed by *S. spectabilis*, *C. megalocarpus* and *G. sepium*; production during the fourth and fifth years after planting ranged between 2.8 and 4.9 t ha^{-1} yr^{-1}. Crop production in the agroforestry treatments was always lower than in sole crops due to below-ground competition for water and, in seasons with higher water availability, shading by the trees. Of the agroforestry systems examined, seed production for beans was highest under *M. volkensii* and *G. sepium*, followed by *C. megalocarpus* and *S. spectabilis*. Grain production in maize was greatest under *C. megalocarpus*, followed by *G. sepium*, *S. spectabilis* and *M. volkensii*. Mean annual above-ground biomass production including maize grain and stover, bean seed, woody biomass and tree leaves in the *M. volkensii* treatment exceeded that for the sole crop plots, even though rainfall during 1996 and 1997 was only 61 and 95 % of the long term average. Although the biomass production of leaves was not estimated for *S. spectabilis* and *G. sepium*, the results obtained suggested that biomass production was greater than that obtained under sole crop cropping.

The inverse correlation between tree and crop yield suggests that the value of the tree products must exceed the associated crop losses if benefits are to be obtained from agroforestry. *M. volkensii* is valued in areas of Kenya where markets for its products exist and therefore shows great promise for extension in semi-arid areas; where necessary, pruning may be used to reduce competition with crops and increase the length of clear bole. *C. megalocarpus* is widely used as a shade tree in East Africa and seems well suited for this purpose as its impact on adjacent crops was least of all the tree species examined. *S. spectabilis*, although having straight unbranched stems, exhibited a level of competition with adjacent crops that would necessitate a high value for its timber products to warrant its adoption. The least suitable tree species of those examined was *G. sepium*, whose poor form and susceptibility to attack by fungal pathogens and insects severely undermined its potential value for use in agroforestry systems.

1 INTRODUCTION

1.1 ENVIRONMENTAL ISSUES

Large areas of forest, particularly savanna woodland and open forests in semi-arid regions, are being steadily degraded without this deterioration being reflected by deforestation statistics (World Bank, 1989). Increasing population pressure in many low rainfall areas of the world is threatening both the natural and human environments (Brown, 1999), and in Africa deforestation is seen as one of the greatest threats to ecological stability and food production (Njoroge, 1996). The demand for timber, fuelwood, poles and other forest products has exceeded production, leading to the depletion of indigenous forests in many semi-arid areas of Africa (Malaisse and Binzangi, 1985; Grainger, 1986; Viswanathan, 1986; Weaver and Temu, 1987; Mgeni and Nsolomo, 1995; Dewees, 1996) and India (Verma, 1990; Shyam Sunder, 1992; Dhyani and Tripathi, 1999). In East and Central Africa, the estimated annual reduction in closed forest cover ranges between 0.6-0.7 %, although in India forest cover is relatively stable (FAO, 1997). Population growth, which underlies the problems of forest clearance and degradation, may provide a more reliable indication of the threat to open forest and scrubland. It is predicted that the global population will increase by 3.3 billion during the next 50 years, almost exclusively in the developing world; some of the largest increases are expected to occur in India and sub-Saharan Africa (United Nations, 1996), extensive areas of which are classified as semi-arid (Hudson, 1987). The main causes of deforestation are expanding agricultural and livestock populations and increasing demand for timber and wood for construction and fuel (World Bank, 1989). Local consequences of deforestation are that tree products must be sought further afield, soil productivity is reduced, and the increased use of crop residues and dung to replace fuel wood leads to the erosion and nutrient depletion of agricultural soils (Pimentel *et al.*, 1986). Larger scale consequences include the increased incidence of flooding, decreases in biological diversity and climate change (Viswanathan, 1986; World Bank, 1989; Dixon, 1995). The combined effects of soil exhaustion and erosion resulting from non-sustainable agricultural practices and fuelwood harvesting have already resulted in severe desertification of 30 % of the world's arid and semi-arid lands (Grainger, 1985).

The dependence of plant growth and productivity on water availability exacerbates the severity of these problems. Above-ground dry matter production declines globally with decreasing rainfall from c. 25 t ha^{-1} yr^{-1} when annual precipitation exceeds 2500 mm to 5-16 t ha^{-1} yr^{-1} in areas with annual rainfall of 500-800 mm (Lieth, 1978). Habitat aridity, to which plant physiognomy and production are more closely related, is a function of both rainfall and potential evapotranspiration (Baumer, 1990). UNESCO (1977) classified the semi-arid zone as having an average annual ratio of rainfall to potential annual evapotranspiration ranging between 0.2-0.5. In tropical semi-arid zones, dry matter production in forest and dry savanna systems ranges between 7 and 17 t ha^{-1} yr^{-1}, compared to 27-30 t ha^{-1} yr^{-1} in humid evergreen forest (Rodin, Bazilevich and Rozov, 1978). Crop yields in semi-arid climates are inherently limited by the availability of soil moisture to support gas exchange during photosynthetic carbon assimilation (Sinclair, 1988). Indeed, Brown (1999) identified shortage of water as the dominant constraint on efforts to expand global food production. The reduced reliability of rainfall as mean annual rainfall decreases and the limited moisture-retaining capacity of many soils in semi-arid areas pose further problems (Hudson, 1987). Temperature extremes may also inhibit germination (Vandenbeldt and Williams, 1992), while erosion is a risk wherever high winds and dry soil occur concurrently (Baumer, 1990).

FAO (1997) identified agroforestry and other sustainable management systems for natural forests and plantations as potentially providing the most effective means of increasing fuelwood production, whilst Baumer (1990) recognised agroforestry as an effective means of combating desertification and environmental degradation. Agroforestry has an important role in Africa, where incorporation of trees into farm land may be the most appropriate means for households to meet their requirements for forest products, and may also provide additional income (FAO, 1997). The potential benefits and disadvantages of agroforestry are manifold (Szott, Fernandez and Sanchez, 1991; Kessler and Breman, 1991; Rao, Nair and Ong, 1997); the aim of agroforestry research is to determine the relative importance of factors which may influence the success and performance of agroforestry systems under a range of aerial and edaphic environments, including relevant anthropological and sociological factors.

1.2 AGROFORESTRY IN THE SEMI-ARID TROPICS

Agroforestry provides a means by which the imbalances brought about by deforestation may be redressed, environmental services restored, and productivity increased relative to that offered by traditional cropping systems. Trees form effective windbreaks which may be important in reducing erosion (Tibke, 1986) and ameliorating crop microclimate (Brenner, 1995). Young (1989) outlined the potential of agroforestry to promote effective nutrient cycling and assist in controlling soil erosion by providing surface cover and barriers to downslope water flow. The importance of tree roots in providing a safety net by capturing nutrients leached from the crop rooting zone was initially proposed by van Noordwijk *et al.* (1996) and supported by recent measurements of ^{15}N uptake from different depths below hedgerow agroforestry systems in Indonesia (Rowe *et al.*, 1999). Agroforestry may also maintain more favourable organic matter contents and soil physical properties than agricultural systems (Nair, 1984; Young, 1989), although such results have not yet been widely reported (Sanchez, 1995). Trees may also provide a wide range of products ranging from timber, poles, fuelwood, mulch and fodder to medicine, fibre, oil, nuts and fruit (Leakey, 1994).

In tropical semi-arid regions, there is substantial potential for increasing water use by implementing agroforestry as existing cropping systems often use less than half of the available rainfall due to substantial losses caused by evaporation from the soil surface, runoff and drainage (Wallace, 1996). Low rainfall use efficiencies occur primarily because the fraction of rainfall used for transpiration is low and the ratio of evaporation to transpiration is high when the crop canopy is sparse (Unger, Jones and Steiner, 1988). Ong *et al.* (1992) reported that a sorghum/pigeonpea intercrop on the Deccan plateau in India used 41 % of the annual rainfall, while the rest was lost as runoff (26 %) and deep drainage (33 %). In agroforestry systems, runoff may be reduced by the barrier effect of closely planted tree rows, as outlined above, while deep drainage may be limited by water extraction by tree roots located beneath the crop rooting zone (van Noordwijk *et al.*, 1996). The water savings attributable to reductions in soil evaporation in agroforestry systems relative to sole cropping are likely to be greater outside, as opposed to during cropping seasons, as shown by results for an experiment carried out at Machakos, Kenya, in which soil evaporation in an agroforestry system was only marginally lower than in the equivalent sole maize treatment, but was 28 % less than that from bare soil (Jackson and Wallace, 1999). Similarly, exploitation by trees of soil water remaining after crop harvest and off-season rainfall may also increase rainfall use efficiency (Ong *et al.*, 1996).

The choice of tree species for use in agroforestry is likely to be based on a combination of product value, interactions with crops, availability and price of seedlings, management inputs, and the environmental services provided. Attention has recently turned to indigenous tree species, partly because of the perception that fast-growing exotic species are extravagant in their use of water (Florence 1986), but also due to a realisation of their value to local communities (Nair, 1998) and importance in providing environmental services, whilst moving the source of tree products away from natural forests (Leakey and Simons, 1998). Recent research has highlighted the economic and social potential of the various products provided by indigenous trees, including timber (Stewart and Blomley, 1994), fruit

(Maghembe, 1994) flavouring oils (Ejiofor and Okafor, 1997) and medicine (Leakey and Simons, 1998). Indigenous species may be less susceptible to attack by pests and have better survival rates, but often exhibit lower growth rates than exotic species providing wood of similar quality (Haggar, Briscoe and Butterfield, 1998). However, there is great potential for the improvement of the quality and growth rates of wild indigenous trees through domestication, genetic improvement, and development of suitable management strategies (Leakey and Simons, 1998).

The use of nitrogen-fixing trees to improve soil fertility has received much attention in systems containing widely scattered trees such as *Faidherbia albida* in the arid and semi-arid tropics, and in hedgerow intercropping in the sub-humid tropics, where *Leucaena leucocephala* and *Gliricidia sepium* may rapidly increase soil fertility (Ong, 1996). However, benefits have only been found where the soil is fertile and there is sufficient rainfall and labour (Sanchez, 1995). In the semi-arid tropics, hedgerow intercropping has not met with the success initially anticipated as the fertility improvements obtained have failed to offset competition for water and nutrients (Rao, Nair and Ong, 1997). *G. sepium*, one of the species included in the present study, has been shown to contribute substantial quantities of nitrogen to the soil-plant system in the humid and sub-humid tropics (Liyanage, Danso and Jayasundara, 1994; Heineman *et al.*, 1997). However, a modelling study by Shepherd *et al.* (1996) showed that agroforestry would not significantly reduce nitrogen deficiency unless a high proportion of the tree biomass was returned to the soil as fixed nitrogen was removed in material harvested from the trees. Similarly, (Avery and Rhodes, 1990) reported that less than 1 % of the nitrogen fixed by *L. leucocephala* trees was taken up by sorghum in agroforestry systems under nitrogen-limiting soil conditions.

1.3 TREE-CROP INTERACTIONS

Some of the more important interactions for light and water in agroforestry systems are reviewed in the following sections. As a result of the complexity of the interactions involving rainfall interception, evaporation, transpiration and the effects of shading on leaf energy balance and photosynthesis, care must be taken not to bias expectations by attributing positive or negative effects to individual factors when other influential factors may be operating at a similar or finer scale to negate the hypothesised outcome or lead to unforeseen or opposing effects under altered conditions. For convenience, the interactions discussed here are separated into those predominantly acting above- or below-ground; however, it is must be emphasised that both act in unison to regulate tree and crop growth.

1.3.1 ABOVE GROUND

In canopies which are closely coupled to the bulk atmosphere, stomatal conductance provides the primary control on transpiration and photosynthesis at the canopy scale (Jarvis, 1995). Thus in the canopies of isolated tree rows, leaf area, leaf area density, and stomatal and boundary layer conductances determine the rates of photosynthesis and soil water extraction. As well as controlling transpiration and photosynthesis, the behaviour of stomata under differing conditions also influences water use efficiency (Jones, 1992). Canopy size and leaf area density affect the penetration of photosynthetically active radiation (PAR) to understorey crops and influence the radiative balance of adjacent surfaces. The temporal pattern of leaf area during the cropping season is therefore a fundamental determinant of tree-crop interactions. Huxley (1996) has drawn attention to the lack of research concerning the effects of tree phenology in agroforestry systems despite its obvious potential impact. The importance of canopy development in providing temporal separation of resource use has been demonstrated for pigeonpea/ sorghum mixtures in which seasonal light interception exceeded that of equivalent sole crops due to differences in the duration and timing of canopy development in the two species involved (Willey *et al.*, 1987). Ralhan, Singh and Dhanda (1992) showed that the performance of wheat in poplar plantations in India was enhanced by leaf fall from the trees in winter, and that the small reductions in crop yield were more than offset by the production of tree biomass. The classic example of temporal separation of tree and crop growth is that of *Faidherbia albida* (Vandenbeldt, 1992), where crop growth is generally improved by a combination of tree characteristics (Sanchez, 1995) including their 'reverse' phenology whereby the leaves are shed at the onset of the rains and flushing occurs at the beginning of the ensuing dry season. Such an exceptional phenological pattern may not be essential to alleviate the effects of competition, as late development of the tree canopy may allow the crop to become established prior to major increases in shading and water extraction by the trees (Huxley, 1994).

Although water deficits affect a wide range of plant processes including cell division, leaf duration and assimilate partitioning to the roots and shoots, the most important factor in decreasing dry matter production is generally the reduction in leaf area resulting from reductions in cell turgor pressure and assimilation rate (Jones, 1992). Yields in various dryland crops have been shown to increase approximately linearly over a wide range of water availability (Stewart, 1988), although the timing of water supplies in relation to crop developmental stage, as determined by rainfall and water extraction by the trees in agroforestry systems, may also have substantial effects. Thus Reshid and Getahun (1987) found that maize yields were significantly reduced when substantial rainfall occurred during the early stages of the cropping season, as this caused leaching of nutrients from the soil surface layers, and also by moisture stress during the reproductive growth phase. The sensitivity of yield in annual crops to water deficits during reproductive growth is widely documented; for instance, failure of pollination and reduction in assimilate production during grain filling may greatly reduce both harvest index and grain yield (Norman, Pearson and Searle, 1995; Monhouche, Ruget and Delecolle, 1998). Although seasonal rainfall and its temporal distribution are of primary importance in determining soil moisture content, the high potential evaporation in arid and semi-arid zones increases the potential influence of incident radiation and tree shading on crop water status.

Shading influences crop growth by decreasing assimilate production due to reduced PAR receipts (Caldwell, 1987), and also by reducing the radiative load, which may alleviate the effect of limited soil water availability (Allen *et al.*, 1976). In agroforestry, shading and soil moisture deficits resulting from water extraction by the trees often occur concurrently, with the result that the impact of reduced PAR on crop performance may be limited if stomatal conductance is also decreased by low soil water availability. This view is supported by observations that the reductions in the yield of maize grown under artificial shade were greater when soil water availability was increased during seasons of high rainfall (Lott *et al.*, 2000b) or by irrigation (Howard, 1995). The potential of tree shading to alleviate water stress was illustrated by Belsky *et al.* (1993) who showed that the productivity of herbaceous species grown under *Acacia tortilis* and *Adansonia digitata* trees was greater than in open grassland at two sites which differed in rainfall. The differences in productivity between areas under tree canopies and in the open were greater at the lower rainfall site, suggesting that this effect may become more pronounced under increasing aridity. These results were supported by Lott *et al.* (2000b) who showed that maize yield was increased under neutral density shade nets during drier seasons. The effect of reductions in PAR on C3 and C4 species may be expected to differ due the higher light saturation levels of C4 plants; however, differences between leaves grown under contrasting light conditions may be greater than those attributable to photosynthetic pathway (Jones, 1992). Thus, although overall production may be greater in agroforestry systems containing C4 crops due to their reduced tendency to become light saturated, the effect of shading may differ little from that on C3 species. The higher assimilation rates commonly found in C3 than C4 plants at lower temperatures (Jones, 1992) are unlikely to be important given the relatively small temperature differences induced by shading by tree canopies.

Temperature affects plant growth by influencing reaction rates for a wide range of metabolic processes (Jones, 1992). Above a base temperature where the process begins, the rate of the process increases linearly up to an optimum, before decreasing linearly to a maximum temperature where the process ceases. The cardinal temperatures (base, optimum and maximum) vary depending on the species and metabolic process concerned (Squire, 1990). The concept of thermal time has been developed to provide a measure of the influence of temperature on the timing and duration of specific growth phases. Thermal time (degree days, °Cd) is often determined by summing the mean daily values for mean temperature minus the base temperature for particular species and processes; however, the relationship is reversed above the optimum and rate decreases with increasing temperature. The temperature optimum for yield may be either above or below that for growth due to the influence of temperature on the duration of the structures associated with yield (Squire, 1990). Although the occurrence of optimum temperatures during vegetative development increases the rate of germination (Mohamed, Clark and Ong, 1988a) and canopy expansion (Mohamed, Clark and Ong, 1988b), so increasing yield, increases in temperature between 20 and 30 °C often reduce the reproductive yield of annual crops by decreasing canopy duration and the panicle or pod filling period (Squire, 1990).

Interactions between temperature and other limiting factors may induce various effects; for example, increases in temperature may improve yield if the consequent reduction in crop duration results in avoidance of end-of-season drought (Brenner, 1995). In agroforestry systems, shading by the trees may influence crop development and yield by altering temperature. Corlett *et al.* (1992a) found that leaf temperatures in millet grown adjacent to *Leucaena leucocephala* hedges were decreased relative to sole millet by shading during the day and increased at night due to a reduction in the long wave flux resulting from the presence of the hedges. However, the calculated differences in thermal time attributable to the hedges were small, amounting to a delay in development of approximately two days over 50 day period (Corlett *et al.*, 1987). Lott (1998) reported that flowering in maize was delayed by up to 24 days in a *Grevillea robusta* agroforestry system relative to adjacent sole crops, although water stress resulting from the presence of trees may have contributed to the delay.

Rows of trees are planted in many climatic zones because of their ability to reduce windspeed and ameliorate crop growing conditions (Brenner, 1995). Shelter from wind promotes various microclimatic modifications. However, although the effects of shelterbelts are clearly advantageous for crop growth where soil moisture is freely available, results are less clear in areas where water supplies are limiting (Davis and Norman, 1988). Daytime temperatures in areas protected by shelterbelts are generally increased as a result of reductions in the heat flux away from the crop surface (Brenner, 1995), whereas evaporation is usually decreased (Rosenberg *et al.*, 1983). Transpiration rate may either increase or decrease depending on the impact of shelter on vapour pressure deficit, which is likely to decrease if the crops are transpiring rapidly, although the situation may be reversed when water supplies are limited (Wallace *et al.*, 1990). The influence of shelter on transpiration therefore depends on the relative values of the variables controlling water use (Brenner, 1995).

1.3.2 BELOW GROUND

Anderson, Muetzelfeldt and Sinclair (1993) highlighted the need for further studies of root architecture and dynamics and competition between roots to improve understanding of the functioning of agroforestry systems. Below-ground competition for water and nutrients between trees and crops is mediated by the degree of spatial and temporal interaction between tree and crop rooting patterns and the activity of the roots as influenced by the development of the tree and crop canopies. Several studies have shown that exclusion of tree roots from the crop rooting zone increases crop yield by reducing competition (Singh, Ong and Saharan, 1989; Corlett *et al.*, 1992b; Okorio *et al.*, 1994), and efforts have been made to identify potentially beneficial tree rooting characteristics.

Huxley (1983) proposed that exploitation of different soil volumes by tree and crop roots may increase resource capture in agroforestry systems without introducing intense competition. Although this is an attractive idea which is supported by observations of stratification of rooting depths for competing species in natural ecosystems (Schroth, 1999), pot experiments (Berendse, 1981), and an irrigated alley cropping system (Lehmann, *et al.*, 1998), there are some theoretical caveats to its potential for increasing productivity through water uptake in semi-arid agroforestry systems. In semi-arid areas without deep water tables and only limited deep drainage, trees with deep rooting patterns may be less competitive for water with shallow rooting crops, but are likely to be slower growing than trees which exhibit more extensive surface rooting patterns because they do not access available moisture in the surface soil layers. This may be important when crop yield is of paramount importance, but does not necessarily provide complementarity of resource use. However, in areas where rainfall exceeds crop requirements for transpiration, deep rooting trees may provide a "safety net" by capturing water draining from the crop rooting zone (van Noordwijk *et al.*, 1996). The potential for complementarity is also likely to be greater in areas where a water table is present beneath the maximum crop rooting depth, but within reach of the tree roots (Smith, Jarvis and Odongo, 1997b). In rainfed systems, these limitations may apply to a lesser degree to nutrients, as their supply is less directionally discrete unless the supply of nutrients resulting from leaching from the surface soil horizons is important.

As cropping seasons are not usually immediately consecutive, system productivity may also be increased by separation of tree and crop rooting activity in time as well as in space. Temporal separation of water uptake by tree and crops roots may increase yields without increasing competition, as demonstrated by the reverse phenology of *Faidherbia albida* in which water uptake by the roots is effectively arrested by leaf fall during the cropping seasons (see above). The potential for increasing resource use, as opposed to reducing tree-crop competition, is likely to be greater in situations where out-of-season rainfall constitutes a significant proportion of the annual rainfall, or where adequate moisture for continued tree growth remains in the soil profile after crop harvest (Ong *et al.*, 1996).

Most previous studies have shown that trees and crops share the same rooting depths (Jonsson *et al.*, 1988; Daniel, Ong and Kumar, 1991; Odhiambo *et al.*, in press), or that tree rooting densities are greatest in the surface horizons (Dhyani, Narain and Singh, 1990; Toky and Bisht, 1992; Mwihomeke, 1992). These results, in combination with the limited opportunity for increasing productivity through root separation in semi-arid areas outlined above, suggest that complementary root system architecture may not be the key to success in simultaneous agroforestry systems, as suggested by van Noordwijk *et al.* (1996). However, increased understanding of the causes and consequences of seasonal variations in fine root density, the timing of root flushing (e.g. Odhiambo *et al.*, in press) and the effects of branch pruning on water uptake by trees (Lehmann, *et al.*, 1998; Jones, Sinclair and Grime, 1998) may reveal opportunities for the management of water extraction. Recent studies (Emerman and Dawson, 1996; Burgess *et al.*, 1998) have demonstrated the extent to which soil water may be redistributed by tree roots, the consequences of which have not yet been established for agroforestry systems.

1.4 PREVIOUS RESEARCH

A considerable amount of agroforestry research has focussed on hedgerow intercropping in the humid and sub-humid tropics, where the aim has been to increase crop yields by improving soil fertility (Ong *et al.*, 1996). Most such systems have not met with the success originally anticipated and benefits are predicted only under specific conditions, which include the presence of fertile soil, relatively high rainfall and sufficient labour to maintain the systems (Sanchez, 1995). Increases in crop yield in hedgerow intercropping systems are rare in the semi-arid tropics as improvements in fertility are insufficient to offset competition for water and nutrients (Rao, Nair and Ong, 1997). In the more commonly practised forms of agroforestry, where trees are of greater direct value to the farmer, the aims differ in that a compromise between tree and crop yield is acceptable depending on the relative value of the tree and crop products and the environmental services performed.

Most studies of overstorey agroforestry systems in arid and semi-arid regions of India and sub-Sahelian Africa have unsurprisingly shown reductions in crop yields adjacent to trees. The effects on crops predominantly result from competition for water (Malik and Sharma, 1990; Corlett *et al.*, 1992b; Howard *et al.*, 1995; Lott *et al.*, 2000b; Jones, Sinclair and Grime, 1998), although the effects of shading are also important (Kater *et al.*, 1992; Kessler 1992; Singh *et al.*, 1993; Yadav, Sharma and Canna, 1993; Okorio *et al.*, 1994; Osman, Emmingham and Sharrow, 1998). However, these reductions in crop yield do not necessarily constitute a failure of the system, and where calculations of overall productivity or economic benefits have been made, those offered by agroforestry systems have exceeded those from sole stands (Singh *et al.*, 1990 in Ong, 1996; Akyeampong *et al.*, 1995; Lott *et al.*, 2000b). Reductions in crop yield have been recorded at distances of up to 10 m from trees (Malik and Sharma, 1990; Yadav, Sharma and Khanna, 1993), although their severity may vary greatly. The effects of trees on crop yields are generally negligible or much reduced during the first 2-3 years after tree establishment (Ralhan *et al.*, 1992; Rao *et al.*, 1993; Akyeampong *et al.*, 1995; Lott *et al.*, 2000b).

Increases in crop yield in the vicinity of trees are less common, but do occur under certain circumstances. The best known and most widely studied systems are those containing *Faidherbia albida*, which increases in crop yield are associated with a range of tree characteristics known as the "albida effect"; these include improved supplies of nitrogen associated with the characteristic shedding of the tree leaves at the beginning of the cropping season (Sanchez, 1995; Rao, Nair and Ong, 1997). However, beneficial effects may not become apparent for 20-40 years after planting due to the slow rate of improvement of soil fertility (Poshen, 1986). Other observed increases in crop yield have also been associated with nutritional effects. For instance, yield increases in maize and beans were observed in sub-humid areas of Uganda for systems containing *Alnus acuminata*, a slow growing, nitrogen fixing species (Okorio *et al.*, 1994), while in West Africa the effects of *Vitellaria paradoxa* (Karité) on cotton yield were found to be negligible (Kater, Kante and Budelman, 1992).

Because of the commonly observed reductions in crop yield, the focus in agroforestry research has turned towards the improvement of existing farming practices, such as boundary and scattered planting of trees. The preference for boundary planting in many areas, as opposed to more spatially integrated forms of agroforestry, results from the reduced above-ground extent of the tree-crop interface and the low management inputs, which can largely be confined to the dry season (Ong *et al.*, 1996). Boundary planting of overstorey trees is practised by farmers to demarcate field and property boundaries, stabilise land, act as terrace risers and produce timber, poles, fuelwood and fodder (Malik and Sharma, 1990; Verma, 1990; Rao, Nair and Ong 1997). Little research has been carried out to examine the productivity of crops and trees grown in rows which simulate boundary planting situations (Malik and Sharma, 1990; Okorio *et al.*, 1994; Heineman *et al.*, 1997), although a greater body of work is available for systems containing scattered trees. The challenge in such systems is to maximise their overall value, which is less closely linked to the maintenance of crop yields when more valuable tree species are used.

1.4.1 MODELLING

Mathematical modelling of agroforestry systems provides a means of structuring existing hypotheses to predict system behaviour under a wide range of environments otherwise precluded from study by the scale and cost of establishing and conducting experimental trials. The complexity of physical interactions in agroforestry systems and the relatively advanced state of knowledge concerning plant physiology, particularly above ground, renders modelling an attractive opportunity for advancing knowledge in the field. The importance of computer models for testing hypotheses in novel systems and environments and their value in familiarising researchers with the structure and functioning of agroforestry systems were highlighted by Ong, van Noordwijk and Coe (1999).

Muetzelfeldt (1995) argued the case for the adoption of a modular approach to modelling, whereby model structure has a high degree of clarity and plasticity to ease the problems associated with the inflexibility and opacity of conventional models. This approach is likely to be the way forward as the sub-routines required for many of the calculations involved in agroforestry modelling, e.g. light interception, evaporation and water infiltration, can generally be agreed upon or alternatives provided where there is equivocation so that a well structured and clearly written model may achieve many objectives. Several models are currently available for modelling tree-crop interactions for light, nutrients and water. These include WaNuLCas (van Noordwijk and Lusiana, 1999), which was developed to cope with a wide range of agroforestry systems and focuses on above and below-ground interactions for light and nutrients, and HyPAR (Mobbs *et al.*, 1998; Cannell, Mobbs and Lawson, 1998), which involves an amalgamation of tree and crop models and focuses on light, water and temperature. The model, Maestra, (Medlyn, 1999) has also been used in an earlier form (Maestro; Lawson *et al.*, 1995) for agroforestry applications. Maestra/Maestro is physiologically explicit at the leaf level and allows canopy level photosynthesis and transpiration to be calculated in three dimensions for isolated plants, thereby including agroforestry situations.

The study conducted by Cannell, Mobbs and Lawson (1998) using HyPAR parameterised for sorghum and generic broad-leaved trees suggested that agroforestry would be disadvantageous in areas where rainfall was below 800 mm yr^{1} and there was no water table within reach of the tree roots unless the tree component was of greater value than crop yield. It was estimated that, although the capture of light and water may be increased in agroforestry systems, grain yield for sole crops would exceed grain yield plus net primary production by the overstorey trees due to the adverse effect of tree shade, competition for water and the lower light and water use efficiencies of C3 trees relative to C4 crops understorey crops. These conclusions provide an opportune subsidiary hypothesis for the work reported in the present thesis.

1.5 AGROFORESTRY PARADIGMS

Various hypotheses and paradigms have been used to help determine the principles upon which efforts may be focussed to improve understanding of agroforestry systems and assist in the design and interpretation of agroforestry experiments. These have either been adopted from the fields of intercropping and plant ecology or have been developed specifically for agroforestry systems as scientific attention has increased (Mead and Willey, 1980; Vandermeer, 1989; Ong and Black, 1994; Sanchez, 1995; Ong *et al.*, 1996; Cannell *et al.*, 1996). The most important theory is that of competitive exclusion/ coexistence (Gause, 1934), in which the fundamental niche requirements and relative competitive abilities of species are the basic components (Aarssen, 1983). Competitive and facilitative production principles were subsequently developed in theoretical ecology to explain the structure and function of mixed species communities (Vandermeer, 1989). Competitive production occurs when one species exerts a negative effect on another, but the species mixture uses resources more effectively than monocultures. Facilitation is where the response of one species to the environmental modification provided by another is positive. These principles are paralleled by the land equivalent ratio (LER) method for estimating intercrop performance (Mead and Willey, 1980). LER is calculated as the sum of the ratios of yields for the individual intercropped components relative to their yields in equivalent monocultures i.e.

$$\mathrm{LER} = \frac{A_I}{A_S} + \frac{B_I}{B_S} \qquad [1.1]$$

where A and B denote yields for each species and subscripts I and S represent the intercropping and sole cropping systems. LER values above 1 are indicative of competitive production and/or facilitation, whereas values below 1 suggest competitive exclusion, although there are exceptions (Vandermeer, 1989). Ong and Black (1994) regarded competition as a process which resulted in LER values below 1 being obtained, whilst the term "complementarity" was used to describe situations where LER exceeded 1 (Ong *et al.*, 1996). Competition may be more severe between similar species than between species with contrasting niches or growth habits (Vandermeer, 1989). However, Ong *et al.* (1996) suggested that densely planted monocultures may capture resources more efficiently unless one or more resource is limiting, when productivity may be improved by species mixtures if the component species capture more of the available resources or use them more effectively for growth.

These paradigms provide a valuable structure for assessing the performance of species mixtures, irrespective of whether these involve annual crops or tree-crop combinations. However, as the products of trees and crops are not interchangeable other than by weight, energy content or economic return, the use of such approaches is reduced where there is limited opportunity for growing trees and crops separately, or where trees are used for other purposes such as demarcating farm boundaries or providing anti-erosion barriers along the edges of terraces. As Vandermeer (1989) pointed out, when perennial species are inter-planted with annual crops, the focus is primarily on combining a satisfactory yield from the annual crop with an acceptable growth rate for the tree component, rather than comparing intercrop yields with those of sole crops. Van Noordwijk and Purnomosidhi (1995) pointed out that, if the tree and crop are of similar direct value to farmers relative to the area occupied, weak complementarity is sufficient to justify agroforestry, whereas complementarity has to be more pronounced if the trees have little or no direct value. Therefore, notwithstanding the longer term indirect value of trees, the use of tree species yielding valuable products provides the best opportunity for increasing the value of the system as opposed to simply increasing resource utilisation. Although it is not suggested that the inclusion of trees will always be profitable in all climatic regions, an assumption that Kessler and Breman (1991) specifically warned against, the fact that trees provide valuable products and environmental services dictates that a central objective of agroforestry should involve the optimisation, improvement and tailoring of outputs to meet the needs of farmers rather than a more esoteric justification.

1.6 AIMS AND OBJECTIVES

The work presented in this thesis focuses on single row agroforestry systems containing two indigenous East African tree species (*Croton megalocarpus* and *Melia volkensii*) and two exotic tree species from Central America (*Senna spectabilis* and *Gliricidia sepium*) and examines their effects on adjacent maize (*Zea mays*) and bean (*Phaseolus vulgaris*) crops in the semi-arid highlands of Kenya. The tree species were chosen from a range of eight species grown as overstorey trees in the **R**oots **A**nd **C**ompetition experiment (RAC) at the Machakos Research Station of the International Centre for Research in Agroforestry (ICRAF). *C. megalocarpus* was chosen as a representative evergreen species, indigenous to and popular in East Africa, while *M. volkensii* was chosen as a fast growing indigenous deciduous species currently gaining popularity in certain areas of Kenya. *G. sepium* and *S. spectabilis* were selected as nitrogen fixing and non-fixing exotic species with differing canopy phenologies. The crops chosen are typical of those commonly grown in East Africa and possess contrasting C3 (bean) and C4 (maize) photosynthetic pathways. The overall objective was to provide guidelines for efforts to improve the productivity, economic value and sustainability of agricultural systems in the semi-arid areas tropics. Specific aims were to:

(i) determine the patterns of leaf phenology in *Croton megalocarpus*, *Melia volkensii*, *Senna spectabilis* and *Gliricidia sepium* in relation to cropping seasons;

(ii) establish seasonal patterns for transpiration and photosynthesis in *C. megalocarpus* and *M. volkensii*;

(iii) establish seasonal patterns of shading beneath the canopies of *C. megalocarpus* and *M. volkensii*;

(iv) determine the growth and productivity of the trees and the yields of understorey maize and bean crops;

(v) establish the impact of rainfall interception, water uptake and shading by the trees on the yields of understorey maize and bean crops.

Details of the experimental location and design and the tree and crop species studied are given in Chapter 2.

2 LOCATION, CLIMATE AND SPECIES

2.1 THE EAST AFRICAN BIOME

The East African biome covers a series of habitats, ranging from montane, humid forest and lacustrine to savanna, thorn bushland and semi-desert. It is accepted that climate is the principal determinant of vegetation type, particularly the combined effect of rainfall and radiation on water availability. Rainfall in East Africa is lower than normal for equatorial regions, which was attributed by Gill (1991) to the desiccating effect of the surrounding desert areas. Temperatures throughout the region are generally warm rather than hot and can be distinctly cool at some times of year. In Kenya, March is the warmest month, while July or August is the coolest (Griffiths, 1972). The wildlife populations of East Africa, which were influential in shaping the vegetation of the area are now greatly reduced but, at least until 20 years ago exercised a considerable influence on vegetation communities and land development (Pratt and Gwynne, 1977). This is still the case in some areas, although cattle and goats account for the majority of herbivore effects in most areas. Man's first extensive influence on Kenyan vegetation began with forest disturbance about 1000 years ago, although disturbances in other parts of east and north-east Africa considerably predate this (Friis, 1992).

The land area of Kenya (582646 km^2) is slightly greater than that of France The population in 1986 was 21.2 million, with an annual average growth of around 4 % (World Bank, 1998). Between 1981 and 1990, the annual deforestation rate was 0.6 %; the corresponding figures for the neighbouring countries of Uganda and Tanzania were 1.0 and 1.3 % respectively. In 1990, 80 % of Kenya's labour force was involved in agriculture, and similar figures applied in Uganda and Tanzania. The proportion of cropland in Kenya rose from 3 % in 1980 to 8 % in 1993, while that in Tanzania increased from 1 to 4 %; in contrast, the proportion used for cropping in Uganda decreased from 41 to 34 % (World Bank, 1996). Thus the predominantly agricultural populations are increasing rapidly, leading to deforestation and encroachment into lower potential areas, although urbanisation has to some extent decreased the demand for land (Gichuki, 1998).

Rainfall in East Africa is concentrated mainly on the upland regions, while the semi-desert areas are restricted to lower altitudes in eastern and northern Kenya. However, altitude is not as important as relief, aspect and slope in determining rainfall (Pratt and Gwynne, 1977). East Africa has a characteristically seasonal rainfall regime whereby eastern Kenya and north-eastern Tanzania generally have bimodal rainfall patterns, whereas areas towards each tropic experience a summer maximum (Pratt and Gwynne, 1977). The bimodal regions, including the experimental site at Machakos, receive rainfall predominantly between March and May (long rains) and November and December (short rains) depending on their position relative to the passage of the inter-tropical convergence zone (cf. Section 2.2). Uganda experiences the highest mean annual rainfall, regularly receiving 750 mm yr^{-1} in over 75 % of its territory, while Tanzania receives the same amount over half of its land area. In contrast, Kenya reliably receives 750 mm yr^{-1} over one-seventh of its land area and 500 mm in four out of five years in just under three-quarters (Griffiths, 1972). When plant growth is considered, the influence of specific quantities of rainfall is modified by evaporation rate and the water-retaining capacity of the soil. Considerable rainfall may also be lost as runoff due to the frequently short and intense nature of tropical rainfall, which often occurs at night when windspeeds are low and droplet size is large (Pratt and Gwynne, 1977). The diurnal pattern of rainfall may also influence the interaction between radiation, saturation deficit and evaporation. For instance, Griffiths (1962) concluded that limited rainfall is received throughout Kenya between 0900 and 1200 h, heavy rainfall occurs in the highlands between 1500 and 1800 h, while the greatest rainfall in Nairobi is received between 2100 and 2400 h during the short rains. This link between rainfall and cloud cover is also important in determining effects on plant growth, as evidenced by the results for the 1997/98 short rains reported here.

As noted by Pratt and Gwynne (1977), rainfall in East Africa is erratic, exhibiting substantial variability in its timing, quantity and distribution within seasons; the spatial patterns of inter-annual rainfall anomalies are also complex (Ogallo, 1993). This is of great significance to agriculture and adds to the problems faced by efforts to increase productivity and yield. In an attempt to forecast rainfall, annual 'probability' tables have been compiled (Griffiths, 1972; Pratt and Gwynne, 1977) and cyclic analyses attempted (e.g. Pratt and Gwynne, 1977; Tiffen *et al.*, 1994). However, true probability can only be established if rainfall varies systematically around the averages calculated for the relatively short periods over which records are usually available. Even then, the values obtained may be of little use in established agricultural systems where farmers are already familiar with the prevailing weather conditions. Similarly, cyclic analyses are theoretically weak as they have no physical basis and usually rely even more heavily upon the repetition of previously observed patterns. The primary requirement of agriculture is for reliable guidance on forthcoming seasonal rainfall and long term shifts, neither of which is provided by the approaches described above. These methods also promote a static and retrospective view of natural systems which is detrimental to improved understanding. However, modern meteorological analytical approaches are providing an improved understanding of global weather patterns and, notwithstanding the possibility of chaotic behaviour on substantial spatial and temporal scales, may provide the key to some of the problems faced.

2.2 CLIMATE IN EAST AFRICA

The importance of rainfall in East Africa and the significance of the El Niño/Southern Oscillation (ENSO) in determining extreme events demands an understanding of the prevailing weather systems, their genesis and likely changes in their future pattern. Ogallo (1993) stated that any changes in natural environmental conditions within the region would have far-reaching socio-economic consequences and that semi-arid areas are amongst the most vulnerable to climate change. Unfortunately, our understanding is currently incomplete and there is, for example, no coupled atmosphere/ocean global climate model which provides fully realistic simulations of ENSO events (Trenberth and Hoar, 1996). However, an improved understanding of the complex and highly interactive climatic processes involved, aided by increased international collaboration, is allowing long range forecasts to be published for low latitudes (Hastenrath, 1990). Such predictions of seasonal weather and climate change used in conjunction with simple plant growth models should allow contingency plans to be developed to help neutralise the consequences of unusual or extreme weather events for the large agrarian communities of East Africa.

The dominant factor in determining East African weather systems is the annual oscillation of the Intertropical Convergence Zone (ITCZ). The ITCZ is the convergence of the northern and Southern Hemisphere trade winds which causes air to be deflected upwards, resulting in cooling and rainfall. As the sun moves seasonally over the equator and back again, the atmospheric pressure zones caused by the heating move in tandem with a lag of about one month (Griffiths, 1962). The double peak of rainfall experienced around the equator (including the Machakos experimental site) is a response to the overhead passage of the sun, and hence the ITCZ, at the equinoxes (Gill, 1991). The ITCZ migrates at a latitude of around 6 °N rather than around the equator itself due to the relative predominance of water in the Southern Hemisphere (Barry and Chorley, 1992). Consequently the ITCZ spends less time south of the equator, accounting for the relatively brief interval between the short and long rains at Machakos. The long rains between March and May and the short rains between November and December arise respectively from the slow northward and fast southward movement of the ITCZ over the region (Nieuwolt, 1977). The marked temporal and spatial variability of precipitation in the area results from the diffuse nature of the ITCZ, which is a consequence of the meteorological disturbances caused by Lake Victoria and the East African topography (Griffiths, 1972; Ogallo, 1988).

The transitional stages between the two synoptic subdivisions, signalled by the rains from the passing ITCZ, occur in May and late October (Griffiths, 1972), although the exact timing depends on location and annual irregularities. For example, the region around Mount Kilimanjaro, approximately 150 km south of Machakos, experiences the northward passage of the ITCZ between March and May and its southward passage in November and December (Griffiths, 1962). The onset of monsoonal rains is generally sharp: in India the monsoon breaks when the south-west winds arrive following a few scattered showers from the north-east winds as the ITCZ passes overhead (Barry and Chorley, 1992). In Machakos, although events are less marked, it is nonetheless usual for a few light showers to precede the first heavy downpour.

Wind direction is important for agroforestry systems involving wind breaks or tree rows (Brenner, 1995; Darnhofer *et al.*, 1989), as in the present study, since the passage of the ITCZ brings seasonal wind reversals around the equinoxes. In the Southern Hemisphere, north-easterly monsoonal winds are generally experienced in summer and south-westerly winds in winter (Gill, 1991). However, conditions vary around the globe, and in East Africa the north-easterly monsoonal flow during the austral summer is replaced by a south-easterly flow in winter (Barry and Chorley, 1992). The prevailing wind directions in Nairobi are east/north-east between October and November (before the southward passage of the ITCZ) and north-east from December to April (before its northward return; Griffiths, 1972). The monsoon circulation and the associated trade winds are, however, highly variable from year to year (Webster and Yang, 1992) depending on the intensity, location and orientation of the major semi-permanent anticyclones (high pressure areas) of Africa (Ogallo, 1988). The convergence between the African south-west monsoon and the south-east monsoon from the Indian Ocean creates further peculiarities in wind flow over eastern parts of East Africa (Friis, 1992). Furthermore, Barry and Chorley (1992) noted that, as wind does not reach a geostrophic balance at low latitudes due to the weak Coriolis effect, wind direction provides no guide to the weather pattern.

Besides the monsoon, other factors including tropical cyclones, waves in the easterly monsoon winds, jet streams, global teleconnections and extra-tropical weather systems also influence regional rainfall (Hastenrath, 1991; Ogallo, 1993). Thus the relatively recently discovered Somali jet moves up from the south-east to cross East Africa between April and July and is associated with rainfall in eastern and coastal areas (Hastenrath, 1994), while the easterly tropical jet stream which overlays the monsoon produces rainfall to its left, i.e. on its southern side, in Africa (Barry and Chorley, 1992) and may also affect the Machakos area.

2.2.1 THE EL NIÑO/SOUTHERN OSCILLATION

The effects of the El Niño/Southern Oscillation are evident over longer time scales, particularly during the East African short rains (Ogallo, 1988). Major ENSO events occur with a frequency of 2-10 years, but less severe events occur at approximately three year intervals (Barry and Chorley, 1992). However, patterns have been changing during recent decades, and according to Wang (1995), the background conditions from which El Niño evolves and which determine the characteristics of the onset of warming throughout the Pacific basin has changed considerably since the late 1970s. Furthermore, the longest ENSO since 1882 occurred between 1990 and 1995, which Trenberth and Hoar (1996) suggested may be evidence of climate change, rather than resulting from an unusually long fluctuation. These findings pose an unprecedented challenge for reliable long-range forecasting.

Nicholson and Kim (1997) reported that the modulation of rainfall in Africa by ENSO is strongest in eastern equatorial and south-eastern areas, and suggested that ENSO tends to produce opposite anomalies in equatorial and southern Africa. Their conclusion that negative rainfall anomalies occur in eastern equatorial Africa during the first half of the ENSO cycle and positive anomalies during the second half, with the opposite occurring in Southern Africa, was supported by Hastenrath (1991). However, relationships between East African weather and ENSO are further complicated by season-specific rainfall anomalies.

Based on records between 1923 and 1984, Ogallo (1988) found that the strongest correlations with ENSO in East Africa occurred between October and December, with positive rainfall anomalies being associated with low phases of SO (El Niño event) and negative anomalies with high phases. In 1997, the global climate was affected by both extremes of ENSO, with a weak Pacific cold episode occurring in January and February and one of the strongest Pacific warm episodes (El Niño) in history being recorded during the remainder of the year. The most affected regions included equatorial East Africa, which received above average rainfall during October-December; in many regions, opposite anomalies developed between 1996/early 1997 and mid/late 1997 (Bell and Halpert, 1997). Thus the 1996/97 short rains were well below average during the first part of the ENSO cycle, whereas the 1997/98 short rains brought well above average rainfall during the second half, which continued well into 1998 (Table 2.3)

2.3 THE KENYA HIGHLANDS AND MACHAKOS

The following description is based largely on information from IGDA (1976). The Kenya Highlands cover 80000 km^2 and are divided in two by the Great Rift Valley. The western Rift Highlands have a single rainy season, while the eastern Highlands have a bimodal pattern (Pratt and Gwynne, 1977); the agricultural highlands (>1500 m) have a variable mean annual rainfall exceeding 800 mm. Crops are grown in the higher, wetter regions and the more productive areas are associated with well-drained soils. Livestock is reared in the drier areas and nomadic pastoralism is practised below 1500 m in the arid or semi-arid plains and plateaux. Mean annual maximum and minimum temperatures are closely linked to altitude, but rainfall is less closely correlated and is usually a reflection of major topographical features. Both the eastern and western highlands have areas of high agricultural potential in the higher, wetter areas away from the dry north. Machakos is an isolated area of agricultural activity in a residual hill mass towards the eastern edge of the eastern Rift Highlands, and is composed of rocks of the basement system (pre-Cambrian crystalline). Ukambani, the district in which Machakos is situated, is densely populated, has an annual rainfall below 800 mm in the drier areas, and light friable soils which pose erosion problems. Land use is subsistence agriculture, the chief crops being maize, beans and cowpea.

Land tenure in Machakos district resembles private ownership (Tiffen *et al.*, 1994) in which the sons inherit shares of the land. As a result of the rapid population growth in recent decades, farm sizes are small (Table 2.1); private ownership nevertheless provides a secure base for tree planting. In recent years, increasing numbers of people have been making a living away from the land, thus decreasing further division of the farms. Fees are paid for cattle and goat grazing on government land where cultivation and tree felling are forbidden.

Table 2.1. Percentage of farmers by land ownership category from a survey of farms in Machakos and Kitui districts conducted in 1977 (Consortium, Report 3, 1978; Tiffen *et al.*, 1994).

Land area (ha)	Percentage of farms (%)
0-0.4	1.2
0.4-1.2	18.0
1.2-3.6	46.5
3.6-12	34.3
>12	0.0

The soils in Machakos District are highly variable, with some areas being rocky, and nitrogen deficiency is common, as demonstrated by the presence of chlorotic maize crops during high rainfall seasons. McCown *et al.* (1992) reported that soil fertility is generally low in Machakos and Kitui Districts and that large areas are degraded due to a lack of awareness of the need to take measures to protect the soil. The problem of erosion, so often cited as a case for the adoption of agroforestry (Young, 1989), has particular resonance in Machakos District where a unique and extensive study was carried out by Tiffen *et al.* (1994). As early as the 1920s and 1930s, Machakos District was perceived to be suffering from severe erosion caused by deforestation, overstocking, cultivation of hillslopes, and over-cultivation. Despite early efforts to plant trees on farms, with tens of thousands of seedlings being distributed to farmers since 1921, Machakos was still very bare of trees in the 1950s (Peberdy, 1958, cited by Tiffen *et al.*, 1994). This was thought at the time to be partly due to farmers' attitudes, but perhaps more important was the lack of suitable tree species (Eucalyptus and cypress were most commonly planted), ill-informed management and poor understanding of land tenure. However, the situation had changed by 1990, with a marked increase in the density and average size of trees on farms, planted as woodlots, windbreaks, hedges and in gullies to protect against erosion.

Thus, agroforestry is to some extent already successful in East Africa and fruit trees including banana, avocado, mango, paw paw and citrus are particularly popular. *Eucalyptus* sp. are common in the wetter areas closer to the Iveti hills and *Grevillea robusta* remains popular despite its susceptibility to termite attack. Of the tree species studied here, *Croton megalocarpus* is very common in Machakos District and other wetter parts of Kenya where the trees grow much larger. *Melia volkensii* does not occur naturally in Machakos District, but is common in the drier, hotter and lower-lying areas towards the coast and to the east of Mount Kenya. *Senna spectabilis* is often seen by roadsides in towns, where it is planted as an ornamental, but *Gliricidia sepium* is uncommon in the area. Interestingly, planting density in the Machakos area is inversely related to farm size (Tiffen *et al.*, 1994), suggesting that the reduction of crop yields resulting from competition is not a major factor. The increased density may result from the preference for boundary planting of trees to demarcate property and field boundaries (Ong *et al.*, 1996).

Tiffen *et al.* (1994) stated that, although past surveys suggested that the wood resources in Machakos District had and were still being overexploited, there was currently no objective evidence to suggest anything more serious than a limited scarcity of wood. In support of this view, they argued that many households were self-sufficient, the amount of time required to collect firewood was not excessive, and the firewood market was not strongly developed. However, it is likely that cheap imports of timber from other areas and illegal felling on government land caused some market distortions and limited the demand for farmed trees. A proliferation of tree felling on government land for charcoal manufacture is common in the weeks before Christmas, suggesting that revenue from sale rather than the fuel itself is sought. Tiffen *et al.* (1994) suggested that a scarcity of fuel-wood will assist further development of agroforestry, with fruit trees being most important, followed by exotic species, but with indigenous trees still having a role to play. Furthermore, population growth and the subdivision of land-holdings provide an incentive for the conversion of more grazing land to arable land and increased planting of trees.

2.4 THE RAC EXPERIMENT

The Roots and Competition (RAC) experiment was set up in 1993 to elucidate the key elements of tree/crop interactions by planting a range of tree species with differing geographic origins, phenology and nutritional characteristics (e.g. exotic *vs.* indigenous, leguminous *vs.* non-leguminous). In designing the experiment, particular attention was paid to the common practice of planting trees around the boundaries of small-holdings which is enforced by the limited space available (Table 2.1). The trees were therefore planted as single rows rather than in a grid pattern or other form of dispersed planting arrangement. The experimental design and objectives originated from the supposition that the greatest advances in improving complementarity of resource use in agroforestry systems would emerge from studies of below-ground interactions owing to the disproportionate emphasis previously placed on above-ground interactions, which had resulted in the importance of below-ground interactions being somewhat overlooked (Ong *et al.* 1991; Anderson, Muetzelfeldt and Sinclair, 1993). However, this supposition has proved difficult to verify as field studies of rooting characteristics and function are extremely laborious and generally yield information only on spatial and temporal root distribution patterns, which is still several steps away from providing a reliable understanding of the corresponding patterns of water uptake. A combination of measurements of soil moisture content with a detailed knowledge of the above-ground behaviour of the trees and crops may offer a more effective means of inferring the spatial and temporal patterns of water use. Notwithstanding the difficulty of achieving the original objectives, the experimental design of the RAC trial proved suitable for several purposes, not least because the east-west orientation of the tree rows and the continuous canopies resulting from the close spacing of the trees simplified crop shading patterns, while the deep soil and range of tree species present were ideal for studies of processes occurring at the tree/crop interface. The experiment was managed to determine atmospheric and edaphic effects on yield; thus browsing by livestock, attack by insects and poor management practices that might have adversely affected system performance on farms were eliminated to the greatest possible extent. Several institutions other than the University of Nottingham and ICRAF participated in the experiment; these included the Institute of Terrestrial Ecology and the Universities of Dundee, Makarere and Bangor.

2.4.1 LOCATION AND CLIMATE

ICRAF's Machakos Field Station is located 75 km south-east of Nairobi (1° 33' S, 37° 14' E) at an altitude of 1660 m (ICRAF, 1994). The site, shown in Plate 2.1, represents the drier end of the bi-modal highlands, with a long term annual average rainfall of c. 740 mm, divided approximately equally between the two rainy seasons. Table 2.2 shows rainfall recorded at two local sites over two different periods since 1963 to illustrate possible effects of El Niño on rainfall during the short rainy season. Potential evaporation at the experimental site varies between 95 and 165 mm month^{-1} (Huxley *et al.*, 1989) and greatly exceeds rainfall. According to the rainfall probability map produced by Tiffen, Mortimore and Gichuki (1994), Machakos receives c. 250-300 mm during the long rains in six out of ten years and c. 200-250 mm during the short rains. Topography is generally consistent with that of the highlands region of Kenya; Machakos Research Station comprises a convex upper area which gives way to a 7-20 % slope leading down to the Maruba River. The local soils are underlain by petroplinthite (murram), are dark reddish-brown, well-drained, moderately leached, weakly acidic with moderate levels of organic matter, and are susceptible to erosion (ICRAF, 1991). Soil composition within the 10-20 cm horizon was 48 % sand, 14 % silt and 37 % clay (J. Caldwell, unpublished data). Soil cores extracted during the installation of neutron probe access tubes showed that the soil profile in RAC varied between 1 and 2 m in depth. Soil nutrient status was shown not to be limiting for crop performance using maize cover crops planted prior to establishment of the RAC trial and results obtained from previous adjacent experiments.

Table 2.2. Long-term rainfall (mm) at Machakos Research Station (1991-1997) and the nearby Maruba Dam site (1963-1971).

Location	Long rains (1 Mar – 31 July)	Short rains (1 Oct – 28 Feb)	Annual total
Maruba Dam (1963-1971)	359	350	782
Machakos Station (1991-1997)	230	480	667

The US soil classification provides a detailed and useful ecophysiological tool in areas for which information is available. The soil at the experimental site is defined as an alfisol according to the United States seventh classification. A working definition of a tropical alfisol is given by Mongia and Bandyopadhyay (1993); such soils have a clay horizon containing low levels of essential nutrients, are deficient in the major elements and may also be deficient in micronutrients. Moisture stress and susceptibility to erosion are major constraints, while low aggregate stability and surface capping by rainfall, which impede seed germination and establishment and increase runoff, are common. The Soil Survey Staff (1975, as amended by ICOMLAC, 1986), indicates that soil water potential falls below wilting point (-1.5 MPa) for at least three months each year at times when the soil is sufficiently warm for plants to grow. Kandic Rhodustalfs, as occurred at the Machakos experimental site, are dark red with a clay-enriched sub-surface horizon and are found in ustic (monsoonal) or marginally aridic moisture regimes. Native plants are mostly annual species or are dormant when the soil is dry (Soil Survey Staff, 1987, quoted in Fanning and Fanning, 1989).

The classification of ecoclimatic zones on the basis of moisture index (derived from monthly rainfall and evaporation, the latter being based on radiation, air temperature, saturation deficit and windspeed, weighted for altitude and latitude) given by Pratt and Gwynne (1977) places Machakos within the dry sub-humid to semi-arid category. However, despite the fact that rainfall and temperature are of dominant importance in determining vegetation type, the classification devised by Pratt and Gwynne (1977) is of limited agricultural relevance due to the exclusion of the influence of soil type on moisture availability. Another problem associated with this type of classification is the lack of resolution in regions such as Machakos where orographic influences greatly affect rainfall and vegetation over short distances. This variability also poses problems for extension work as, although broad-brush approaches to species recommendations may increase overall productivity in specific areas, a proportion of farmers may suffer due to local environmental anomalies (Burley, 1982). The designation usually given for the dryland vegetation of the Kenya Highlands is *Acacia-Themeda* woodland (Odingo, 1971), the latter referring to *Themeda triandra* or red oat grass. Prior to its conversion to agriculture, the natural vegetation in the vicinity of Machakos Research Station included *Acacia* woodland and deciduous/semi-evergreen woodland corresponding to the semi-arid classification of Pratt and Gwynne (1997). Additional species, with their associated characteristic ecoclimatic zones, were also present, e.g. *Acacia seyal* (semi-arid ecoclimatic zone), *A. nilotica, A. tortilis, Terminalia brownii* (dry sub-humid to semi-arid to arid), *Comiphora africana* (semi-arid and arid) and *A. xanthophlea.*

Rainfall varied greatly during the four cropping seasons examined (Table 2.3), with only 98 mm (9.3 %) falling outside the cropping seasons. The two bean cropping seasons (short rains) experienced contrasting rainfall (45 and 174 % of the long term average), whereas rainfall receipts during the two long cropping seasons when maize was grown were 62 and 88 % of the long term average. Monthly climatic data are presented in Figure 2.1. The observed climatic variations resulted primarily from the seasonality of rainfall, which affected both water availability and vapour pressure deficit, and the increase in cloud cover towards the end of the long rains, which decreased temperature and radiation receipts. The 1997/98 season was unusual for its high rainfall and frequency of cloud cover, which reduced radiation receipts (Figure 2.1). Extremes of temperature were uncommon at the experimental site and the annual variation is generally small; temperature tended to increase during the short rains and decrease during the long rains.

Table 2.3. Seasonal total rainfall during the experimental period (long rains, 1 Mar – 31 July; Short rains, 1 Oct – 28 Feb).

Season	Rainfall
Long rains 1996	224
Short rains 1996/97	158
Long rains 1997	316
Short rains 1997/98	608 [1]

1- 734 mm fell in total between sowing and harvest dates.

2.4.2 LAYOUT AND MANAGEMENT

The trial was planted on 20 April 1993 after deciding on the blocking arrangement following visual assessment of the land and the performance of a maize cover crop. The site (Plate 2.1), previously covered by scrub dominated by *Acacia*, had no cropping history. The experimental design was a randomised complete block containing four replicates (Figure 2.2). The plots were fenced at the beginning of the 1996/97 short rains to prevent wild pigs and porcupines from damaging the crops. The plots were 18 x 18 m square and contained a central row of 19 numbered trees (586 trees ha^{-1}) with an east-west orientation (Figure 2.3). Soil depth generally exceeded 1.75 m, although some areas were as shallow as 1 m. To limit root interference between neighbouring plots, trenches were dug at the beginning of each cropping season to a depth of 2 m around each plot. The trees were lightly pruned before the onset of the rains to maintain a uniform canopy shape.

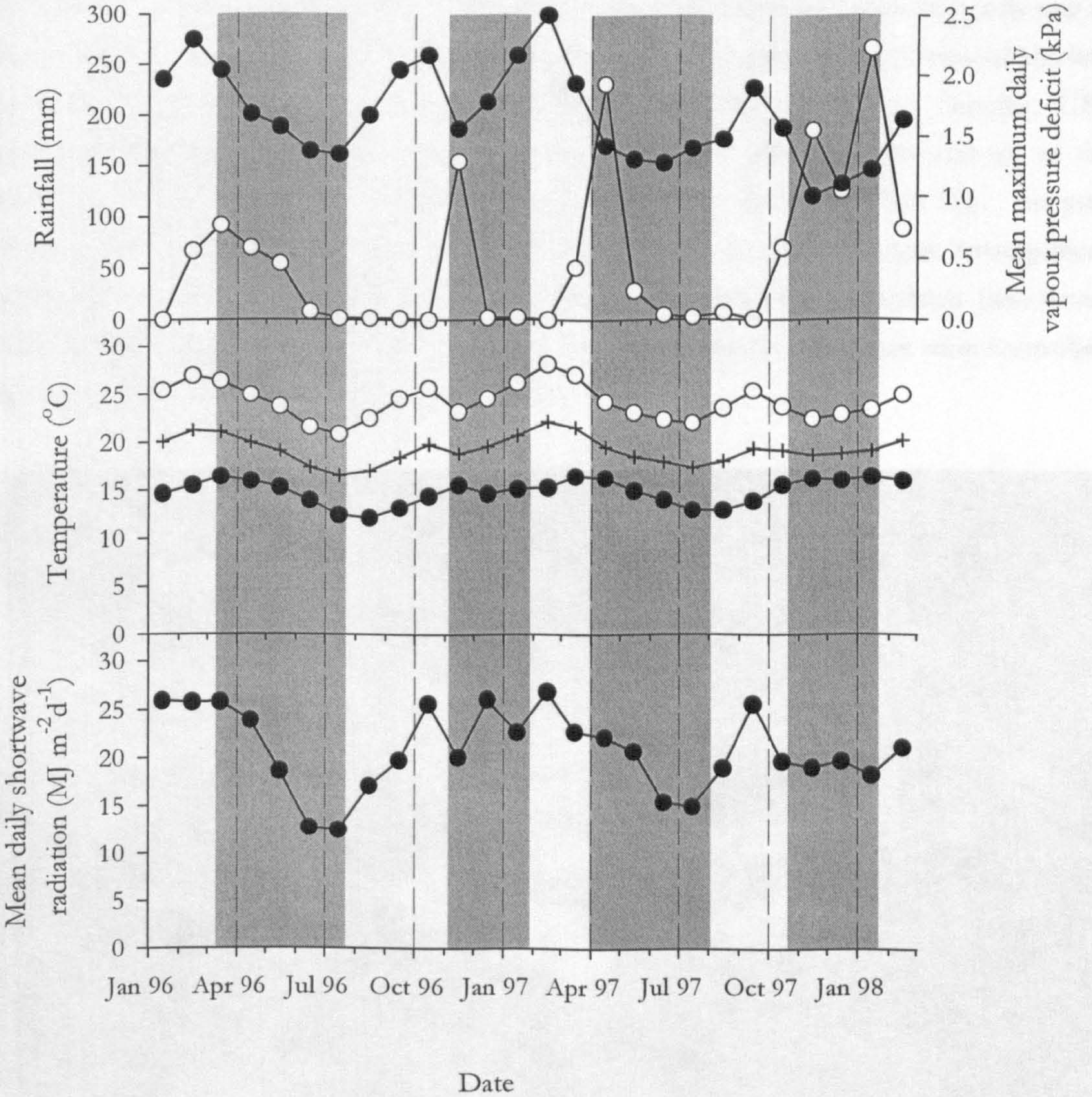
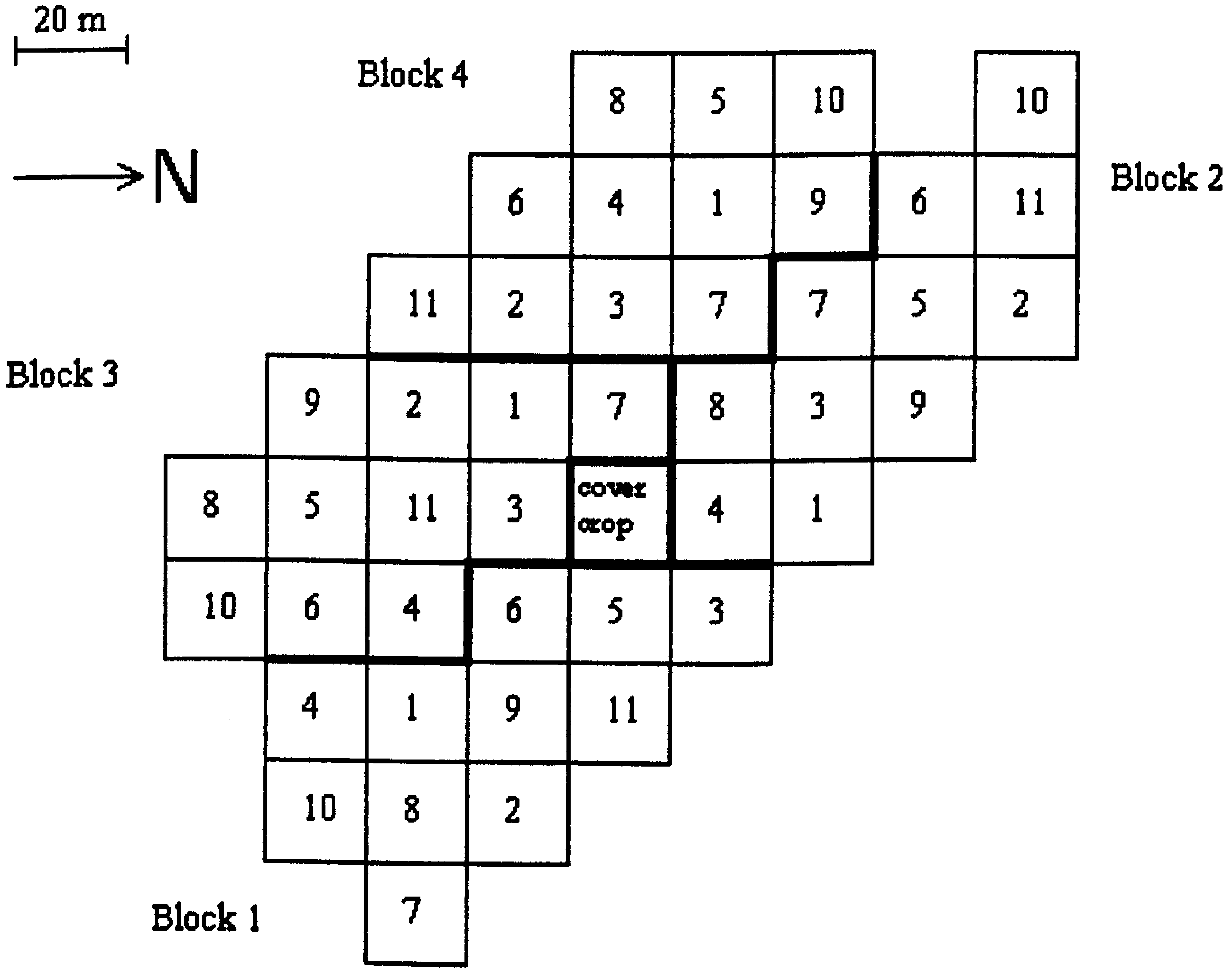


Figure 2.1. Top, Monthly rainfall (O) and vapour pressure deficit (●); middle, maximum (O), mean (+) and minimum (●) mean daily temperature; and bottom, mean daily shortwave radiation receipts, 1996 – 1998. Shaded areas represent cropping seasons.

Katumani composite maize (*Zea mays*) was sown during the long rains at a density of c. 44444 plants ha^{-1}. Seeds were planted at a spacing of 1 m between rows and 25 cm within rows, with nine rows on either side of each tree row. French beans (*Phaseolus vulgaris*) cv. Rosecoco were planted at a density of c. 111111 plants ha^{-1} during the short rains, with a spacing of 60 cm between rows and 15 cm within rows (15 rows either side of each tree row). Two or three seeds were sown at each planting point and the seedlings thinned after emergence to leave one plant at each point. The plots were marked out prior to sowing to ensure a regular planting arrangement was achieved. The whole trial required 2-4 days to sow, although the treatments reported in the present study were planted within a single day in all except the first maize season. Crop yields were determined by harvesting each row in the central 6 m wide section of each plot (Figure 2.3). To determine the effects of shading on crop growth, shade nets with neutral spectral qualities (Lowes of Dundee, UK) nominally extinguishing 25 and 50 % of incident shortwave radiation, were set up on the southern sides of the sole crop plots in each replicate as shown in Plate 7.1. An area between the nets with no shading was harvested as a control. Routine management procedures included weeding, thinning and insecticide applications (Ambush insecticide, Zeneca, Haslemere, UK) to control caterpillar and beetle attacks. Termites were controlled by excavating the nest and removing the queen.

Plate 2.1. The experimental site with a bean crop during the 1997/98 short rains.

To elucidate important tree-crop interactions and draw meaningful generalisations regarding agroforestry in semi-arid areas, four tree species were selected from the eight included in the experiment. *C. megalocarpus* was chosen as a representative evergreen species, indigenous to and popular in East Africa, while *M. volkensii* was selected as a fast growing indigenous, deciduous species currently gaining popularity in areas of Kenya. *G. sepium* and *S. spectabilis* were chosen as nitrogen-fixing and non-nitrogen-fixing exotic species with differing patterns of leafing phenology. There has been little previous research concerning the two native species, *Melia volkensii* and *Croton megalocarpus*, although casual observations indicate that both grow successfully in different areas of Kenya, with the former generally being confined to drier areas and the latter growing to a larger size in wetter areas. The eleven treatments, including the sole crop are shown in Figure 2.2.



1. **Senna spectabilis** (trees)
2. *Senna spectabilis* (hedge)
3. ***Croton megalocarpus*** (trees)
4. ***Gliricidia sepium*** (trees)
5. *Gliricidia sepium* (hedge)
6. *Grevillea robusta* (trees)
7. Leucaena colinsii (trees)
8. ***Melia volkensii*** (trees)
9. *Leucaena leucocephala* (trees)
10. *Casuarina equisitifolia* (trees)
11. **Sole crop**

Figure 2.2. Experimental layout for RAC with treatment numbers 1-11 shown for each block. Treatments shown in bold text were examined in work reported here.

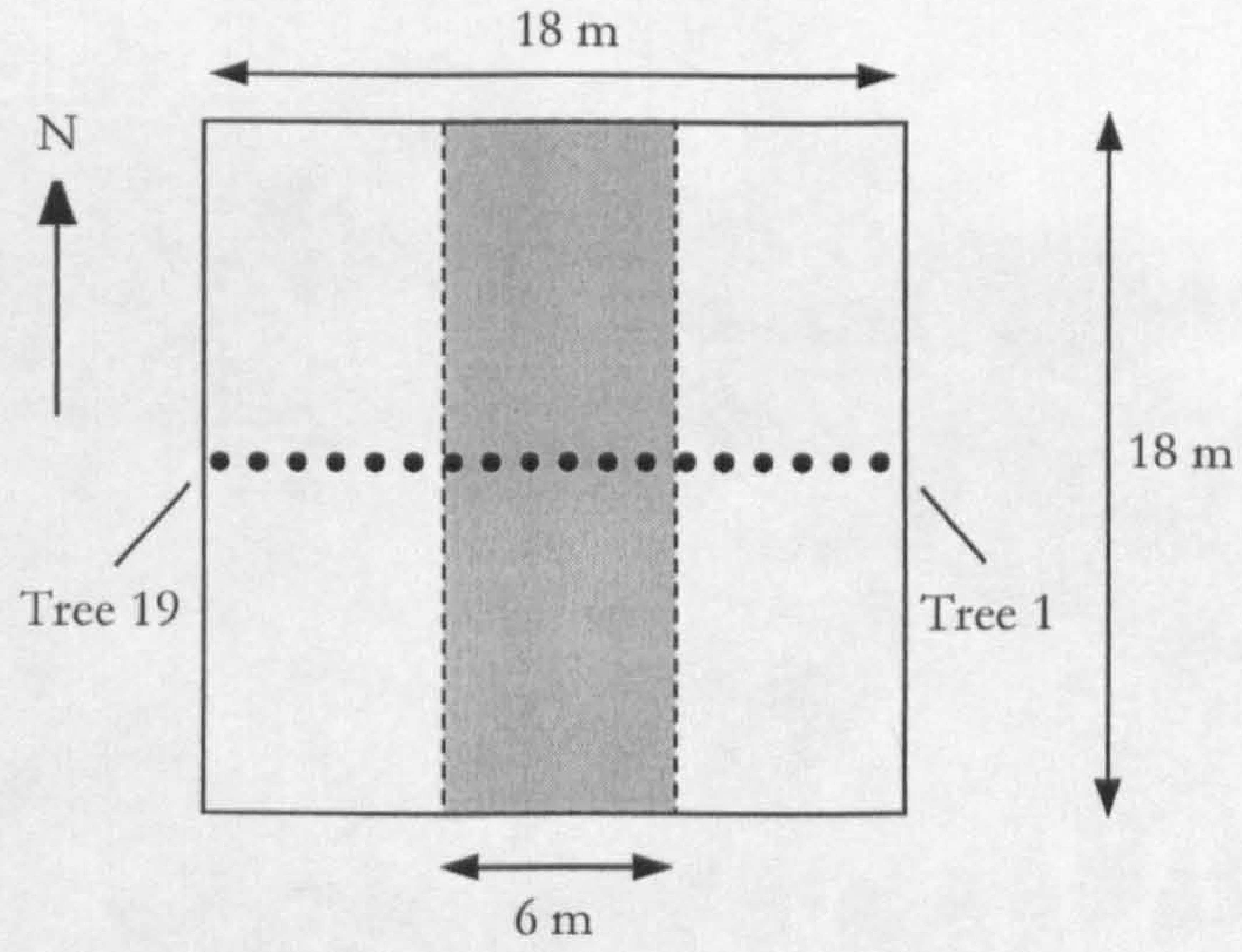


Figure 2.3. Plot layout showing tree row position and the central 6 m area where crops were harvested (shaded).

2.5 CROTON MEGALOCARPUS

Croton megalocarpus (Euphorbiaceae) Hutch (1912), shown in Plate 2.2, was described by Smith (1987) as a large monoecious or occasionally dioecious tree growing to a height of 35 m, though more commonly to 15-25 m, with a clear bole up to 20 m and a spreading crown. The leaf blades (Plate 2.3) are ovate, elliptic-ovate, elliptic-lanceolate or oblong lanceolate, 7-14 cm long and 3-7 cm wide, and are dark green above and densely silvery lepidote (covered with scales or spots) below. Its distribution includes Uganda, Kenya, Tanzania, Zaire, Rwanda, Burundi, Zambia, Malawi and Mozambique in a typical habitat of evergreen forest 1200-2400 m. *C. megalocarpus* is closely related to *C. mubango* Muell. Arg., which is native to Zaire, although it is possible that the differences may be insufficient to merit their present separation into distinct species (Smith, 1987). The seed used in the RAC experiment was collected from the Karura Forest, Nairobi.

Croton megalocarpus is commonly found along roadsides and in smallholdings around Machakos, where it provides shade throughout the dry season. Although the species is evergreen, it usually flushes after the onset of the rains and loses leaves during the long dry season (July-October), when they become ragged and parched; in drier years the trees shed all their leaves. The main uses for *C. megalocarpus* recorded by Rocheleau *et al.* (1988) are firewood, charcoal, pole-making and the provision of mulch. However, in hotter, drier areas such as Machakos, dry season shade is undoubtedly an important function.

Plate 2.2. *C. megalocarpus* trees during the 1996/97 short rainy season showing shade cast to the northern side of the trees.

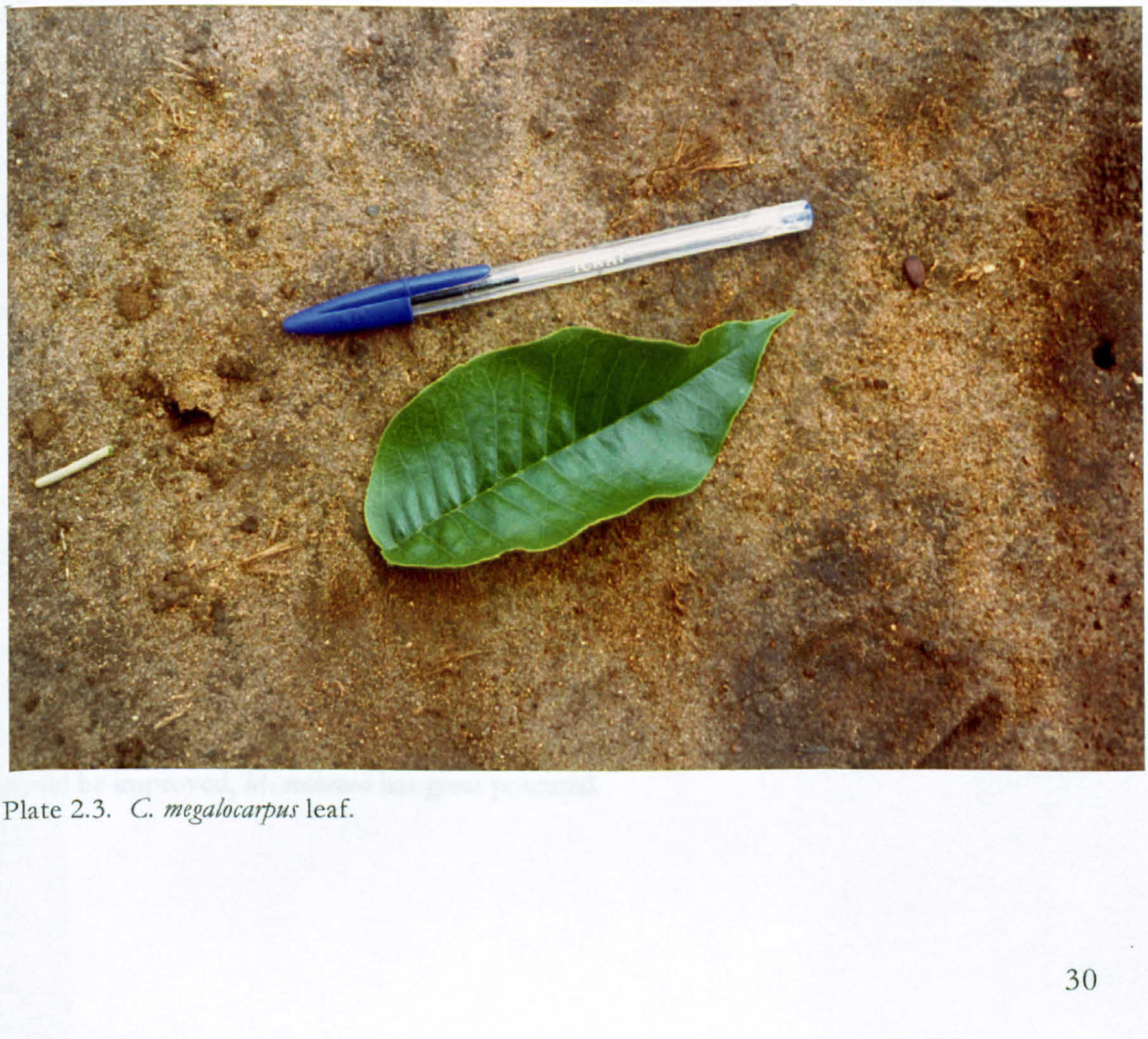


Plate 2.3. *C. megalocarpus* leaf.

2.6 MELIA VOLKENSII

Melia volkensii (Meliaceae) Gürke (1895), shown in Plate 2.4, is described by Styles and White (1991) as a tree which grows to 15-20 m in height and whose crown often shows a browse-line produced by giraffe; its leaves are up to 35 cm in length and are divided, as shown in Plate 2.5. *Melia volkensii* is widely distributed in Kenya, Tanzania, Ethiopia and Somalia, where it is commonly found as an overstorey species in deciduous bushland dominated by *Acacia* or *Commiphora*; it is occasionally found fringing seasonal watercourses and growing on rock outcrops at altitudes between 350 and 1675 m. Stewart and Blomley (1994) reported that its distribution is restricted to eastern Kenya, though it does not grow naturally in the area of the research station. Its timber is easily worked and planed and of high value. Pratt and Gwynne's (1977) classification included *M. volkensii* within their arid ecoclimatic zone. The seed used in the RAC experiment was collected in the Kibwezi area of Kenya.

M. volkensii is deciduous, shedding most or all of its leaves twice yearly during the dry seasons and regaining them around the beginning of the rains. It is used in East Africa for the production of timber used for construction and carving, fuel, fodder (fruits), mulch and green manure. As its seed germination rates are low, root suckers and wildings are more suitable for propagation (ICRAF, 1992). *M. volkensii* did not suffer from any noticeable attacks by pests and diseases during the experimental period reported here and it appears that, with the exception of goats, this is also true on farms (Tedd, 1997). Although farmers' knowledge and experience of *M. volkensii* was mixed, and occasionally conflicting, it is interesting to note that farmers around Kibwezi believed that, of the commonly grown crops, maize was most severely affected by proximity to *M. volkensii*, while beans were least affected (Tedd, 1997). A minority of farmers in Kibwezi grow *M. volkensii*, although some were precluded from doing so by the small size (<0.8 ha) of their shambas (smallholdings); adoption of *M. volkensii* was greatest in shambas larger than 2.8 ha. In Lower Embu, to the north of Machakos District, where *M. volkensii* grows wild, many farmers have begun to plant this species and some are giving up their crops because of the high value of the timber. However, although the timber is valuable in some areas, especially in Lower Embu (J. Mulatya, pers. comm.), no developed market exists in other areas. The local success of the species therefore depends upon on its biological suitability and the market for timber within specific areas. Tedd (1997) concluded that, although management and knowledge could be improved, *M. volkensii* has great potential.

Plate 2.4 *M. volkensii* trees in the experimental plot during the 1997/98 short rainy season showing a canopy platform from which leaf gas exchange measurements were made.

Plate 2.5. *M. volkensii* leaf.

2.7 SENNA SPECTABILIS

Senna spectabilis (Caesalpiniaceae), formerly *Cassia spectabilis* native to tropical America, is a medium sized deciduous tree growing to a height of 15 m (Little, Woodbury and Wadsworth, 1974). In the bimodal rainfall areas of Kenya, it sheds its leaves prior to the long rains and regains them before their onset. Casual observations suggest that *S. spectabilis* has a widespread rooting system and is suited to lighter soils (Rocheleau *et al.*, 1988). Its termite-resistant wood is used for poles, fuelwood, charcoal, and tool handles, while its foliage may be used as mulch (ICRAF, 1992). The seed used in this study was collected in Luanda, Angola. The natural range of Senna extends from Southern Mexico through central America to Colombia (Little, Woodbury and Wadsworth, 1974), where rainfall patterns vary between aseasonality and May-December rains (Meteorological Office, 1977).

2.8 GLIRICIDIA SEPIUM

Gliricidia sepium (Papilionaceae) is a native of Central America growing to 7-8 m; the Retalhuleu provenance used in RAC was of Guatemalan origin (~14-16 °N), where the rainy season extends from approximately May to November but may continue throughout the year in some areas (Meteorological Office, 1977). *G. sepium* is a small to medium sized tree with a spreading crown which usually attains a height of 10-12 m. Its leaves are odd-pinnate, growing to a length of 30 cm with ovate or elliptic leaflets 2-7 cm long and 1-3 cm wide (Little and Wadsworth, 1964). In its native habitat, *G. sepium* is largely deciduous during the January to May dry season (Simons and Stewart, 1994), although Whiteman *et al.* (1986) reported that the leaves were shed when night temperatures fell below 15 °C. It is leguminous and considered to be a pioneer species in its native habitat, and is often toxic and unpalatable to livestock (Simons and Stewart, 1994). *G. sepium* is more commonly used in the humid tropics and in coppice form for alley cropping and fodder (Gutteridge and Shelton, 1994), although Heineman *et al.* (1997) found that incorporation *G. sepium* leaves into the soil in experimental plots in Western Kenya improved soil nutrient status. Although the Retalhuleu provenance showed stable and superior production for both leaf and wood production across a wide range of sites in an international trial (Simons and Stewart, 1994), the trees in RAC suffered from insect and fungal attack and were generally in poor condition, possibly reflecting the poor drought resistance (Shelton, 1994) and reduced yield under cooler conditions reported by (Swasdiphanich, 1993). In Kenya, *G. sepium* is deciduous, shedding its leaves during the July-October dry season and not flushing until near the end of the year. The trees are termite-resistant and are used for the production of fuel, charcoal, timber, poles, mulch, green manure, food (vegetable and oil), fodder and furniture (ICRAF, 1992). It is suitable for use on acidic, basic and infertile soils (Rocheleau *et al.*, 1988).

2.9 CROPS

Two crop species were used in the experiment reported here, maize during the long rains and beans during the short rains. These crops were chosen because of their local popularity, a staple food being boiled maize and beans, and their suitability to their chosen seasons with regard to their relative yielding properties and drought resistance. In addition, the use of C3 and C4 species enabled the effects of the modified light/water regimes imposed by the trees on crops with contrasting photosynthetic pathways and shade responses to be examined.

2.9.1 MAIZE

Zea mays L. (Katumani composite B), a short duration variety which flowers within approximately two months of planting and reaches maturity within four months, was used (Acland, 1971). Katumani composite was developed for drier areas with unreliable rainfall at the Kenya Agricultural Research Institute (KARI) station at Katumani, a few kilometres from Machakos Research Station, and was selected in 1968 on the basis of its drought escape characteristics (i.e. rapid maturity) rather than drought resistance from over 500 lines (Tiffen *et al.*, 1994). Composite maize comprises a variety of genotypes selected and grown together to spread the risk of crop failure by inclusion of drought resistant and high yielding genotypes. Katumani composite is cross-pollinated, allowing farmers to save and plant their own seed; indeed, one third of 40 farmers interviewed in the Machakos area use Katumani maize exclusively, while another third also used local or hybrid varieties (Tiffen *et al.*, 1994).

The popularity of maize in the East African Highlands results from its high yields relative to indigenous cereals, its natural resistance to attack by pests, diseases and birds, and the lack of any requirement for threshing or winnowing (Acland, 1971). In deep, well-drained fertile soils, its roots may extend to a depth of 3.6 m (Acland, 1971), although Purseglove (1985) reported a maximum rooting depth of 2.5 m and that some roots may grow horizontally for 0.5-1.0 m before turning sharply downwards. Young plants are susceptible to high soil moisture contents, while excessively wet soils around sowing may reduce yield. The most critical stage of development is the 30 day period of maximum growth which precedes pollination, when low temperature or water deficits result in yield reductions (Purseglove, 1985). Towards harvest, dry conditions are needed to aid grain maturation and prevent ear rot. Maize requires well-drained soil with a good nutrient supply. Nitrogen deficiency is evident from the yellowing of the lower leaves, from which nitrogen is redistributed to younger leaves, commencing at the tip and extending along the midrib (FAO, 1980). The growth stages most commonly considered during field studies of maize are those between sowing, germination, floral initiation, tasselling, silking, physiological maturity (maximum grain dry weight) and final harvest (FAO, 1980). Yields are greatest when Katumani is grown at a population of c. 99000 plants ha^{-1} under unlimited rainfall conditions, although water stress may pose a serious risk during drought periods at such a high density. Ineffective weed control is one of the main contributory factors limiting yields in East Africa as the plants may never fully recover if checked by weeds during early growth. Yields of up to 3350 kg ha^{-1} are obtained in Machakos District, although mean yields are considerable lower (C. Ong, pers. comm.).

2.9.2 BEANS

French beans (*Phaseolus vulgaris* L. cv. Rosecoco) were grown during the short rains. Nodulation of the roots is very variable as the common strains of *Rhizobium* bacteria present in East Africa belong to the cowpea group, which do not colonise *Phaseolus* sp. effectively. Beans are almost completely self-pollinating under most conditions. The taproot grows rapidly to a depth of up to 1 m depending on soil conditions, while extensive lateral rooting is confined mainly to the top 15 cm (Purseglove, 1968). The period between sowing and first flowering is approximately five weeks at an altitude of 1200 m and continues for about two weeks. During this period, excessive rain may cause flower drop (Purseglove, 1968). Approximately two weeks is required for flowers to produce fully expanded pods and a further 4-5 weeks is necessary for these to mature and dry out, giving a total growth period of approximately three months. Although beans are not drought resistant and require good moisture supplies throughout their life-cycle, excessive rain increases the incidence of disease (Purseglove, 1968). Rainfall towards the end of the season may also create problems by delaying drying and inducing attack by various pests and diseases. Yields are greatest on freely draining soils with a reasonably high nutrient content, but are nevertheless notoriously low, usually being between 220-670 kg ha^{-1} in East Africa. However, yields of up to 1100 kg ha^{-1} may be obtained with higher inputs (Acland, 1971).

3 PHENOLOGY

3.1 INTRODUCTION

Lieth (1974) defined phenology as the study of: (i) the rhythm of repetitive biological events; (ii) the biotic and abiotic causes of these events; and (iii) the relation between the phenophases (i.e. periods during which a specific phenological event is taking place) of individual or different species. In agroforestry systems, the rhythms and causes of tree phenophases and their temporal relationship with cropping periods are important in determining the pattern of tree-crop interactions. Knowledge of these rhythms and their origins is necessary both for the extrapolation of experimental results to other climatic regions and to provide criteria for selecting genotypes for specific climatic regions or agroforestry systems.

The phenology of tropical forests is distinct from that of temperate vegetation owing to the more limited seasonal variation in temperature and the relative absence of photoperiodic and thermoperiodic adaptations (Reich, 1995). Thus an increasing proportion of tropical tree species become deciduous as the dry season becomes increasingly severe, while both evergreen and deciduous species often produce leaves episodically (Reich, 1995). In tropical savannas exhibiting a seasonal climate, temporal growth patterns are linked to the rhythms of the wet and dry seasons (Williams *et al.*, 1997). Reich and Borchert (1984) concluded that seasonal variation in water availability is important in determining the seasonal development of tropical trees as changes in the physiognomy of tropical forests result primarily from seasonal variation in rainfall which, in conjunction with soil moisture availability, is the principle determinant of tree water status. Thus, in semi-arid areas such as Machakos District in the Central Highlands of Kenya, where ground water is absent and seasonal variation in rainfall determines water availability and hence the cropping period, temporal convergence between tree and crop growth is likely. Agroforestry systems in which the trees and crops occupy the same above-ground space and soil horizons are therefore likely to be constrained in the extent to which temporal complementarity, sensu Ong *et al.* (1991a) may be realised. However, tree water status is a function not only of seasonal variation in water availability, but also of its structural and functional state (Reich, 1995); thus periods of maximum leaf cover do not always correspond closely with the rainy seasons. Indeed, a small number of 'hygrophobic' species shed their leaves during the wet season and flush again prior to or at the onset of the ensuing dry season (Koriba, 1958). *Faidherbia albida*, a species well known to agroforestry, displays such phenological patterns in areas with a single annual rainy season (Dunham, 1991; cf. Sanchez, 1995 for agroforestry review) by accessing deep water tables (Roupsard, *et al.*, 1999). Elucidation of the phenological patterns of tree species in relation to climate and cropping periods, although often neglected, is therefore central to the comprehension of the functional aspects of agroforestry systems. Such information is especially useful where trees have been introduced from different climatic regions and also for genotype selection where the extent to which phenophases are under endogenous (genetic) or exogenous (environmental) control determines heritability (Falconer and Mackay, 1996).

The prevailing bimodal rainfall pattern in Machakos District provides an attractive environment for phenological comparisons of species which are naturally distributed in zones with differing annual rainfall patterns. Thus the considerable seasonal and interannual variability in the quantity, duration and timing of the rains at Machakos is conducive to elucidating the links between phenophases and water availability. As daylength between latitudes between 0 and 5° varies by between 2 and 35 minutes over the annual cycle (List, 1966), and by only 10 minutes between solstices at the experimental site (calculated according to Monteith and Unsworth, 1990), photoperiod is unlikely to have been a factor in determining phenophases. The work described in this chapter focuses on two indigenous species, *Melia volkensii* and *Croton megalocarpus*, which occur naturally in the bimodal rainfall areas of East Africa, and two exotic species, *Senna spectabilis* and *Gliricidia sepium* which are native to the monomodal rainfall areas of central America. *C. megalocarpus* grows naturally in the Central Kenyan Highlands, but is more common in higher rainfall areas; casual observation suggests that Machakos is towards the drier end of its range. *M. volkensii* does not occur naturally in the vicinity of the experimental site, but is widely distributed in lower, drier areas in the arid ecoclimatic zone (Pratt and Gwynne, 1977). The natural range of *Senna spectabilis* extends from Southern Mexico (c. 20 °N) through Central America to Colombia (c. 0 °N; Little, Woodbury and Wadsworth, 1974), where rainfall varies between aseasonality and a monomodal rainfall distribution (May-December; Meteorological Office, 1977). The *Gliricidia sepium* provenance used in the experiment was of Guatemalan origin (c. 14-16 °N) where the rainy season extends from May to November, with aseasonality being prevalent in some areas (Meteorological Office, 1977). In its native habitat, *G. sepium* is largely deciduous during the dry season between January and May (Simons and Stewart, 1994).

The aims of the work described here were to determine for each species: (i) the seasonal patterns of leaf cover, leaf flushing and leaf fall; (ii) the inter-annual variation in these patterns; (iii) the degree of inter-specific variation in deciduousness; (iv) whether the leaf phenophases are synchronous within and between species; and (v) whether the phenophases are associated with changes in climatic variables.

3.2 METHODS

3.2.1 PHENOPHASE SCORING

Leaf phenophases were assessed for all four species at c. 14 d intervals between March 1996 and January 1998, a period spanning the 1996/97 and 1997/98 short rains (October-February) and the 1997 long rains (March-July); however, measurements did not begin until after the major phenophasic changes at the beginning of the 1996 long rains had taken place. Trees 5-15 (Figure 2.3) were scored individually for leaf cover, leaf flushing and leaf fall in all four replicate plots. Trees 1-4 and 16-19 were ignored to eliminate edge effects which were unrepresentative of the population as a whole. The phenological status of the trees was characterised as follows:

(i) **leaf cover**; the proportion of the potential canopy, as defined by the extent of the outer branches, covered with leaves. The scores ascribed were 0 (absent), 1 (low), 2 (intermediate) and 3 (high).

(ii) **flushing**; the proportion of the canopy provided by young foliage; new foliage could be distinguished in all species by its colour and size. Scores ascribed to categories 0-3 as described above.

(iii) **leaf fall**; scoring involved assessing both the proportion of the canopy which consisted of senescent leaves and the quantity of newly fallen leaves (discernible by colour) under the trees. Scores were ascribed to the categories described above.

Trees flowering and fruiting periods were also recorded, but are not reported here as the focus of the present study was directed towards processes affecting light interception and transpiration.

3.2.2 CLIMATIC CONDITIONS

Climatic data comprising rainfall, atmospheric vapour pressure deficit (D), air temperature and total short-wave radiation were compiled from half-hourly records from an automatic weather station located close to the experimental plots (Model WS01, Delta T, Cambridge, U.K.). Vapour pressure deficit was calculated according to Buck (1981, cited in Jones, 1992). Volumetric soil moisture content was measured at weekly intervals using a Wallingford neutron probe (Institute of Hydrology, Wallingford, UK; cf. Appendix 1, Section7.2.2). Measurements were made at 20 cm intervals between 20 and 160 cm depth at distances of 1.0, 2.5, 4.0, 5.5, 7 and 8.5 m from the northern side of the tree rows. For the purposes of analysis in this chapter, measurements at a depth of 20 cm, averaged over measurement points within 5.5 m of the tree row, were used to represent the surface soil horizon which responded rapidly to rainfall, whilst measurements made at 120 cm depth were used to represent water stored in deeper soil horizons.

3.3 RESULTS

3.3.1 CLIMATE

Rainfall during the measurement period fluctuated seasonally, exhibiting the bimodal annual pattern typical of the area (Figure 2.1). Total rainfall receipts (Table 3.1) were close to the 1991-97 field station average of 230 mm during the 1996 long rains and above average in 1997. Seasonal rainfall during the 1996/97 and 1997/98 short rains fell on either side of the 1991-97 average of 480 mm and differed greatly, with over 4.5 times as much rainfall being received during the latter season. The first significant rainfall event (defined here as exceeding 10 mm d^{-1}) of the 1996 long rains arrived 40 days earlier than in 1997, while the first significant rainfall event of the 1996/97 short rains was 21 days later than in 1997/98 (Table 3.1).

Table 3.1. Date of first rains (>10 mm d^{-1}) and total seasonal rainfall during the measurement period.

Season	Rainfall[1]	Date of first rain >10 mm d^{-1}
Long rains 1996	224	18 February 1996
Short rains 1996/97	158	11 November 1996
Long rains 1997	316	30 March 1997
Short rains 1997/98	608	21 October 1997

1 – Rainfall totals are for the periods between 1 March-31 July (long rains) and 1 October-28 February (short rains).

Maximum daily vapour pressure deficit (D) decreased as rainfall increased (Figure 2.1), with the highest values being recorded before the onset of the rainy seasons, after which the values declined rapidly to their seasonal minimum. The high rainfall during the 1997/98 short rains is reflected by low D values. Variations in the pattern of maximum daily temperature (Figure 2.1) showed a similar seasonal periodicity to D, with a maximum being observed prior to the rains followed by decline once the rainy season commenced. Minimum daily temperature varied less and remained relatively constant or increased during the rainy seasons, presumably because of the increased night-time cloud cover. Mean daily solar radiation receipts (Figure 2.1) reached a minimum during June and July, when conditions are commonly overcast in the region. Radiation receipts were also lower during the wetter seasons, as was particularly noticeable during the 1997/98 short rains when cloud cover was abundant. Soil moisture contents at saturation, field capacity and wilting point measured close to the experimental site are shown for reference in Table 3.2. During the study, soil moisture content at a depth of 20 cm increased rapidly to >25 % following rainfall and returned to <15 % in approximately 3 months in all plots, as shown in Figures 3.5-3.8. Soil moisture at 120 cm remained relatively constant throughout the measurement period except during the latter part of 1997, when the values increased to a maximum approaching 30 %.

Table 3.2. Volumetric soil moisture content (%) at saturation, field capacity and wilting point (Kiepe, 1995).

Depth (cm)	Saturation (0 kPa)	Field capacity (-10 kPa)	Wilting point (-1.5 MPa)
30	40	26	11
110	38	34	16
150	37	32	16

3.3.2 SEASONAL AND ANNUAL PHENOPHASE PATTERNS

The seasonal patterns for leaf cover, flushing and leaf fall are shown in Figures 3.1-3.4 for all four species throughout the experimental period, together with the cropping periods and daily rainfall. The bars show the standard error of the replicate means and hence are indicative of the degree of asynchronicity between replicates. The episodic nature of the phenophases shown by all four species comply with Reich and Borchert's (1984) assertion that such patterns are typical of both evergreen and deciduous trees in tropical areas experiencing more severe dry seasons (decreasing precipitation and increasing D). The principal differences in leaf cover patterns were between the indigenous and exotic species. Thus the exotics, *S. spectabilis* and *G. sepium*, exhibited one main period of low leaf cover annually, corresponding approximately to the dry season preceding the short rains, whereas *M. volkensii* and *C. megalocarpus* showed reduced leaf cover during both dry seasons. *C. megalocarpus* was the only species to maintain permanent leaf cover. Figures 3.5-3.8 show the percentages of trees in each replicate which began to flush or commenced leaf fall following periods of complete cessation, and are referred to in the following synopsis of species responses.

Croton megalocarpus

C. megalocarpus (Figure 3.1) exhibited the least episodic phenophases of the four species examined as all trees retained leaf cover throughout the measurement period. Flushing increased after the first rains of the season and continued into the following dry season, but decreased towards the end of the dry season when periods of low leaf cover occurred. Only a limited number of trees ceased flushing during the driest months. Full leaf cover was not attained until midway through the 1996/97 and 1997/98 short cropping seasons; however, during the 1997 long rains, rapid flushing resulted in full cover being achieved earlier in the cropping period. Limited leaf fall occurred almost continuously, decreasing to zero only during the wettest periods.

Although complete cessation of flushing was infrequent (Figure 3.5), the intensity of flushing consistently increased in all trees after the first 10 mm d^{-1} rainfall event of each rainy season, when soil moisture content at 20 cm began to increase (Table 3.3). It should be noted that, as flushing occurred almost continuously in *C. megalocarpus*, Table 3.3 shows the dates when flushing increased, whereas flushing onset dates are shown for all other species. On the single occasion when leaf fall ceased for some trees in all replicates, it recommenced when soil moisture content at depths of 20 and 120 cm fell to c. 27 % (Table 3.4). This result may be less meaningful than for the other species examined as limited leaf fall was normal for *C. megalocarpus* at the Machakos research site.

Interannual variation in the phenophases for *C. megalocarpus* was largely attributable to the timing of rainfall. Thus the increase in flushing at the beginning of the short rains occurred one month later in 1996 than 1997, and on both occasions followed the first significant rainfall event (10 mm d^{-1}), which was 21 days later in 1996 (Table 3.3). The flushing period at the onset of the 1997 long rains was later than in 1996, when the first significant rainfall occurred 41 days earlier (17 February 1996); however, the precise date could not be established because flushing commenced before scoring began. The higher flushing intensity during 1997 than 1996 reflected the higher rainfall. As leaf fall in *C. megalocarpus* was continuous and rarely ceased completely, comparison of the onset dates for leaf fall between seasons and years was not possible.

Melia volkensii

M. volkensii (Figure 3.2) was characterised by major reductions in leaf cover during the dry seasons which preceded both the short and the long rains. Flushing consistently began prior to the onset of the rains following periods of high leaf fall and low leaf cover, and leaf cover reached maximum levels during the early stages of the cropping seasons. Leaf fall ceased completely only for short periods following flushing, and when leaf fall recommenced following cessation this occurred predominantly during the rainy seasons (Figure 3.6). Leaf fall increased sharply during the latter stages of the rainy seasons and this, in combination with the reduced flushing, resulted in a decline in leaf cover prior to crop harvest. Leaf fall increased rapidly under the very moist conditions prevailing during the early stages of the 1997/98 short rains, as is discussed further below.

The onset of flushing in *M. volkensii* invariably occurred when soil moisture content at a depth of 20 cm was below field capacity (c. 9-10 %) and either falling or stable, as shown in Table 3.3. Flushing began approximately one month before the onset of the 1997 long rains even though rainfall during the previous season had been unusually low (Table 3.1), suggesting that stored water was available either in the soil or within the trees themselves. Leaf fall began when mean soil water content at 120 cm was 16.5-17.5 % except for the 1997/98 short rains when the values at 120 cm were unusually high. No consistent relationship between soil moisture content at 20 cm and the onset of leaf fall was apparent.

M. volkensii showed extensive interannual phenophasic variation that was apparently not attributable to differing climatic patterns. Thus the flushing period prior to the short rains began approximately six weeks earlier in 1996 than 1997, preceding the first significant rainfall event in 1996 by almost three months and by one month in 1997 (Table 3.3). Flushing also preceded the first significant rainfall event of the 1997 long rains by approximately one month. The periods of leaf fall, which peaked during the early stages of the dry season (Figure 3.2), were variable in intensity and length, although the duration of leaf fall during the short dry season preceding the 1997 long rains was shorter and less intense than others. The onset dates for leaf fall (Figure 3.6) indicate that, although substantial interannual variation was apparent, the leaf fall predominantly commenced towards the end of the rainy seasons.

Senna spectabilis

S. spectabilis (Figure 3.3) lost almost all of its leaf cover prior to the short rains but maintained full cover during the dry season preceding the long rains. The single major annual flushing period occurred prior to the onset of the short rains after leaf fall ceased. Maximum leaf cover was maintained throughout the short growing season, but decreased towards the end of the long rains. Leaf fall was less episodic than in *M. volkensii* and remained constant between January and July following a flushing peak.

In common with *M. volkensii*, all flushing onset dates occurred when soil moisture content was below field capacity and falling (Table 3.3). Also in common with *M.*

volkensii, flushing followed periods of low leaf cover, although a minor flushing event occurred around the time of the first significant rainfall of the 1997 long rains, when leaf cover had not previously fallen (Figure 3.3). Leaf fall began when soil moisture content at 120 cm was 17-18 % except during the 1997/98 short rains when, in common with the other species examined, leaf fall commenced when soil moisture content was unusually high (Table 3.4); this is discussed further below. During both the 1996/97 and 1997/98 short rains, leaf fall began when surface soil layers were still relatively moist.

S. spectabilis flushed approximately 11 weeks prior to the first significant rainfall of the 1996/97 short rains and, similarly to *M. volkensii*, approximately one month prior to the 1997/98 short rains (Table 3.3). Although *S. spectabilis* flushed slightly later than *M. volkensii* in 1996, both species showed an identical pattern of events prior to the 1996 and 1997 short rains. Little difference in leaf fall patterns between years was evident; during both 1996 and 1997, leaf fall ceased towards the end of August, when the trees were predominantly leafless, and recommenced during late November following flushing. During 1997, leaf fall remained relatively constant and was synchronous in all replicates for most of the year. In 1996, however, when rainfall was lower, leaf fall was more episodic and reached higher intensities (Figure 3.3).

Gliricidia sepium

G. sepium (Figure 3.4), in common with *S. spectabilis*, maintained leaf cover during the dry season preceding the long rains but, in sharp contrast, major flushing events occurred twice annually. The peak period of flushing onset preceded the first significant rainfall (>10 mm d^{-1}) of the 1997/98 short and the 1997 long rains, but occurred after the first significant rainfall of the 1996/97 short rains (Table 3.4). However, even during the latter season, a number of trees began flushing before the onset of the rains (Figure 3.8). Prior to the 1997 long rains, flushing was not preceded by increased leaf fall or a major reduction in leaf cover as was the case for the other flushing events, suggesting that, on this occasion, flushing may have been triggered by an exogenous stimulus. Although flushing began before the onset of the rains, it did not attain its full intensity until after the rainy season had commenced (Figure 3.4). Leaf cover during both short rainy seasons did not attain its maximum levels until near the end of the cropping period, but was maintained at near-maximal levels throughout the long rains.

The peak period for the onset of flushing at the beginning of the 1996/97 short rains occurred between 4 and 14 days after the first significant rainfall, when rehydration of the surface soil horizons had taken place (Table 3.3). However, as stated above, a number of trees began flushing during the preceding dry season, when soil moisture content at 20 cm was below the wilting point. Flushing began between 6 and 20 days before the first significant rainfall of the 1997/98 short rains, and between 16 and 27 days before the 1997 long rains, at times when soil moisture content was low and falling (Table 3.3). The flush which preceded the 1997 long rains did not reach its maximum intensity until one month later following rainfall, suggesting that insufficient soil moisture was available. Leaf fall began when soil moisture content at 120 cm was 16-17 % and exhibited a similar pattern to *S. spectabilis*, in which leaf fall began 1-2 months earlier when soil moisture contents were slightly higher (cf. Figures 3.3 and 3.4). In common with the other species examined, leaf fall during the 1997/98 short rains began when soil moisture content at both the 20 and 120 cm soil depths was relatively high.

The peak periods of flushing onset varied between years in accordance with the date of the first significant rainfall, despite occurring in advance of rainfall. Thus the onset of flushing at the beginning of the 1996 short rains occurred over one month later than in 1997, when the first significant rainfall was received 21 days earlier (Table 3.3). Leaf fall patterns were broadly similar in both years, reaching a peak in September which was followed by a reduction during the short rains and a resumption in December/January, towards the end of the short rains (Figure 3.4). The onset of leaf fall (Figure 3.8) followed a similar pattern to *S. spectabilis*, occurring at approximately the same time during both the 1996/97 and 1997/98 short rains. In common with *S. spectabilis*, leaf fall did not cease during the 1997 short rains, as had occurred in 1996 when rainfall was lower.

The onset events for leaf fall in all species during the 1997/98 short rains were unusual in that volumetric soil moisture content was well above the wilting point. Between the two scoring occasions when leaf fall began, maximum soil moisture contents for all four species reached 26-28 % at 20 cm and 28-30 % at 120 cm, close to field capacity (Table 3.2). The resumption of leaf fall in *C. megalocarpus* and *G. sepium* was less remarkable as leaf fall had been almost continuous and had not previously reached such a low a level. Similarly, leaf fall in *S. spectabilis* was limited during this period and had been close to zero during the preceding 3-4 months. A similar pattern occurred during the 1996/97 short rains (Table 3.4). *M. volkensii*, however, showed a more dramatic promotion of leaf fall, which rapidly increased to a maximum as soil moisture content at 120 cm increased to c. 31 % (Table 3.4). Leaf cover therefore decreased although flushing continued (Figure 3.2). In contrast to other leaf fall periods, leaves were lost whilst still green. Similar though less conspicuous events occurred during the 1997 long rains, when yellowed leaves began falling whilst soil moisture content at 20 cm remained high (Table 3.4).

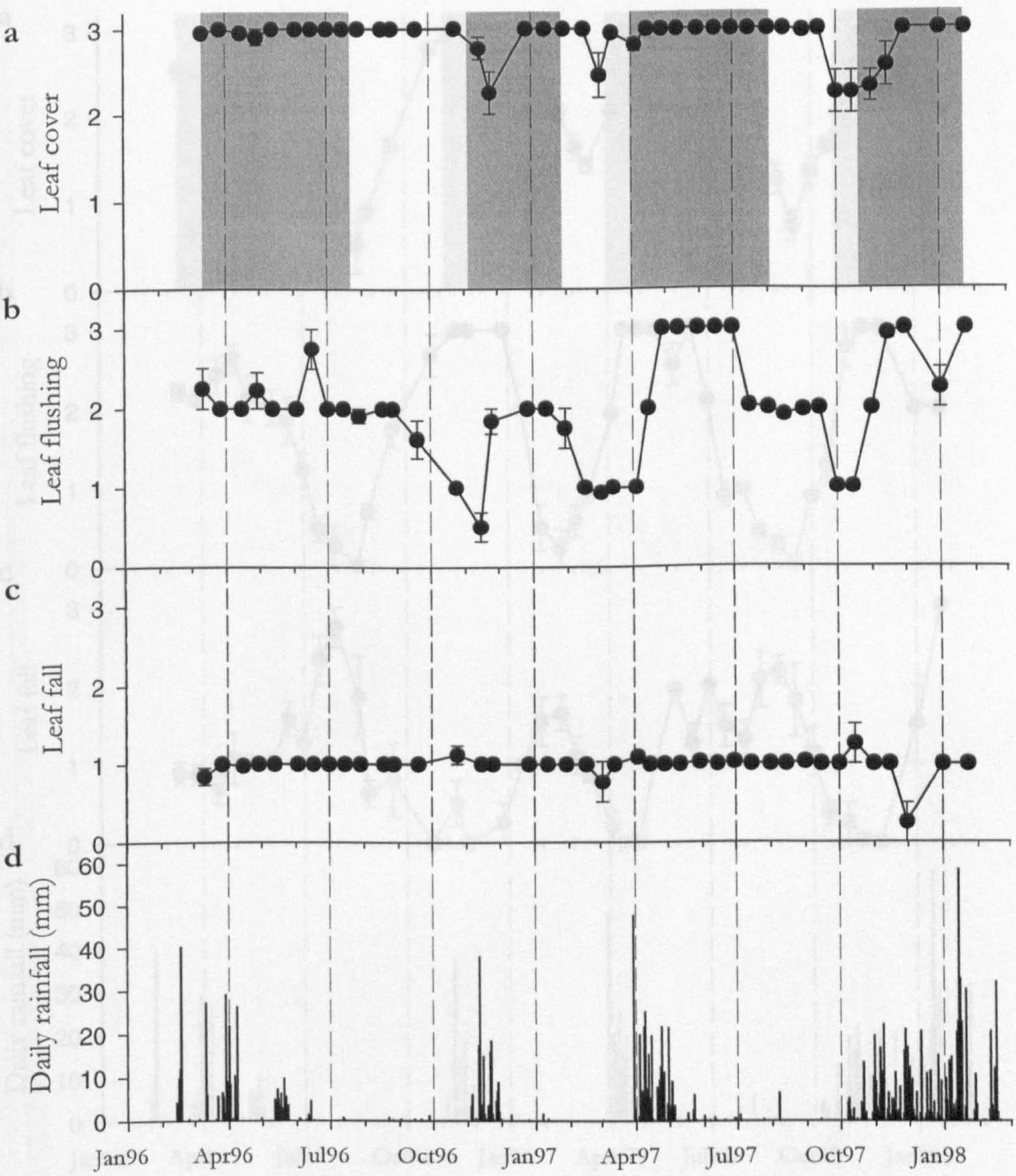


Figure 3.1. *C. megalocarpus*: (a) leaf cover and duration of the cropping periods (shaded areas), (b) flushing, (c) leaf fall, and (d) daily rainfall during the measurement period. Dates indicate the first day of the month. Standard errors of the replicate mean are shown where these are larger than the symbols in panels (a), (b) and (c).

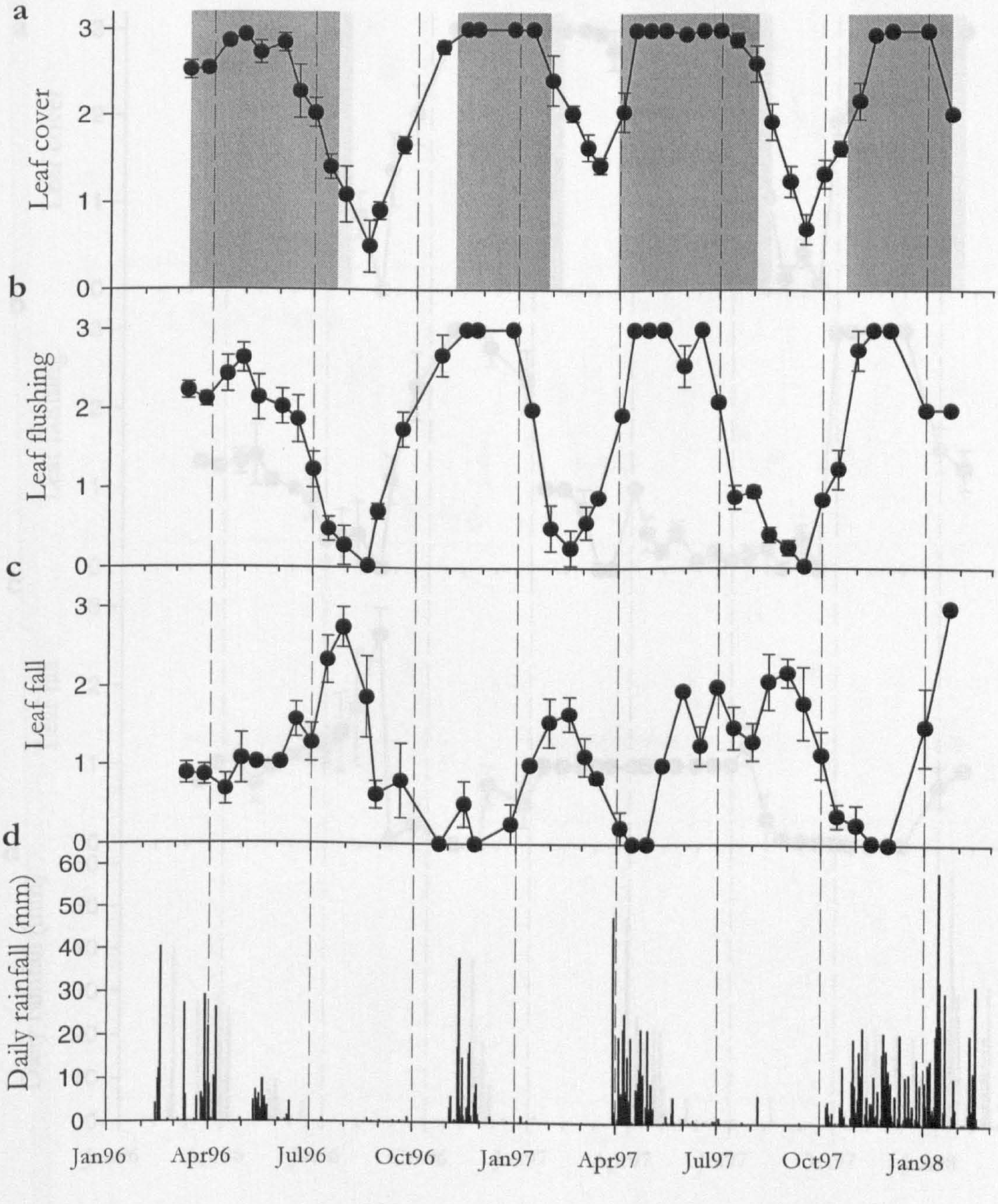


Figure 3.2. *M. volkensii*: (a) leaf cover and duration of the cropping periods (shaded areas), (b) flushing, (c) leaf fall, and (d) daily rainfall during the measurement period. Dates indicate the first day of the month. Standard errors of the mean are shown where these are larger than the symbols in panels (a), (b) and (c).

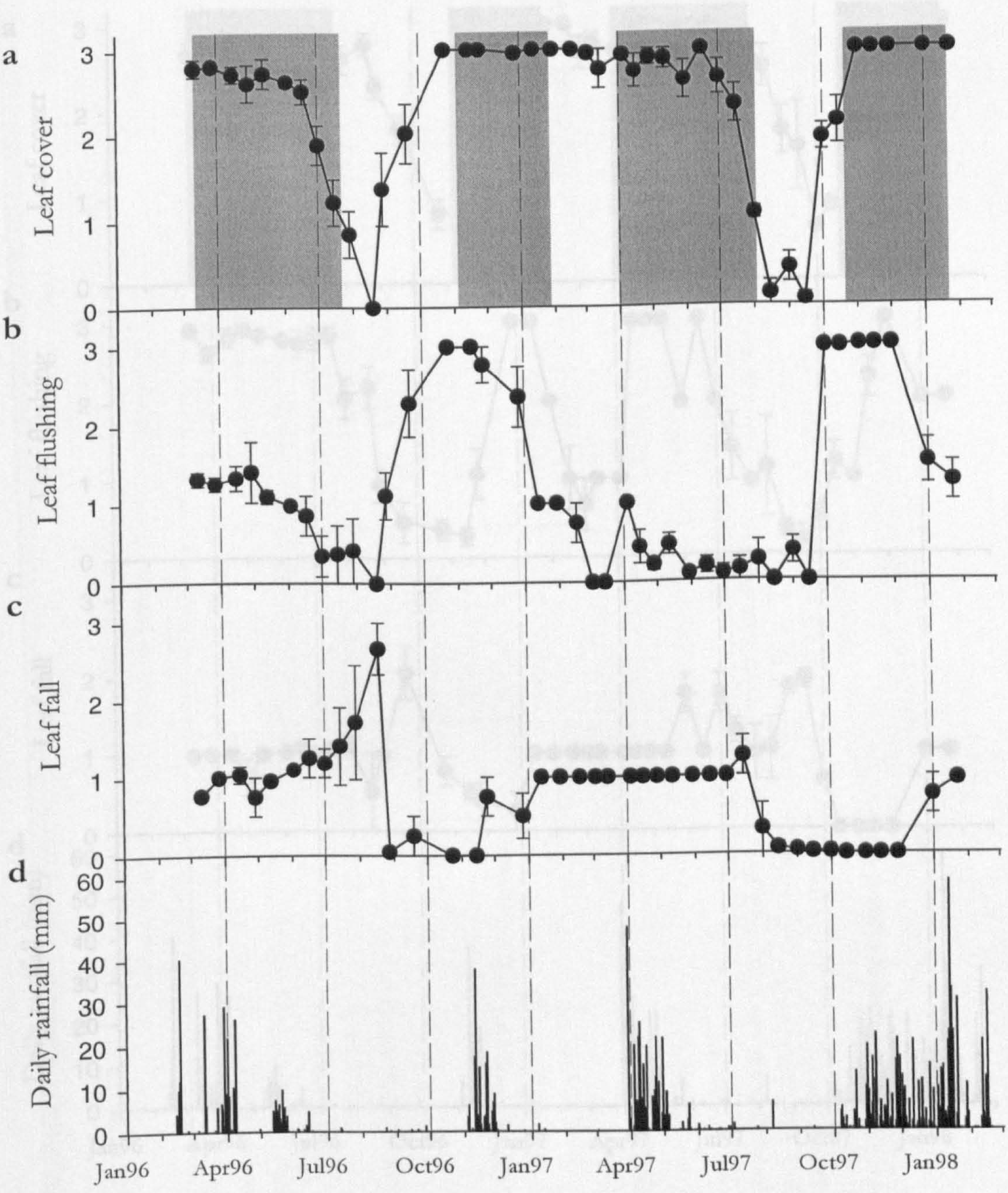


Figure 3.3. *S. spectabilis*: (a) leaf cover and duration of the cropping periods (shaded areas), (b) flushing, (c) leaf fall, and (d) daily rainfall during the measurement period. Dates indicate the first day of the month. Standard errors of the mean are shown where these are larger than the symbols in panels (a), (b) and (c).

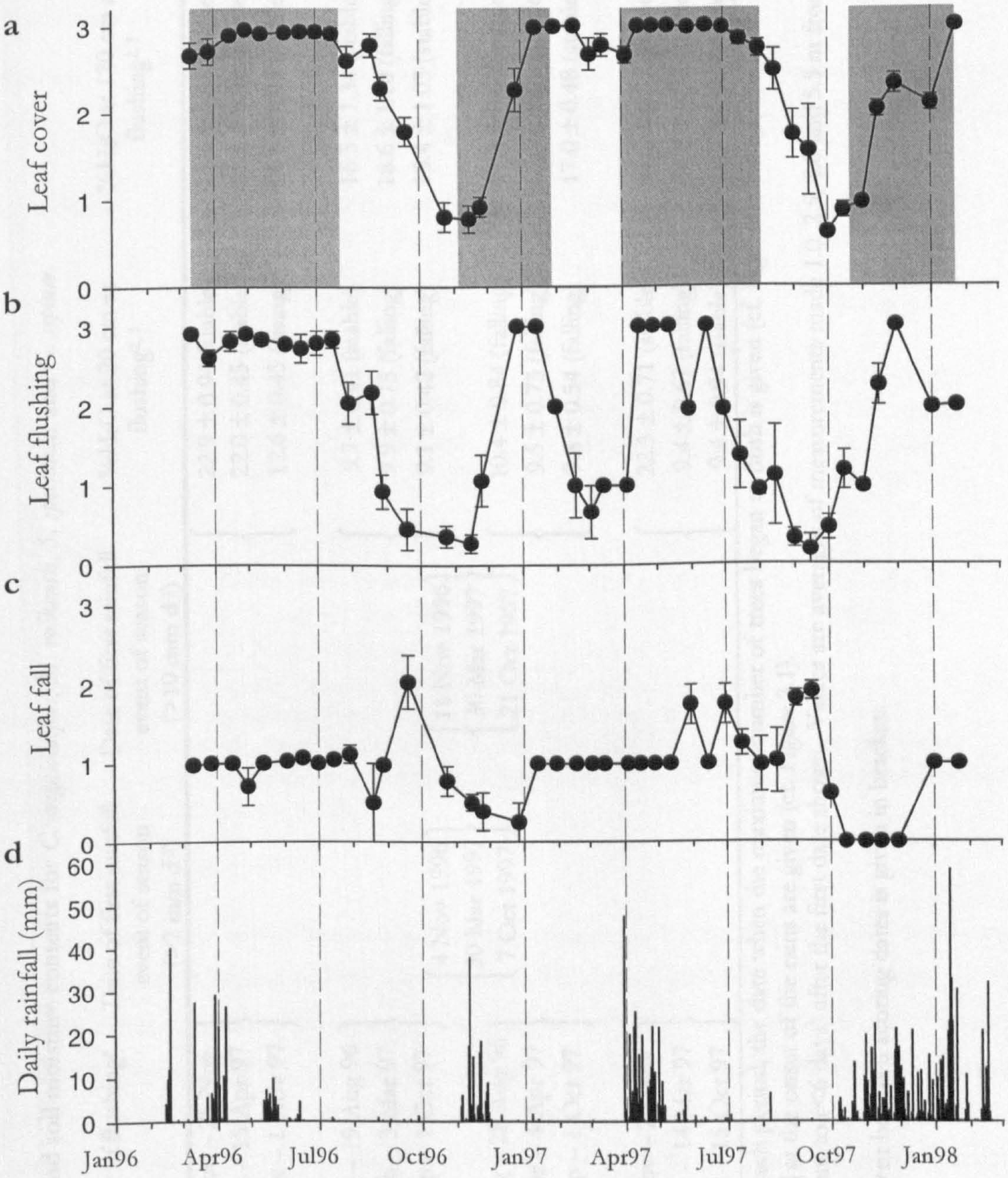


Figure 3.4. *G. sepium*: (a) leaf cover and duration of the cropping periods (shaded areas), (b) flushing, (c) leaf fall, and (d) daily rainfall during the measurement period. Dates indicate the first day of the month. Standard errors of the mean are shown where these are larger than the symbols in panels (a), (b) and (c).

Table 3.3. Flushing dates, rainfall timings and soil moisture contents for *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium*.

Species	Season	Onset of flushing[1]	Date of first rainfall event of season (>2 mm d^{-1})	Date of first rainfall event of season (>10 mm d^{-1})	%H_2O at 20 cm at flushing[2, 3]	%H_2O at 120 cm at flushing[2, 3]
C. megalocarpus	1996/97 short rains	15 Nov – 25 Nov	4 Nov 1996	11 Nov 1996	22.9 ± 0.94 (stable)	17.5 ± 0.68 (stable)
	1997 long rains	4 Apr – 15 Apr 97	30 Mar 1997	30 Mar 1997	22.0 ± 0.45 (stable)	18.4 ± 0.98 (stable)
	1997/98 short rains	15 Oct – 1 Nov 97	7 Oct 1997	21 Oct 1997	12.6 ± 0.45 (rising)	16.6 ± 0.43 (stable)
M. volkensii	1996/97 short rains	29 Jul – 19 Aug 96			9.7 ± 0.41 (stable)	16.5 ± 1.34 (stable)
	1997 long rains	17 Feb – 3 Mar 97			9.9 ± 0.75 (falling)	18.6 ± 1.10 (falling)
	1997/98 short rains	15 Sep – 1 Oct 97			9.1 ± 0.42 (falling)	15.4 ± 1.03 (stable)
S. spectabilis	1996/97 short rains	19 Aug – 28 Aug 96			10.4 ± 0.84 (falling)	17.8 ± 0.84 (stable)
	1997 long rains	14 Mar – 4 Apr 97			9.5 ± 0.73 (falling)	17.4 ± 0.68 (stable)
	1997/98 short rains	15 Sep – 1 Oct 97			9.8 ± 0.54 (falling)	17.0 ± 0.48 (stable)
G. sepium	1996/97 short rains	15 Nov – 25 Nov			22.3 ± 0.71 (stable)	17.0 ± 0.74 (stable)
	1997 long rains	3 Mar – 14 Mar 97			9.4 ± 0.67 (falling)	16.8 ± 0.76 (stable)
	1997/98 short rains	1 Oct – 15 Oct 97			9.6 ± 0.94 (stable)	16.7 ± 0.52 (stable)

1-Dates between which flushing began. For each period, the date when the maximum number of trees began to flush is given (cf. Figures 3.5-3.8). For *C. megalocarpus*. the dates when flushing increased at the onset of the rains are given (cf. Figure 3.1).

2-Soil moisture measurements made subsequent to (<6 days) after the first date shown. Values are averages of measurements made 1.0, 2.5, 4.0 and 5.5 m from tree row on northern side (cf. Section 3.2.2).

3-Description of change in soil moisture content between scoring dates is given in brackets.

Table 3.4. Dates of onset of leaf fall following cessation and soil moisture contents for *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium*.

Species	Onset of leaf fall [1]	% H_2O at 20 cm at onset of leaf fall[2]	% H_2O at 120 cm at onset of leaf fall[2]
C. megalocarpus	30 Nov 97 – 1 Jan 98	27.6 ± 0.43	27.7 ± 1.40
M. volkensii	15 Apr – 29 Apr 1996	16.4 ± 1.02	16.5 ± 1.53
	27 Dec 1996 – 13 Jan 1997	11.2 ± 0.31	17.6 ± 0.64
	28 Apr – 12 May 1997	21.4 ± 1.62	17.1 ± 0.33
	30 Nov 1997 – 1 Jan 1998	26.1 ± 0.55	24.2 ± 2.06
S. spectabilis	29 Apr – 13 May 1996	13.3 ± 1.22	18.6 ± 0.59
	29 Jul – 19 Aug 1996	10.6 ± 0.60	17.7 ± 0.78
	15 Nov – 25 Nov 1996	22.0 ± 0.33	17.6 ± 1.02
	30 Nov 1997 – 1 Jan 1998	26.6 ± 0.26	27.6 ± 0.99
G. sepium	15 Apr – 29 Apr 1996	16.7 ± 1.42	17.1 ± 0.77
	27 Dec 96 – 13 Jan 1997	12.9 ± 0.9	17.1 ± 0.89
	15 Aug – 1 Sep 1997	9.9 ± 0.81	16.6 ± 0.79
	30 Nov 97 – 1 Jan 1998	26.5 ± 0.94	29.3 ± 0.49

1-Dates prior to and at the onset of leaf fall following complete cessation. For each period, the date when the maximum number of trees commenced leaf fall is given (cf. Figures 3.5-3.8).
2-Soil moisture measurements made after (<6 days) the first date shown. Values shown are averages ± standard error for measurements made 1.0, 2.5, 4.0 and 5.5 m from the northern side of the tree row (cf. Section 3.2.2).

3.3.3 DECIDUOUSNESS

Deciduousness varied between species and seasons with respect both to the percentage of trees that were leafless and the duration of leaflessness (Table 3.5). *C. megalocarpus*, which is generally considered to be an evergreen, was the only species for which all trees retained leaf cover throughout the experimental period. However, a number of trees in Machakos District were seen to lose all of their leaves during the dry seasons, suggesting that the species is facultatively deciduous. Some *M. volkensii* trees were leafless for periods during the dry seasons preceding both the short and long rains, although the periods when the canopy was bare were not necessarily concurrent for all trees. In contrast, *S. spectabilis* and *G. sepium* were leafless only during periods preceding the short rains. Thus 82 and 84 % respectively of the *M. volkensii* trees were leafless for an average of approximately one month before the 1996 and 1997 short rains, although the periods varied greatly between individual trees. This compared with a value of 43 % during the shorter dry season preceding the 1997 long rains, when the duration of leaflessness was also shorter. The majority of *S. spectabilis* trees were leafless prior to the short rains in July and August 1996, and all trees were leafless between August and September 1997. Similarly, 95 and 100 % of the *G. sepium* trees were leafless during August and November in 1996 and 1997 respectively.

Table 3.5. Percentage of trees which were leafless and duration of leaflessness for *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium*.

Species	Season	Percentage of leafless trees [1]	Duration of leaflessness (days) [2] Mean	Minimum	Maximum
C. megalocarpus	pre short rains 1996	0	-	-	-
	pre long rains 1997	0	-	-	-
	pre short rains 1997	0	-	-	-
M. volkensii	pre short rains 1996	82	36	9	101
	pre long rains 1997	43	20	11	46
	pre short rains 1997	84	26	16	61
S. spectabilis	pre short rains 1996	82	27	9	66
	pre long rains 1997	0	-	-	-
	pre short rains 1997	100	32	14	47
G. sepium	pre short rains 1996	95	37	10	121
	pre long rains 1997	0	-	-	-
	pre short rains 1997	100	21	14	78

1-Percentage of trees 5-15 in all replicate plots.
2-Elapsed time between first scoring date when leaflessness was recorded to the date when flushing was first observed.

3.3.4 SYNCHRONICITY OF PHENOPHASES

The synchronicity of phenophases between and within replicates was examined using two methods:

(i) comparison of dates when phenophases (leaf flushing and leaf fall) resumed in individual trees following complete cessation (cf. Figures 3.5-3.8Figure 3.5);

(ii) tests for between-replicate differences in phenological scores for each measurement date using the Kruskal-Wallis one-way analysis of variance; data for each species were analysed separately.

As *C. megalocarpus* (Figure 3.5) ceased flushing infrequently and only for short periods, a full comparison proved difficult. Although the flushing onset event in November 1996 occurred synchronously in all replicates (cf. Figure 3.1), the equivalent event observed at the beginning of March 1997 in Replicates 3 and 4 represents a marginal change in only three trees during the dry season rather than a wider trend. Thus the points when flushing increased following periods of low flushing activity provide a better basis for comparison for *C. megalocarpus* than the onset date for flushing. Such occasions in November 1996, April 1997 and October 1997 (cf. Figure 3.1 and Table 3.3) followed the first significant rains of the season and were synchronous in all trees and replicates. The onset of leaf fall was also infrequent due to the infrequent cessation of leaf fall. The single period when leaf fall ceased and recommenced at the end of November 1997 (Table 3.4) was synchronous in all replicates, suggesting that the phenophases in *C. megalocarpus* were predominantly under exogenous control.

The onset of flushing in *M. volkensii* (Figure 3.6) occurred during the dry season before soil moisture content increased. Although discrete flushing periods were apparent, the degree of temporal dispersion suggests that the initiation of flushing was not the result of an environmental stimulus. The onset of leaf fall occurred more frequently and exhibited greater scatter than flushing throughout the seasons. Periods of intensive leaf fall were closely co-ordinated across replicates, although the pattern for Replicate 2 differed in that trees were less synchronised. As neutron probe measurements were not made for this replicate for logistical reasons, it is not known whether this difference in the pattern of leaf fall reflected differences in soil moisture content between replicates.

The onset of flushing in *S. spectabilis* (Figure 3.7) showed close synchronicity in Replicates 1-3 throughout the measurement period. The anomalous pattern observed for Replicate 4 may reflect differences in soil moisture content, which was consistently higher than in Replicates 1 or 3 throughout the measurement period. The onset of leaf fall occurred synchronously in all replicates during the 1997/98 short rains, when soil moisture content was unusually high, but differed between replicates throughout 1996 and early 1997. In Replicate 2, leaf fall at the end of 1996 did not begin until over one month later than in Replicates 1, 3 and 4; however, as stated above, the absence of neutron probe measurements for Replicate 2 precluded any comparison of soil moisture contents.

The onset of flushing in *G. sepium* (Figure 3.8) occurred over protracted periods prior to and at the beginning of the 1996/97 and 1997/98 short rains. The absence of any onset of flushing prior to the 1997 long rains (Feb-Mar 1997) in Replicates 2 and 4 resulted because flushing had continued throughout the preceding dry season. Figure 3.4 shows that flushing increased synchronously in all replicates approximately one month later, at the beginning of April 1997, following the first significant rainfall (>10 mm d^{-1}). Leaf fall onset occurred predominantly during periods when soil moisture content at 20 cm began to fall in April/May and also November/December 1996. Leaf fall also began synchronously in all replicates during the 1997/98 short rains when soil moisture contents at 120 cm were high.

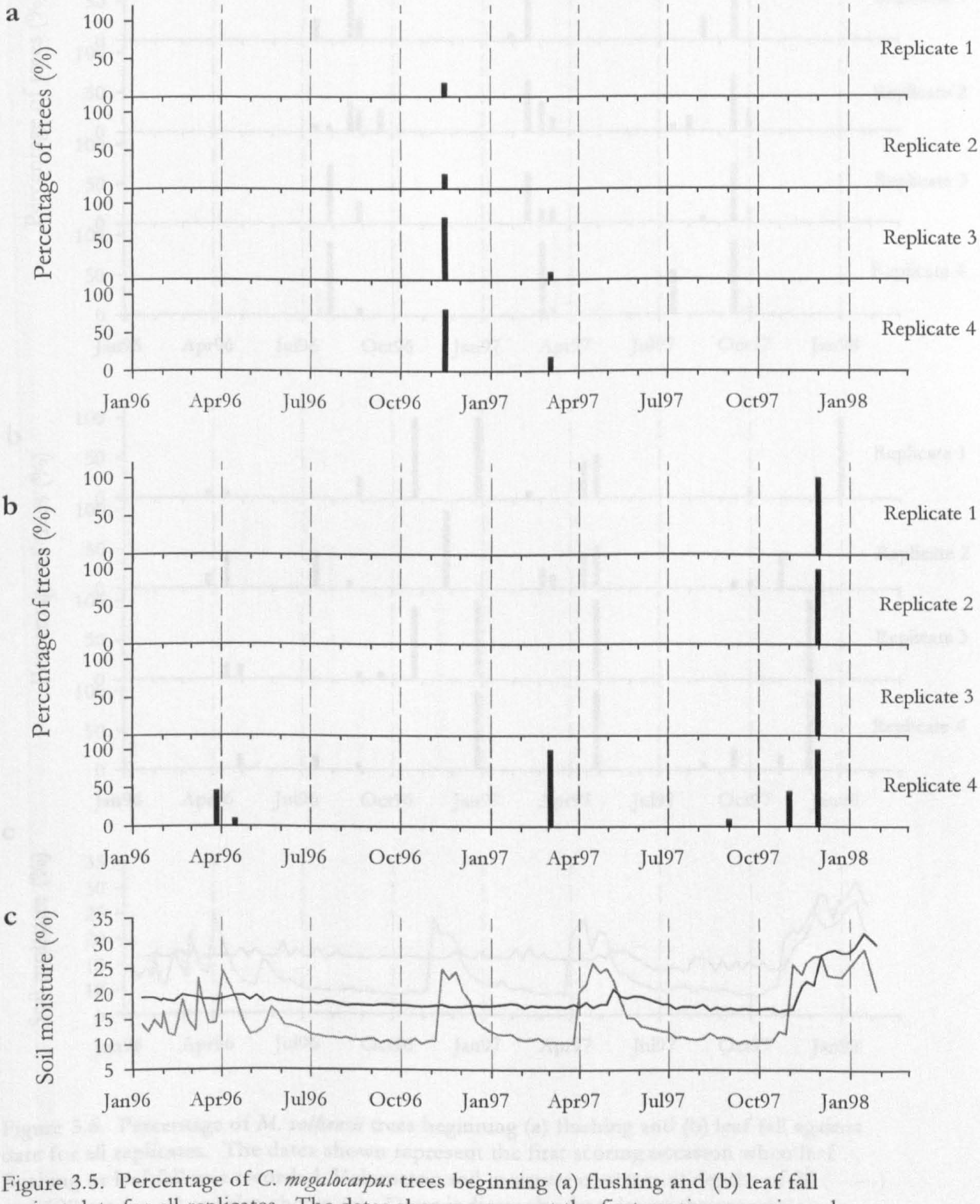


Figure 3.5. Percentage of *C. megalocarpus* trees beginning (a) flushing and (b) leaf fall against date for all replicates. The dates shown represent the first scoring occasion when leaf flushing or leaf fall was recorded. Volumetric soil moisture contents at depths of 20 (——) and 120 cm (——) are shown (b). Dates indicate the first day of the month.

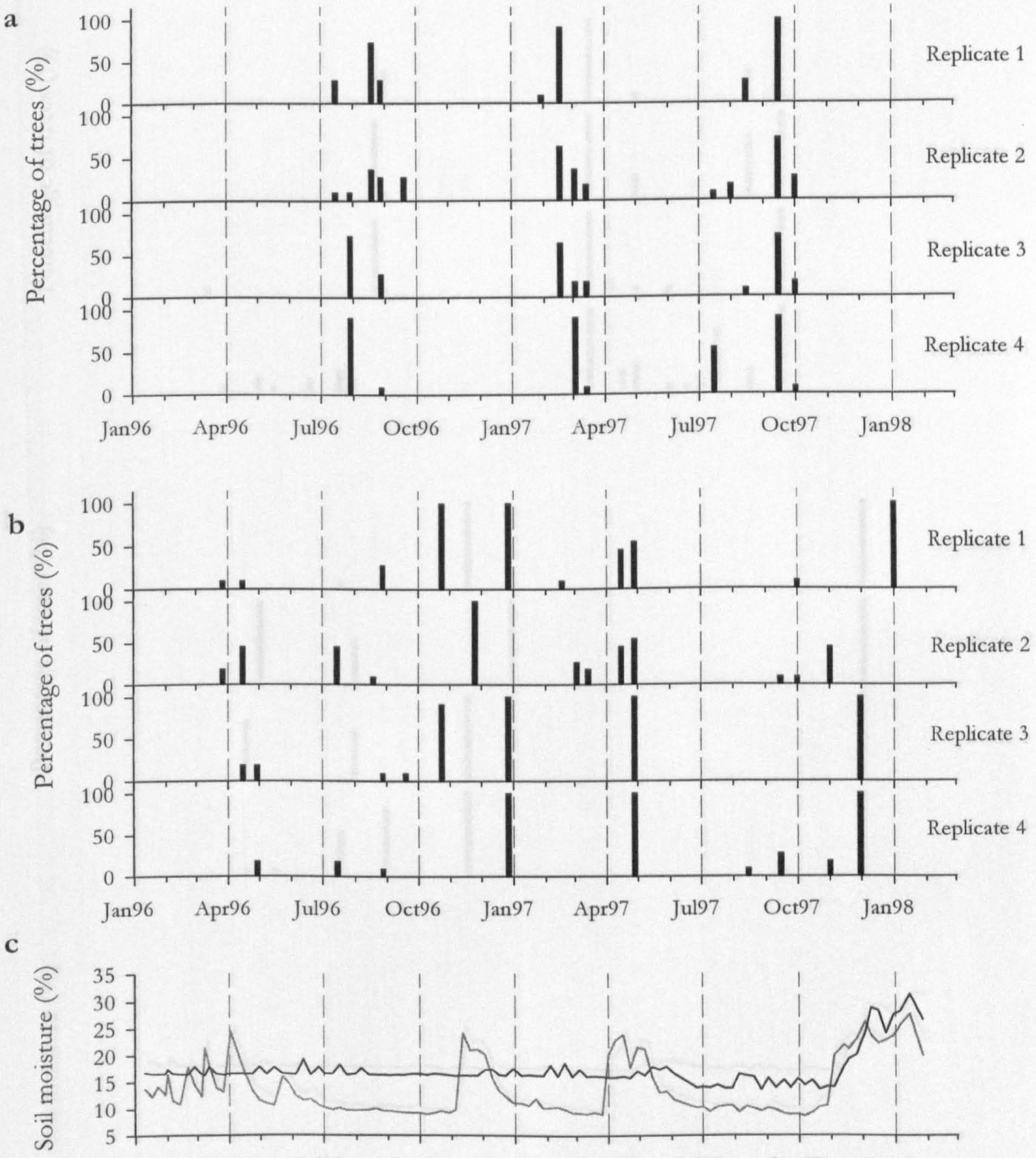


Figure 3.6. Percentage of *M. volkensii* trees beginning (a) flushing and (b) leaf fall against date for all replicates. The dates shown represent the first scoring occasion when leaf flushing or leaf fall was recorded. Volumetric soil moisture contents at depths of 20 (——) and 120 cm (——) are also shown (c). Dates indicate the first day of the month.

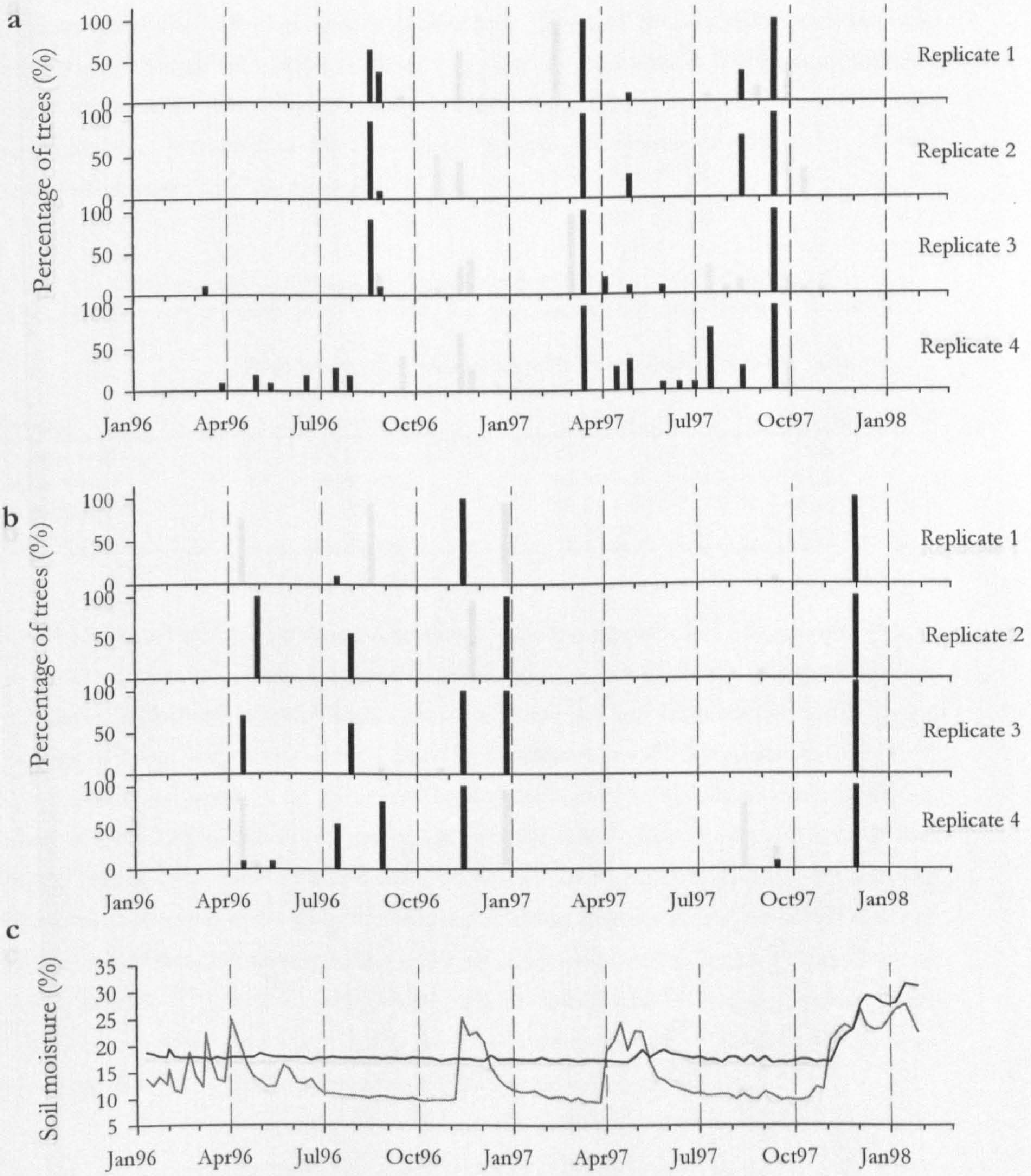


Figure 3.7. Percentage of *S. spectabilis* trees beginning (a) flushing and (b) leaf fall against date for all replicates. The dates shown are the first scoring occasion when leaf flushing or leaf fall was recorded. Volumetric soil moisture contents at depths of 20 (——) and 120 cm (——) are also shown (c). Dates indicate the first day of the month.

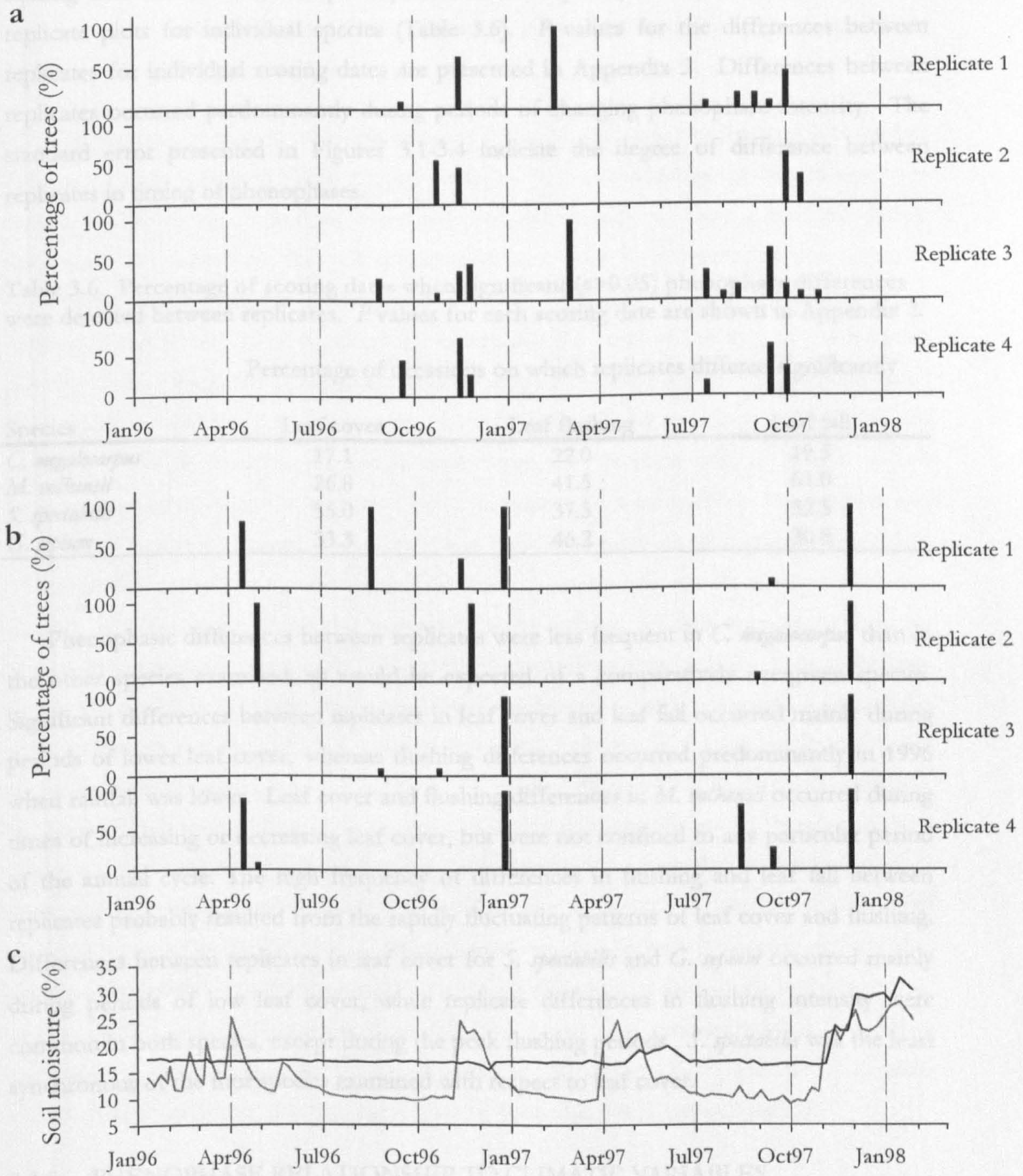


Figure 3.8. Percentage of *G. sepium* trees beginning (a) flushing and (b) leaf fall against date for all replicates. The dates shown represent the first scoring occasion when leaf flushing or leaf fall was recorded. Volumetric soil moisture contents at depths of 20 (——) and 120 cm (——) are also shown (c). Dates indicate the first day of the month.

Kruskal-Wallis tests for the significance of differences between replicates for each scoring date showed that the phenophases were frequently not synchronised across all replicate plots for individual species (Table 3.6). *P* values for the differences between replicates for individual scoring dates are presented in Appendix 2. Differences between replicates occurred predominantly during periods of changing phenophase intensity. The standard error presented in Figures 3.1-3.4 indicate the degree of difference between replicates in timing of phenophases.

Table 3.6. Percentage of scoring dates when significant ($p>0.05$) phenophase differences were detected between replicates. *P* values for each scoring date are shown in Appendix 2.

	Percentage of occasions on which replicates differed significantly		
Species	Leaf cover	Leaf flushing	Leaf fall
C. megalocarpus	17.1	22.0	19.5
M. volkensii	26.8	41.5	61.0
S. spectabilis	55.0	37.5	32.5
G. sepium	33.3	46.2	30.8

Phenophasic differences between replicates were less frequent in *C. megalocarpus* than in the other species examined, as would be expected of a comparatively evergreen species. Significant differences between replicates in leaf cover and leaf fall occurred mainly during periods of lower leaf cover, whereas flushing differences occurred predominantly in 1996 when rainfall was lower. Leaf cover and flushing differences in *M. volkensii* occurred during times of increasing or decreasing leaf cover, but were not confined to any particular period of the annual cycle. The high frequency of differences in flushing and leaf fall between replicates probably resulted from the rapidly fluctuating patterns of leaf cover and flushing. Differences between replicates in leaf cover for *S. spectabilis* and *G. sepium* occurred mainly during periods of low leaf cover, while replicate differences in flushing intensity were common in both species, except during the peak flushing periods. *S. spectabilis* was the least synchronous of the four species examined with respect to leaf cover.

3.3.5 PHENOPHASE RELATIONSHIP TO CLIMATIC VARIABLES

In all except *C. megalocarpus*, flushing began during the dry seasons in the absence of recent rainfall, while leaf fall commenced over a range of soil moisture contents in all species (Table 3.4). To determine whether these events were related to other environmental changes, comparisons were made between the climatic conditions preceding successive flushing and leaf fall events. The principal points of interest were: (i) the ability of *S.*

spectabilis, *M. volkensii* and *G. sepium* to flush prior to the first rains of the season when temperature and vapour pressure deficits were relatively high and soil moisture content was low; and (ii) the initiation of leaf fall in all species, particularly *M. volkensii*, under seemingly advantageous growing conditions.

The patterns of climatic variables between 2 and 60 days prior to flushing and the leaf fall onset events shown in Table 3.3 and Table 3.4 were examined visually for similarity of trends. The climatic variables examined included maximum daily saturation deficit, maximum and minimum daily air temperature and daily short-wave radiation receipts. Correlation coefficients for relationships between sequences of daily climatic variables between 2 and 60 days prior to successive events and the onset of flushing or leaf fall were also calculated. Negative correlations were commonly obtained and the analyses provided little evidence regarding possible triggers. Correlations between sequences of daily climatic variables where no negative correlation coefficients were detected were as follows: for all flushing onset dates in *C. megalocarpus*, daily maximum D, maximum air temperature and short-wave radiation receipts were falling and daily minimum air temperature was rising. These results comply with the observation that *C. megalocarpus* always flushed following rainfall. In contrast, for all flushing onset dates in *M. volkensii*, the daily maximum values for D and air temperature were rising. No variables showed consistent trends prior to flushing or leaf fall events in *G. sepium* or *S. spectabilis*. Examination of daily minimum temperatures prior to the onset of leaf fall in *G. sepium* showed that these events did not occur specifically when night time temperatures fell below 15 °C, as was observed by Whiteman *et al.* (1986) in Mexico. However, as leaf fall in *G. sepium* was almost continuous in the present study, it is doubtful whether attempts to attribute this response to changing climatic factors is meaningful. Further experiments would be necessary to determine whether the observed correlations prior to flushing in *M. volkensii* were causal, although it appears unlikely that drier, hotter growing conditions would provide the stimulus. It also seems unlikely that *G. sepium* would flush and commence leaf fall in response the same stimulus of increasing radiation receipts. Overall, the results obtained for *M. volkensii*, *G. sepium* and *S. spectabilis* suggest that phenophasic patterns are at least partially under endogenous control.

3.4 DISCUSSION

The four species examined exhibited a range of canopy phenologies with respect to the timing of the major leaf phenophases and the degree of synchronicity within and between species. The overall patterns were comparable to those recorded by Huxley and Van Eck

(1974) for 38 indigenous and introduced woody perennials in the bimodal humid tropics of Uganda, where two flushing periods occurred, the more intense coinciding with the beginning of the short rains (November-December), with a slightly less intense period occurring at the beginning of the long rains (March-April). The interannual variation in phenophases for all species examined, in conjunction with the lack of variation in daylength, demonstrates the absence of any link between phenological cycles and photoperiod. In *C. megalocarpus*, increases in soil moisture associated with the onset of the rainy season were the likely trigger for leaf flushing. The cessation of flushing during dry periods and leaf fall during very wet periods further suggests that phenophase control was predominantly exogenous. The water contents of sections of trunks were measured for each species in March 1998 to determine biomass and provide information regarding the functional type of the species involved, which Borchert (1994) has related to phenological strategy. Of the species examined, *C. megalocarpus* had the lowest mean trunk water content corresponding to 63% of the dry weight (range 52-82 %), suggesting that augmentation of stored water within the trees would be necessary for increased flushing intensities to occur. This observation supports Borchert's (1994) conclusion that phenology is correlated with water storage capacity, and that trees with a lower water storage capacity are less likely to remain active during drought periods.

In *M. volkensii*, *G. sepium* and *S. spectabilis*, the occurrence of flushing during the dry seasons and the onset of leaf fall over a range of soil moisture contents suggest that the major leaf phenophases reflected the internal water balance of the tree, as proposed by Reich and Borchert (1984) and supported by Williams *et al.* (1997) and Seghieri, Floret and Pontanier (1995). The lack of temporal synchronicity in flushing and the onset of leaf fall both within and between replicates, in combination with the lack of association with climatic changes, also suggests that the involvement of environmental stimuli was unlikely and that the proximal phenophase cues were endogenous. Huxley and Van Eck (1974) also reported no consistent relationship between climatic factors and leaf fall or flushing across the range of species examined their study. Reich and Borchert (1984) and Borchert (1994) proposed that flushing during drought periods results from the rehydration of bare trees following reductions in water loss associated with leaf fall. This is an attractive basis for explaining the flushing patterns observed in *M. volkensii*, *S. spectabilis* and *G. sepium*, which all flushed following periods of maximum leaf fall and low leaf cover. Huxley and van Eck (1974) also reported that similar associations between leaf fall and subsequent bud break in *G. sepium* in Costa Rica were independent of climatic variations, while Borchert (1994) concluded that flushing occurred after leaf shedding and subsequent rehydration of the trees. The high trunk water contents of *M. volkensii* (138 %, range 117-167 %), *S. spectabilis*

(93 %, range 92-95 %) and *G. sepium* (132 %, range 122-142 %) are comparable with those reported for a group of deciduous softwood species in a Costa Rican savanna, in which flushing or flowering occurred during drought following stem rehydration (Borchert, 1994). The fact that soil moisture content at 120 cm remained above the wilting point during the dry season, and would therefore have allowed rehydration, further supports this hypothesis. Flushing of *M. volkensii* and *S. spectabilis* occurred sooner before the 1996/97 short rains, even though rainfall during the previous season was 30 % less than in 1997, possibly because the more limited water supply during the 1996 long rains induced earlier leaf fall and hence earlier flushing. *G. sepium* did not exhibit similar behaviour, suggesting that comparable mechanisms were not involved and that the proximity of flushing to the onset of the rains may be indicative of an undetected environmental stimulus.

The onset of leaf fall in *M. volkensii* and *S. spectabilis* during periods when soil moisture content at 20 cm was above field capacity may have been a hormonal response to high soil moisture levels as occurred during the 1997/98 short rains (see below). Another possible explanation is that leaf fall was due to a temporary functional disequilibrium between the roots and shoots resulting in water deficits within the trees as hypothesised by Reich (1995). However, Wright and Cornejo (1990), working in a high rainfall area (2600 mm per annum) of Panama, found that maintaining soil water potentials at or above field capacity throughout the dry season did not reduce leaf fall in most species examined. Thus, evidence is conflicting on the effects of water availability, but as soil water deficits were not large in the study area of Wright and Cornejo (1990) a response to changing soil moisture remains the most likely explanation.

The results for *M. volkensii* and *S. spectabilis* suggest that the observed phenological resulted predominantly from the sensitivity of leaf abscission to tree water status, which depends on the functional and structural condition of the tree and interactions with the edaphic and aerial environment. Thus, as Reich (1995) suggested, the mechanisms responsible for leaf loss may be influenced by environmental conditions, even though the proximal cues for phenophases are endogenous. In such circumstances water stored in the soil and the tree itself acts as a buffer against the immediate environment by allowing the tree to maintain leaf cover even though there are no water inputs to the system.

The leaf fall events observed in all species, but especially in *M. volkensii*, when soil water contents were close to field capacity contrasts with the paradigm that the optimal strategy in semi-arid climates consists of growth during wet periods and relative dormancy during dry periods. It is unlikely that anaerobic conditions associated with waterlogging were the cause of leaf fall as soil moisture contents barely reached field capacity and were some way off full saturation. However, high soil moisture contents short of flooding may lead to decreased auxin levels which, in combination with the effects of increased ethylene synthesis, may provide conditions which strongly promote leaf abscission (Addicott, 1982). Hartung and Witt (1968) found that soil moisture levels equivalent to c. 60 % field capacity greatly decreased the quantity of diffusible auxin in the stems of *Helianthus annuus* (sunflower). Similarly, in the leaves of the desert plant, *Anastatica hierochuntica* (a desert annual native to Israel), which responded more sensitively than *H. annuus*, auxin was reduced at soil moisture contents above 60 % of field capacity and fell to undetectable levels at 90 % of field capacity, when the leaves rapidly yellowed. Abscission is usually inhibited by auxin transported from leaf blade, but sensitivity to ethylene is increased at low auxin levels, thereby increasing the likelihood of abscission (Brown, 1997).

It is possible that *M. volkensii* was particularly sensitive to the mildly anaerobic conditions which may have occurred in the soil surface layers and that leaf abscission occurred in response to the additional ethylene produced under such conditions (Jackson, 1997). The presence of excess water, coupled with warm temperatures may have resulted in oxygen shortage within the roots, which may have increased the export of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) to the leaves in the transpiration stream (Michael Jackson *pers. comm.*). ACC reaching the leaves is oxidised to ethylene, which is known to promote cell separation processes within the abscission zone (Jackson, 1997). The sensitivity of the abscission zone to increased ethylene may have resulted from decreased auxin levels, although the available experimental evidence remains contradictory (Michael Jackson *pers. comm.*). However, ethylene production was found to induce leaf abscission in citrus trees following drought stress (Tudela and Primomillo, 1992).

3.4.1 IMPLICATIONS FOR AGROFORESTRY

The differing patterns of leaf cover displayed by the four tree species examined in the present study will influence the temporal patterns of tree-crop interactions in agroforestry systems. The classification of tree species according to their geographic area of origin (e.g. indigenous/exotic) is unlikely reflect specific functional differences pertinent to agroforestry. Instead, the ecoclimatic zone of origin and functional tree type are more likely to provide clues concerning the phenological behaviour of individual species. Leaf cover in *C. megalocarpus* developed fully only following rainfall and after the crops were sown. The effect of this phenological pattern on the functioning of agroforestry systems will depend on the nature of tree-crop interactions but, under conditions where water availability limits crop growth, it is likely to restrict the depletion of water by the tree from adjacent crop rooting zones, thereby decreasing competition during the early stages of crop growth. In contrast, the leaf cover patterns exhibited by *M. volkensii* and *S. spectabilis* are likely to increase competition for water, although the decreases in leaf cover towards the end of the long rains in *S. spectabilis* and both rainy seasons in *M. volkensii* may reduce competition during the later stages of the cropping season. However, increased water availability during the latter stages of crop growth and grain filling is likely to have little effect on crop yield. Conversely, flushing during the dry season provides a degree of temporal complementarity whereby tree growth may be increased without increasing competition for water with associated crops. However, an extensive canopy at the start of the season will increase rainfall interception making the soil close to the trees dryer. The lack of full leaf cover in *G. sepium* during the short rains would decrease competition for water with adjacent crops, but is likely also to decrease tree growth. Whether this pattern is beneficial or disadvantageous within specific agroforestry systems will depend on the relative economic value of the tree and crop components.

The results of this study suggest that the phenophases in *M. volkensii*, *S. spectabilis* and probably *G. sepium* are proximally controlled by endogenous factors and soil water availability. In *C. megalocarpus* the controls appeared to be mainly environmental in origin. As suggested by Borchert (1994), functional tree types representing differing adaptive strategies are likely to provide the most reliable insight into phenological control mechanisms and hence the likely pattern of tree-crop interactions. However, as the relationships between phenophase and climate are complex, the degree of certainty is likely to be low. As the heritability of a trait is dependent on the extent to which the trait is under genetic control (Falconer and Mackay, 1996) selection of *M. volkensii*, *S. spectabilis* and *G. sepium* on the basis of phenophase pattern is likely to be ineffective given that water availability is the ultimate control and endogenous (genetically related) mechanisms provide only proximal control. Thus selection may alter phenological patterns by altering water storage capacity or the sensitivity of leaf abscission to tree water status but changing the phenological pattern *per se* is likely to be ineffective. In *C. megalocarpus*, however, phenophases were under exogenous control and therefore variation in phenological patterns, in common environments, is unlikely to be found.

3.4.2 IMPROVEMENTS

The methods employed here worked well for the desired purposes, although further quantification of phenological traits would have allowed further analysis of correlations with climatic variables. However, the work of Reich (1995), Borchert (1994) and Reich and

Borchert (1984) suggest that more profit would have been gained in uncovering the underlying mechanistic processes by measuring tree water status either directly or indirectly based on trunk girth measurements. If environmental cues were responsible for triggering phenophases, the trees were more sensitive that it was possible to detect under field conditions and it is likely that controlled environments experiments would be necessary to elucidate mechanisms. The method of assessing leaf fall could have been improved by using litter traps if sufficient space had been available under the trees. Although the timing of periods of low leaf cover were in agreement with leaf area measurements detailed in Section 4.3.3, the low amplitude of the fluctuation in leaf cover in *C. megalocarpus* shown in Figure 3.1 did not provide a full measure of the true fluctuations in leaf area. This resulted from the gradual nature of fluctuations in leaf phenophase intensity which were difficult to detect by the subjective methods used here.

4 TREE CANOPY CHARACTERISATION

4.1 INTRODUCTION

The quantity and pattern of radiation interception, upon which plant growth ultimately depends, is related to the quantity and spatial distribution of above-ground canopy elements. In agroforestry systems, the tree canopy is important not only in determining tree-environment interactions, but also because it modifies the microclimatic conditions experienced by associated crops (Jackson and Palmer, 1987; Tournebize and Sinoquet, 1995; Brenner, 1996) and influences soil moisture content as a result of changes in water uptake and transpiration (Ong *et al.*, 1991; Howard *et al.*, 1995). Norman and Campbell (1989) suggested that descriptions of canopy structure may reveal the strategy adopted by individual species in dealing with the evolutionary processes of adaptation to the prevailing physical, chemical or biotic factors by reflecting their inherent patterns of activity. The latter is of interest when species with natural distributions tending towards different climatic zones are compared in a common environment.

Canopy structure is usually quantified in terms of leaf area and the spatial and geometric organisation of the individual elements within a defined canopy envelope. The difficulty involved in quantification generally increases with the size and temporal and spatial heterogeneity of the canopy. Ideally, a complete three-dimensional description of the quantity, distribution and orientation of foliage over time is desirable, although this is often not possible because of practical considerations. Assumptions are therefore used to describe canopy shape and approximate the distribution and orientation of leaves in order to determine whole canopy processes from limited numbers of measurements. In practice, the closeness of the coupling between radiation exchange and canopy structure often enables canopy characteristics to be inferred from radiation measurements. However, cases where these assumptions are not valid, i.e. where the foliage is non-randomly distributed (Norman and Jarvis, 1975; Cohen, Monsoni and Meron, 1995) or arranged (Lang, Yueqin and Norman, 1985), or canopies are discontinuous (Jackson and Palmer, 1979) must be recognised and problems rectified.

Norman and Campbell (1989) broadly classified the various methods available for quantifying canopy structure as being either direct or indirect. The former may involve measuring variables such as leaf area and inclination using a planimeter and protractor, but also includes measurements of variables which may be related to leaf area by regression analysis, such as sapwood conducting area, leaf dimensions or leaf dry weight. These methods are often reliable but are usually destructive and become excessively laborious when applied to large or temporally heterogeneous canopies. Indirect methods based on radiative transfer theory developed from the Monsi and Saeki/Beer's law equation (Monsi and Saeki, 1953; Anderson, 1966; Ross, 1975) provide a more rapid means of assessment. However, assumptions concerning canopy structure, such as those outlined above, must be attuned to canopy characteristics if errors are to be minimised. This is particularly important where discontinuous or isolated canopies are concerned (Jackson and Palmer, 1979; Lang and Yueqin, 1986; Brenner *et al.*, 1995).

The aim of the work described in this Chapter was to determine canopy structural parameters for *M. volkensii* and *C. megalocarpus* in order to provide input variables for canopy simulations and allow direct comparisons of the two species. It was assumed that the canopies within individual tree rows were elliptical in cross-section and homogeneous within each 1 m row length, and that the leaves were randomly distributed within the canopy and symmetrically distributed with respect to the azimuth. It was also assumed that non-leafy surface area densities of structural canopy elements remained constant throughout the 20 month measurement period. This assumption is valid if the number and size of branches increase with a coincident increase in canopy volume; this was found to be the case in this study.

4.2 METHODS

During 1996 attempts were made to develop allometric relationships between branch cross-sectional area and leaf area similar to those established by other workers (Nygren, Rebottaro and Chavarria 1994; Lott *et al.*, 2000c). The continual and rapid fluctuation of leaf cover in *M. volkensii* and, to a lesser extent *C. megalocarpus*, however, rendered this approach impractical for these species. The physical size and height of the trees also prevented direct measurement of canopy characteristics without felling them. Therefore an indirect method was devised using an LAI-2000 canopy analyser. Measurements were made at intervals coinciding with full leaf cover during the 1996/97 short rains, 1997 long rains and 1997/98 short rains. Further measurements were made for both species during a period of low leaf cover prior to the 1997/98 short rains. To assess seasonal fluctuations in leaf area, photographs of the tree rows taken at monthly intervals were related to leaf areas estimated using the LAI-2000 canopy analyser (see below) using ranking and regression analysis procedures.

4.2.1 LEAF AREA MEASUREMENTS

A LAI-2000 Plant Canopy Analyzer (Li-Cor Inc., Lincoln, NE, USA.) was used to determine leaf areas for *M. volkensii* and *C. megalocarpus* using a modification of the isolated tree technique described by Li-Cor (1992). The instrument was originally designed to estimate the leaf area index of canopies, but has also been used with isolated trees in previous studies with varying degrees of success (Brenner *et al.*, 1995; Villalobos *et al.*, 1995; Grace and Fownes, 1998). Its use for estimating canopy size in isolated tree rows has not previously been documented. The LAI-2000 (Welles and Norman, 1991; Li-Cor, 1992) has a hemispherical lens and optical sensors which detect radiation at five zenith angles. Gap fractions at each angle are determined from measurements of diffuse radiation made above and below the canopy (Figure 4.1); inversion and numerical integration of the transmission data are then used to estimate leaf area density (LAD). Measurements are made under diffuse light conditions as the presence of even small amounts of direct radiation may introduce large errors (Welles, 1990). View caps may be used to restrict the azimuthal view range of the lens if large gaps in the canopy are present or an isolated plant canopy is asymmetric. It is assumed that: 1. the foliage elements are small relative to the area of view at each zenith angle, 2. the foliage is randomly orientated with respect to the azimuth and randomly distributed within a defined envelope, and 3. the foliage does not reflect or transmit radiation below 490 nm (Li-Cor, 1992).

Theory

The theory used to calculate foliage area is based on the gap fraction or contact frequency technique developed by Warren-Wilson and Reeve (1959), and is described in detail by Welles and Norman (1991) and Li-Cor (1992). Assuming azimuthal symmetry, the probability of transmission (T) of a ray of zenith angle θ is given by:

$$T(\theta) = \exp[-G(\theta)\mu S(\theta)] \qquad [4.1]$$

where $G(\theta)$ is the fraction of foliage projected in direction (θ), μ is foliage density and $S(\theta)$ is the path length through the canopy. Rewriting gives:

$$G(\theta)\mu = -\frac{\ln(T(\theta))}{S(\theta)} \equiv K(\theta) \qquad [4.2]$$

where $K(\theta)$ is the contact frequency, or the average number of contacts per unit length that a probe would make on passing through the canopy at the zenith angle (θ). The analytical solution for foliage density is given by Miller (1967):

$$\mu = 2\int_0^{\pi/2} \frac{-\ln(T(\theta))}{S(\theta)}\sin\theta d\theta \qquad [4.3]$$

Numerical integration over the five zenith angles gives:

$$\mu = 2\sum_{i=1}^{5} \frac{-\ln(T_i)}{S_i}W_i \qquad [4.4]$$

where T_i denotes the proportions of radiation transmitted at the five zenith angles and W_I represents $\sin\theta_i d\theta_i$ values computed by breaking the 0 to 90° interval into five uneven intervals based on the centre zenith angle assigned to detector rings 1-5 (7°, 23°, 38°, 53°, 68°) and normalising (i.e. scaling values so that their sum is equal to 1). The $d\theta$ values correspond to the zenith interval covered by the detector rings. Substitution from equation 4.2 gives:

$$\mu = 2\sum_{i=1}^{5} K_i W_i \qquad [4.5]$$

Measurement of isolated plants for which the horizontal extent of the canopy is less than three times plant height requires the path length, S, to be estimated for each zenith angle (Li-Cor, 1992). In the present study, measurements were made using a 90° view cap with the sensor positioned centrally between adjacent trees and directed perpendicular to the tree row towards either the north or south. This procedure restricted the canopy view to a volume approximated by a 90° segment of an ellipsoid with semi-axis dimensions defined by direct measurements of the canopies (Figure 4.1), and also decreased the number of measurements required to define the canopy perimeter. Path length (S) was calculated from this defined ellipse and the measured sensor height for each LAI-2000 measurement as follows (cf. Appendix 3 for derivation).

$$S = \frac{2ab(b\cos\alpha + a\sin\alpha\tan\beta)}{\cos\beta(b^2 + a^2\tan^2\beta)} \qquad [4.6]$$

where a represents the distance from the centre of the tree row to the canopy edge, b denotes half the distance between the top and bottom of the canopy, θ is the zenith angle and β = 180-θ. α denotes the ellipse angle defining the entry point of a notional ray and is defined as:

$$\alpha = \sin^{-1}\left(\frac{-pb\tan^2\theta \pm a(a^2+\tan^2\theta(b^2-p^2))^{1/2}}{a^2+b^2\tan^2\theta}\right) \qquad [4.7]$$

where p is the vertical distance between the sensor and the centre of the ellipse (see Appendix 3 for derivation).

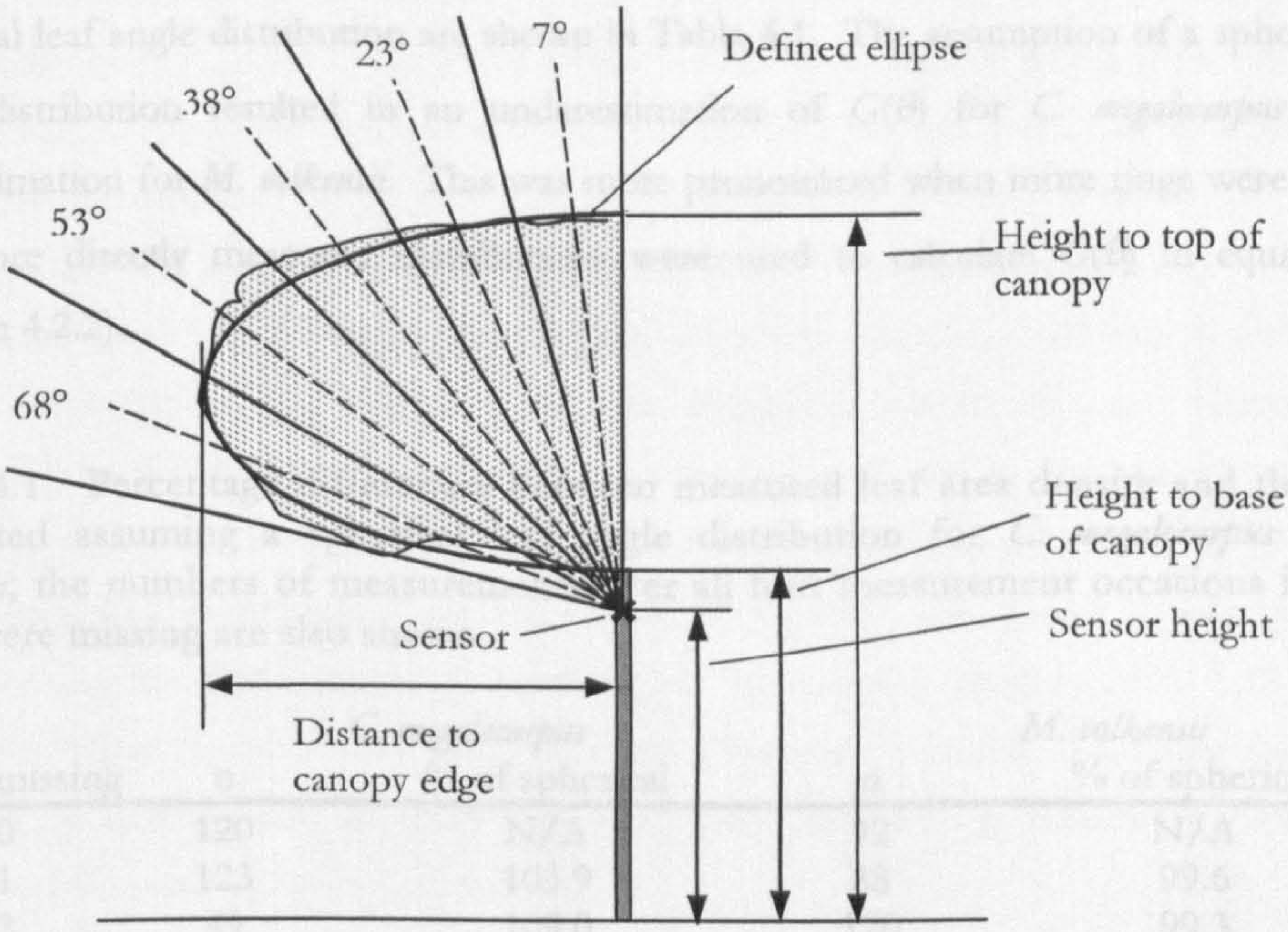


Figure 4.1. Cross-section of a tree canopy showing the five regions of diffuse radiation interception corresponding to the LAI-2000 light detecting rings 1-5 centred on zeniths 7, 23, 38, 53 and 68°. Also shown are dimensions recorded at 50 cm intervals along the row to enable path length and canopy volume to be estimated for the defined ellipse.

Depending on the position of the sensor relative to the canopy, light received by one or more of the outer detector rings may not actually pass through the canopy. In such cases, foliage density (μ) was assumed to be the same as for the outermost measured ring such that, by substituting for μ in equation 4.2, the following may be written:

$$\frac{K_i}{G_i} = \frac{K_{i-1}}{G_{i-1}} \qquad [4.8]$$

the value of K_i required to estimate canopy leaf area density (Eq. 4.5) can then be approximated as:

$$K_i = \frac{G_i}{G_{i-1}} K_{i-1} \qquad [4.9]$$

where G_i represents the fraction of foliage projected in the direction of the five zenith angles (i) calculated from directly measured leaf angle distributions (described below). Comparisons between measured values $G(\theta)$ values and those calculated assuming a spherical leaf angle distribution are shown in Table 4.1. The assumption of a spherical leaf angle distribution resulted in an underestimation of $G(\theta)$ for *C. megalocarpus* and an overestimation for *M. volkensii.* This was more pronounced when more rings were missing. Therefore directly measured distributions were used to calculate $G(\theta)$ in equation 4.9 (Section 4.2.2).

Table 4.1. Percentage differences between measured leaf area density and the values calculated assuming a spherical leaf angle distribution for *C. megalocarpus* and *M. volkensii*; the numbers of measurements over all four measurement occasions in which rings were missing are also shown.

	C. megalocarpus		*M. volkensii*	
Rings missing	n	% of spherical	n	% of spherical
0	120	N/A	92	N/A
1	123	103.9	88	99.6
2	49	109.0	120	99.3
3	2	111.1	19	92.3

Measurements

Measurements were made for all four replicates on four occasions (4 January 1997, 24 June 1997, 22 October 1997 and 23 December 1997). A 90° view cap was used on all occasions to restrict the azimuthal range of the sensor. Measurements were made to the north and south of each tree row at 1 m intervals between trees 5 to 15, providing 20 measurements per replicate except in Replicates 2 and 4, in which the canopy level platforms located to the south of trees 13 and 14 precluded measurements at these locations. In practice, an 'above canopy' measurement made c. 10 m from the tree rows was followed in close succession by a series of five measurements beneath the canopy at adjacent points along the row. The sensor head was levelled using the integral spirit level and directed with the aid of a compass towards the north or south azimuth for both above and below canopy measurements. Data were downloaded onto a PC and subsequent calculations were performed using a spreadsheet. Dimensions to define the ellipse for path length and canopy volume calculations were taken as the averages of three sets of canopy measurements made in line with, and at distances of 50 cm on either side of, the sensor measurement positions. These comprised the top and bottom heights of the canopy and distance to the edge of the canopy from the centre of the tree (Figure 4.1).

Calibration

An empirical calibration was carried out in February 1998 by measuring leaf area directly, immediately after completing the LAI-2000 measurements. The LAI-2000 measurements were made as described above before removing the leaves from the trees for measurement. An effort was made to encompass the range of leaf area densities present within the measurement set by subjectively selecting two 5 m row sections for each species with relatively low and high leaf area densities. Due to the practical difficulty of stripping leaves from trees and calculating the volume of canopy sections with complex profiles, it was assumed that the leaf area density of the volume viewed by the canopy analyser was comparable to that of a 1 m wide section running perpendicular to the tree row centred on the measurement point. Leaf area was determined directly by measuring the dry weight of leaves removed from individual trees and multiplying the values obtained by the corresponding specific leaf area determined for sub-samples using an ADC LA-2000 leaf area meter (Analytical Development Company, Hoddesdon, Herts). Leaf area density was obtained by dividing the leaf area values by the corresponding volume for the section estimated from canopy measurements.

4.2.2 LEAF INCLINATION

The inclination angles of c. 150 leaves sampled randomly from both *C. megalocarpus* and *M. volkensii* were measured on 20 January 1997 during the short rains to provide input for the canopy model described in Chapter 5 and estimation of $G(\theta)$ values for the missing LAI-2000 measurements (Section 4.2.1). Because leaves were only accessible from the canopy-level platforms, measurements were limited to the southern sides of the canopies in Replicates 2 and 4. Measurements were made at all levels in the canopy using a protractor with a weighted dial mounted at its centre, as described by Norman and Campbell (1989).

In order to estimate missing LAI-2000 K_i values (Section 4.2.1), the measured leaf angle distributions were used to calculate $G(\theta)$ values for zenith angles corresponding to the LAI-2000 view angles (7°, 23°, 38°, 53°, 68°). For each zenith angle $G_\alpha(\theta)$, the fraction of foliage inclined at angle α projected in direction θ, was calculated for nine leaf angle classes centred at 10° intervals between 5 and 85°. The formulae follow Welles and Norman (1991), but with a correction applied to the second equation (J. Welles, *pers. comm.*). Thus:

$$G_\alpha(\theta) = \cos\alpha\cos\theta \qquad (\mathit{for}\ \alpha + \theta \leq \pi/2) \qquad [4.10]$$

$$G_\alpha(\theta) = \frac{2}{\pi}\sin\theta\ \sin\alpha\ \sin\beta + \left(1 - 2\frac{\beta}{\pi}\right)\cos\theta\cos\alpha \qquad (\mathit{for}\ \alpha + \theta \leq \pi/2) \qquad [4.11]$$

and

$$\cos\beta = \frac{\cos\alpha\cos\theta}{\sin\alpha\sin\theta} \qquad [4.12]$$

G_i values, which provide a measure of the fraction of foliage projected in the direction of the five zenith angles, were calculated by summing the product of G_{ij}, the fraction of foliage in leaf inclination angle class *j* projected in direction *i*, and f_j, the fraction of leaves in leaf inclination angle class *j* as follows:

$$G_i = \sum_{j=1}^{9} G_{ij} f_j \qquad [4.13]$$

4.2.3 SEASONAL LEAF AREA

Long term changes in leaf area were assessed visually by ranking projected leaf areas using colour photographs of the tree canopies taken at monthly intervals in all replicates. Examples of photographs taken during periods of high and low leaf area are shown in Plates 4.1 and 4.2. The ranks of the photographs were then related to leaf area determined using the LAI-2000 canopy analyser by regression analysis, as detailed below. Grace and Fownes (1998) successfully used a similar method to determine leaf area in a silvopastoral system where browsing and seasonal leaf fall precluded the use of allometric relationships. Photographs of the tree canopies were taken at the end of each month between June 1996 and February 1998, with the exception August 1996 and July and August 1997. The camera, fitted with a 50 mm lens, was positioned at the same point 9.5 m from the northern side of the tree rows and perpendicular to the centre of the row; the photographs included the canopies of the central seven trees in each row. Whenever possible the canopies were photographed under diffuse radiation conditions to avoid uneven illumination, although this was not always possible owing to the prevailing weather conditions.

Plate 4.1. Replicate 4 *C. megalocarpus* canopy photographs during May (above) and November 1997 (below).

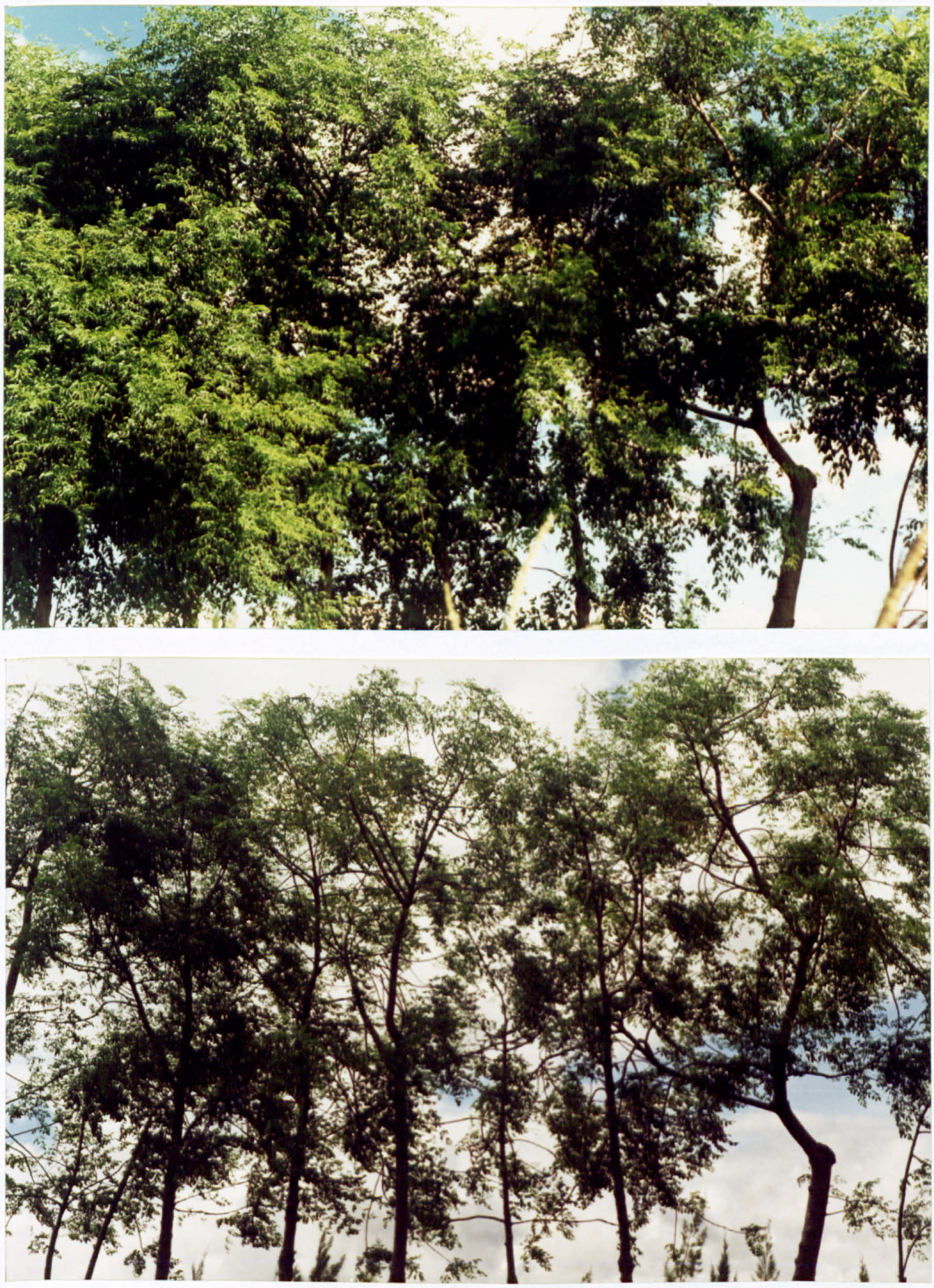


Plate 4.2. Replicate four *M. volkensii* canopy photographs during May (above) and November 1997 (below).

To reduce subjective bias the procedure for relating the photographic images to leaf area was carried out on two occasions using ranks supplied by two independent observers (Levy and Jarvis, 1999). The photographs for the two species were ranked separately and those photographs that were taken concurrently with each of the four LAI-2000 leaf area measurement dates were used to determine mean leaf area values per unit rank for each species. Leaf area estimates for each replicate for specific months were obtained by multiplying the ranks associated with each photograph by the corresponding value of leaf area per unit rank linearly interpolated between the LAI-2000 measurement dates. Because visibility through canopies decreases as leaf area increases (Grace and Fownes, 1998) this method reduced possible errors arising from the effects of canopy size and leaf area on ranking. Average leaf area for each month was then calculated for both *C. megalocarpus* and *M. volkensii*; finally, the estimated leaf areas derived from the two independent sets of ranks were averaged to provide a monthly value for each species.

The data presented in this chapter were analysed using Genstat 5, Release 4.1 for Windows (Lawes Agricultural Trust, UK), and were visually inspected for non-normality using histograms and normal plots.

4.3 RESULTS

4.3.1 LEAF AREA

The relationships between the estimated and measured leaf area density (LAD) values for *C. megalocarpus* and *M. volkensii* are shown in Figure 4.2. The intercepts with the y axis were positive and significantly different from zero (Table 4.2), indicating the presence of non-leafy plant material such as branches and trunks, which caused LAD to be overestimated at low measured leaf area densities. The larger positive intercept for *C. megalocarpus* reflected the greater proportion of branch surface area within its smaller, denser canopy. The fact that the gradients of the linear regressions were less than 1 probably resulted from the leaves being clumped rather than randomly distributed within the canopy as shown in Plate 4.3. This is a common cause of underestimation when leaf area is determined using indirect methods (Cohen *et al.*, 1995; Hanan and Bégué, 1995). Overall, the underestimation of LAD was greater in *M. volkensii* than in *C. megalocarpus*, in which the fitted regression provided estimates which corresponded more closely to the measured values. If this interaction between the slope of the regression and the intercept is not to introduce errors, the non-leaf surface area density would have to remain constant as canopy size increases, as is likely to have occurred during the relatively short measurement period examined here.

Plate 4.3. *C. megalocarpus* (above) and *M. volkensii* (below) canopies photographed from below.

Table 4.2. Regression statistics for leaf area density (LAD) estimated using the LAI-2000 canopy analyser and measured directly for *C. megalocarpus* and *M. volkensii*.

	Response variate	Explanatory variate	slope ± SE	intercept ± SE	r^2	n
C. megalocarpus	Estimated LAD	Measured LAD	0.83±0.080 (p<0.001)	0.70± 0.024 (p=0.009)	0.85	20
M. volkensii	Estimated LAD	Measured LAD	0.63±0.092 (p<0.001)	0.13±0.063 (p=0.05)	0.72	20

The larger scatter around the regression line for *M. volkensii* resulted, in part, from within-row variation in canopy characteristics, as shown by the higher within-row coefficients of variation for leaf area and canopy dimensions (Table 4.3). The increased influence of branch surface area on radiation transmission associated with the lower LAD values for the *M. volkensii* canopy may also have increased errors, as has been reported for sparse eucalypt canopies (Whitford *et al.*, 1995). Changes in sky brightness distribution, which can affect repeatability of measurements by about 10% (Welles and Norman, 1991), may also have increased variance in both species.

Table 4.3. Mean within-row coefficients of variation for leaf area, distance to the canopy edge and height to the bottom and top of canopy as determined by direct measurements made during calibration of the LAI-2000 canopy analyser.

	Leaf area[1]	Distance to edge[2]	Canopy bottom height[2]	Canopy top height[2]
C. megalocarpus	31.2	8.8	14.0	5.6
M. volkensii	43.9	10.2	21.1	5.0

[1] Mean for four sets of five consecutive directly measured 1 m row sections

[2] Mean of four sets of 10 canopy measurements made at 0.5 m intervals for canopy sections corresponding to the LAI-2000 measurements.

As the residuals from the regression analysis showed no apparent skewing, it was concluded that no obvious relationships in the data for either species remained unaccounted for. The random variation is of little importance given the repetition of measurements carried out during the estimation of leaf area for 1 m row sections. On average, leaf area density (LAD) was overestimated by 1% in *C. megalocarpus* and underestimated by 16% in *M. volkensii*. It is not usual for indirect methods to overestimate leaf area unless the leaves are more evenly distributed in space than random models assume (Cohen *et al.*, 1995; Hanan and Bégué, 1995; Levy and Jarvis, 1999). A similar method employed by Brenner *et al.*

(1995) for isolated *Retama sphaerocarpa* bushes also overestimated surface area, although the authors suspected that measurement errors may have been responsible. Measurements for *C. megalocarpus* gave larger overestimates at lower LAD values (Figure 4.2). At higher LADs, where the effect of non-leaf surface area is reduced (Smolander and Stenberg, 1996), the estimated values corresponded more closely to direct measurements (±10%). In contrast, leaf areas in *M. volkensii* were underestimated, particularly at higher LAD values, an effect which was probably attributable to the more clumped nature of its canopy as shown in Plate 4.3. Cohen *et al.* (1995) found that canopy clumping increased with leaf area index in apple trees, possibly contributing to the underestimation of leaf area at higher leaf area densities. The overestimation obtained at low LAD values were again attributable to non-leafy material.

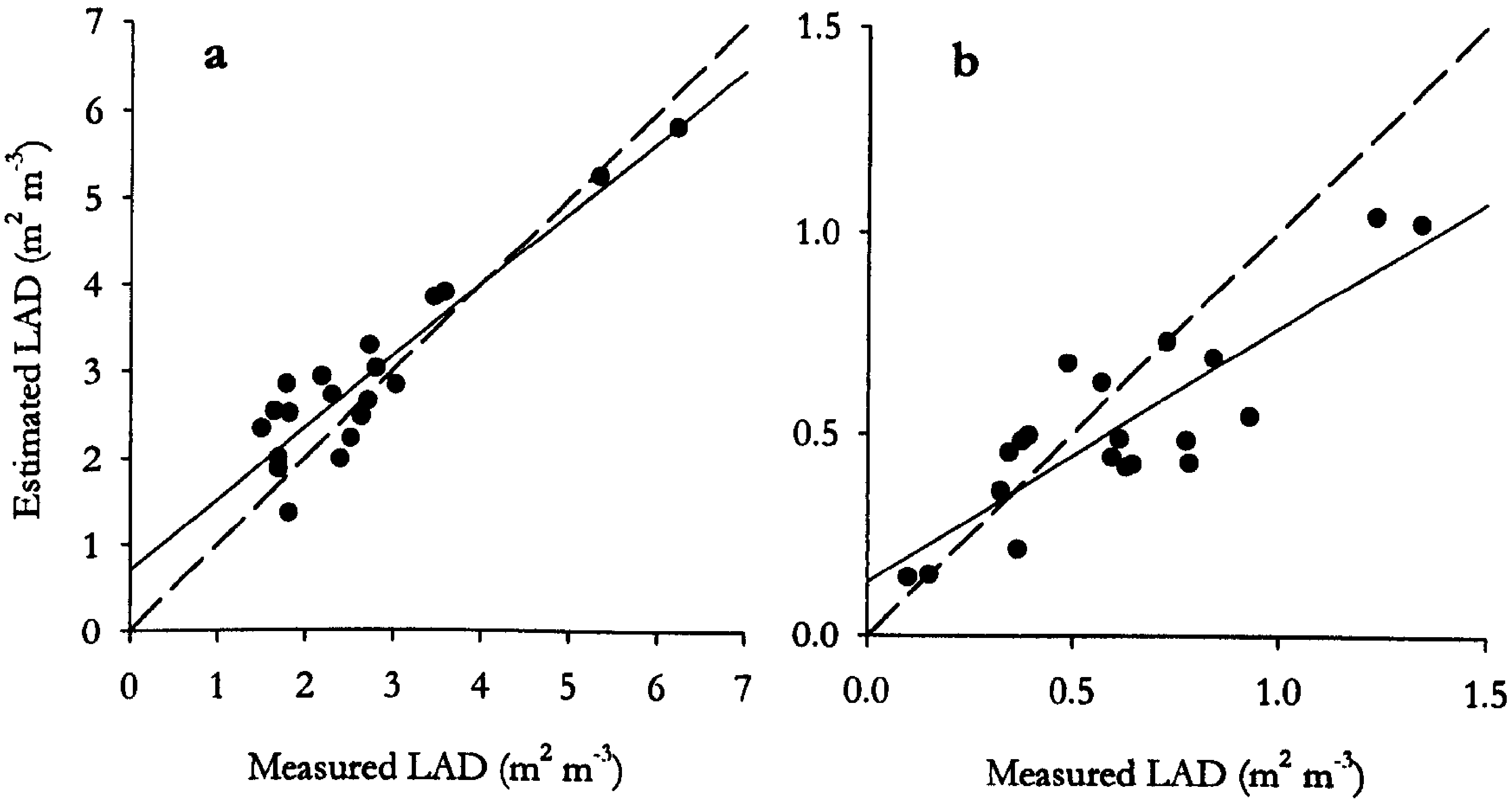


Figure 4.2. Relationship between leaf area density (LAD) estimated from LAI-2000 canopy analyser measurements and measured directly for (a) *C. megalocarpus* and (b) *M. volkensii*. Solid lines show the linear regressions fitted to the data; dashed lines show the 1:1 relationship.

A second method for estimating the leaf area of tree canopies was compared with that described above. This method differed from that above in that, instead of being estimated from canopy dimensions, path lengths were calculated as 1/cosθ, thereby providing an estimate of leaf area index (Welles and Norman, 1991) or, in the present case, leaf area per unit ground area covered by each 1 m row length. This method is generally used for horizontally continuous canopies (Li-Cor, 1992), but was found by Brenner *et al.* (1995) to provide reliable estimates for isolated hemispherical bushes. In the present study, however, regression against direct measurements of leaf area provided poorer fits and larger underestimates than the method described above, particularly for *C. megalocarpus.*

t-tests showed that the differences in leaf areas between the northern and southern sides of the canopies were non-significant for all measurement dates in both *C. megalocarpus* ($0.22 \leq p \leq 0.72$) and *M. volkensii* ($0.11 \leq p \leq 0.93$). Leaf area in *M. volkensii* was significantly greater than in *C. megalocarpus* during the 1996/97 short rains, 1997 long rains and prior to the 1997/98 short rains. However, during the 1997/98 short rains leaf area in *C. megalocarpus* increased to a far greater extent, relative to the values for the 1997 long rains, than in *M. volkensii* (Table 1.4) and values were not significantly different. *M. volkensii* also lost a large proportion of its leaves as a result of the high soil moisture contents following the high rainfall during the 1997/98 short rains (Chapter 3). Leaf area densities were significantly greater in *C. megalocarpus* than in *M. volkensii* during the 1997 long and 1997/98 short rains, but not during the 1996/97 short rains nor prior to the 1997/98 short rains, when leaf areas were lower. These results demonstrate the greater amplitude of the changes in leaf area for the consistently and significantly larger *M. volkensii* canopies (Table 4.4). The decrease in canopy volume between 24 June 1997 and 22 October 1997 in both species reflected a reduction in the dimensions of the canopy resulting from leaf fall during the dry season.

Table 4.4. Mean leaf area, leaf area density and canopy volume for 1 m row-lengths of *C. megalocarpus* and *M. volkensii* averaged across all replicates.

	Date	*C. megalocarpus*	*M. volkensii*	*p* value[1]
Leaf area	4 January 1997	5.1 ± 1.25	10.6 ± 1.76	<0.001 ***
(m^2)	24 June1997	17.3 ± 1.50	27.3 ± 3.37	<0.001 ***
	22 October 1997	2.00 ± 0.31	6.3 ± 0.39	<0.001 ***
	23 December 1997	23.5 ± 3.90	24.7 ± 1.42	0.647 ns
Leaf area density	4 January 1997	1.1 ± 0.31	0.9 ± 0.19	0.168 ns
(m^2 m^{-1})	24 June 1997	2.76 ± 0.22	1.66 ± 0.16	<0.001 ***
	22 October 1997	0.38 ± 0.08	0.47 ± 0.06	0.382 ns
	23 December 1997	2.42 ± 0.44	1.42 ± 0.06	<0.001 ***
Volume	4 January 1997	5.30 ± 0.49	12.52 ± 0.84	<0.001 ***
(m^3)	24 June1997	6.45 ± 0.22	16.55 ± 0.94	<0.001 ***
	22 October 1997	6.20 ± 0.62	14.20 ± 0.84	<0.001 ***
	23 December 1997	10.49 ±1.09	18.02 ± 1.00	<0.001 ***

[1] Test for significant differences between species. Values from ANOVA using a randomised block design: n.s., not significant; *, significant at $p<0.05$; **, significant at $p<0.01$; ***, significant at $p<0.001$.

Analysis of variance was used to test for differences in leaf area between replicates that may have affected crop performance. Leaf area did not differ significantly between replicate plots in *C. megalocarpus*, except during the 1996/97 short rains, when rainfall was 45% of the long term average (Table 4.5). Leaf areas in *M. volkensii* differed significantly between replicates during the 1996/97 short rains and 1997 long rains, but not before and during the 1997/98 short rains. Replicate 2 exhibited the lowest and Replicate 4 the highest leaf area during the 1996/97 short rains, although this situation was reversed during the 1997 long rains (Table 4.5), suggesting that the differences may have resulted from the relative timing of phenophases rather than long term differences in leaf area.

Table 4.5. Leaf area per 1 m row-length in replicate plots of *C. megalocarpus* and *M. volkensii*.

		Replicate				
	Date	1	2	3	4	p value[1]
C. megalocarpus	4 Jan 1997	7.1 ± 1.13	1.8 ± 0.99	6.9 ± 1.44	4.6 ± 1.87	0.034 *
	24 Jun 1997	19.8 ± 2.43	13.1 ± 1.55	19.1 ± 2.58	17.4 ± 2.52	0.188 ns
	22 Oct 1997	1.5 ± 0.71	1.6 ± 1.77	2.8 ± 0.64	1.9 ± 0.95	0.819 ns
	23 Dec 1997	26.7 ± 4.60	13.2 ± 3.45	22.4 ± 0.87	31.5 ± 6.99	0.148 ns
M. volkensii	4 Jan 1997	15.1 ± 2.22	6.5 ± 0.95	10.1 ± 1.63	10.7 ± 1.07	0.005 **
	24 Jun 1997	20.8 ± 3.30	34.3 ± 4.57	22.3 ± 2.26	31.9 ± 4.37	0.033 *
	22 Oct 1997	5.3 ± 1.14	6.4 ± 1.83	7.3 ± 1.52	6.3 ± 1.61	0.853 ns
	23 Dec 1997	27.6 ± 2.78	23.5 ± 3.51	21.3 ± 3.76	26.4 ± 3.67	0.574 ns

[1] Test for significant differences between replicates. Values from one-way ANOVA with no blocking: n.s., not significant; *, significant at $p<0.05$; **, significant at $p<0.01$; ***, significant at $p<0.001$

4.3.2 LEAF INCLINATION

Mean leaf inclination angles were significantly greater ($p<0.01$) in *C. megalocarpus* (mean=60.3 °) than in *M. volkensii* (mean=51.1 °). The distribution of measured leaf inclination angles in *C. megalocarpus* showed a higher frequency of more steeply inclined leaves than in *M. volkensii* (Figure 4.3). The spherical leaf angle distribution is also shown for comparison, where the frequency of leaves in the n^{th} leaf angle class is given by:

$$f(n)=\cos((n-1)\delta)-\cos(n\,\delta) \qquad [4.14]$$

where δ denotes class width in degrees. Although casual observation suggested that the leaves of *C. megalocarpus* became more steeply inclined during periods of low water availability, insufficient time was available to make direct measurements.

Mean leaf inclination angle was also calculated from the LAI-2000 output using the methodology described by Norman and Welles (1991), who suggested that constraints should be applied for extreme leaf angles due to uncertainties in the empirical relationship used to relate radiation measurements to leaf angle. The frequency for which constraints were required to constrain leaf angle to between 0 and 90 ° for the data collected here suggested that the method proposed by Norman and Welles (1991) was not applicable. The unsuitability of the method was partially attributable to the small, non-horizontally homogeneous canopies of the trees violating the implicit assumption in substituting K ($=G(\theta)\mu$) from equation 4.2 into equation 4.5 that G and μ are constant and that the contact frequency, K, is altered only by changes in zenith angle. In reality, G and μ may often not be constant throughout isolated canopies in which leaf area density and/or leaf angles may be greatest at the edges of the canopy.

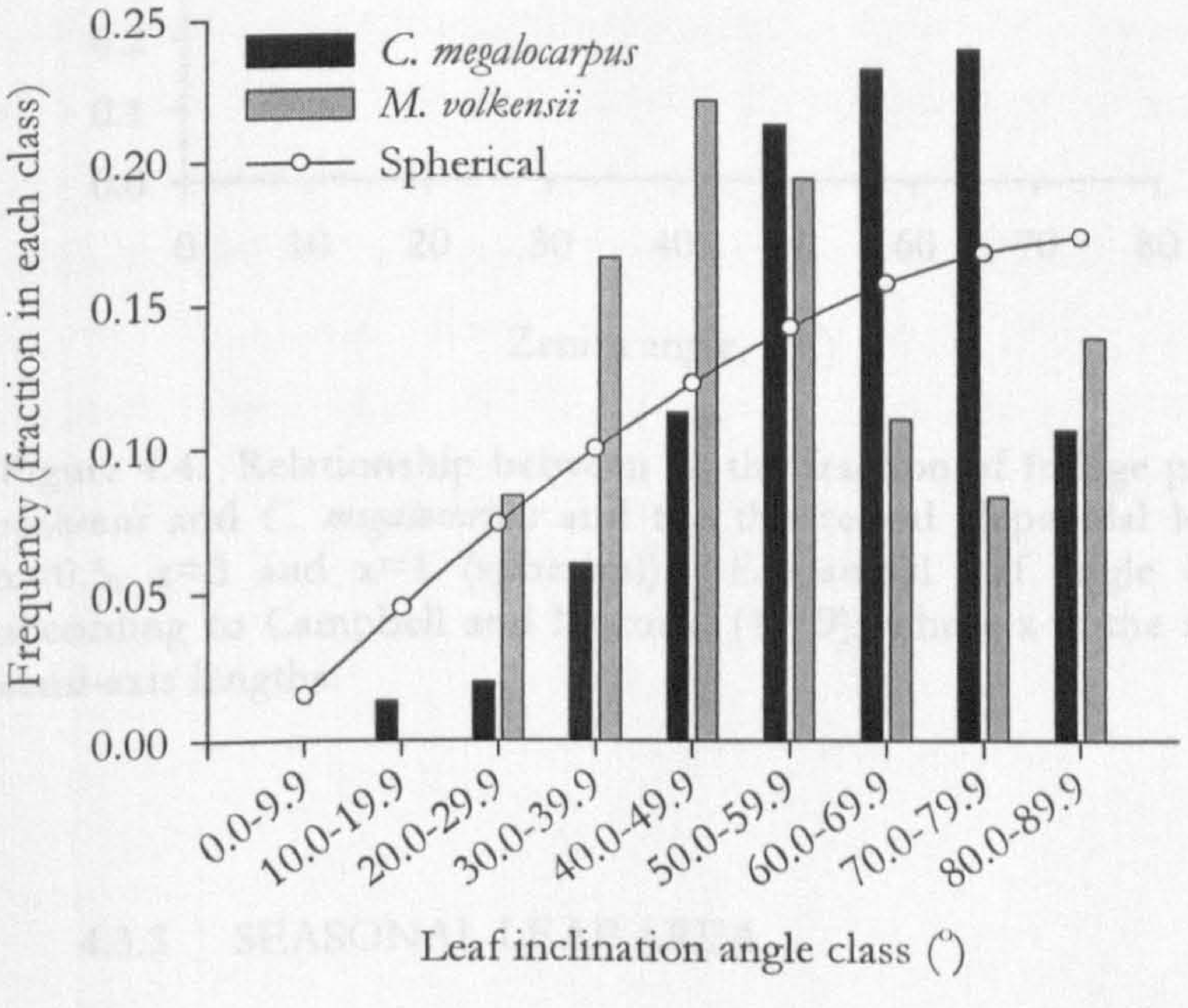


Figure 4.3. Leaf angle distributions for *M. volkensii*, *C. megalocarpus* and the theoretical spherical function, where inclination angle represents elevation above the horizontal.

Figure 4.4 shows $G(\theta)$, the fraction of foliage projected in direction θ, for both species, as well as values for the theoretical spherical and ellipsoidal leaf angle distributions where the ratios of semi-axis lengths are 0.5 and 3.0. A larger proportion of the foliage of *M. volkensii* was projected towards more horizontal angles than in *C. megalocarpus*, as illustrated in Figure 4.3. These values were used to estimate leaf area densities for LAI-2000 measurements with missing measurement rings (Section 4.2.1). The larger values of *G* obtained at lower zenith angles for *M. volkensii* meant that the standard assumption of a spherical leaf angle distribution (J.M. Welles, *pers. comm.*) for missing measurement rings resulted in overestimation of leaf area density. The opposite was true for *C. megalocarpus*, for which *G* was smaller at lower zenith angles (Table 4.1).

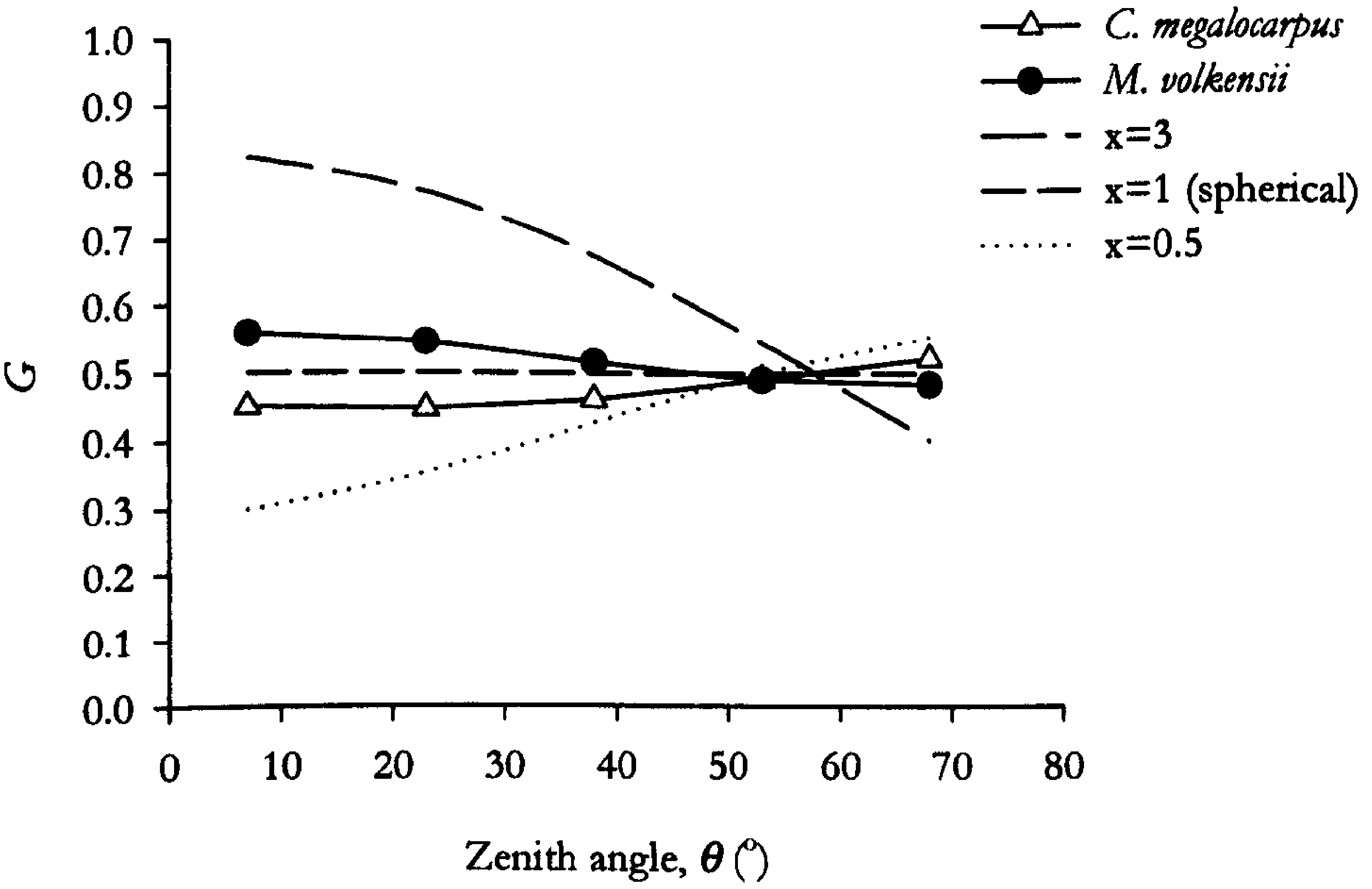


Figure 4.4. Relationship between *G*, the fraction of foliage projected in direction θ for *M. volkensii* and *C. megalocarpus* and the theoretical ellipsoidal leaf angle distributions where x=0.5, x=3 and x=1 (spherical). Ellipsoidal leaf angle distributions were calculated according to Campbell and Norman (1989), where x is the ratio of horizontal to vertical semi-axis lengths.

4.3.3 SEASONAL LEAF AREA

The seasonal fluctuations in leaf area were broadly concurrent in *C. megalocarpus* and *M. volkensii* (Figure 4.5), and their periodicities reflected the timing of the rainy seasons. Although *M. volkensii* exhibited a wider variation of leaf areas than *C. megalocarpus*, it would be an oversimplification to assume that they are respectively deciduous and evergreen. Leaf areas increased sooner and more rapidly in *M. volkensii* than in *C. megalocarpus* prior to all three rainy seasons when measurements were made. These phenological differences are considered further in Chapter 3. Both species had relatively low leaf areas during the

1996/97 short rains, when precipitation was particularly sparse (158 mm) and the bean crop failed. Leaf areas in *C. megalocarpus* were greater towards the end of the 1996 long rains than during the 1996/97 short rains, suggesting that low rainfall rather than differences in tree size was responsible for the low leaf areas. Leaf area in *M. volkensii* was lower during the 1997/98 short rains than during the 1997 long rains, whereas the opposite was true for *C. megalocarpus*;: these differences may reflect adaptations to the climatic conditions experienced within their natural ranges (cf. Section 2.5). *M. volkensii* showed a marked decrease in leaf area during December 1997 and January 1998 when conditions were unusually wet (Chapter 3), but leaf areas began to increase again in February 1998. Leaf area in *C. megalocarpus* increased progressively during the same period.

The small differences between estimates obtained using the LAI-2000 and photographic methods for the four LAI-2000 measurement dates (Figure 4.5) result from using average leaf area per unit rank to estimate leaf area of individual replicates according to the ascribed rank. The qualitative nature of the photographic method does not allow errors to be completely quantified, although the main source of error is likely to be associated with observer bias. The leaf area per unit rank values provided by the two observers for each LAI-2000 measurement occasion agreed to within 10% for *C. megalocarpus*. Agreement was also within 10% for *M. volkensii* with the exception of the measurements made in October 1997, at a time of relatively low leaf area, when the ranks differed by 32%. The two sets of ranks used individually gave a mean difference in leaf area per 1 m row-length of 0.75 m^2 or 8% for *M. volkensii*, with a maximum of 2.19 m^2 (8%). For *C. megalocarpus*, the average difference was 0.91 m^2 or 13%, with a maximum 1.96 m^2 (18%).

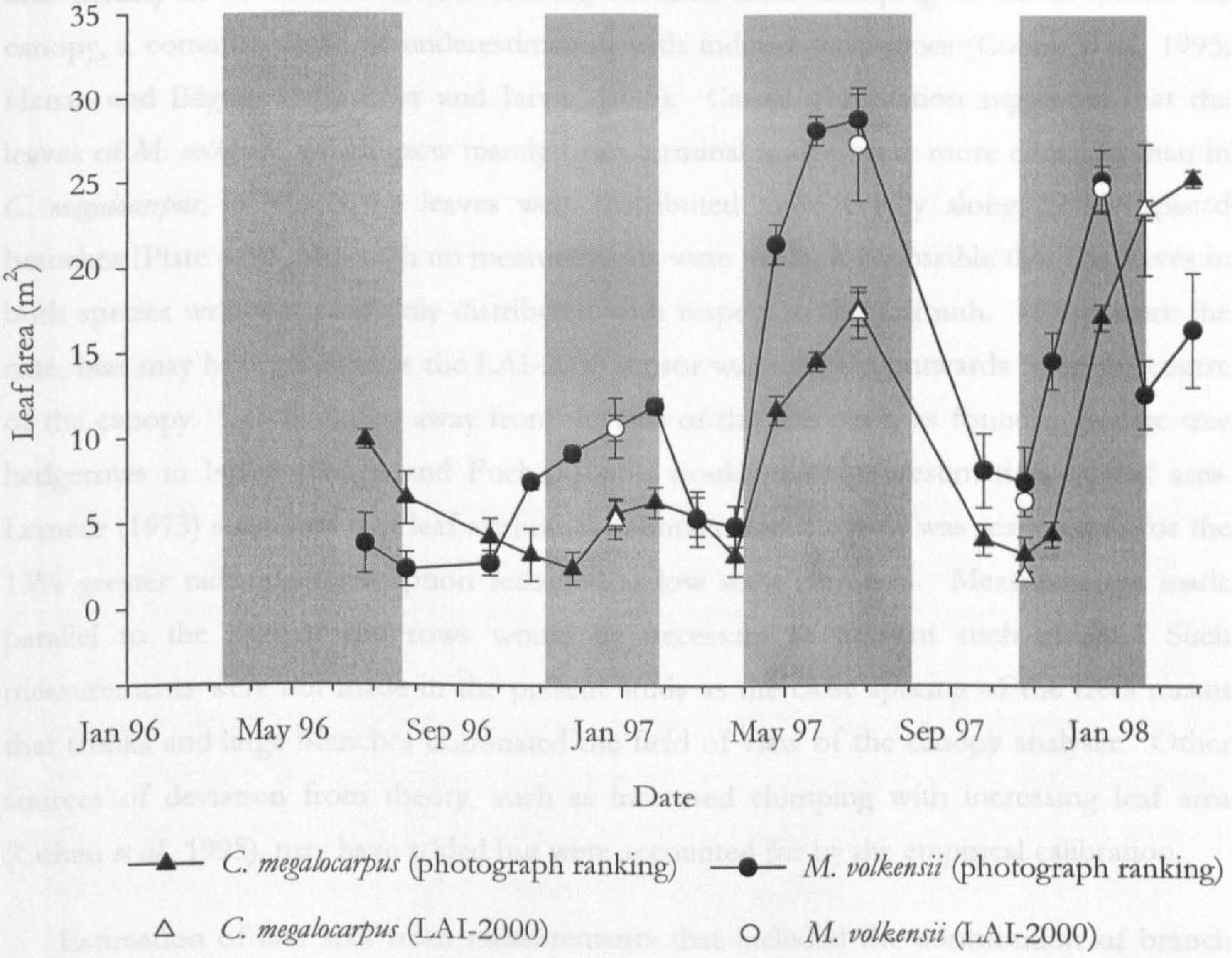


Figure 4.5. Leaf areas per 1 m row length between June 1996 and February 1998 estimated by ranking photographs for *C. megalocarpus* and *M. volkensii*. Error bars represent double standard errors of the replicate means averaged over the two sets of ranks. Also shown are LAI-2000 estimates with double standard errors of the replicate means.

4.4 DISCUSSION

The agreement between direct and indirect estimates of leaf area demonstrates that the theory first described by Welles and Norman (1991) and further developed in the present study may be reliably used to calibrate LAI-2000 output for isolated tree rows. Although measurements involving a wider range of canopy sizes would have been desirable if trees of appropriate size had been available, the absence of smaller canopies in the calibration dataset is unlikely to have been important as canopy size was taken into account in the theory and calculations. The success of the approach for *C. megalocarpus* was attributable to its greater canopy homogeneity expressed in terms of leaf area and canopy dimensions as compared to *M. volkensii*. As the high leverage of the two points representing the greatest leaf area density (Figure 4.2a) may have biased the calibration for *M. volkensii*, further confirmatory measurements would have been advantageous. The underestimation of leaf area density in *M. volkensii* almost certainly resulted from clumping of leaves within the canopy, a common cause of underestimation with indirect techniques (Cohen *et al.*, 1995; Hanan and Bégué, 1995; Levy and Jarvis, 1999). Casual observation suggested that the leaves of *M. volkensii*, which grew mainly from terminal nodes, were more clumped than in *C. megalocarpus*, in which the leaves were distributed more evenly along closely spaced branches (Plate 4.3). Although no measurements were made, it is possible that the leaves in both species were not randomly distributed with respect to the azimuth. If this were the case, bias may have resulted as the LAI-2000 sensor was directed outwards from the centre of the canopy. Leaves facing away from the axis of the tree rows, as found in orange tree hedgerows in Israel (Cohen and Fuchs, 1986), would cause overestimation of leaf area. Lemeur (1973) suggested that leaf azimuthal orientation in *Zea mays* was responsible for the 13% greater radiation interception recorded at low solar elevation. Measurements made parallel to the axis of the rows would be necessary to prevent such errors. Such measurements were not made in the present study as the close spacing of the trees meant that trunks and large branches dominated the field of view of the canopy analyser. Other sources of deviation from theory, such as increased clumping with increasing leaf area (Cohen *et al.*, 1995), may have added but were accounted for by the empirical calibration.

Estimation of leaf area from measurements that included the contribution of branch surface area was achieved here through empirical calibration. Lang (1991) advocated that directly measured surface areas of branches should be subtracted from indirect estimates to obtain leaf surface area. However, this method is unsuitable for isolated canopies, for which the sensor position affects the proportion of branch area projected in the direction of the sensor, as branches are generally inclined upwards and outwards from the main stem. Thus, if the sensor is positioned adjacent to the stem, as suggested by Li-Cor (1992), the branch surface area projected in the direction of the sensor will be smaller than if the sensor is placed at the edge of the canopy. Therefore, although an empirical calibration is in some ways less attractive than a fully mechanistic method, the lack of appropriate theory to account for branches makes calibration desirable.

Differences in measurement techniques makes comparisons with the results obtained by other workers difficult. The LAI-2000 has not been used extensively with isolated canopies in previous studies and its use with isolated tree rows has not been documented. The results obtained for *M. volkensii* at higher leaf area densities are consistent with the isolated tree technique used for *Acacia koa* by Grace and Fownes (1998), in which leaf area was underestimated by approximately 54%. However, Brenner *et al.* (1996) found that the LAI-2000 overestimated the total surface area of isolated *Retama sphaerocarpa* bushes by c. 14%, attributing these errors to estimation of path length. Measurement of the leaf area of isolated canopies is challenging and represents an extreme test of indirect methods. Although the method developed here involved some data manipulation to avoid the use of doubtful assumptions, the time required could be greatly reduced in future studies. Practical problems were encountered with the rapid failure of light following sunset at equatorial latitudes, while the lack of overcast days during some seasons limited the opportunity to make measurements under diffuse radiation conditions. With further validation, the method has potential for use with isolated tree rows although, in the absence of independent measurements of additional canopy structural parameters and incorporation of these into theory, validation and calibration are necessary.

The higher mean leaf inclination angle of *C. megalocarpus* relative to *M volkensii* and the observed increase in inclination angle during the dry season are likely to decrease both the irradiance incident upon the leaves and leaf temperature, thereby limiting consequent injury and photoinhibition. Werner, Correia and Beyschlag (1999) found that the horizontally orientated leaves of semi-deciduous Mediterranean macchia plants were highly susceptible to photoinhibition and photodamage during drought, whereas a more upright posture appeared to protect the leaves. Similarly, in an investigation of the functional roles of contrasting morphologies in *Heteromeles arbutifolia*, an evergreen Californian chapparal shrub, Valladares and Pearcy (1998) concluded that the steeply inclined leaves of sun plants maximised carbon gain whilst minimising the period when leaves were exposed to potentially photoinhibitory photon flux densities. The greater leaf angles observed in *C. megalocarpus* were accompanied by other features which suggest adaptation to drought-prone environments, such as silvery hirsute abaxial leaf surfaces and a degree of leaf rolling. These attributes are more important in evergreen species which cannot escape drought by shedding leaves, and were not apparent in the drought-deciduous *M. volkensii* either at Machakos or within its more arid natural range.

In conjunction with estimates of leaf area provided by the LAI-2000 canopy analyser, the photographic method provided results that served the desired purpose of tracking relative changes in leaf area between LAI-2000 measurement dates. The greatest source of error was probably associated with observer bias in ranking photographs and differences in leaf area per unit rank for different sampling dates arising from the non-linear relationship between rank and leaf area. These problems would have been partly resolved and the reliability of the results improved if destructive measurements of leaf area had been made more frequently for comparison with the photographic rankings.

Leaf area and the seasonal pattern of variation affect both tree and crop growth. Light interception by *M. volkensii* was greater than in *C. megalocarpus* for most of the measurement period, due to the lower leaf area densities and higher leaf areas in the former species (Chapter 7). The effects of clumping and leaf angle distribution are likely to have been less important, because the clumpiness of the *M. volkensii* canopies and the more steeply inclined leaves of *C. megalocarpus* reduced the interception of radiation and increased light transmission to the crop at higher solar elevations. Owing to the energy-dependency of evaporation, the patterns of transpiration and water extraction closely followed those for light interception (Chapter 5). Smith, Jarvis and Odongo (1997a) found that most of the radiation absorbed by windbreak canopies in a semi-arid region of the Sahel was dissipated by transpiration during wetter periods when stomatal and canopy conductances were high. However, transpiration was also shown to be strongly affected by advection and vertical entrainment of air, and is predominantly driven by the vapour pressure deficit at the leaf surface. These results indicate the dependence of transpiration on canopy structure owing to its influence on radiation interception and canopy and aerodynamic conductances. It is interesting to note that *C. megalocarpus*, whose natural range is in higher rainfall areas than Machakos, produced greater leaf areas during wetter seasons than *M. volkensii*, which has a natural range in areas drier than Machakos. These characteristics increased the growth of *M. volkensii* relative to *C. megalocarpus* in drier seasons and *vice versa* in wetter seasons (Chapter 5). With respect to crop growth, shading by taller overstorey trees may decrease assimilate production (Caldwell, 1987) or, alternatively, protect shaded plants from water stress (Allen, Sinclair and Lemon, 1976). These topics are discussed further in Chapter 5.

The observed differences in the timecourses of leaf area, whereby *M. volkensii* produced greater leaf areas during the two drier cropping seasons while *C. megalocarpus* had a higher leaf area during the wetter 1997/98 short rains, resulted in a greater water extraction by *M. volkensii* during drier seasons and by *C. megalocarpus* at the end of the 1997/98 short rains (Chapter 5). However, the increase in leaf area prior to the onset of the rains, particularly in *M. volkensii*, would be expected to increase both the extraction of water and the severity of competition with associated crops; this aspect is discussed further in Chapter 7. The balance between the benefits of shading and competition for water depends primarily on rainfall, crop species, crop position relative to the trees and transpiration and light interception by the trees; these issues are discussed further in Chapter 7.

5 TREE PHOTOSYNTHESIS AND TRANSPIRATION

5.1 INTRODUCTION

In many agroforestry studies, it has been customary to focus on the physiological impact of trees on crop growth in order to isolate determinants of crop yield (e.g. Ong *et al.*, 1991; Howard *et al.*, 1995; Tournebize and Sinoquet, 1995; Brenner, 1996). However, as the trees in agroforestry systems are competitively dominant once established (e.g. Huxley, 1994; Lott *et al.*, 2000a), the growth and yield of crops and the performance of the trees and the system overall may be better defined by establishing patterns of tree behaviour in relation to environmental variables than by simply studying the effects of specific variables on crop growth. Crop growth may then be quantified in terms of seasonal tree functioning. This approach is particularly applicable to seasonally variable environments where the architecture and function of the canopy and roots of the tree component cannot be assumed to remain constant even over relatively short periods. Furthermore, treating the tree component as a static source of microclimatic modification ignores the genetic and ecological basis of tree behaviour upon which the seasonal pattern of crop microclimatic modification is founded. This reduces the potential scope of the findings obtained by precluding the inclusion of tree phenology as a factor influencing system performances in the longer term. In the past, various considerations have constrained detailed ecophysiological studies of the tree component of agroforestry systems, not least the practical difficulty of making routine growth and physiological measurements on large organisms.

Measurement of photosynthesis and transpiration under field conditions was made possible by the advent of portable infra-red gas analysers which enable the gas exchange of individual leaves or whole branches enclosed in chambers to be determined (e.g. Dufrêne, Pontailler and Saugier, 1993). However, measurements of individual canopy elements are of limited value in determining the photosynthesis and transpiration of the whole canopy due to the difficulty of sampling adequate numbers of leaves under fluctuating microclimatic conditions. Wolf, Burk and Isebrands (1995) discussed some of the difficulties and approaches involved in overcoming the problems associated with instantaneous measurements of whole tree photosynthesis. However, by using mathematical models to take account of the structural complexities of tree canopies, the problems associated with the dependence of radiation interception by individual leaves on neighbouring leaves may be overcome. Thus fluxes at specific points within the canopy may be estimated from reference measurements made outside the canopy. Similarly, the use of models to describe the response of leaf-scale physiological processes at different points within the canopy allows integration to determine canopy-scale functioning. Fitting models to physiological responses at the individual leaf level also solves problems associated with the strong correlations which exist between specific environmental variables, such as radiation, temperature and vapour pressure deficit under field conditions (Jarvis, 1976). Such an approach is necessary where non-linearity in the functional relationships between specific processes and their driving variables invalidates simple averaging procedures for measurements made on smaller temporal or spatial scales (Jarvis, 1995). Thus if the y-variate is a non-linear function of the x-variate, the mean of y is not a simple function of the mean of x, but is instead the mean of function values calculated over each spatial and/or temporal interval.

The degree of canopy disaggregation within specific models represents a compromise between realism and simplicity. For example, single layer canopy models may be appropriate where the vegetation represents a permeable lower boundary to the atmosphere, but are inadequate when it is necessary to resolve detail within the canopy (Raupach and Finnigan, 1988). The spatial structure of agroforestry systems in which the tree canopies are isolated or grouped in rows necessitates the use of three-dimensional as opposed to horizontally homogeneous canopy models. Layering within the canopy with respect to leaf area distribution and the input parameters required for physiological models are likely to be of secondary importance where smaller canopies are concerned.

The model used here, MAESTRA, is a development of MAESTRO (Wang and Jarvis, 1990), in which three-dimensional canopy architecture is represented with a high degree of specificity. Widely accepted equations and sub-models are used to determine processes on a spatial scale of individual leaves within the tree canopy and a timescale of hours. In the present study, a modification of the model developed by Jarvis, Miranda and Muetzelfeldt (1985) was used to estimate assimilation, while a modification of the Jarvis (1976) model was used to estimate stomatal conductance. Both models were written into the source code of MAESTRA by the author as they are not supported by the current version. MAESTRA was used to estimate canopy-scale photosynthesis and transpiration for *M. volkensii* and *C. megalocarpus* over three of the four cropping seasons examined. In rainfed semi-arid agroforestry systems, transpiration by the trees is particularly important in determining crop growth as water is, of necessity, largely extracted from the soil volume occupied by the roots of both components. Shading of adjacent crops by trees also has potentially important effects and was estimated using MAESTEST, a companion model to MAESTRA which calculates incident photosynthetic photon flux density (Q) below tree canopies. The results of these analyses are presented in Chapter 7. MAESTEST was also used to validate the radiative transfer routines in MAESTRA, including the leaf area estimates, by comparing modelled output to quantum sensor measurements made beneath the tree canopies. Subsidiary objectives were to examine the effects of the quantity and spatial arrangement of leaf area on canopy assimilation and transpiration in order to determine their relative importance to the functioning within the systems examined.

5.2 MATERIALS AND METHODS

5.2.1 LEAF GAS EXCHANGE

Leaf gas exchange measurements for *Croton megalocarpus* and *Melia volkensii* commenced during the 1996/97 short rains and continued until January 1998, with the exception of the period between June and September 1997. A CIRAS-1 portable photosynthesis system was used in combination with a narrow Parkinson leaf cuvette (PLC(N)) with dimensions of 45 x 20 mm (PP Systems, Hitchin, Herts, UK.). The CIRAS-1 employs four independent infra-red gas analysers, two each for determining carbon dioxide and water vapour concentrations. One pair of CO_2 and H_2O analysers measure the reference air supply whilst the second pair measures the sample air, i.e. air that has passed through the leaf cuvette. The accuracy of the analysers is maintained during operation by frequent zeroing, whereby CO_2-free dry air is passed through the analysers. A second zeroing method whereby reference air is passed through all four analysers is used to balance readings for each pair of cells. Leaf temperature may be measured either using a thermistor placed in contact with the leaf or an energy balance approach. Air temperature within the cuvette is measured by a second thermistor, while photosynthetic photon flux density is determined by a quantum sensor positioned beside the leaf chamber. Regular maintenance of the instrument included periodic replacement of air filters and renewal of the air conditioning chemicals when colour changes indicated exhaustion. Chamber seals were checked for leaks by breathing around the closed cuvette with all CO_2 removed from the inlet air; replacement was necessary on only one occasion. Details of the calibration of the various sensors and measurements of boundary layer resistance within the cuvette are given in Appendix 4.

Measurements were made from platforms constructed using two pairs of 10 m tall eucalyptus poles set in concrete and cross-braced using 1 m long ½ inch diameter steel rods (cf. Plate 2.4). The two pairs of poles were supported by steel stays and two or three platforms were suspended at different levels to provide access to the full vertical extent of the canopy. To avoid disruption of crop growth in the central area of the plots, the platforms were positioned on the southern side and at the western end of the tree rows to provide access to the canopies of 5-6 adjacent trees.

Before each day of measurement, the CIRAS-1 system was left to equilibrate for >10 minutes to allow the sensors to stabilise and flush stagnant air from the air conditioning columns and air-lines. Reference air was drawn via a tube attached to a 8 m bamboo pole raised above the tree canopy and passed through a five litre container to buffer changes in air composition. Flow rates were set between 300-350 cm^3 min^{-1} to provide a typical CO_2 depletion of between 5 and 30 ppm, as recommended by the manufacturer. Leaf temperature was measured using the thermistor held against the underside of the leaf. Leaf temperatures obtained agreed closely with those calculated using the leaf energy balance approach. However, the energy balance method for determining leaf temperature was not used routinely as the location of the quantum sensor outside the cuvette precluded correct measurement of leaf temperature when the external light source was used. Following each measurement, the leaf section enclosed within the cuvette was excised and sealed in a zip-lock plastic envelope until its area could be determined using an portable leaf area meter (ADC, Hoddesdon, Herts, UK).

Measurement methods

Two types of measurement were made using the CIRAS-1 gas analyser:

1. "Ambient" measurements were made under the prevailing environmental conditions to determine photosynthetic rate and stomatal conductance. During these measurements, sample CO_2 and H_2O concentrations were monitored for c. 30-90 s to allow the values to stabilise before being recorded. Although stomatal conductance may decrease by 50 % within 2-5 minutes, and in some cases within as little as 1 minute in response to decreases in irradiance (Jones, 1992), the reductions in illumination within the leaf cuvette were limited; this method was therefore considered preferable to making almost immediate measurements and using ambient air conditions to parameterise the physiological models. Instantaneous measurements may also introduce problems associated with incomplete flushing of air from the cuvette and gas lines and possible overestimation of transpiration resulting from rapid changes caused by heating within the cuvette.

2. "Light response" measurements were made by manipulating the photosynthetic photon flux density (Q) incident upon the leaves to determine the responses of carbon assimilation. Figure 5.1 shows a typical light response curve for *M. volkensii*. A light source supplied by PP Systems was used in conjunction with a plastic diffuser and metal mesh filters of varying porosity to adjust Q. The illumination unit contained two 12 V, 20 W quartz halogen bulbs and an interference filter to remove infra-red radiation with a

wavelength below 3 µm and minimise heating. Q within the cuvette was determined by placing the quantum sensor at leaf level under the cuvette window with the light unit switched on. The shading effect provided by specific filters was determined and several were selected to provide a sequence of Q values for use in field measurements. As the experimental site was some distance from a mains electricity supply, the unit was powered by two fully charged 12 V lead acid batteries connected in parallel to minimise voltage drop. As Leverenz (1988) showed that the illumination sequence has no significant effect on the shape of the light response curve, measurements were carried out in a sequence intended to minimise leaf heating by beginning at the highest Q value, i.e. with no diffuser or filters, and continuing with a series of successively lower Q values. A period of >30 s was allowed to elapse following changes in Q before values were recorded. Finally, a measurement was made in darkness using thick cloth to cover the cuvette window and exclude light. Depth within the canopy and distance from the edge of the canopy were recorded for each leaf examined. Attempts to reduce heating of the leaves using a Peltier module attached to the cuvette proved ineffective. Light response measurements were therefore generally made early in the day during periods of hot weather to minimise heating effects.

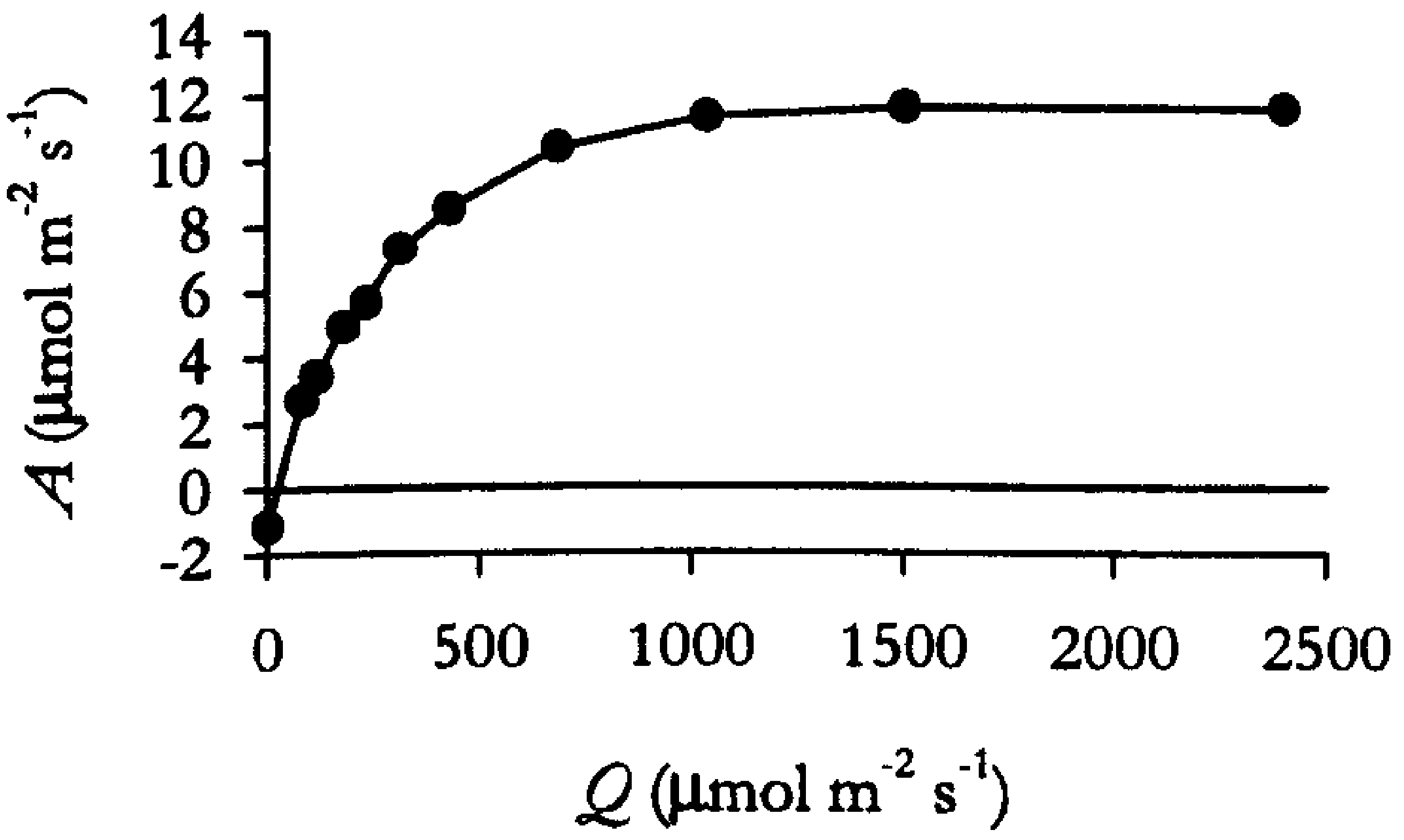


Figure 5.1. Typical light response curve for *M. volkensii.*

Sampling strategy

The sampling strategy differed for the two methods of measurement. Ambient measurements were made for 20-30 tagged leaves distributed throughout the width and depth of the southern side of the tree canopies in Replicates 2 and 4. Measurements were made for each tagged leaf twice during the same day at two week intervals. Light response measurement were made in alternate weeks to the ambient measurements, with 5-10 response curves being constructed on each sampling date. Every effort was made to spend two days constructing response curves for each species during each round of measurements, one for each replicate examined, although time-constraints occasionally prevented this from being achieved. Several additional sets of measurements were made to enable comparison of the responses of measured and modelled assimilation rates under changing conditions. These were made for single leaves, with automatic measurements being made at 5 minute intervals over periods of several hours on several occasions towards the end of 1997.

For all measurements, the data were downloaded to a PC at the end of the day and calculations were performed in a spreadsheet using measured leaf areas and the photosynthesis equations provided by PP Systems (1994).

Stomatal distribution

The surfaces of several leaves of *M. volkensii* and *C. megalocarpus* were examined to establish stomatal distribution and to determine whether the calculations of gas exchange should be based on one or both leaf surfaces. Stomata were located exclusively on the abaxial leaf surface of *M. volkensii* and predominantly on the abaxial leaf surface of *C. megalocarpus*, with much smaller numbers being present on the adaxial surface. The assumption that leaves were hypostomatous was therefore used in the gas exchange calculations.

Leaf temperature

Leaf temperature measurements were made with the intention of being used as model input. However, difficulties associated with the operation of leaf thermocouples for extended periods and failure of the data logger caused the dataset to be discontinuous; air temperature measurements were therefore used as a substitute in MAESTRA. Measurements were made in Replicate 3 for *C. megalocarpus* and Replicate 4 for *M. volkensii* using x-shaped thermocouples, the extremities of which were attached to the underside of individual leaves using small strips of porous surgical tape. Six sets of five 0.2 mm copper-constantan thermocouples, waterproofed with a thin layer of nail varnish and wired in parallel, were used to provide temperature measurements for different sections of the canopies of each species. These were visually divided into three equally spaced levels, and three sets of thermocouples, one at each level, were assigned to the north and three to the south side of the tree row. A series of measurements made between 17-26 October 1997 at the beginning of the 1997/98 short rains is shown in Figure 5.2.

5.2.2 ASSIMILATION

Two leaf-level sub-models, one describing assimilation and the other stomatal conductance, were parameterised for use in MAESTRA. The model of Jarvis, Miranda and Muetzelfeldt (1985), a modification of that developed by Reed *et al.* (1976), describes photosynthesis in terms of Q, stomatal conductance, CO_2 compensation point, mesophyll conductance, CO_2 concentration and dark respiration using the following relationships; ***Photosynthesis*** is defined here as gross carbon fixation and ***assimilation*** as ***photosynthesis*** less the quantity of carbon lost by dark respiration.

1. Photosynthesis (P) is related to Q by a non-rectangular hyperbola whereby

$$\theta P^2 - P(\alpha Q + P_{\max}) + \alpha Q P_{\max} = 0 \qquad [5.1]$$

and

$$P = A + \mathrm{R_d}, \quad P_{\max} = A_{\max} + \mathrm{R_d} \qquad [5.2]$$

where A denotes carbon assimilation rate, θ defines the convexity and α the initial slope of the A-Q relationship.

2. Assimilation is linearly related to intercellular carbon dioxide concentration (C_i) over the range of interest (Ludlow and Jarvis, 1971):

$$A_{\max} = (C_i - \Gamma) g_{mt} \qquad [5.3]$$

where A_{max} represents the maximum assimilation rate, Γ is the carbon dioxide compensation concentration and g_{mt} denotes mesophyll conductance (see below).

3. C_i depends on the rate of assimilation and stomatal conductance (Jarvis, 1971):

$$C_i = C_a - A / g_s \qquad [5.4]$$

where C_a represents the ambient carbon dioxide concentration at the stomata entrance and g_s is stomatal conductance to CO_2.

4. Leaf dark respiration (R_d) is an exponential function of leaf temperature:

$$\mathrm{R_d} = \mathrm{R_0} \exp(k T_l) \qquad [5.5]$$

where R_0 represents the dark respiration rate at 0 °C, k is a temperature coefficient and T_l denotes leaf temperature. Brooks and Farquhar (1985) found that dark respiration in leaves is inhibited in the light to an extent which depends on the availability of ATP and NADPH from photosynthesis. For instance, Villar, Held and Merino (1995) reported that dark respiration rates were inhibited in the light by 62 and 51 % respectively in a deciduous (*Lepechinia fragrans*) and an evergreen (*Heteromeles arbutifolia*) Californian chapparal species. It was therefore assumed in the present study that leaf dark respiration at incident *Q* values above 10 µmol m^{-2} s^{-1} was 60 % of its value in darkness at the same temperature.

Mesophyll conductance was described by a bell-shaped temperature response curve defined by Reed *et al.* (1976) as:

$$g_{\mathrm{mt}} = g_{\mathrm{m0}}(b_1(T_1 - T_{\mathrm{min}})(T_{\mathrm{max}} - T_1)^{b_2}) \qquad [5.6]$$

$$b_1 = \frac{1}{(T_0 - T_{\mathrm{min}})(T_{\mathrm{max}} - T_0)^{b_2}} \qquad [5.7]$$

$$b_2 = \frac{(T_{\mathrm{max}} - T_0)}{(T_0 - T_{\mathrm{min}})} \qquad [5.8]$$

where g_{mt} denotes mesophyll conductance at leaf temperature, g_{m0} represents the maximum mesophyll conductance, T_l is leaf temperature, T_{max} and T_{min} respectively represent the upper and lower temperatures at which mesophyll conductance is 0, while T_0 is the temperature where mesophyll conductance is optimal. The parameters must be constrained so that $T_{\mathrm{max}}>T_0>T_{\mathrm{min}}$ and T_{max} and T_{min} must respectively be above and below the minimum and maximum recorded temperatures within the modelled period to prevent the function becoming undefined.

The CO_2 compensation point, Γ, was calculated according to Brooks and Farquhar (1985):

$$\Gamma = g_{\mathrm{w}} + 1.88(T_1 - 25) + 0.036\,(T_1 - 25)^2 \qquad [5.9]$$

where g_{w} is the conductance for CO_2 transfer from the sub-stomatal cavities to the carboxylation sites for tobacco (36.9 mol m^{-2} s^{-1} bar^{-1}; Von Caemmerer *et al.*, 1994). Equations 5.1 to 5.4 combine to give a quadratic equation, of the form shown in equation 5.10, relating *A* to the leaf variables, the negative root of which gives appropriate assimilation values.

$$A = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} \qquad [5.10]$$

$$a = \theta + \frac{g_{\mathrm{m}}}{g_0} \qquad [5.11]$$

$$b = R_{\mathrm{d}}(2\theta + \frac{g_{\mathrm{m}}}{g_0} - 1) - \alpha Q(1 + \frac{g_{\mathrm{m}}}{g_0}) - g_{\mathrm{m}}(C_{\mathrm{a}} - \Gamma) \qquad [5.12]$$

$$c = \alpha Q g_{\mathrm{m}}(C_{\mathrm{a}} - \Gamma) + R_{\mathrm{d}}(R_{\mathrm{d}}\theta - R_{\mathrm{d}} - g_{\mathrm{m}}(C_{\mathrm{a}} - \Gamma)) \qquad [5.13]$$

where g_0, the total conductance of the leaf (stomatal plus boundary layer conductance), is given by:

$$g_0 = \frac{g_s g_a}{g_s + g_a} \qquad [5.14]$$

where g_s and g_a respectively represent stomatal and boundary layer conductances.

The model described by equation 5.1 was fitted to the pooled ambient and light response data for each species to provide initial values for the more complex model described by equations 5.6-5.14. The dark respiration function was fitted to measurements made in darkness. All models were fitted using non-linear least squares regression procedures in Sigma Plot for Windows Version 4.

5.2.3 STOMATAL CONDUCTANCE

A modified version of the empirical model of Jarvis (1976) was used in MAESTRA to describe stomatal conductance in terms of photosynthetic photon flux density and vapour pressure deficit.

1. Stomatal conductance was related to absorbed Q using a normalised hyperbolic function:

$$f\,Q = Q/(Q + Q_0) \qquad [5.15]$$

where Q_0 is an arbitrary fitted parameter determining the curvature of the relationship (equivalent to PAR_0 in MAESTRA documention).

2. Stomatal responses to vapour pressure deficit remain in question as a causal relationship has not been established (Monteith, 1995), although a linear or curvilinear relationship is commonly found. The relationship with vapour pressure deficit (D) is described in this model by a normalised exponential function following that of Levy

(1995), which generally provides a better description of experimental data than a linear response:

$$fD = \exp(-(D^2)/D_0) \qquad [5.16]$$

where D_0 is an arbitrary parameter defining the decrease in g_s with D (equivalent to VPD$_0$ in MAESTRA documention). It is assumed that there is no interaction between variables, giving the following relationship:

$$g_s = (g_{s\,\mathrm{ref}} - g_{s\,\mathrm{min}}) \cdot fQ \cdot fD + g_{s\,\mathrm{min}} \qquad [5.17]$$

where $g_{s\mathrm{ref}}$ and $g_{s\mathrm{min}}$ represent the measured maximum and minimum stomatal conductances respectively.

No response to C_a was included as the range over which measurements were made was small (30 μmol mol^{-1}) and no response was apparent within the data obtained. A temperature response analogous to that in equations 5.6-5.8 was fitted to the data but was not used for further analyses as no improvement in the fit of the model was achieved and no temperature relationship was apparent in the data. The limited temperature range over which measurements were made (c. 10 °C) may have been responsible for this apparent lack of response.

To determine whether soil moisture content (cf. Section 7.2.2) was an influential variable, stomatal conductance was plotted against weekly soil moisture contents averaged across measurement points to a depth of 1.6 m on the north side of the trees at distances of up to 5.5 m from the tree row. No trend was evident and linear responses failed to improve the fit of the model for either species and so were not used.

5.2.4 CANOPY-SCALE GAS EXCHANGE

The model MAESTRA (Medlyn, 1999) was used to estimate whole-tree photosynthesis and transpiration in *M. volkensii* and *C. megalocarpus* and to test the relative importance of changes in leaf area and canopy volume. MAESTRA is a revision of the model MAESTRO (Wang and Jarvis, 1990) which has undergone development and modification since the 1970s (Norman and Welles, 1983). MAESTRO/MAESTRA is a three dimensional model of canopy radiation absorption and photosynthesis, in which the stand or forest canopy is represented as an array of tree crowns with specified shapes, positions, dimensions, leaf areas and leaf angle distributions. These attributes make the model particularly applicable to agroforestry systems in which the tree crowns are isolated, receive direct radiation from various directions depending on solar angle and cast discreet shadows on understorey crops. The shading patterns may be quantified with the associated program, MAESTEST (cf. Section 5.1), further extending the applicability of the model to agroforestry situations. The model also allows for changes in leaf areas and crown dimensions over time, thereby enabling phenological changes and canopy growth to be represented. Calculations are performed for specified "target trees", the canopies of which are sub-divided into a number grid locations, where absorbed radiation is calculated in three wavebands (PAR, NIR and thermal), with direct, diffuse and scattered radiation being considered separately. The direct fraction of incident radiation is calculated from the ratio of measured incident radiation above the canopy to a theoretical value for the same solar position with a cloudless sky. Penetration of direct radiation to the specified sub-volumes within the canopy takes into account solar position and the area and angle distributions of leaves in neighbouring sub-volumes along the ray path, including those in surrounding trees. First order scattering is calculated according to Norman and Welles (1983) and transmission of diffuse radiation to each sub-volume is calculated as a Lambert-Beer extinction function from a number of hemisphere points. Woody parts of the canopy are ignored for the purposes of determining radiation penetration. Weighted averages of photosynthesis and transpiration are calculated for the target tree based on the leaf area in the volume of the canopy represented by each grid point. Temperature and humidity are held equal to the bulk atmosphere outside the canopy. Absorbed Q at each grid point and associated microclimatic information drive the photosynthesis and transpiration sub-models, with transpiration being calculated for each gridpoint using the Jarvis and McNaughton (1985) formulation of the Penman-Monteith equation:

$$\lambda E = \frac{\varepsilon R_n + 2c_p D_a G_H / \gamma}{\varepsilon + G_H / G_V} \qquad [5.18]$$

where λ represents the latent heat of vaporisation of water, E is the evapo-transpiration rate, s is the slope of the relationship between saturation vapour pressure and temperature, γ is the psychrometric constant, $\varepsilon = s/\gamma$ (strongly dependent on temperature), c_p is the molar heat capacity of dry air at constant pressure, D_a is the water vapour saturation deficit of air, G_H is the total conductance for sensible heat and G_V is the total conductance for water vapour. Inputs are the calculated net radiation flux density incident upon the leaf surface, the water vapour saturation deficit of the ambient air and leaf boundary layer, and stomatal conductance. The photosynthesis sub-model outlined in Section 5.2.2 was written into the model source code, as MAESTRA only handles the Farquhar and von Caemmerer (1982) model which, given its biochemical basis, is more difficult to parameterise with field measurements. The model is written in Fortran and runs in a DOS environment with text input and output files.

The model has been successfully tested against canopy transmitted radiation data (Wang and Jarvis, 1990) and CO_2 flux data measured by eddy covariance in Sahelian crops and savanna (Levy, 1995), Amazonian rain forest (Kruijt *et al.*, 1994) and Boreal spruce forest (Rayment *et al.*, 1995).

5.2.5 MODEL PARAMETERISATION AND USE

Model parameters are submitted to MAESTRA via name lists in text files. Five text input files, the contents of which are reproduced in Appendix 5, are required, with an additional file for MAESTEST (cf. Section 5.1). There is some flexibility in the choice of sub-models; for instance, three models are available for describing stomatal conductance, while the meteorological data may be presented in several ways. In the model runs reported here, the routines for calculating wood and root growth and maintenance respiration were not used as appropriate input data were not collected. Model output was therefore limited to assimilation and transpiration rather than growth *per se*. The following sections outline the main features of each input file and the sources of the parameters. The model was run with an hourly time-step between 1 July 1996 and 28 February 1998. The input files are as follows:

1. confile.dat

'Confile.dat' contains switches to control the simulation, states the number of trees, the target tree, the number of layers in the canopy and the number of zenith and azimuth angles over which the integration is carried out. For all model runs, six canopy layers were specified to provide 72 canopy grid points (12 points per layer) as Levy (1995) showed that absorbed radiation reaches an asymptote with upwards of ~60 grid points, below which radiation absorption may be underestimated. The numbers of zenith and azimuth angles were set at the default values of 5 and 11 respectively.

2. met.dat

The meteorological data input specification is also flexible to some extent (Medlyn, 1999). In the present study, the data comprised hourly means of windspeed at reference height above the canopy, air temperature, soil temperature at a depth of 5 cm, vapour pressure deficit and photosynthetically active radiation (PAR). Windspeed at the experimental site was measured at a height of 8 m using an anemometer attached to one of the canopy measurement towers using a horizontal pole. As global radiation rather than

PAR was recorded by the meteorological station, a conversion factor of 0.5 was used; a conversion factor of 4.57 was used to transform the values from units of J m^{-2} s^{-1} to μmol m^{-2} s^{-1} (Jones, 1992). The latitude and longitude of the site were taken from ICRAF (1991). Barometric pressure was specified as 86900 Pa, the average value obtained from measurements made over a period of several months during the field period using a Vaisala PTB100 barometric pressure sensor (Vaisala, Helsinki, Finland).

3. phy.dat

This file specifies the physiological parameters used in the model. The physiological parameters for assimilation (Eqs. 5.5-5.14) and stomatal conductance (Eq. 5.17) shown in Table 5.3 were included in the model source code and not in the input file, as would be the case if the standard MAESTRA model structure was used. The reason for this was that the input name lists do not accommodate the use of these equations and modification of the program source code and name lists was not considered a worthwhile investment of time.

Leaf reflectance and transmittance in the photosynthetically active and near infra-red wavebands were derived from measurements of the leaves of four Sahelian species reported by Levy (1995). Values for leaves in the thermal waveband and all reflectance and transmittance values for soils were estimated according to Monteith and Unsworth (1990). Leaf width, required for the calculation of boundary layer conductance, was taken as the mean of measurements for 10 leaves (leaflets in the case of *M. volkensii*) for each species.

4. str.dat

This file specifies canopy structural parameters. Crown shape may assume any of six forms: upright cylinder, paraboloid, box, cone, ellipsoid and half ellipsoid. 'Box', a six sided volume with 90° opposed straight edges, was used to create an array of 19 canopies edge-to-edge to simulate the tree row (see trees.dat). Elliptical leaf angle distributions were used for parameterisation of leaf incidence angle. The equations of Campbell and Norman (1989) were fitted to the measured leaf angle distributions for *C. megalocarpus* and *M. volkensii* shown in Figure 4.3. Good fits were achieved for both species ($r^2>0.9$).

5. trees.dat

'trees.dat' contains plot details, including crown dimensions and positions. Plot dimensions were set at 20 x 20 m to contain 19 trees at a 1 m spacing, forming a row along the centre of the plot. The *x*-axis of the plot was given a bearing of 90° from the south to denote the east-west orientation of the tree rows. All crowns were given the same dimensions with an *x*-radius of 0.5 m which, with a 1 m spacing between trees, left no gap between the edges of adjacent canopies. *y*-radii, crown height and trunk height were specified on four occasions coinciding with LAI-2000 leaf area measurements, when crown dimensions were recorded (cf.

Table 4.4). As measured leaf areas were for a volume with an elliptical cross-section (cf. Section 4.2.1), the specified *y* radii were set at 75 % of the measured values to retain the measured leaf area densities within ±4 % with the box-shaped canopies. All trees were allocated equal leaf areas which were defined on 18 occasions according to the estimates obtained for 1 m row lengths (cf. Section 4.3.3) of each species using the procedures described in Section 4.2.3.

6. points.dat

This file contains *x*, *y* and *z* co-ordinates of points for calculation of below-canopy *Q* and is not used by MAESTRA itself, but by the companion program MAESTEST, which calculates radiation flux at defined points within the plot. The file is primarily intended for validation purposes, but was also used in Chapter 7 to predict *Q* values incident on the crops adjacent to the trees.

Validation

To test the radiative transfer routines within the model and measured canopy attributes, *Q* measurements were made using quantum sensors (Skye Instruments, Llandrindod Wells, UK) at defined points within and beneath the canopies of *C. megalocarpus* and *M. volkensii* in Replicates 3 and 4 respectively. The quantum sensors were mounted on telescopic steel tubes which could be fixed at varying heights. The sensors were moved every few days to a new position within 1 m of the centre of the tree row and between trees 5 and 15 (cf. Figure 2.3). The height of the sensors and position relative to the tree row were recorded with each movement of the sensor. Measurements were recorded using a datalogger (21X, Campbell Scientific, Shepshed, UK) at five minute intervals and hourly means were calculated prior to and during the 1997/98 short rains. Only the measurements made at the bottom of the canopy were ultimately used, as it was subsequently decided that, as a result of time-constraints, the tree canopy would be modelled without horizontal layering, negating the need for validation at different levels in the canopy.

Originally, a selection of tube solarimeters, some constructed by ICRAF staff and others supplied by Delta-T Devices (Cambridge, UK) were used to measure incident shortwave radiation under the trees to enable validation of the canopy model. However, numerous problems were encountered with these instruments. Condensation frequently formed within the tubes, necessitating the removal and oven-drying of the solarimeter; calibration factors were also found to drift between successive calibrations. As the reliability of the data obtained was questionable, it was decided to switch to the more robust point sensors.

Sensitivity testing

As the stomatal conductance model fitted to *C. megalocarpus* measurements gave some skewing of residuals, as outlined below, a sensitivity test was carried out to determine the effects of altering the stomatal conductance model input parameter, Q_0, on photosynthesis and transpiration. The model was run for the period between 1 June and 31 December 1997 with Q_0 being increased or reduced by 20 %.

Alternative scenarios

In addition to the originally parameterised model runs, two separate scenarios were used to test the extent to which variation in leaf area and canopy volume affected photosynthesis and transpiration in *C. megalocarpus* and *M. volkensii*. For both species, leaf area and canopy volume were doubled independently and data for the period between 1 October and 31 December 1997 were used to drive the model. This period was chosen for two reasons, firstly because the transition between the dry and wet seasons occurred when leaf areas were increasing and climatic changes were taking place, and secondly because leaf areas were determined at the beginning and end of this period using the LAI-2000 canopy analyser (cf. Section 4.3.1).

5.3 RESULTS

5.3.1 LEAF TEMPERATURE

Under ideal circumstances, IRGA measurements for the purposes here would be carried out under the conditions experienced by unenclosed leaves. However, enclosure in the leaf cuvette increased leaf temperature, particularly when the illumination unit was used. To determine the extent of heating, leaf temperature within the cuvette during measurement was compared with air temperature measured at hourly intervals at the meteorological station. Under ambient radiation conditions, mean leaf temperatures in *C. megalocarpus* and *M. volkensii* were respectively 3.6 and 2.1 °C above air temperature. However, the temperatures of unenclosed leaves were also higher than air temperature during the day. For the period shown in Figure 5.2 leaf temperatures were on average 0.8 °C higher in *C. megalocarpus* and 0.6 °C in *M. volkensii* between 6 am and 6 pm. The increased irradiance provided by the external light source resulted in mean leaf temperatures being 7.9 and 7.5 °C above air temperature in *C. megalocarpus* and *M. volkensii* respectively. Leaf heating is likely to remain a problem with portable gas analysers which lack the refrigeration capacity necessary to maintain leaf temperature close at near ambient levels under hot climatic conditions. Although the temperature responses included in the photosynthesis models may circumvent this problem, with semi-empirical models it is preferable to maintain measurement conditions as close to ambient as possible.

During the central hours of the day (10 am-2 pm), leaf temperatures were significantly higher (p<0.001) in *C. megalocarpus* than in *M. volkensii*, as shown in Figure 5.2, probably because of lower stomatal conductances. Despite the high degree of coupling with ambient temperature expected in isolated canopies, leaf temperatures were often 1-2 °C above air temperature during the middle of the day. The elevated leaf temperatures in both treatments at night (cf. Figure 5.2) was probably the result of condensation. Given these differences between leaf and air temperature, substitution of air temperature for leaf temperature in MAESTRA may be expected to cause some underestimation of transpiration and respiration during the day and an overestimation of respiration at night.

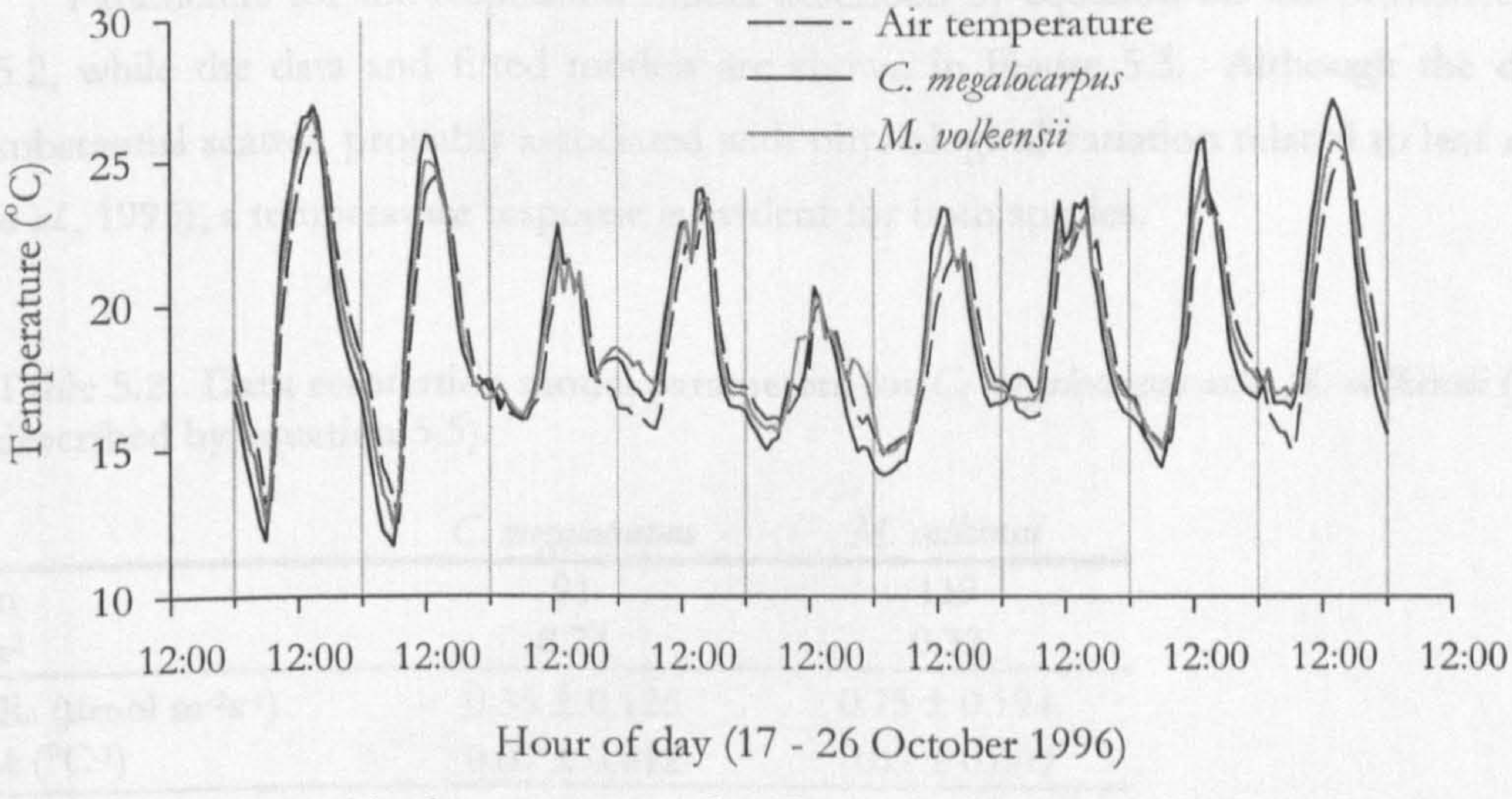


Figure 5.2. Air and leaf temperatures for *C. megalocarpus* and *M. volkensii* for the week beginning 17 October 1997.

5.3.2 ASSIMILATION

Assimilation rates under saturating light (>1200 µmol m^{-2} s^{-1}) were 22 % higher in *M. volkensii* than in *C. megalocarpus* (p<0.001; Table 5.1). The values obtained are low compared to the range of 14-40 µmol m^{-2} s^{-1} reported for C3 plants by Jones (1992), but fall within the limits reported for a range of evergreen and deciduous savanna species (Eamus *et al.*, 1999) and six semi-deciduous forest trees from Panama (Hogan, Smith and Samaniego, 1995).

The mean dark respiration rates for both species (Table 5.1) are slightly higher than those reported for three deciduous Sahelian shrub species, *Combretum micranthum* (1.46 μmol m^{-2} s^{-1}), *Combretum nigricans* (2.01 μmol m^{-2} s^{-1}) and *Guiera senegalensis* (1.43 μmol m^{-2} s^{-1}) over a similar temperature range (Levy, 1995). Villar, Held and Merino (1995) found that respiration rates in the dark were higher in the leaves of a deciduous Californian chapparal shrub species (*Lepechinia fragrans*) than in a co-occurring evergreen (*Heteromeles arbutifolia*), although the differences were not significant. Similarly, the mean dark respiration rate in the deciduous *M. volkensii* was higher than in the evergreen *C. megalocarpus* (Table 5.1), although the differences were again not significant.

Table 5.1. Dark respiration and assimilation rates under saturating light (>1200μmol m^{-2} s^{-1}) for *C. megalocarpus* and *M. volkensii.*

	Dark respiration (R_d, μmol m^{-2} s^{-1})			Assimilation (A, μmol m^{-2} s^{-1})		
	Mean	n	*p*[1]	Mean	n	*p*[1]
C. megalocarpus	2.38 ± 0.13	91	<0.21	8.59 ± 0.189	373	<0.001
M. volkensii	2.57 ± 0.09	139		10.47 ± 0.193	287	

[1] 1-probability of difference between species

Parameters for the respiration model described by equation 5.5 are presented in Table 5.2, while the data and fitted models are shown in Figure 5.3. Although the data show substantial scatter, probably associated with physiological variation related to leaf age (Villar *et al.*, 1995), a temperature response is evident for both species.

Table 5.2. Dark respiration model parameters for *C. megalocarpus* and *M. volkensii* (Model described by equation 5.5).

	C. megalocarpus	*M. volkensii*
n	91	139
r^2	0.24	0.33
R_0 (μmol m^{-2}s^{-1})	0.35 ± 0.125	0.75 ± 0.194
k (°C^{-1})	0.07 ± 0.012	0.05 ± 0.009

The variation of assimilation rate with temperature is shown in Figure 5.4. The outer limit of the scatter shows a broadly bell-shaped response in both species. However, the fitted curve parameters for mesophyll conductance shown in Table 5.3 indicate that in *C. megalocarpus* the relationship was not bell-shaped, but approximated a straight line, with T_0 being very close to T_{max}. This may have occurred because the temperature response apparent in Figure 5.4 was removed by co-variance of temperature with other variables within the model. In *M. volkensii* both the upper and lower constraints were reached, again suggesting temperature effects were not pronounced for the range over which measurements were made.

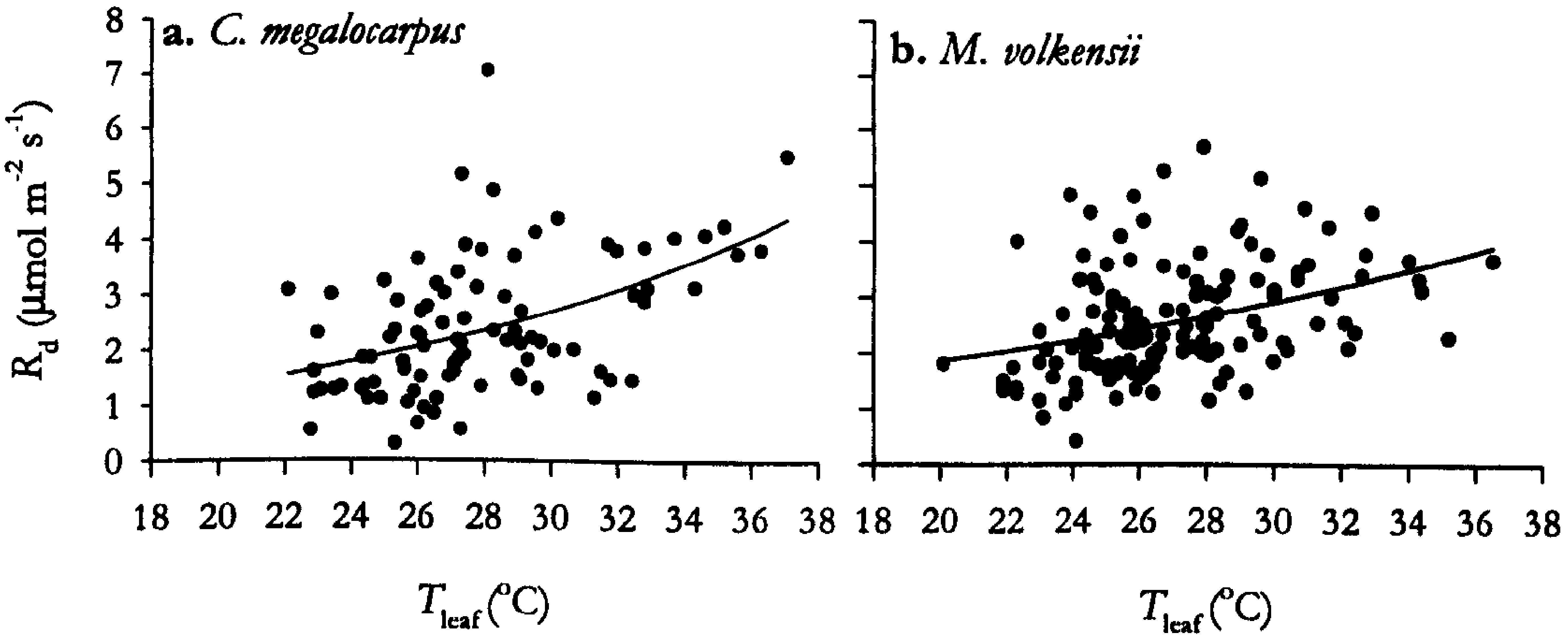


Figure 5.3. Relationship between dark respiration and leaf temperature with fitted curves (Eq. 5.5) for a). *C. megalocarpus* and b). *M. volkensii*.

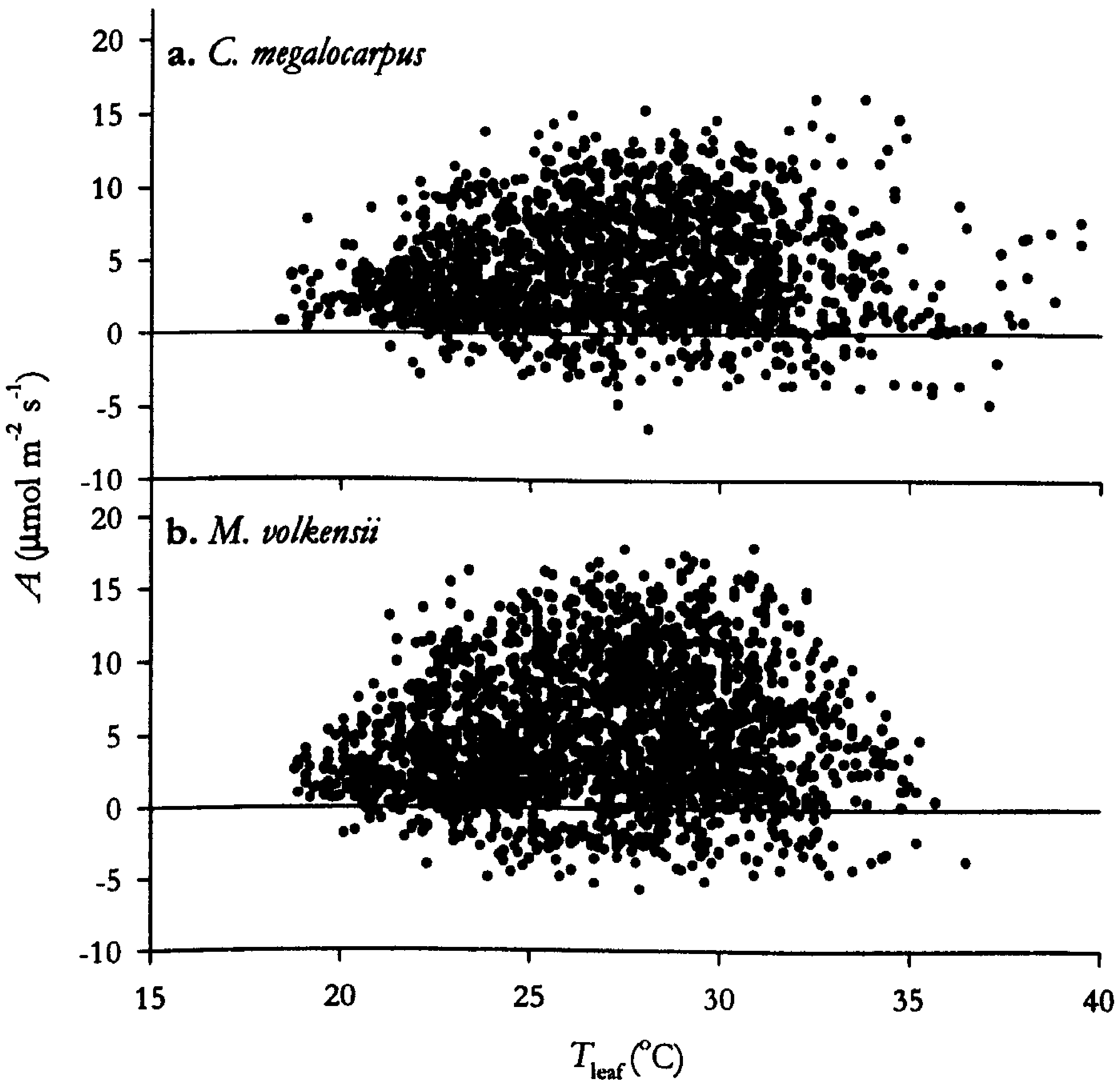


Figure 5.4. Relationship between assimilation rate (A) and leaf temperature for a). *C. megalocarpus* and b). *M. volkensii* derived from ambient and light response measurements.

Figure 5.5 shows light response curves for *C. megalocarpus* and *M. volkensii* for three ranges of stomatal conductance. The fitted lines are output from the partial model relating assimilation to *Q* using the non-rectangular hyperbola described by equation 5.1. The model was fitted separately to data falling within each stomatal conductance category using the mean R_d values shown in Table 5.1.

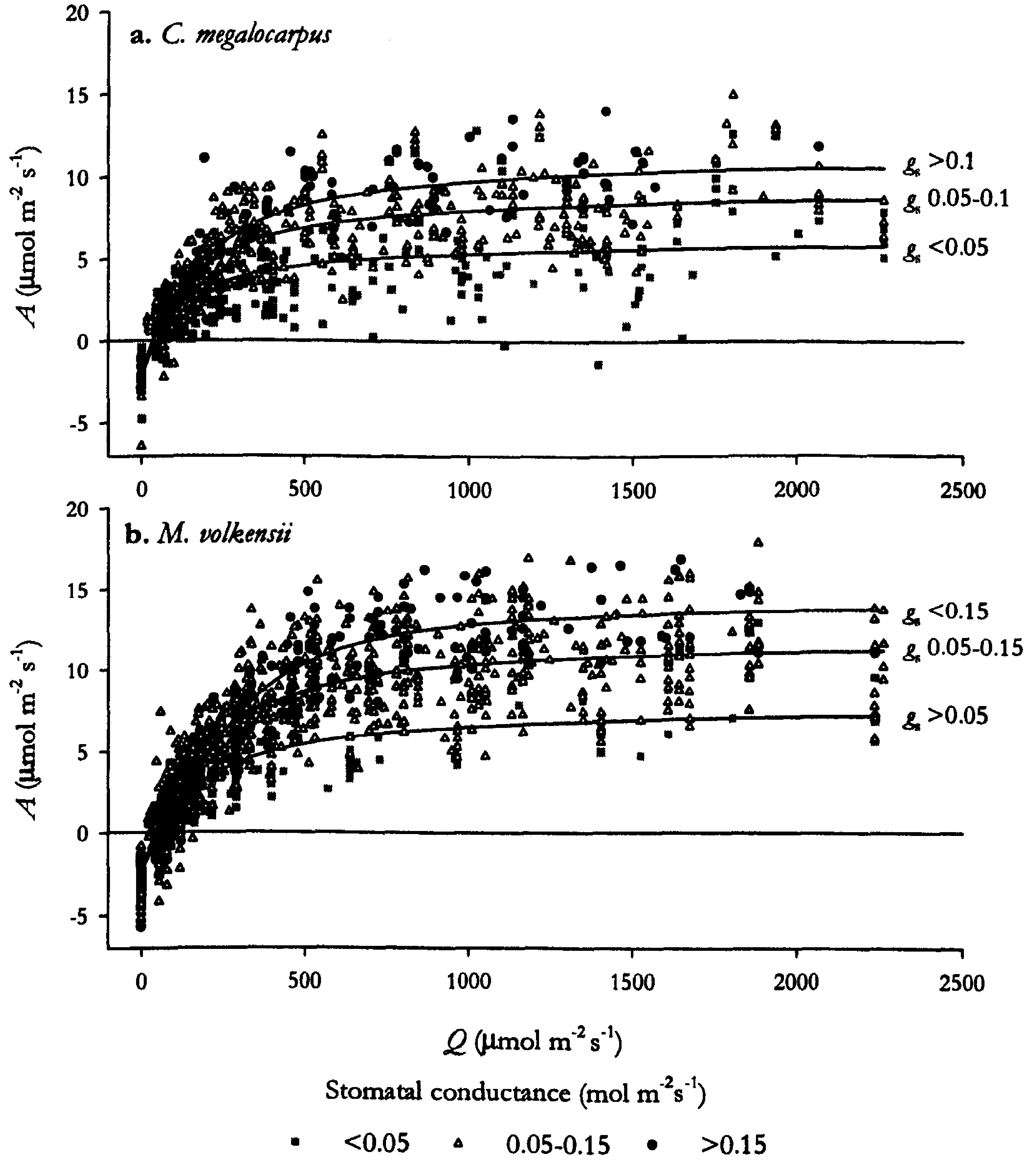


Figure 5.5. Non-rectangular hyperbolae relating measurements of assimilation rate (*A*) to *Q* for three stomatal conductance ranges ($g_s<0.05$, $0.05<g_s<0.01$, $g_s>0.01$) for a) *C. megalocarpus* and b) *M. volkensii*.

Although assimilation rates within each conductance category exhibited considerable scatter, separation between the various categories is apparent. *M. volkensii* exhibited light saturation of photosynthesis at higher Q values and greater rates of assimilation than *C. megalocarpus*.

Parameters fitted to the photosynthesis model are shown in Table 5.3, together with r-squared regression coefficients for both species. Both models generally fitted the experimental data closely, as shown by Figure 5.6. However, high measured assimilation rates were underestimated by the modelled values in both species. This effect may be attributable to too few or ill-fitting function(s) within the model, resulting in the measurements made at high assimilation rates being effectively averaged rather than explained. The possibility of deviations of this type is inevitable in non-mechanistic models in which the underlying physiological and biochemical mechanisms within the leaf are not exactly represented. The values for θ, the convexity of the light response, are lower than reported by Leverenz (1988) for a range of coniferous species and Ögren (1993) for *Salix* species, indicating a low convexity and high saturation point for the light response curve, and hence a lower photosynthetic efficiency over the intermediate light range. This may have originated partly because the use of numerous data points for different periods resulted in a loss of resolution, or as a result of model parameters trading off against one another during the fitting procedure, leading to the best fit being achieved for the entire model, but with individual parameters not necessarily being close to their theoretical values. However the relatively high incident Q values experienced by the two species are consistent with the possibility that leaf chlorophyll content was also high, which would decrease curve convexity (Leverenz, 1988). Mesophyll conductance (Table 5.3) was within the range (0.067-0.143 mol $m^2 s^{-1}$) reported for C3 plants by Jones (1992).

Table 5.3. Photosynthesis model parameters ± SE and regression co-efficients for *C. megalocarpus* and *M. volkensii*. (Model described by equations 5.5-5.14).

	C. megalocarpus	*M. volkensii*
n	1779	2287
r^2	0.78	0.86
α	0.057 ± 0.0001	0.052 ± 0.001
θ	0.33 ± 0.077	0.364 ± 0.0269
$g_{m(l)}$	0.09 ± 0.003	0.07 ± 0.001
T_o	41.7 ± 0.96	29.2 ± 0.10
T_{max}	41.8 ± 1.45	38.1 ± 7.46 [1]
T_{min}	4.1 ± 0.85	7.7 ± 0.85 [1]

1-constraint reached

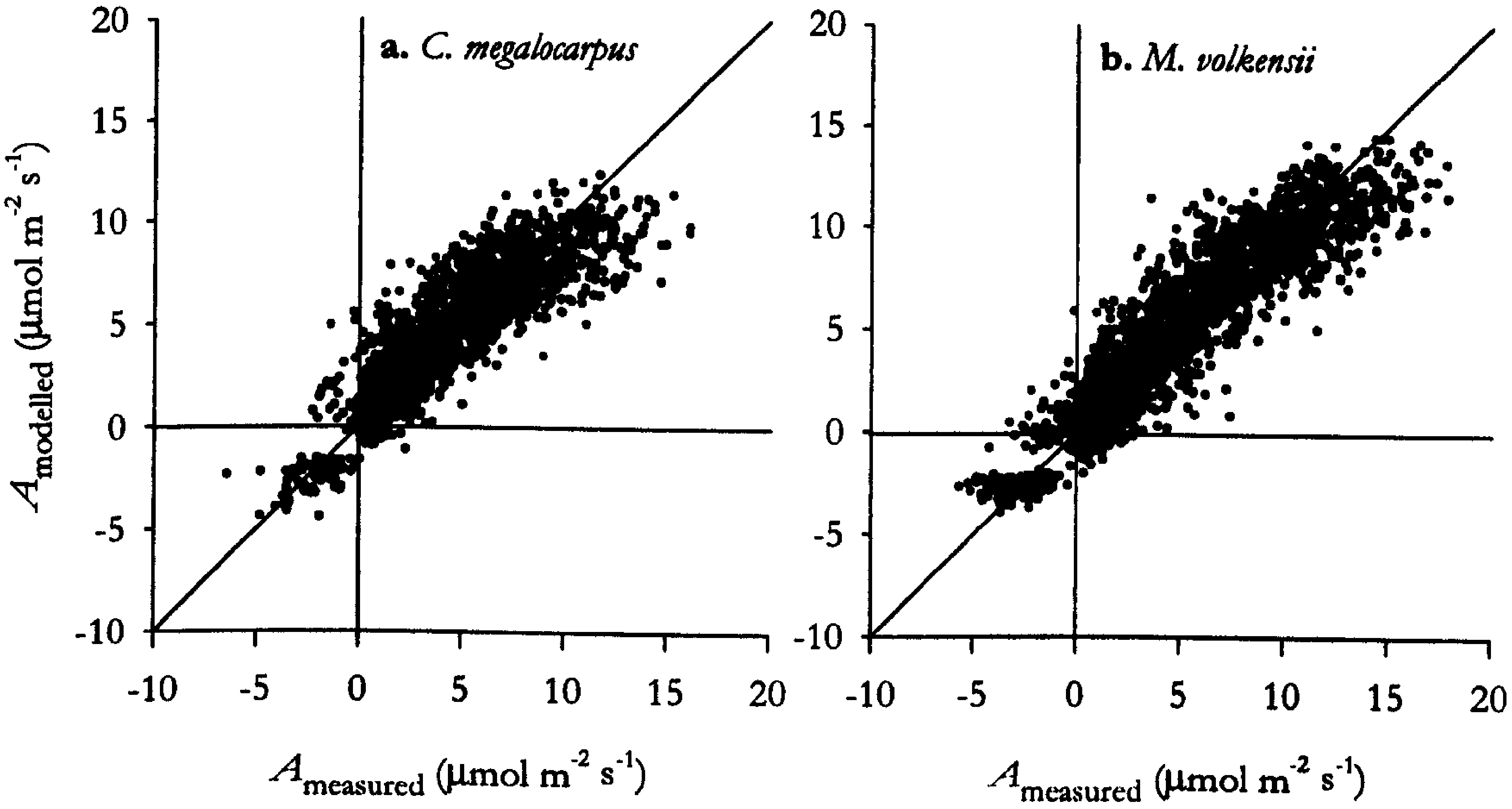


Figure 5.6. Relationship between observed and modelled assimilation rates for a). *C. megalocarpus* and b). *M. volkensii*. 1:1 lines are shown.

Residual analysis

Figures 5.7 and 5.8 show plots of residual values against other parameters and independent variables. Inappropriate models would lead to lack of fit and non-random error, introducing bias into parameter estimates and the distribution of residuals (Reed *et al.*, 1976). No skewing is evident for the models fitted to either species with respect to predicted assimilation, stomatal conductance, *Q* or leaf temperature. The lack of any systematic deviation between observed and calculated values show that the equations provided an adequate description of the shape of the response curves. Slight overestimation of assimilation is apparent at the beginning of the short rains in October and November 1997 in *C. megalocarpus*, but not in *M. volkensii*. This effect may have resulted from differences in leaf age whereby old leaves still present at the end of the dry season assimilate more slowly than new leaves produced after the onset of the rains. With respect to the differing positions of leaves within the canopy, the even distribution of the residuals indicates that the model adequately explained the variance resulting from the commonly observed differences between sun and shade leaves (Gratani, 1993; Zhang, Sharifi and Nobel, 1995).

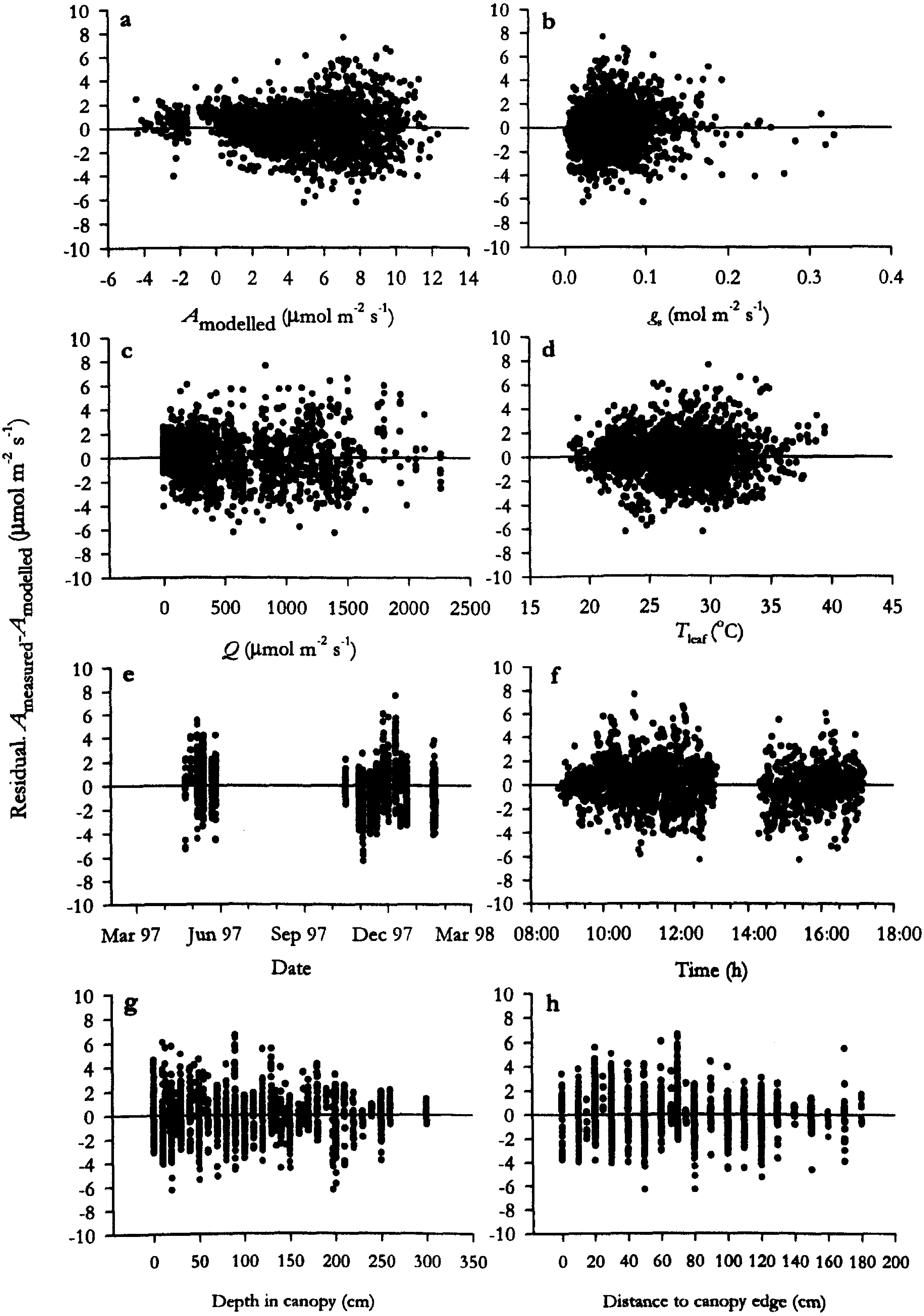


Figure 5.7. Distribution of residuals (measured A – modelled A derived from the fitted model for: a) assimilation; b) stomatal conductance; c) Q; d) leaf temperature; e) date; f) time; g) depth within the canopy; and h) distance to edge of the canopy for *C. megalocarpus*.

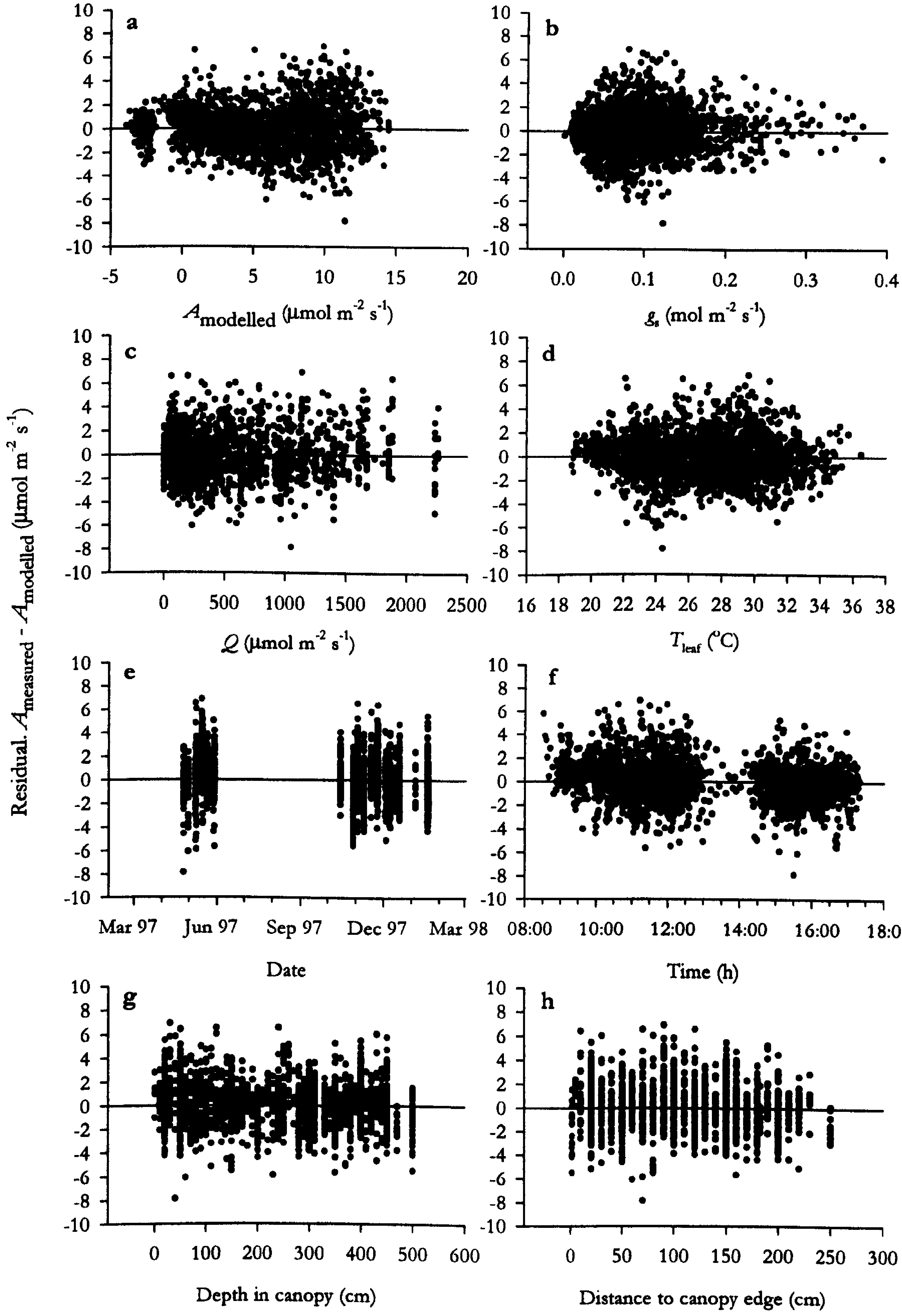


Figure 5.8. Distribution of residuals (measured *A* – modelled *A* derived from the fitted model for: a) assimilation; b) stomatal conductance; c) *Q*; d) leaf temperature; e) date; f) time; g) depth within the canopy; and h) distance to edge of the canopy for *M. volkensii*.

Figures 5.9 and 5.10 show assimilation timecourses constructed for single leaves of *C. megalocarpus* and *M. volkensii* on days of occasional cloud in November 1997, during the short rainy season. The model closely tracked the changing assimilation rates of leaves induced by fluctuating *Q*. The closer tracking of *Q* by the modelled data suggests that the leaves and/or the CIRAS-I gas analyser system may not have responded immediately to changes in ambient conditions. This would not have been a problem during measurements made to parameterise the model, when an equilibration period was used to ensure that stable values were recorded. The underestimation of *A* at high assimilation rates apparent in Figure 5.6 was more pronounced in *C. megalocarpus*, for which incident *Q* was higher.

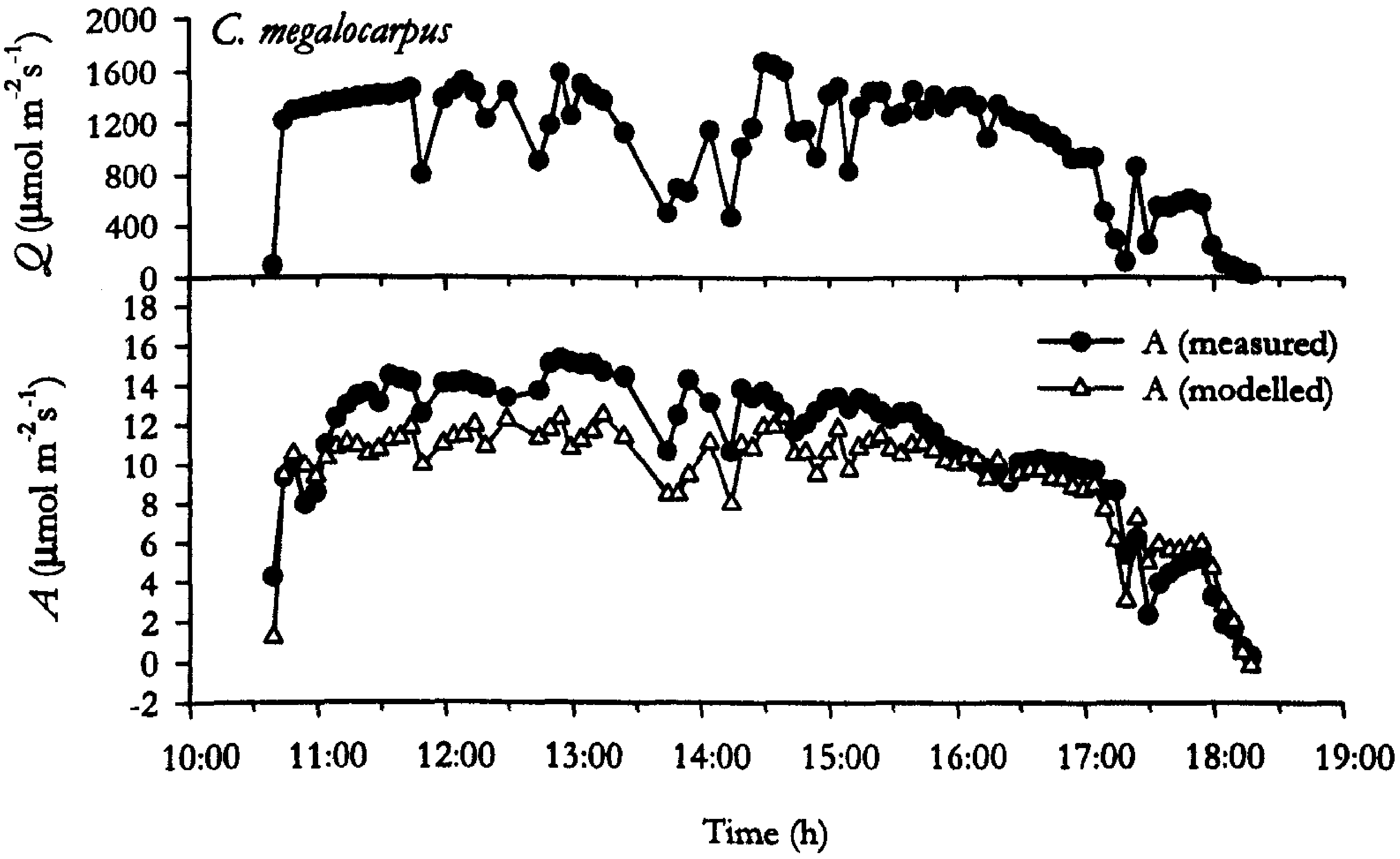


Figure 5.9. Diurnal timecourses for: a) incident photosynthetic photon flux density, *Q*; and b) observed and modelled assimilation rates for *C. megalocarpus*; automatic measurements of assimilation rate were made for a single leaf at 5 min intervals on 23 November 1997.

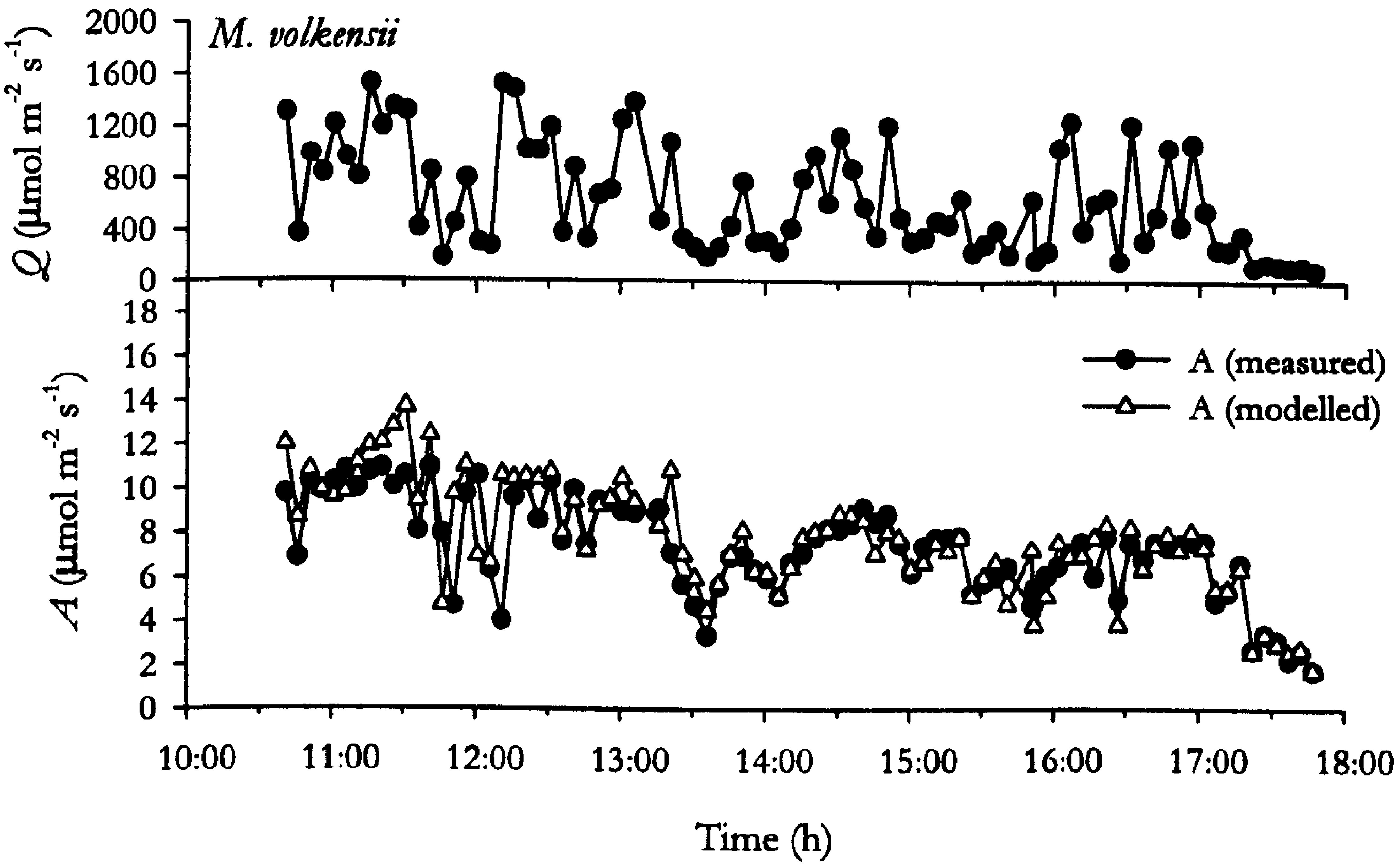


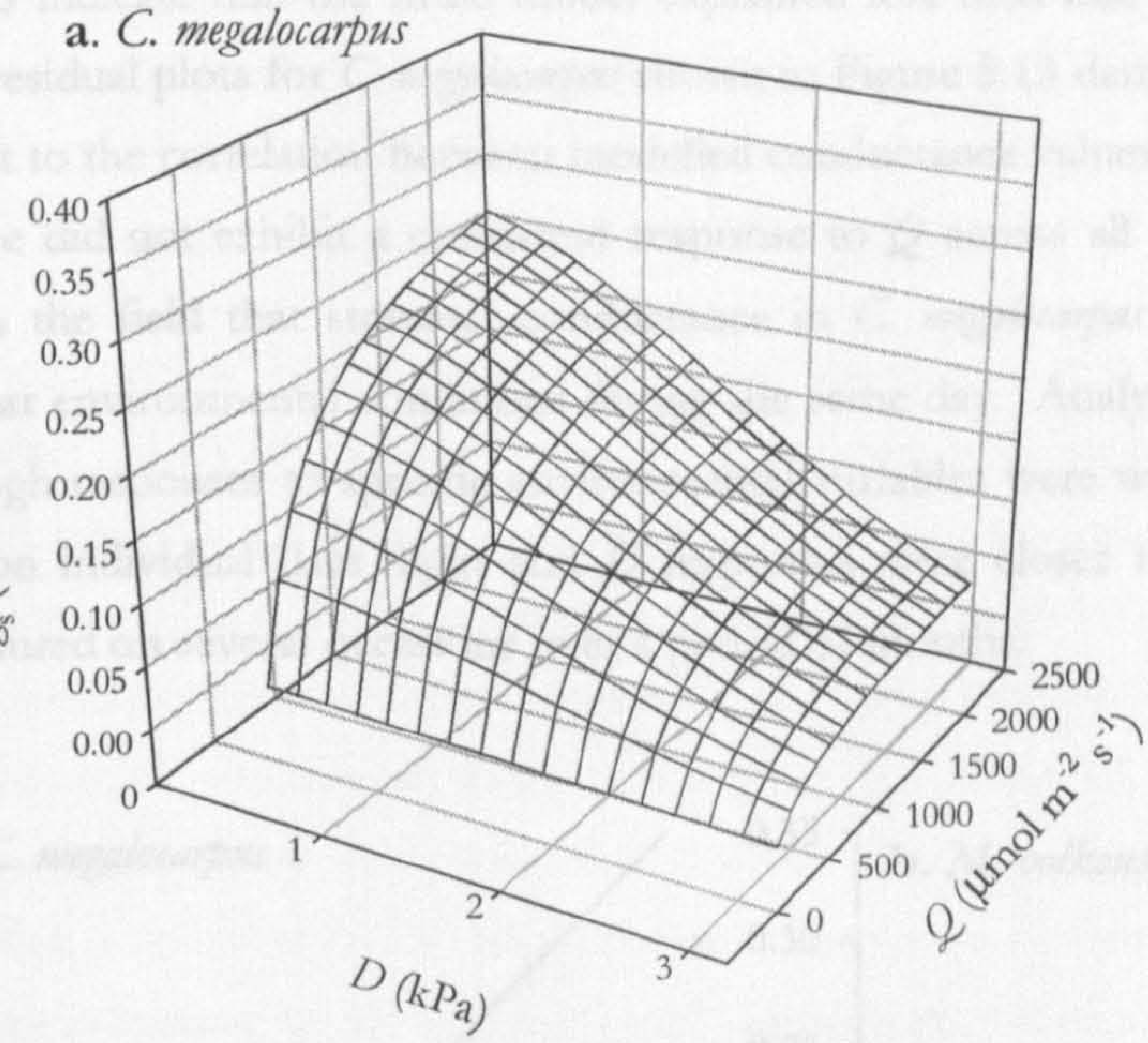
Figure 5.10. Diurnal timecourses for; a) incident photosynthetic photon flux density, *Q*; and b) observed and modelled assimilation rates for *M. volkensii.*; automatic measurements of assimilation rate were made for a single leaf at 5 min intervals on 6 November 1997.

5.3.3 STOMATAL CONDUCTANCE

Mean stomatal conductances to carbon dioxide calculated from the pooled ambient measurements for each species were 21 % higher in *M. volkensii* than in *C. megalocarpus* (p<0.001; Table 5.4). The maximum values for both species (Table 5.5) were higher than those reported by Körner *et al.* (1979) for deciduous and evergreen woody plants, but fell within the same range as those recorded for three woody Sahelian species (Levy, 1995). The response surfaces shown in Figure 5.11 illustrate the shape of the functions describing the relationship between stomatal conductance, D and Q for both species. The greater stomatal conductances recorded for *M. volkensii* and the more dramatic response to Q are evident. However, stomatal conductances were comparable in both species at lower Q values. *M. volkensii* also showed a more pronounced response to D and lower absolute conductances than *C. megalocarpus* at equivalent D values, which may relate to the greater aridity of its natural habitat.

Table 5.4. Mean stomatal conductance to carbon dioxide for *C. megalocarpus* and *M. volkensii* calculated from pooled ambient measurements.

	Stomatal conductance (mol CO_2 m^{-2} s^{-1}) Mean	n
C. megalocarpus	0.067 ± 0.0014	691
M. volkensii	0.085 ± 0.0016	751



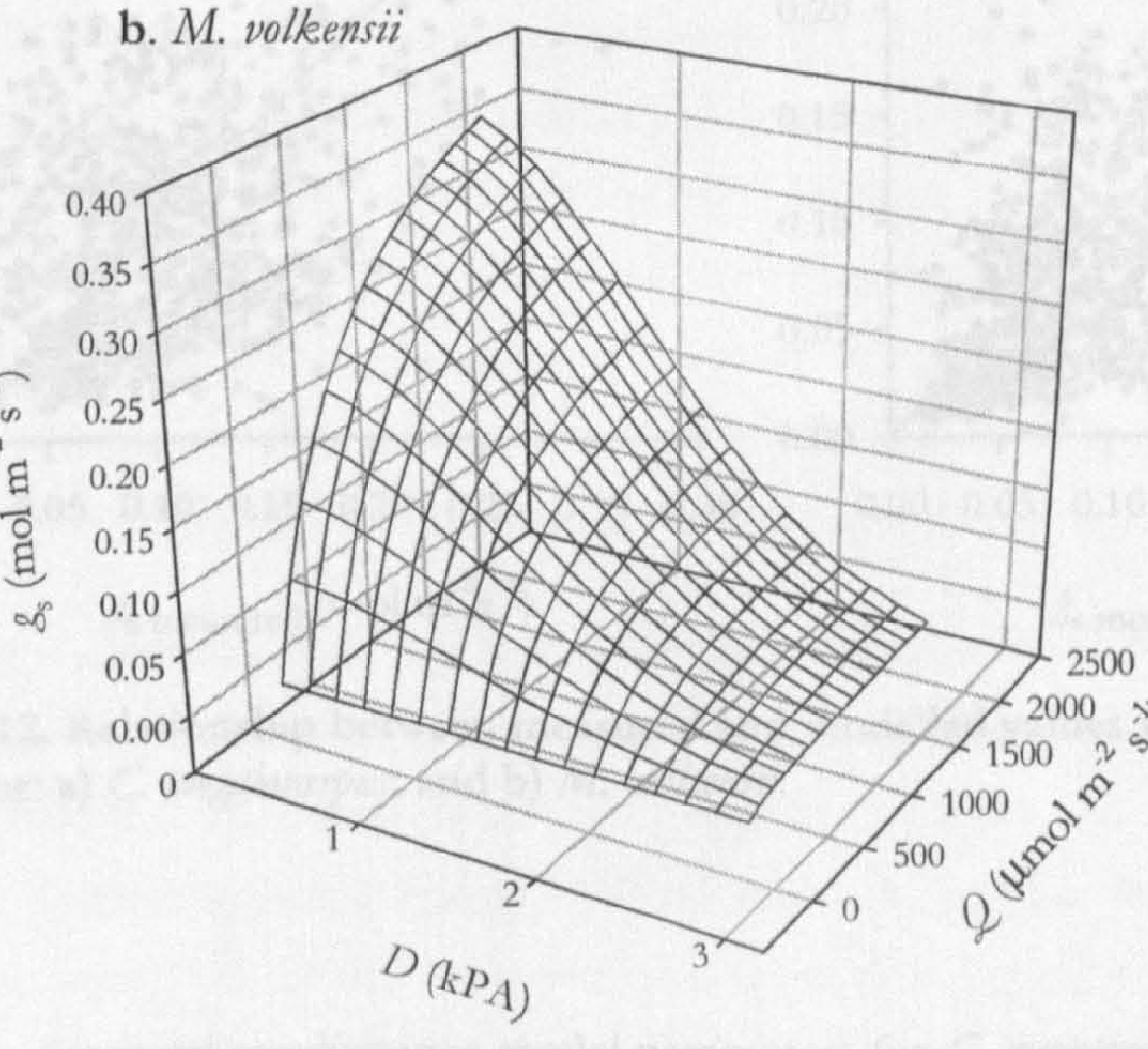


Figure 5.11. Fitted stomatal conductance models for: a) *C. megalocarpus*; and b) *M. volkensii.*

The correlations between measured and modelled stomatal conductances for *C. megalocarpus* and *M. volkensii* shown in Figure 5.12 and the regression coefficients presented in Table 5.5 indicate that the fitted model explained less than half of the variation in the data. The residual plots for *C. megalocarpus* shown in Figure 5.13 demonstrate some skewing with respect to the correlation between modelled conductance values and Q, suggesting that conductance did not exhibit a consistent response to Q across all measurements. It was apparent in the field that stomatal conductance in *C. megalocarpus* varied between leaves under similar environmental conditions during the same day. Analysis of the data revealed that, although responses to specific environmental variables were weak for different leaves measured on individual days, light and D responses were closer for the same individual leaves measured on several occasions over a period of months.

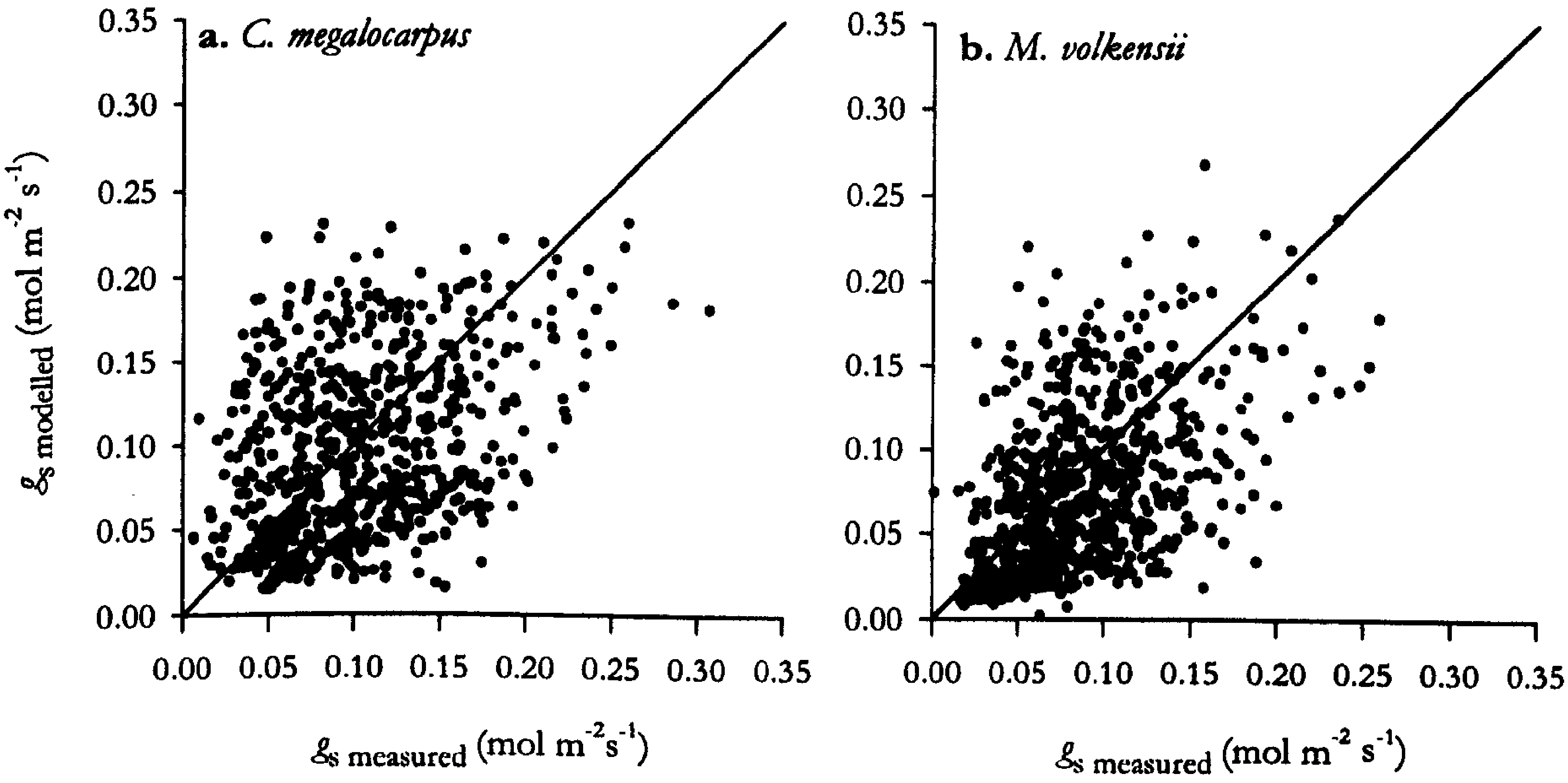


Figure 5.12. Relationship between measured and modelled values for stomatal conductance to CO_2 for: a) *C. megalocarpus*; and b) *M. volkensii*.

Table 5.5. Stomatal conductance model parameters for *C. megalocarpus* and *M. volkensii*.

	C. megalocarpus	*M. volkensii*
n	692	751
r^2	0.36	0.50
$g_{s\,ref}$ ^{1}	0.34	0.481
$g_{s\,min}$ ^{1}	0.004	0.0020
Q_0	371.9 ± 24.53	574.4 ± 32.37
D_0	6.6 ± 0.47	2.8 ± 0.15

1-measured values

The model overestimated stomatal conductance under intermediate photon flux densities. The residuals were evenly distributed with respect to D, leaf temperature, date and time of day, showing that none of these factors were responsible for the overestimation. The lack of response to soil moisture is apparent from the even residual scatter with respect to date. Table 5.5 shows that the model provided a better fit to *M. volkensii* than *C. megalocarpus* data.

Previous studies of *Tectona grandis* and *Gmelina arborea* in Nigeria (e.g. Grace, Okali and Fasehun, 1982) and *Coffea arabica* in Hawaii (Gutiérrez, Meinzer and Grantz, 1994) have shown closer relationships with environmental variables for measurements made over short periods. However, Levy (1995) observed poor correlations between stomatal conductance and environmental variables for measurements made over long periods, while Irvine (1998) found no stomatal response to Q or temperature but observed responses to D and a threshold response to soil moisture deficit in *Pinus sylvestris*. These observations raise the possibility that a response to soil water potential may have occurred in the present study, and the weak responses to the environmental variables examined were a result of the trees being able to access residual soil moisture. The observation that stomatal conductance did not vary with date even though soil moisture content was changing may have occurred because leaf water potential was maintained relatively constant by a dynamic equilibrium between leaf area and soil water availability (cf. Chapter 3), thereby reducing the degree of direct stomatal control of transpiration. A further possibility may be that chemical signals such as abscisic acid (ABA) generated in the roots affected stomatal conductance; however, the work of Triboulot *et al.* (1996) showed that ABA had no effect on stomatal behaviour in oak trees despite its important regulatory function in herbacious species (Jackson, 1997).

As the relationship between measured assimilation rate and stomatal conductance was linear (Figure 5.7b), the poor fit of the model would not necessarily lead to systematic errors in the estimation of canopy-level processes, for the reasons outlined in Section 5.1. However, depending on the frequency distribution of Q within the canopy, the skewing of residuals in relation to Q may cause incorrect estimation. As light is extinguished within the canopy, the resulting distribution of Q is likely to damp the effects of the skewing, with the result that canopy-scale processes may not be greatly affected. However, stomatal conductance may be overestimated under mid-range incident Q (~500-1000 μmol m^{-2} s^{-1}), producing overestimates of photosynthesis and transpiration. A sensitivity analysis was therefore carried out by changing Q_0 and monitoring model output to establish the effects of altering the shape of the stomatal conductance function, as is described below

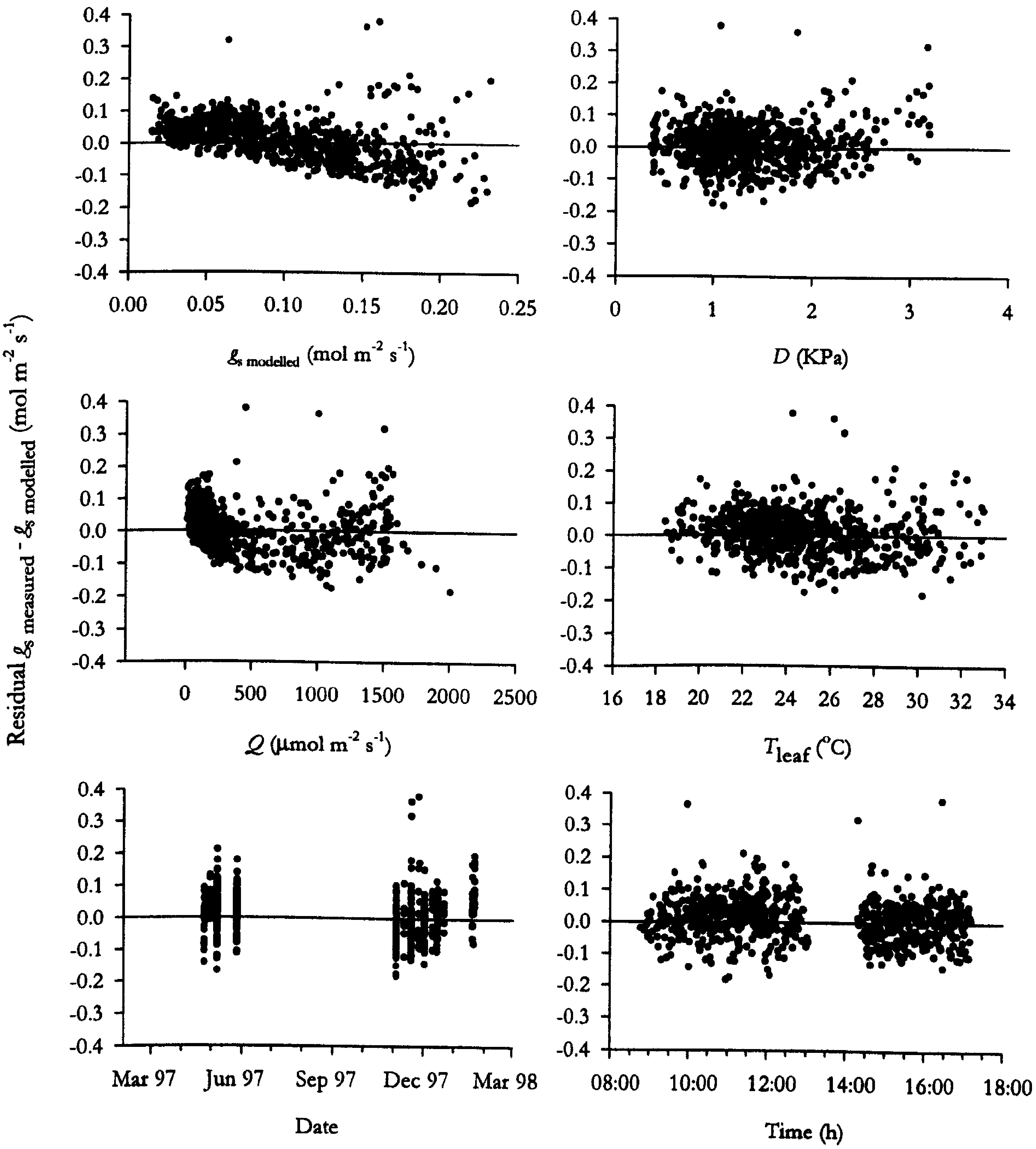


Figure 5.13. Distribution of residuals (measured g_s – modelled g_s derived from the fitted stomatal conductance model (Jarvis, 1976)) plotted against: a) modelled stomatal conductance; b) D; c) Q; d) leaf temperature; e) date; and f) time of day for *C. megalocarpus* ambient measurements.

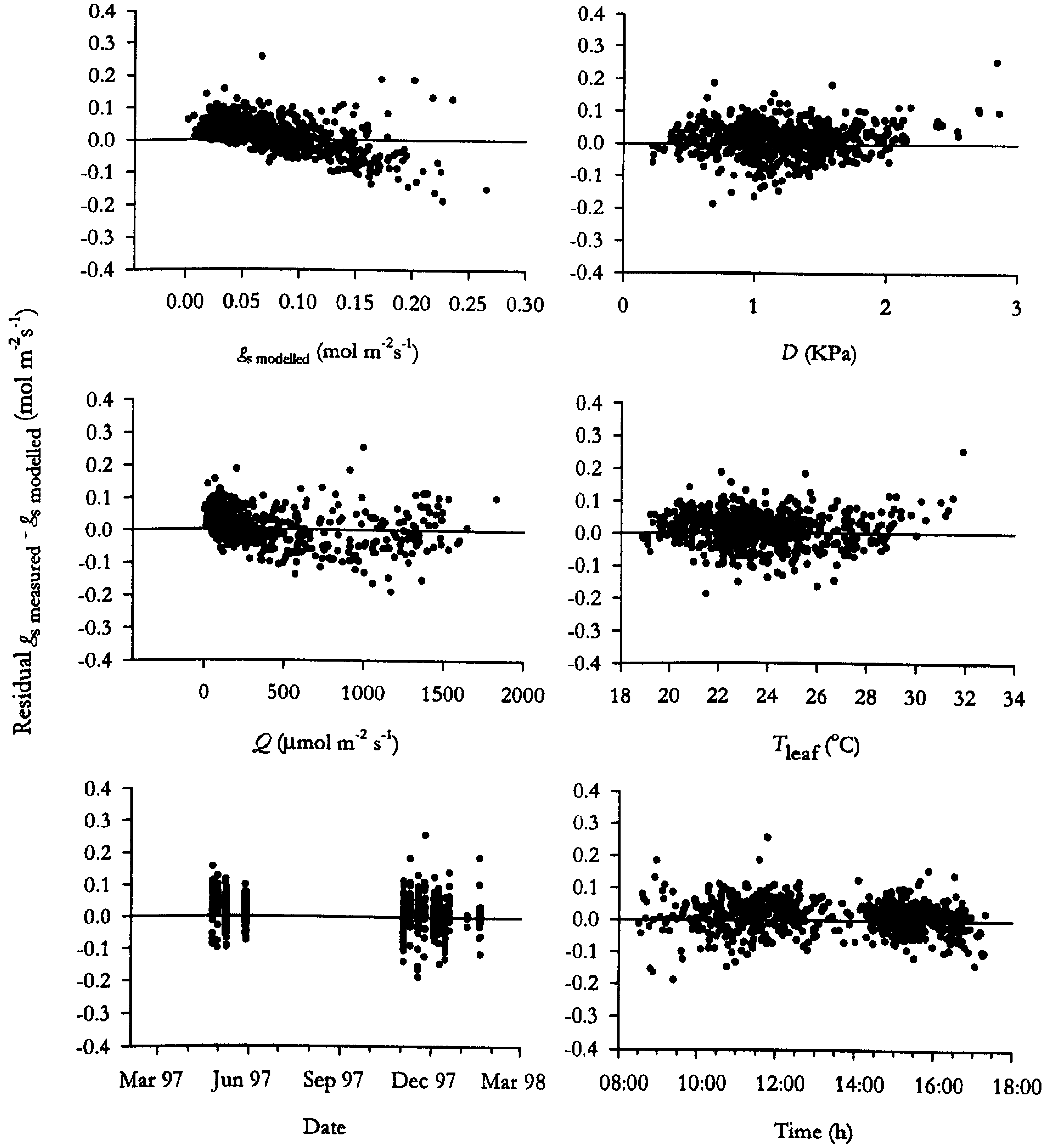


Figure 5.14. Distribution of residuals (measured g_s – modelled g_s derived from the fitted stomatal conductance model (Jarvis, 1976)) plotted against: a) modelled stomatal conductance; b) D; c) Q; d) leaf temperature; e) date; and f) time of day for *M. volkensii* ambient measurements.

Water use efficiency

Following common usage, the ratio of assimilation to water loss, although not a true efficiency, is referred to here as 'water use efficiency' (WUE). Mean instantaneous values calculated from the pooled ambient measurements and measurements made under saturating light are shown in Table 5.6. The lack of any significant difference between the pooled values for each species results in part from the similarity of stomatal conductances and assimilation rates at lower Q values (cf. Figure 5.5). However, a significant species difference ($p<0.001$) was observed under saturating Q, with the value for *M. volkensii* being 1.6 times greater than that for *C. megalocarpus*. This difference resulted primarily from the higher assimilation rate per unit stomatal conductance in *M. volkensii*.

In *M. volkensii* higher values of WUE were obtained under saturating light relative to the mean for all light levels suggesting that this species is better adapted to high light conditions. In *C. megalocarpus*, the reverse was the case (Table 5.6). These differences are in keeping with the natural distributions of the two species and although the values are high compared to other tree species (e.g. Zhang and Marshall, 1994), they are comparable with those recorded by Lindroth and Cienciala (1996) in *Salix viminalis* where the range of D was similar.

Table 5.6. Mean water use efficiency ($A/E \times 10^3$) for *C. megalocarpus* and *M. volkensii* calculated from 1. all ambient measurements or 2. ambient measurements made at saturating Q.

	1. All measurements			2. Q >1200 μmol m² s⁻¹		
	Mean (μmol mmol⁻¹)	N	p^1	Mean(μmol mmol⁻¹)	n	p^1
C. megalocarpus	4.27 ± 0.12	688	0.56	3.68 ± 0.18	94	0.001
M. volkensii	4.18 ± 0.11	749		5.73 ± 0.25	61	

1-significance of difference between species

5.3.4 CANOPY SCALE GAS EXCHANGE

Validation

Validation of the radiative transfer routines within models using point measurements of Q provides an extreme test owing to the horizontally discontinuous and structurally inhomogeneous nature of the tree canopies (cf. Plate 4.3). Figures 5.15 and 5.16 respectively show measurements made under *C. megalocarpus* and *M. volkensii* canopies. The mismatch in measured and modelled peaks are due to temporal differences between the predicted and measured occurrence of sunflecks, as identified by Wang and Jarvis (1990). The measured and modelled values agreed closely throughout the measurement period in *C. megalocarpus*, with overestimates being obtained only for a few isolated days. In *M. volkensii*, the measurements made in September 1997 showed some underestimation of Q, suggesting that the leaf area values in the model were high. This may have resulted from the characteristic rapid changes in leaf area, which may have led to temporary underestimation of modelled incident Q values; thereafter the measured and modelled values agreed much more closely.

Sensitivity testing

The sensitivity of the modelled values for transpiration in *C. megalocarpus* to changes in the stomatal conductance parameter, Q_0, was greater than that for assimilation (Table 5.7). The mean difference in daily total values was nonetheless much smaller than the percentage change in the input parameter. Decreases or increases in Q_0 caused the greatest difference in transpiration relative to the originally parameterised run when absorbed Q was relatively low. A 20 % increase in Q_0 (i.e. decreasing the steepness of the response of stomatal conductance to increasing Q) reduced transpiration, whereas a 20 % decrease in Q_0 increased transpiration. These effects were greatest when leaf areas were higher at the beginning and end of the simulated period (data not shown). Although the transpiration estimates for *C. megalocarpus* should not have been greatly affected by using the fitted responses, the most sensitive periods to alterations in Q_0 were when leaf areas were high and absorbed Q was low i.e. cloudy periods during the rainy seasons (data not shown).

Table 5.7. Percentage change in modelled daily photosynthesis and transpiration output from MAESTRA parameterised for *C. megalocarpus* when the stomatal conductance model parameter Q_0 was increased or decreased by 20 %. The model was run using data for the period 1 June 1997 to 31 December 1997.

Scenario	Photosynthesis expressed as % of initial estimate Mean (range)	Transpiration expressed as % of initial estimate mean (range)
Q_0 decreased by 20%	100.9 (100.6-101.2)	108.6 (104.6-114.6)
Q_0 increased by 20 %	99.9 (99.2-100.6)	94.0 (90.4-96.3)

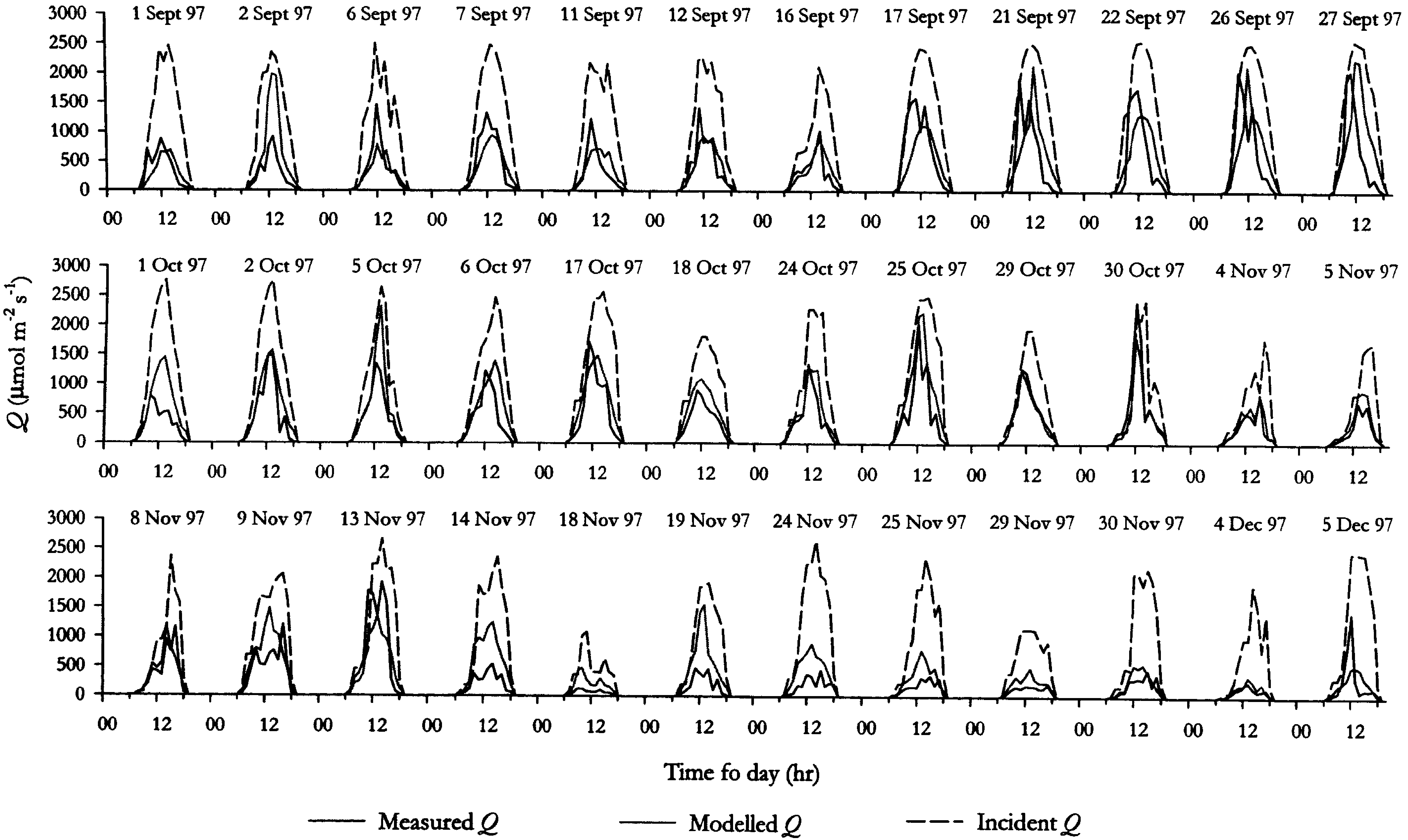


Figure 5.15 Incident Q and observed and modelled below canopy Q in *C. megalocarpus* for 36 days between September and December 1997.

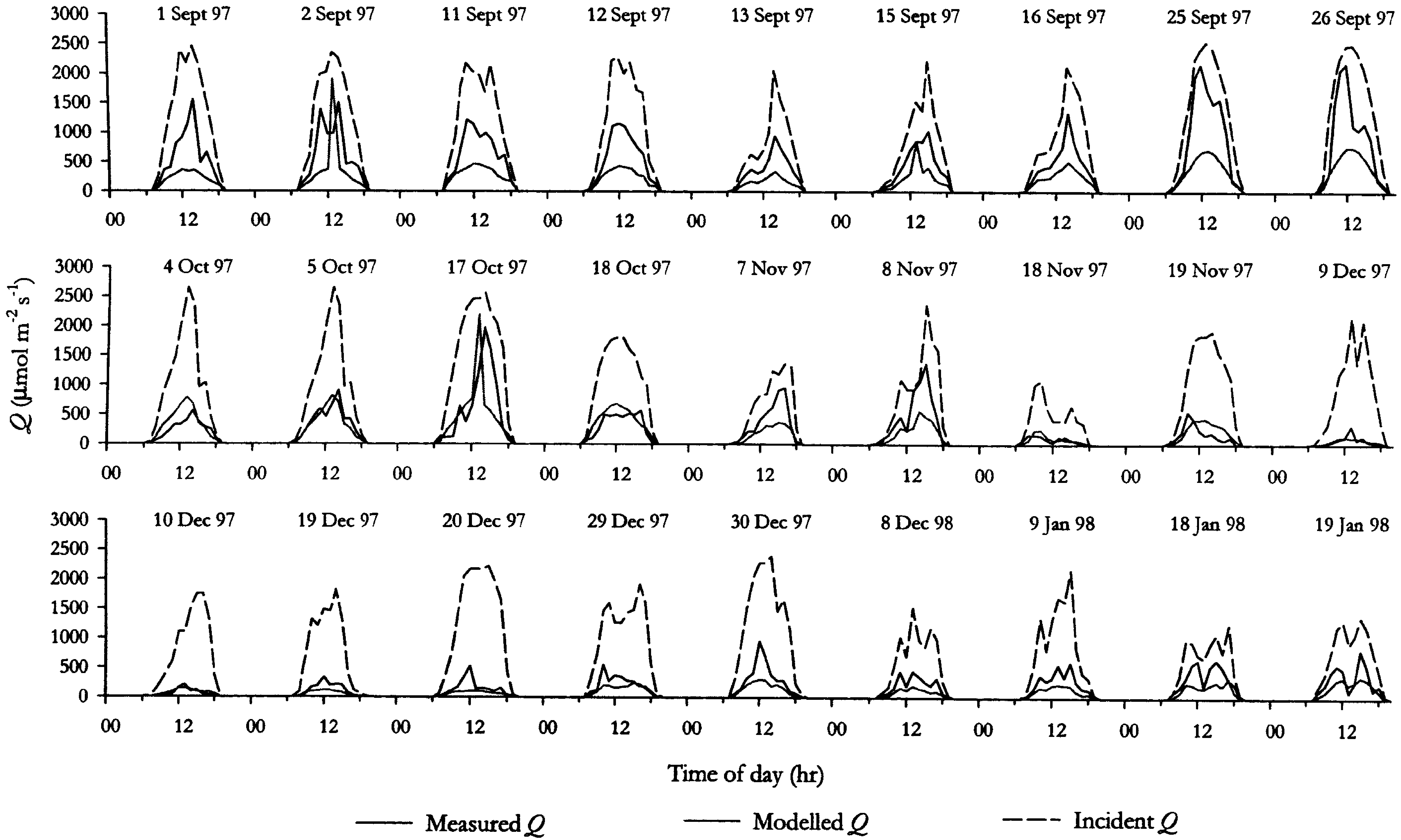


Figure 5.16 Incident Q and observed and modelled below canopy Q in *M. volkensii* for 27 days between September 1997 and January 1998

Figure 5.17 shows model predictions of canopy-scale photosynthesis, assimilation, dark respiration rates and estimated leaf area for *C. megalocarpus* and *M. volkensii* between July 1996 and February 1998. The progressive increase in assimilation and photosynthesis from one season to the next reflects the general increase in leaf area during the observation period. Photosynthesis, assimilation and respiration rates expressed on a per tree basis were consistently lower in *C. megalocarpus* than in *M. volkensii.* Expressed on a leaf area basis, mean canopy assimilation rates during the simulation period were 2.52 (range: 0.54-4.12) and 2.66 μmol m^{-2} s^{-1} (range: 0.72-4.86) for *C. megalocarpus* and *M. volkensii* respectively. The ratio of photosynthesis rates for the periods between and during cropping seasons did not differ significantly between species. The increase in assimilation at the beginning of the rainy seasons occurred sooner in *M. volkensii* and assimilation levels were maintained for longer following cropping periods in *C. megalocarpus* as a result of phenological differences. The effects of the lower Q receipts between May and September, a predominant feature of the local climate, are evident from the lower levels of photosynthesis. Assimilation and transpiration rates expressed on a leaf area basis were at their lowest during this period in both species; rates were also low, particularly in *C. megalocarpus*, between December 1997 and February 1998. The rapid decrease in photosynthesis in *M. volkensii* at the end of the short rains in December – January 1997 reflected the rapid leaf loss induced by the prevailing high soil moisture levels, as discussed in Chapter 3.

Modelled respiration rates during the observation period tracked the fluctuations in leaf area, with temperature exerting a lesser effect which is evident in the daily oscillations (Figure 5.17). During the long rains (Apr-Jul 1997), when leaf areas were high but radiation receipts were relatively low, the relatively high dark respiration and low photosynthesis rates resulted in low assimilation rates. Results suggest that the short rainy season may provide better growth conditions than the long rains owing to these climatic differences.

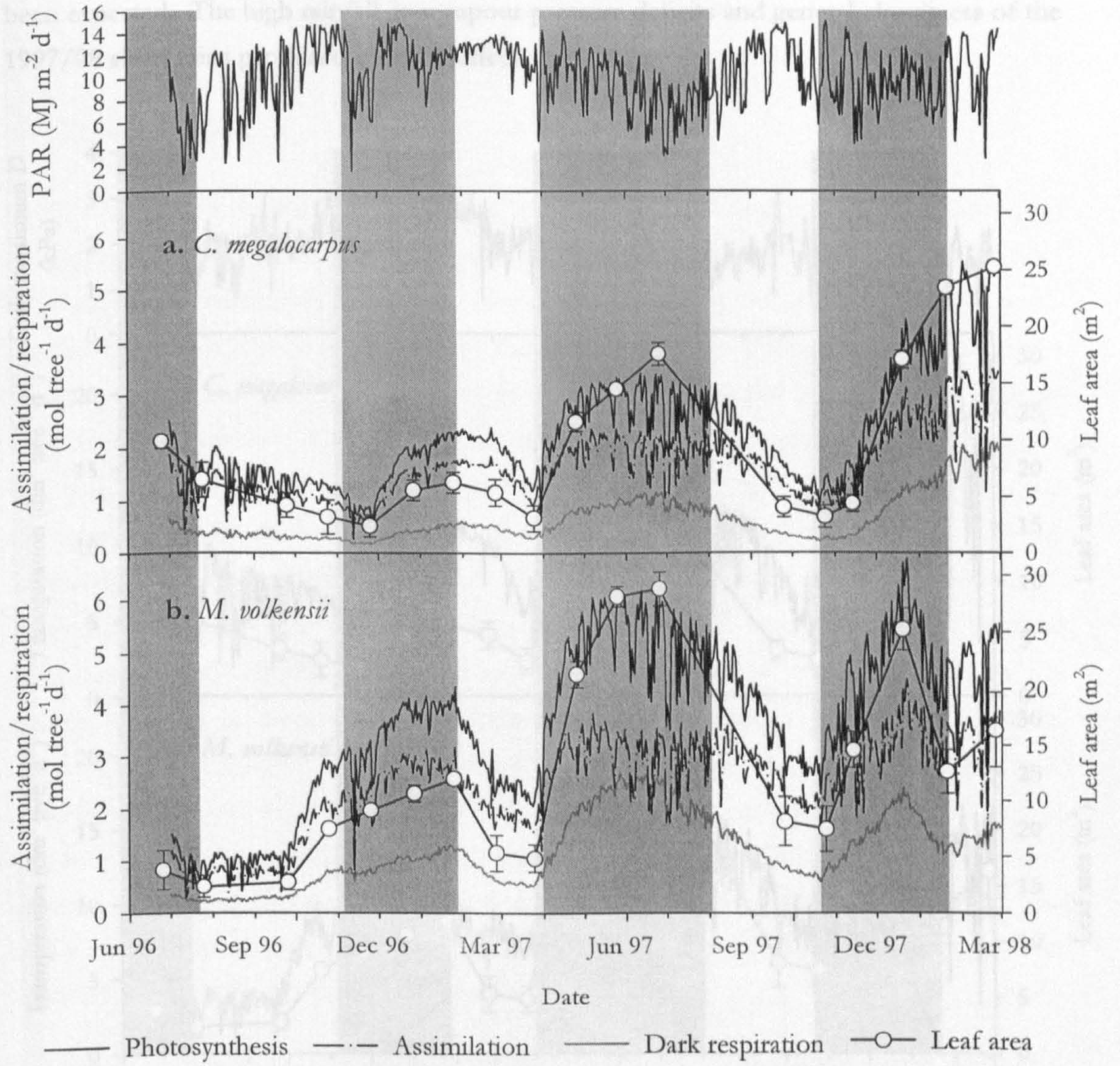


Figure 5.17. Timecourses for modelled daily photosynthesis, assimilation, dark respiration rates and leaf area per metre length of tree row in a) *C. megalocarpus* and b) *M. volkensii* between July 1996 and February 1998; incident daily mean values for photosynthetically active radiation are also shown. Shaded areas represent cropping seasons.

Transpiration rates exhibited similar timecourses to photosynthesis (Figure 5.18), with the values generally being higher in *M. volkensii* than in *C. megalocarpus.* However, transpiration per unit leaf area, averaged over the simulation period, was higher in *C. megalocarpus* than in *M. volkensii*, with respective means and ranges of 0.79 (0.09-1.53) and 0.61 (0.11-1.18) mmol m^{-2} s^{-1} being obtained. This is a result of the more pronounced responses of stomatal conductance to vapour pressure deficit and *Q* in *M. volkensii* than *C.*

megalocarpus (Figure 5.11). The lower incident radiation levels between May and September 1997 resulted in lower transpiration rates during the long rains than might otherwise have been expected. The high rainfall, low vapour pressure deficits and general cloudiness of the 1997/98 short rains produced a similar effect.

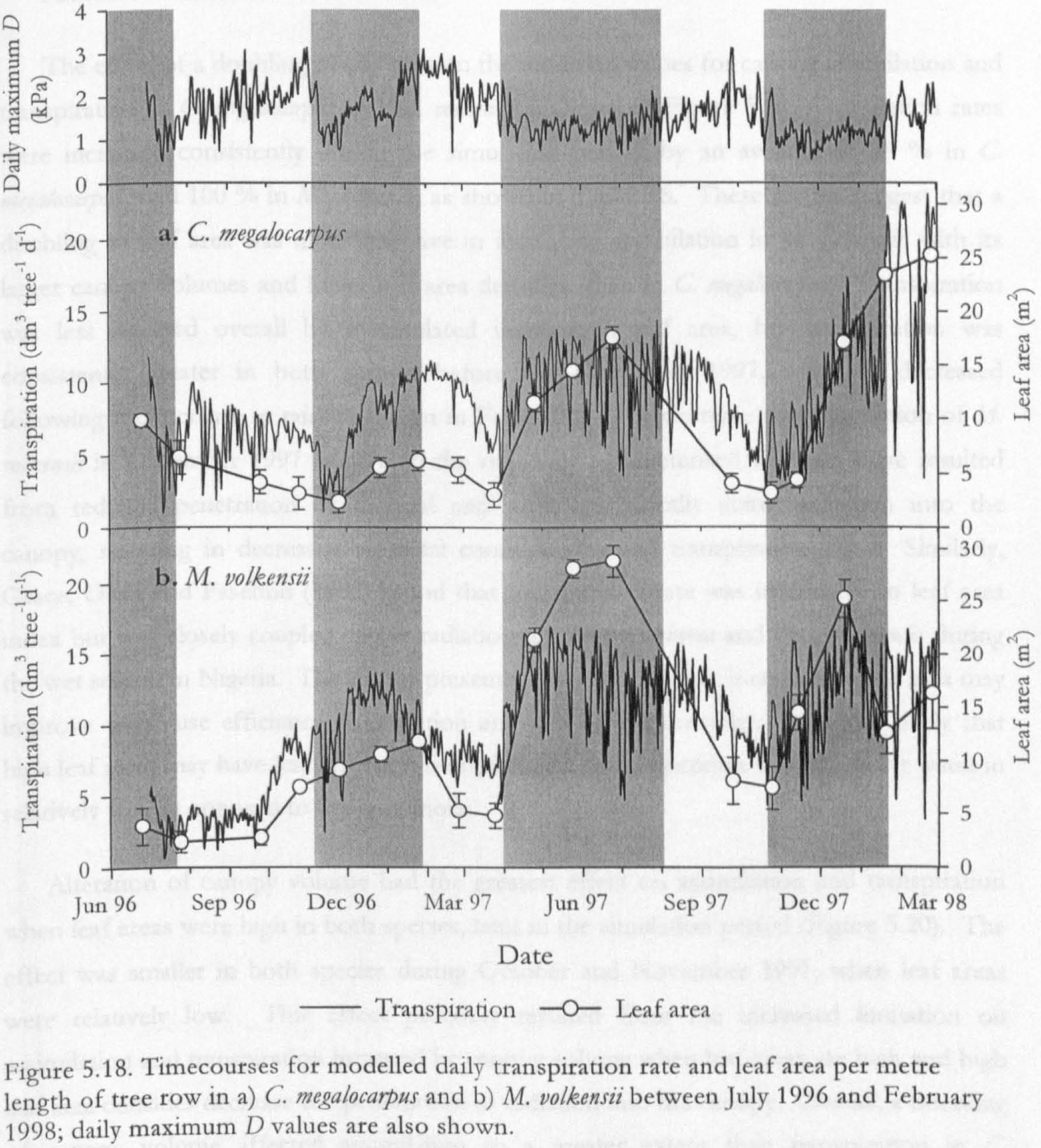


Figure 5.18. Timecourses for modelled daily transpiration rate and leaf area per metre length of tree row in a) *C. megalocarpus* and b) *M. volkensii* between July 1996 and February 1998; daily maximum D values are also shown.

The ratios of transpiration for the periods between and during the cropping seasons did not differ greatly between the two species, suggesting that the deciduous and evergreen habits of *M. volkensii* and *C. megalocarpus* respectively had no great influence on crop water availability. Transpiration rates in *C. megalocarpus* exceeded those for *M. volkensii* in

February and March 1998 as a result of the large increase in leaf area during the season in response to the heavy rainfall, suggesting that the relative behaviour of the two species and their influence on adjacent crops may vary or even be reversed in wetter climates. However, competition with crops for water is less important in wetter climates.

Alternative scenarios

The effect of a doubling of leaf area on the modelled values for canopy assimilation and transpiration in *C. megalocarpus* and *M. volkensii* is shown in Figure 5.9. Assimilation rates were increased consistently during the simulation period, by an average of 88 % in *C. megalocarpus* and 100 % in *M. volkensii*, as shown in Table 5.8. These results suggest that a doubling of leaf area was more effective in increasing assimilation in *M. volkensii*, with its larger canopy volumes and lower leaf area densities, than in *C. megalocarpus*. Transpiration was less affected overall by a simulated increase in leaf area, but transpiration was consistently greater in both species before mid-November 1997, when *D* decreased following the increase in rainfall shown in Figure 2.1. The decrease in transpiration of *M. volkensii* in December 1997 relative to the originally parameterised run may have resulted from reduced penetration of thermal and photosynthetically active radiation into the canopy, resulting in decreased stomatal conductances and transpiration rates. Similarly, Grace, Okali and Fasehun (1982) found that transpiration rate was insensitive to leaf area index but was closely coupled to net radiation in *Gmelina arborea* and *Tectona grandis* during the wet season in Nigeria. The results presented here suggest that increases in leaf area may improve water use efficiency, assimilation and primary productivity. It is also likely that high leaf areas may have less effect on transpiration and competition with crops for water in relatively wet, as opposed to dry conditions.

Alteration of canopy volume had the greatest effect on assimilation and transpiration when leaf areas were high in both species, later in the simulation period (Figure 5.20). The effect was smaller in both species during October and November 1997, when leaf areas were relatively low. This effect probably resulted from the increased limitation on assimilation and transpiration imposed by canopy volume when leaf areas are high and high leaf area densities decrease the penetration of radiation into the canopy. Overall, a doubling of canopy volume affected assimilation to a greater extent than transpiration in *C. megalocarpus*, but had a similar effect in *M. volkensii* (Table 5.8) owing to the greater dependence of assimilation on radiation penetration, which was decreased to a greater degree by the denser canopies of *C. megalocarpus* (cf. Table 4.4).

Table 5.8. Sensitivity of assimilation and transpiration rates to independently altered leaf area and canopy volume in *C. megalocarpus* and *M. volkensii*. Values are expressed as percentages of the originally parameterised run.

Species	Scenario	Assimilation mean (range)	Transpiration mean (range)
C. megalocarpus	Leaf area doubled	187.8 (151.4-217.1)	133.9 (99.3-160.7)
	Canopy volume doubled	138.9 (121.4-169.0)	110.1 (99.4-129.1)
M. volkensii	Leaf area doubled	200.3 (165.2-328.8)	110.2 (90.6-134.9)
	Canopy volume doubled	122.4 (108.7-143.9)	122.6 (110.6-141.9)

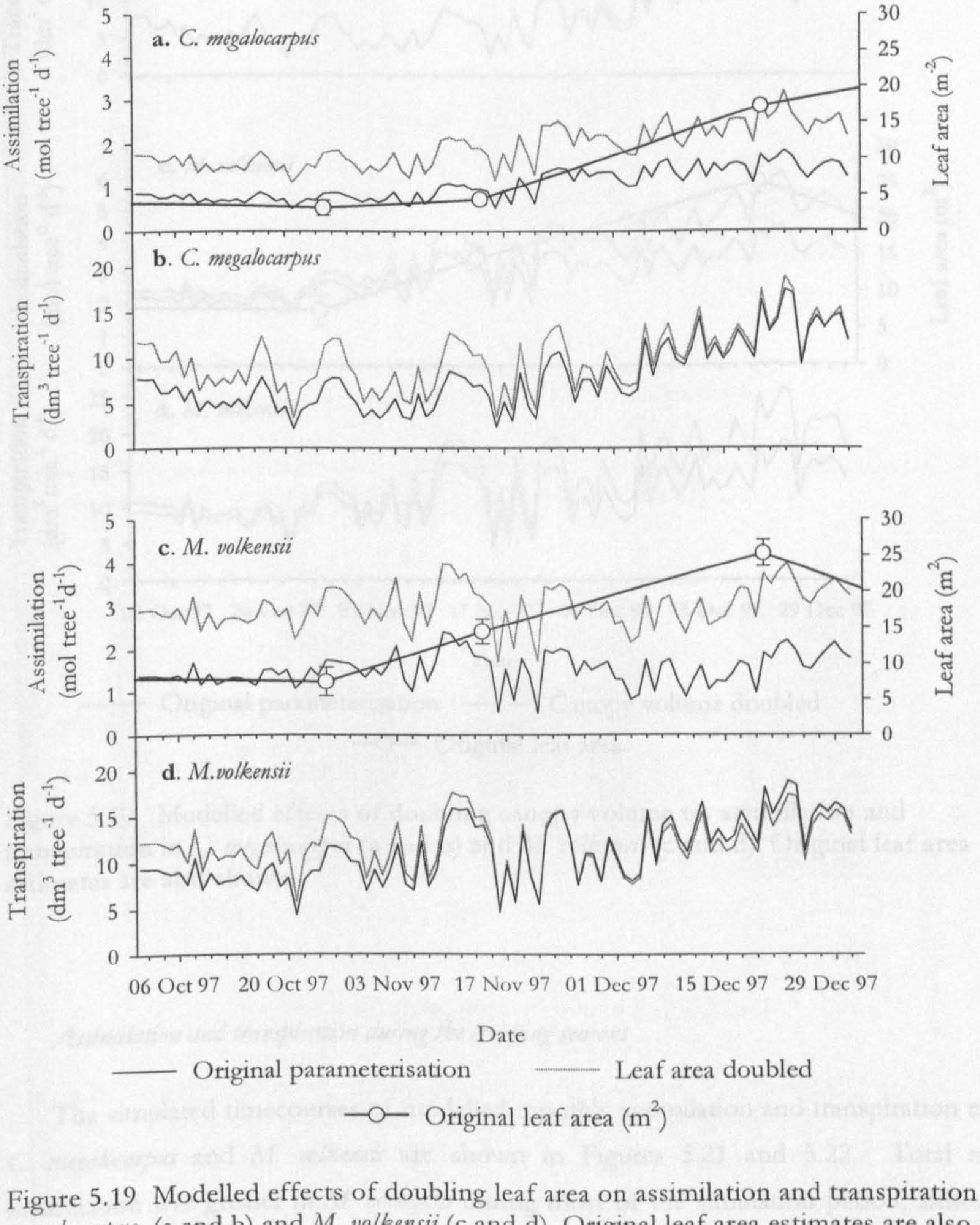


Figure 5.19 Modelled effects of doubling leaf area on assimilation and transpiration in *C. megalocarpus* (a and b) and *M. volkensii* (c and d). Original leaf area estimates are also shown.

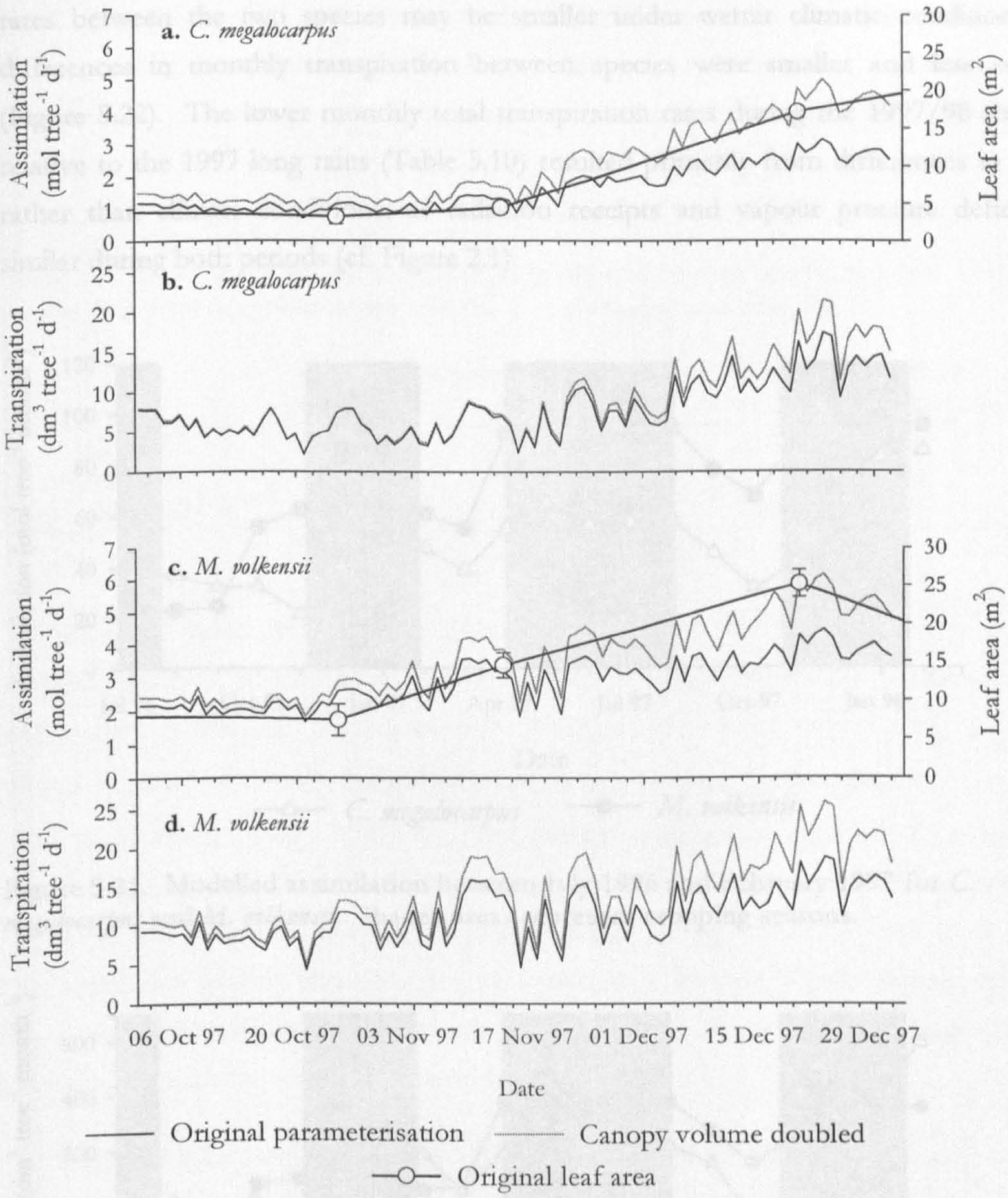


Figure 5.20. Modelled effects of doubling canopy volume on assimilation and transpiration in *C. megalocarpus* (a and b) and *M. volkensii* (c and d). Original leaf area estimates are also shown.

Assimilation and transpiration during the cropping seasons

The simulated timecourses of modelled monthly assimilation and transpiration rates for *C. megalocarpus* and *M. volkensii* are shown in Figures 5.21 and 5.22. Total monthly assimilation was greater in *M. volkensii* during most of the simulation period, although the high rainfall and consequent increase in leaf area in *C. megalocarpus* during the 1997/98 short rains (cf. Figure 5.18) decreased the difference, suggesting that the differences in growth rates between the two species may be smaller under wetter climatic conditions. The differences in monthly transpiration between species were smaller and less consistent (Figure 5.22). The lower monthly total transpiration rates during the 1997/98 short rains relative to the 1997 long rains (Table 5.10) resulted primarily from differences in leaf area rather than climate conditions, as radiation receipts and vapour pressure deficits were similar during both periods (cf. Figure 2.1).

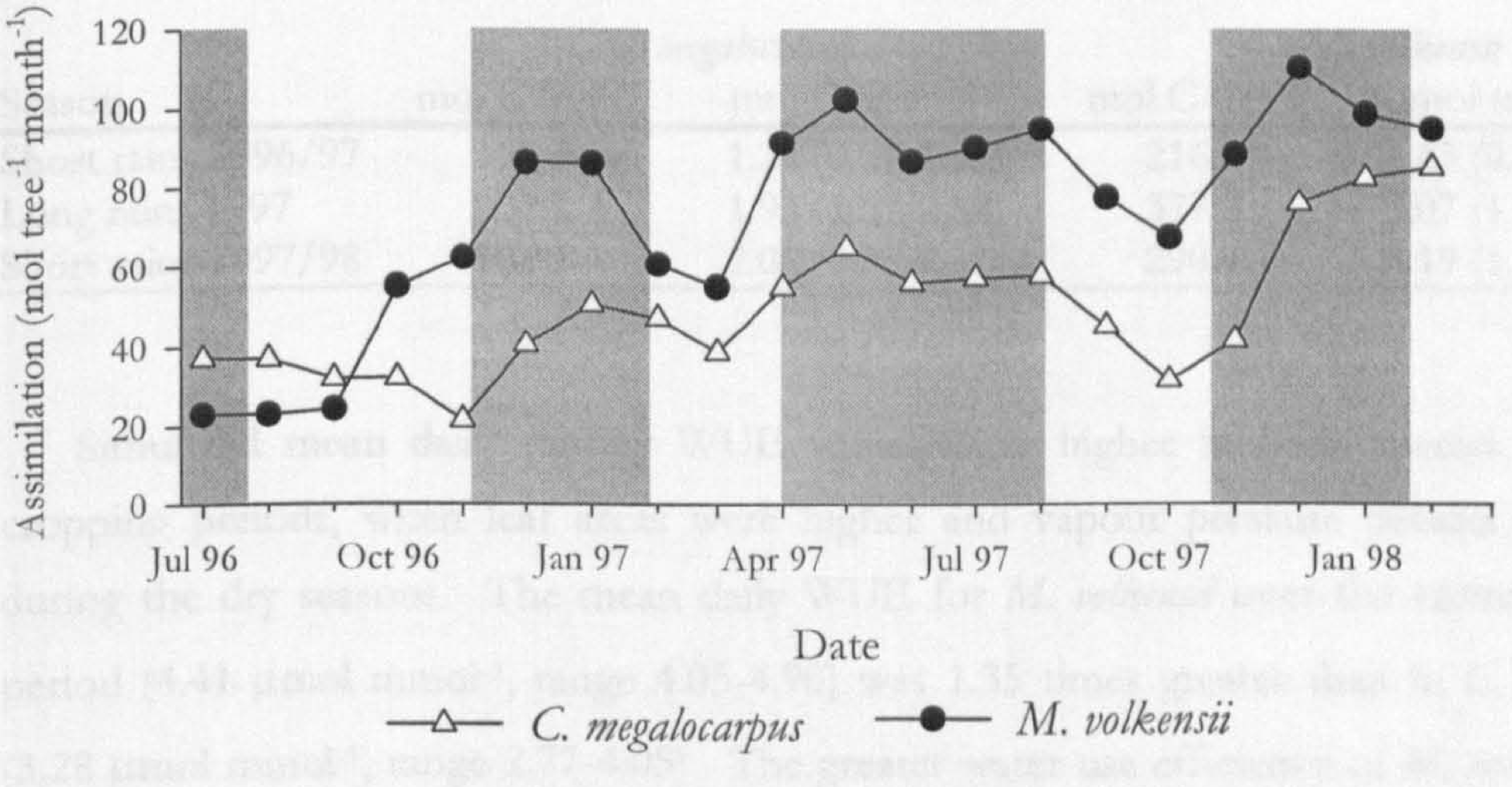


Figure 5.21. Modelled assimilation between July 1996 and February 1997 for *C. megalocarpus* and *M. volkensii.* Shaded areas represent cropping seasons.

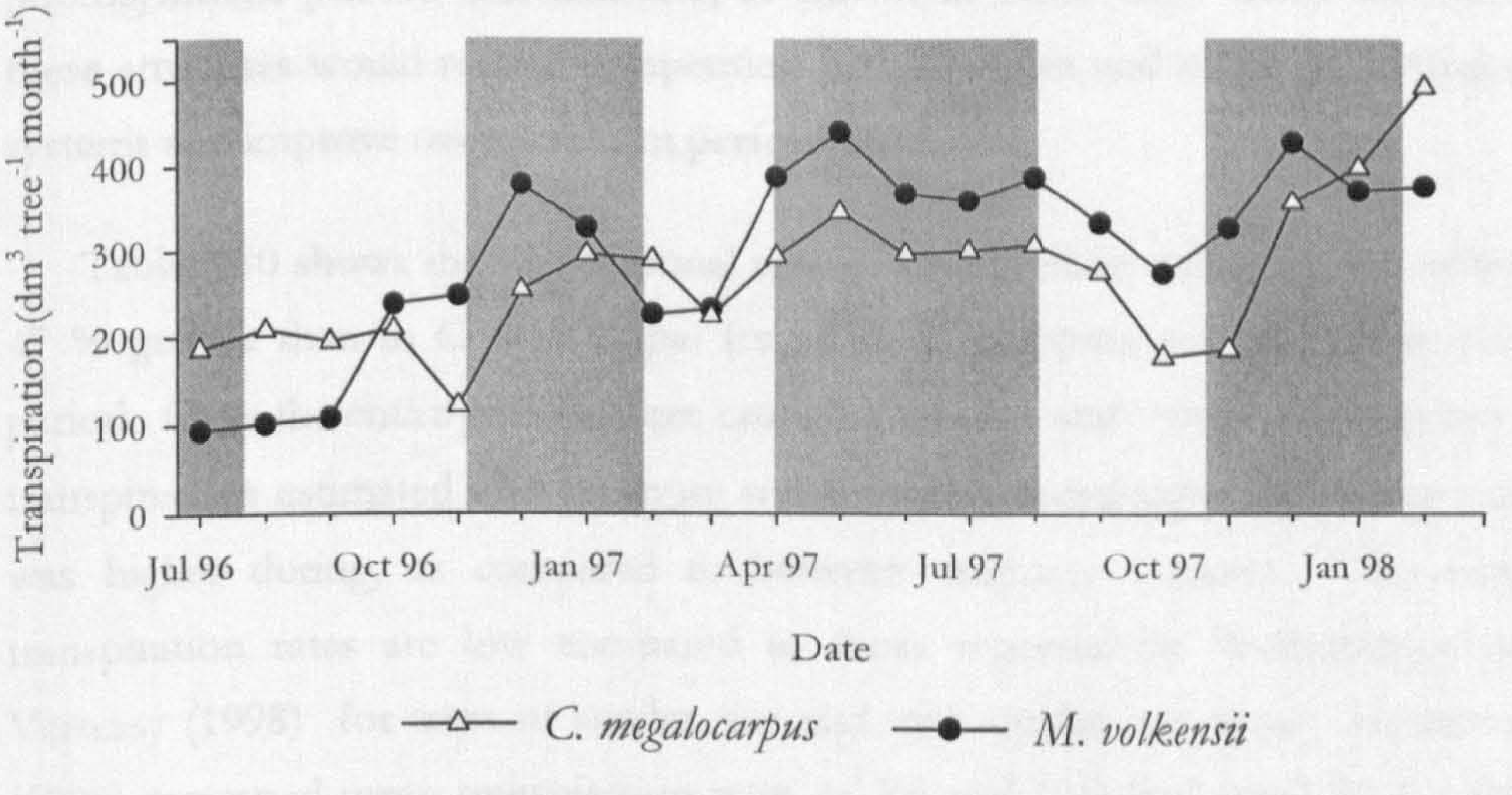


Figure 5.22. Modelled transpiration between July 1996 and February 1997 for *C. megalocarpus* and *M. volkensii.* Shaded areas represent cropping seasons

Assimilation was 49 % greater in *M. volkensii* than in *C. megalocarpus* over the entire simulation period; however, when calculated only for specific cropping periods, assimilation was 112 % greater in *M. volkensii* during the 1996/97 short rains and c. 60 % higher during the remaining two seasons (Table 5.9). The larger differences in assimilation than transpiration between the two species indicate differences in water use efficiency at the canopy scale.

Table 5.9. Simulated total net assimilation (mols carbon) per tree during each cropping season and daily assimilation per tree for *C. megalocarpus* and *M. volkensii.*

	C. megalocarpus		*M. volkensii*	
Season	mol C tree^{-1}	mol C tree^{-1} d^{-1}	mol C tree^{-1}	mol tree^{-1} d^{-1}
Short rains 1996/97	101.9	1.24 (0.27-1.77)	216.0	2.63 (0.72-3.18)
Long rains 1997	237.8	1.93 (1.07-2.38)	377.2	3.07 (1.67-3.87)
Short rains 1997/98	182.2	2.00 (0.83-3.31)	290.4	3.19 (1.84-4.50)

Simulated mean daily canopy WUE values were higher in both species during the cropping periods, when leaf areas were higher and vapour pressure deficits lower than during the dry seasons. The mean daily WUE for *M. volkensii* over the entire simulation period (4.41 µmol mmol^{-1}, range 4.05-4.90) was 1.35 times greater than in *C. megalocarpus* (3.28 µmol mmol^{-1}, range 2.77-4.05). The greater water use efficiency of *M. volkensii* at the canopy level resulted from a combination of increased radiation absorption associated with its lower leaf area densities and a greater WUE at the individual leaf scale at higher photosynthetic photon flux densities, as shown in Table 5.6. Other factors being equal, these attributes would reduce competition between trees and crops in dryland agroforestry systems and improve overall system performance.

Table 5.10 shows that the seasonal canopy transpiration values for *M. volkensii* were 26-47 % greater than in *C. megalocarpus* for all three cropping seasons within the simulation period. Over the entire period (three cropping seasons and ~three dry seasons), *M. volkensii* transpired an estimated 10.9 % more water than *C. megalocarpus*, indicating that water use was higher during, as compared to between cropping seasons. The estimated daily transpiration rates are low compared to those reported by Wullschleger, Meinzer and Vertessy (1998) for trees of similar size and with similar leaf areas. However, Lott *et al.* (1996) measured mean transpiration rates of 3.8 and 12.0 dm^3 tree^{-1} d^{-1} for three year old trees in a *Grevillea robusta*/maize agroforestry system close to the experimental site used here, although on a shallower soil. Ong *et al.* (1992) also reported transpiration rates ranging between c. 4 – 15 dm^3 tree^{-1} d^{-1} for three year old *Albizia lebbek* and *Faidherbia albida* trees grown in combination with sorghum or castor in agroforestry systems at Hyderabad, India.

Table 5.10. Simulated total daily transpiration per tree during the cropping seasons.

	M. volkensii		*C. megalocarpus*	
Season	dm^3 tree^{-1}	dm^3 tree^{-1} d^{-1} (range)	dm^3 tree^{-1}	dm^3 tree^{-1} d^{-1} (range)
Short rains 1996/97	885.9	10.67 (2.4-13.7)	603.7	7.27 (1.1-11.2)
Long rains 1997	1587.1	12.8 (4.7-17.0)	1261.7	10.2 (3.6-14.3)
Short rains 1997/98	1104.7	12.14 (4.6-18.86)	847.4	9.31 (2.4-19.2)

5.4 DISCUSSION

By structuring existing hypotheses into a formal arrangement, canopy models allow further hypotheses to be tested at a scale not otherwise possible. Modelling also highlights areas of uncertainty, provides information to guide further experiments and assists extension workers in decision making (Lawson *et al.* 1995). The limitations of modelling are reduced in comparative studies because the focus is directed towards relative responses of species as opposed to the absolute quantities involved. The accuracy of model predictions is, however, determined by the validity of the component hypotheses. The good fit of the photosynthesis model (Figure 5.6) and the validation of the radiative transfer sub-model (Figures 5.15 and 5.16) demonstrate their robustness. Estimates of daily transpiration with the widely used Penman-Monteith equation have been shown to compare favourably with independent methods (Caspari, Green and Edwards, 1993; Goulden and Field, 1994). However, as indicated above, the reliability of the estimated values, particularly estimated resistances, depends on the accuracy of the input variables (Raupach and Finnegan, 1988). Although assimilation and transpiration were largely insensitive to Q_0 in *C. megalocarpus*, the weak fit showed that the concurrently measured microclimatic variables did not account for a large proportion of the variation in conductances. The weak responses obtained for this species may reflect its evolutionary origin in wetter areas where stomatal control of water loss is of less importance than in more arid areas. An improved mechanistic understanding of stomatal responses in the present study might have been provided by pre-dawn measurements of leaf water potential. However, test measurements showed that the pressure chamber method for determining water potential was unsuitable for *C. megalocarpus* because exudation from resin ducts in the petioles obscured the return of the xylem sap meniscus to the cut end of the petiole. Stem hygrometers or psychrometric measurements may provide more reliable estimates, but were not available for use in the present study. The fact that residuals from the stomatal conductance model were not skewed with respect to date in *C. megalocarpus* (Figure 5.13) and the lack of correlation between soil moisture content and stomatal conductance showed that soil moisture content did not have a direct effect on stomatal conductance. The existence of a dynamic equilibrium between leaf area and soil moisture content as proposed above (Section 5.3.3) would reduce the need for direct stomatal control according to water availability. The reason for the small proportion of variation in stomatal conductance explained by concurrently measured environmental variables therefore may be related to innate variation between leaves or branches which could conceivable be a mechanism allowing staggered leaf loss during drought. The combined stomatal conductance/photosynthesis model of Ball, Woodrow and Berry (1987) provides an alternative method for determining stomatal conductance dependent on intercellular carbon dioxide concentration and humidity. However, the model is weakened theoretically by the interdependence of photosynthesis and stomatal conductance and the questioned validity of stomatal responses to atmospheric humidity (Monteith, 1995).

The combination of higher assimilation rates, stomatal conductances and leaf areas and lower leaf area densities provides an explanation for the greater growth and yield of *M. volkensii* relative to *C. megalocarpus* in the present experiment (cf. Chapter 6). However, similar patterns may not apply in areas of higher rainfall or on heavier, moisture-retaining soils as the associated phenological changes in canopy structure in *M. volkensii* (cf. Chapter 3) relative to *C. megalocarpus* are likely to reduce performance. The higher stomatal conductances in *M. volkensii* resulted in lower adjacent crop yields as a result of higher tree transpiration (cf. Chapter 7). Smith, Jarvis and Odongo (1998) suggested that selection of tree species with lower stomatal conductances would result in reduced competition with crops in agroforestry systems where ground water is inaccessible to trees. However, where the tree has direct value to the farmer this may also result in selection of slow growing trees. Improvements in tree productivity may be achieved without reducing crop yield only if there is spatial or temporal separation of the ecological niches occupied by trees and crops, and/or an improvement in the water use efficiency of the agroforestry system over sole cropping. The greater water use efficiency of *M. volkensii* and its lower transpiration during the dry seasons, when WUE was reduced, are therefore likely to lead to a greater improvement in system performance than may be achieved using a species with lower stomatal conductance such as *C. megalocarpus*.

The model simulations carried out using leaf areas double those observed experimentally suggest that high leaf areas may not necessarily result in increased transpiration rates, especially under wetter conditions, and that water use efficiency may be increased when larger leaf areas are compressed within a defined canopy volume. There are however likely to be interactions between canopy physiognomy and leaf physiology which confound these hypothetical differences in natural occurring canopies. On the basis of model simulations, canopy volume proved less important than leaf area in determining WUE, although productivity is likely to be increased when a specified leaf area is distributed over a larger canopy volume. Increased tree density is likely to increase water uptake as shown by Eastham *et al* (1988) in a *Eucalyptus grandis* system with trees planted in concentric rings at a range of densities. Transpiration was dominated by the pasture component (*Setaria sphacelata*) when the trees were widely spaced but by the trees at higher planting densities. These results show that crop yields may be expected to suffer more with higher planting densities as was found by Lott *et al* (2000b) and strengthen the case for boundary or scattered plantings and manipulation of planting density to control competition with crops.

Cannell, Mobbs and Lawson (1998) used modelling approaches to predict that the trees in agroforestry systems are likely to transpire a greater proportion of the annual precipitation at lower rainfall sites, and WUE will be decreased as a result of associated increases in *D*. Extrapolation of this conclusion to the present study would imply that crop growth would be most severely affected by the presence of trees during dry periods, when crop yields are already likely to be limited even in the absence of trees. However, this was not the case during the two maize cropping seasons here where the larger trees in the higher rainfall 1997 cropping season caused greater yield reductions relative to the sole crop than during the 1996 season. In the bean cropping seasons such an effect was not evident due to the universally low yields during the 1996/97 season, when rainfall was scarce, although during the 1997/98 bean cropping season when rainfall was abundant the effects of tree competition on crop yields were small (cf. Chapter 7). Nonetheless where crop yield is of paramount importance, species with lower stomatal conductance such as *C. megalocarpus* are likely to induce less severe reductions in crop growth than those with higher conductances such as *M. volkensii*. The balance between tree and crop production in the present study is examined further in Chapter 7.

6 TREE PERFORMANCE

6.1 INTRODUCTION

Boundary planting of upperstorey trees is used by farmers to demarcate field and property boundaries, stabilise land, provide terrace risers and produce timber, poles, fuelwood and fodder (Malik and Sharma, 1990; Rao, Nair and Ong 1997). The preference for boundary planting as opposed to a more spatially integrated form of agroforestry stems from the relatively small extent of the aerial tree-crop interface zone and the low management inputs, which may be largely confined to the dry seasons (Ong *et al.*, 1996). However, despite their popularity with farmers, few semi-arid upperstorey agroforestry systems have been studied in detail. A notable exception, both in terms of the nature of the tree-crop interactions and the abundance of publications, are systems containing *Faidherbia albida* (e.g. Jama and Getahun, 1991; Vandenbeldt and Williams, 1992; Okorio and Maghembe, 1994). The increased crop yields which are commonly associated with *F. albida* result predominantly from nitrogen fixation by the trees, their unusual reverse phenology, and the microclimatic amelioration they provide (Vandenbeldt, 1992; Sanchez, 1995). However, although this species is often associated with increased crop yields, most other tree species commonly used for agroforestry in semi-arid areas reduce crop yield by competing for available soil moisture and, to a lesser extent, by imposing excessive shading (see references below). Reductions in crop yield, although widespread, do not detract from the overall value of the system where tree products are in demand and, as pointed out by Rao, Nair and Ong (1997), a 100 m boundary planted tree row which reduces crop yield by 50 % over a distance of 10 m on either side of the tree row will only reduce overall crop yield by 10 % on a 1 ha farm. Indeed, as markets grow, successful production of tree commodities may prove more valuable than crop yields and, as has recently happened with *M. volkensii* in the semi-arid Lower Embu district of Kenya, farmers may begin to disregard crop production in favour of timber production (*pers obs*).

Most studies of upperstorey agroforestry systems have been conducted in India (arid zone: Rao *et al.*, 1993; Puri, Bangarwa and Singh, 1995; semi-arid zone: Malik and Sharma, 1990; Singh *et al*, 1993; Osman, Emmingham and Sharrow, 1998) or sub-Sahelian Africa (semi-arid zone: Howard *et al.*, 1995; Jones, Sinclair and Grime, 1998; Lott *et al.*, 2000a, b; sub-humid zone: Okorio *et al.*, 1994; Heineman *et al.*, 1997). Most of these studies and others concerned only with agroforestry tree species (Ngulube, 1990; Kamara and Maghembe, 1994; Abebe, 1994) have sought to compare the performance of various species at a single site or to determine tree productivity in relation to crop yield, rather than relating tree growth to the prevailing aerial and edaphic environment. As the performance of most tree species has not been studied in detail, environmental effects are difficult to assess and species selection is generally achieved either through trial and error, or by judiciously matching species and provenances to prospective sites based on knowledge of the prevailing ecoclimatic zones. Important factors that have not been adequately addressed include the implications for agroforestry of the decrease in net biomass production as the size and surface area of trees increase (Cannell, 1989); this effect results from the increase in maintenance respiration which occurs as the proportion of non-photosynthetic tissue increases with tree size. The implication for agroforestry is that competition with crops may intensify as gross biomass production increases, yet tree yield increments will decline as net biomass production decreases. The effects may be more pronounced in warmer climates where respiration rates are higher.

To elucidate the determinants of tree growth rates and the characteristics mediating interactions with adjacent crops in border planting systems, four tree species were selected from the eight grown as upperstorey trees in the experiment (cf. Figure 2.2). *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium* were chosen for their differing geographical origins, leaf phenology and nitrogen fixing ability (cf. Section 2.5-2.8). Exotic tree species have commonly been assumed to be fast growing, highly competitive and extravagant consumers of water. Gichuki (1998) suggested that the failure of the huge tree planting efforts in Machakos District in the 1930s may have originated from the use of poorly adapted exotic species, while Haggar, Briscoe and Butterfield (1998) found that, although some exotic species grew well, they were often susceptible to attack by pests. The best performing indigenous species tended to exhibit better survival and greater resistance to pests, but lower growth rates than exotic species which produced wood of similar quality; few indigenous species were therefore attractive for use in plantations. However, the potential of indigenous species at the local level has led ICRAF to focus upon the domestication of indigenous trees providing high value products (Sanchez, 1995). The importance of leaf phenology has been demonstrated for perennial pigeonpea (Daniel and Ong, 1989) and *F. albida*-based systems (Okorio and Maghembe, 1994), as crop growth was increased by the reduced competition resulting from the leaflessness of the upperstorey species during some or all of the cropping season. However, tree growth may be suppressed in such circumstances, and it is doubtless for this reason that leaflessness during rainy seasons is rare.

As sole tree plots were not included in the experiment reported here, it was not possible to assess the effect of the crops on tree growth or determine whether it would be more profitable to grow the trees separately. However, the latter question is of little relevance in highly populated semi-arid regions as sufficient farmland is seldom available to allow planting of separate woodlots. The effects of crops on tree growth have generally been found to be small (Okorio and Maghembe, 1994; Duguma *et al.*, 1994; Lott *et al.*, 2000a); however, where trees are highly valued, an assessment of the positive or negative effects of associated crops on their performance is desirable. The aims of the work reported in this chapter were to determine growth rates and the temporal and seasonal patterns of growth for *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium*, and to estimate timber production in *M. volkensii*. Overall system performance and the effects of the trees on crop yield are described in Chapter 7.

6.2 METHODS

Tree seedlings were planted in April 1993 in east-west rows in randomised complete blocks containing four replicates (Figure 2.2). Maize and beans were grown adjacent to the trees during the long and short growing seasons respectively (cf. Chapter 7) and 1 m deep trenches were dug around the plots at the beginning of each growing season to prevent interference resulting from the growth of tree roots between adjacent plots. Fallen leaves and fruits were not removed, and were mostly deposited in the plots from which they originated. Although insect attack was rare, *C. megalocarpus* trees were sprayed with Ambush insecticide (Zeneca, Haslemere, UK) during the 1997 long growing season to control an outbreak of caterpillars, while *G. sepium* was periodically sprayed to protect against aphids and other sap-sucking insects which constantly attacked the trees. The trees were lightly pruned at the beginning of each cropping season to maintain an even canopy profile within rows and simplify the estimation of leaf area (cf. Section 4.2.1). The prunings were removed from the plots and their dry weight determined (cf. Appendix 6) after drying sub-samples to constant weight at 70 °C. Pruning of *S. spectabilis* and *G. sepium* was discontinued after the beginning of the 1996/97 short rains as time constraints precluded assessment of leaf area. It was assumed that pruning did not alter the allometric relationships between tree dimensions and biomass. The agreement between the two methods for estimating tree biomass (cf. Section 6.3.1) indicates that the errors introduced by pruning were unlikely to have exceeded the residual errors resulting from variability between trees.

6.2.1 HEIGHT, DIAMETER AND BIOMASS

Measurements of *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium* were made in all replicate plots at approximately monthly intervals between December 1993 (8 months after planting) and February 1998 (59 months after planting). Tree height and trunk diameter were measured for trees 5-15 (cf. Figure 2.3) within individual rows. Height was measured using a telescopic pole held adjacent to the tree and recorded as the height to the highest living branch tip. The largest trunk diameter was measured using callipers c. 5 cm above ground level, where butt-swell ceased. To estimate above-ground woody dry weight (trunk + branches), allometric relationships were constructed using data from destructive measurements of trees cut at ground level in March 1998. As the number and position of the sampled trees was limited by the continuing needs of the experiment, trees near the ends of the rows (excluding the last tree) were used. Fresh weights were measured separately for the main stem and branches of each felled tree; sub-samples were dried to constant weight at 70 °C to determine the fresh:dry weight ratio.

Comparison of several relationships between above-ground woody dry weight (B) and tree dimensions for *M. volkensii* and *C. megalocarpus* revealed that the relationship between dry weight and the square of trunk diameter ($B = \mathrm{a}\, d^2 + \mathrm{b}$) provided closer predictions than that between dry weight and the square of trunk diameter * height ($B = \mathrm{a} d^2 h + \mathrm{b}$) or log relationships with diameter or diameter * height. However, as the fitted relationships for both species showed negative y-intercepts, thereby predicting a negative dry weight at low trunk diameters, the more flexible relationship used successfully by Ouellet (1983) for a range of tree species was adopted i.e.:

$$B = \mathrm{a} d^{\mathrm{b}} h^{\mathrm{c}} \qquad [6.1]$$

where B represents dry weight, d is diameter, h denotes height and a, b and c are constants. Due to time constraints, only two trees for each of *S. spectabilis* and *G. sepium* were used to determine above-ground dry weight. As there were insufficient data to fit more complex relationships, biomass was fitted to the square of trunk diameter using a linear relationship with the y-intercept constrained to zero:

$$B = \mathrm{a} d^2 \qquad [6.2]$$

To test the applicability of the relationships for *M. volkensii* and *C. megalocarpus* to the larger population of trees in the central areas of the plots (trees 5-15), non-destructive measurements of these trees were made during February 1998 to allow tree volume to be estimated. Measurements of trunk and branch diameters above and below individual branches and the distances between branching points were used to estimate trunk volume, based on the assumption that the sections approximated the frustrum of a cone. The dry weight of the apical portions of branches whose diameters were too small (<5 cm for *C. megalocarpus* and 8 cm for *M. volkensii*) or branch numbers too great to be practically measured were estimated using a relationship between diameter at the base of the branch and the woody dry weight.

$$B = \mathrm{a}d^{\mathrm{b}} \qquad [6.3]$$

where a and b are constants. Factors for converting volume to dry weight were established by determining the fresh volume of branch and trunk sections by displacement before drying these to constant weight at 70 °C. All relationships were fitted using non-linear regression procedures in Sigma Plot 4.0 for Windows.

These approaches were also used to determine timber volumes for *M. volkensii* in February 1998, 58 months after planting. Measurements of overbark diameter at the base of the trunk and below the first branch and the length of the trunk between these points were used to calculate volume. To estimate the volume of heartwood, which was easily distinguished by its reddish colour (Plate 6.1), measurements were made for the trees felled for allometric relationships. Two measurements were made for each tree, one at the base of the trunk and one immediately below the first branch. Linear regression was used to establish a correlation between heartwood and overbark diameters.

6.2.2 LEAF BIOMASS

Leaf dry weight was estimated for *C. megalocarpus* and *M. volkensii* from the corresponding values for leaf area (cf. Section 4.3.3) using measured values for specific leaf area (SLA). SLA was determined for samples of leaves from a range of canopy positions on four occasions during the first two cropping seasons; 24 samples each containing 15-35 leaves were collected for *C. megalocarpus* and 23 samples containing 2-10 leaves were collected for *M. volkensii*. Leaf areas were measured using a portable leaf area meter (Analytical Development Company, Hoddesdon. UK). In the case of *M. volkensii*, all leaflets were removed from the petioles prior to measurement. The leaves were dried to constant weight at 70 °C and weighed. As the leaves of *M. volkensii* are composite, an additional factor was used to account for the weights of the leaf and leaflet petioles. To determine the ratio of leaflet to whole leaf dry weight, five samples each comprising 30-60 leaves were taken on two occasions (March 1996 and April 1997) and separated into leaflets and petioles before being dried and weighed. Leaf dry weight production between the beginning of consecutive cropping seasons was calculated using this procedure.

6.3 RESULTS

6.3.1 WOODY BIOMASS

M. volkensii and C. megalocarpus

Parameters relating diameter, height and dry weight for *C. megalocarpus* and *M. volkensii* are shown in Table 6.1. The correlation coefficients for the linear regressions between the estimated and measured values (Figure 6.1) were 0.80 and 0.94 for *C. megalocarpus* and *M. volkensii* respectively. The greater scatter and lower r^2 values for *C. megalocarpus* probably resulted from its more variable growth habit, as the trunks often bifurcated within 1 m of ground level. The large standard errors for the parameters indicate that there is high covariance between parameters and that individually, they do not explain a large proportion of the variation in the data.

Table 6.1. Parameters for the relationship between trunk diameter c. 5 cm above ground level (m), height (m) and dry weight (kg) for *C. megalocarpus* and *M. volkensii*: $B = ad^bh^c$ and a, b and c are constants.

Species	n	a	b	c
C. megalocarpus	8	1276.7 ± 390.8	2.28 ± 1.048	0.47 ± 0.206
M. volkensii	10	11915.0 ± 1481.6	2.78 ± 0.557	-0.47 ± 0.391

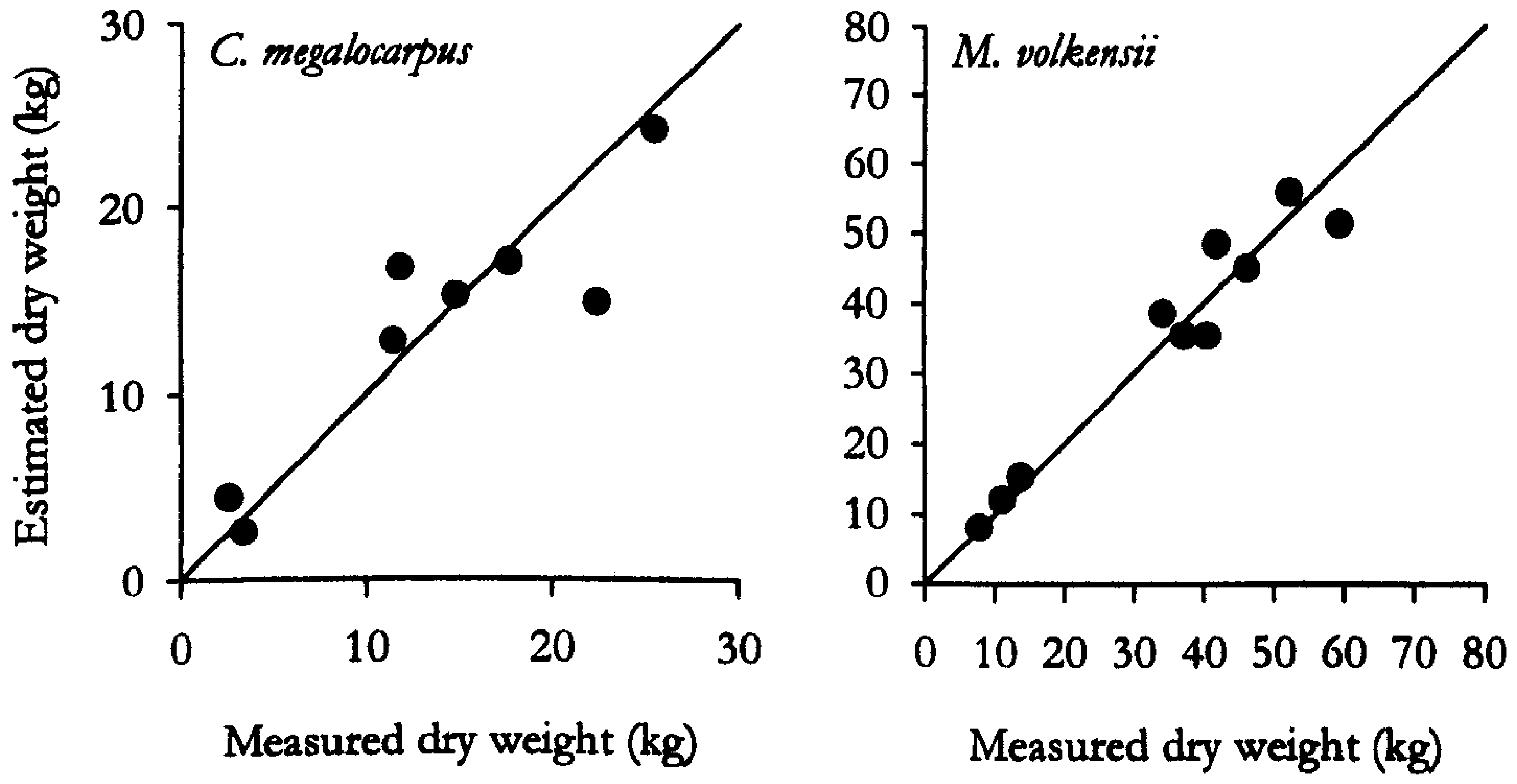


Figure 6.1. Relationship between estimated and measured above-ground woody dry weight for *C. megalocarpus* and *M. volkensii*. Lines show 1:1 relationships.

The parameters for the allometric estimation of branch dry weight (Eq. 6.3) used in the volume method of biomass determination are shown in Table 6.2. The r^2 values for the estimated/measured data (Figure 6.2) were 0.97 and 0.85 for *C. megalocarpus* and *M. volkensii* respectively.

Table 6.2. Parameters for the relationship between branch diameter (cm) and branch dry weight (kg) in *C. megalocarpus* and *M. volkensii*: $B = ad^b$; a and b are constants.

Species	n	a	b
C. megalocarpus	46	9041 ± 3133.2	2.64 ± 0.104
M. volkensii	71	4572 ± 2567.6	2.66 ± 0.203

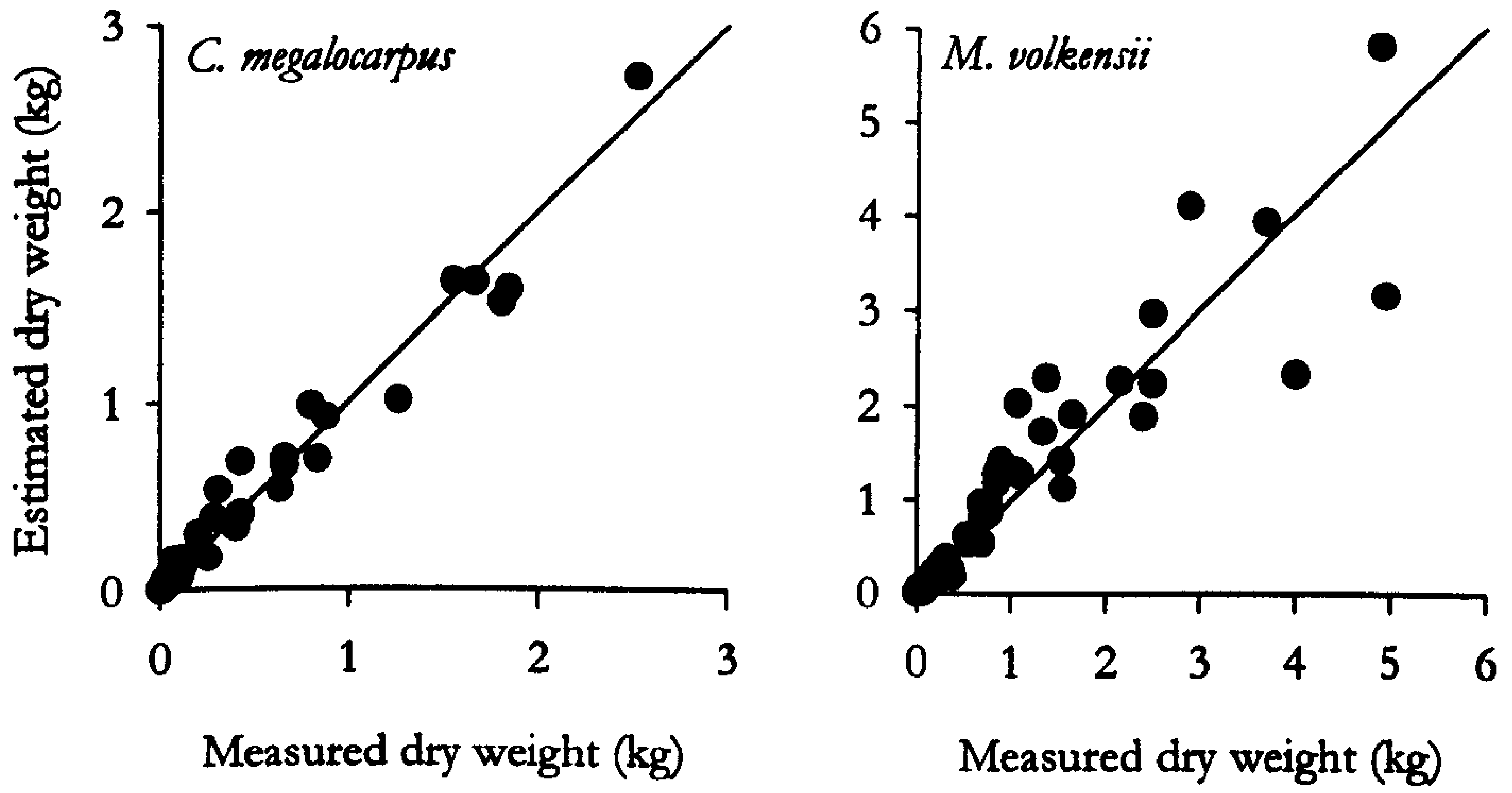


Figure 6.2. Relationship between estimated and measured branch biomass for *M. volkensii* and *C. megalocarpus*. Lines represent 1:1 relationships.

The wood density values used to derive dry weight from estimated trunk and branch volumes in the volumetric method for determining dry weight are shown in Table 6.3. Wood density in *C. megalocarpus*, the slowest growing species in terms of above-ground woody dry weight, was 69 % greater than in *M. volkensii*, the fastest growing species, whilst the two exotics with intermediate growth rates also exhibited intermediate wood densities.

Table 6.3. Trunk and branch dry weight (g) to fresh volume ratio (cm^3) with standard errors for *C. megalocarpus*, *M. volkensii*. *S. spectabilis* and *G. sepium*.

Species	Trunk	n	Branch	n
C. megalocarpus	0.67 ± 0.021	4	0.47 ± 0.019	4
M. volkensii	0.39 ± 0.020	4	0.30 ± 0.010	3
S. spectabilis	0.52 ± 0.000	2	0.49 ± 0.010	2
G. sepium	0.43 ± 0.019	2	0.41 ± 0.038	2

Figure 6.3 shows the close relationships between the estimates of dry weight obtained using equation 6.1 and the volumetric method. The slopes of regression lines relating the two sets of data were not significantly different from unity (p=0.06 and p=0.38 for *C. megalocarpus* and *M. volkensii.* respectively); r^2 values were 0.87 for *C. megalocarpus* and 0.91 for *M. volkensii.* It is concluded that the allometric relationships between tree diameter, height and dry weight were not affected by pruning and can therefore be used to provide a reliable estimates of tree dry weight.

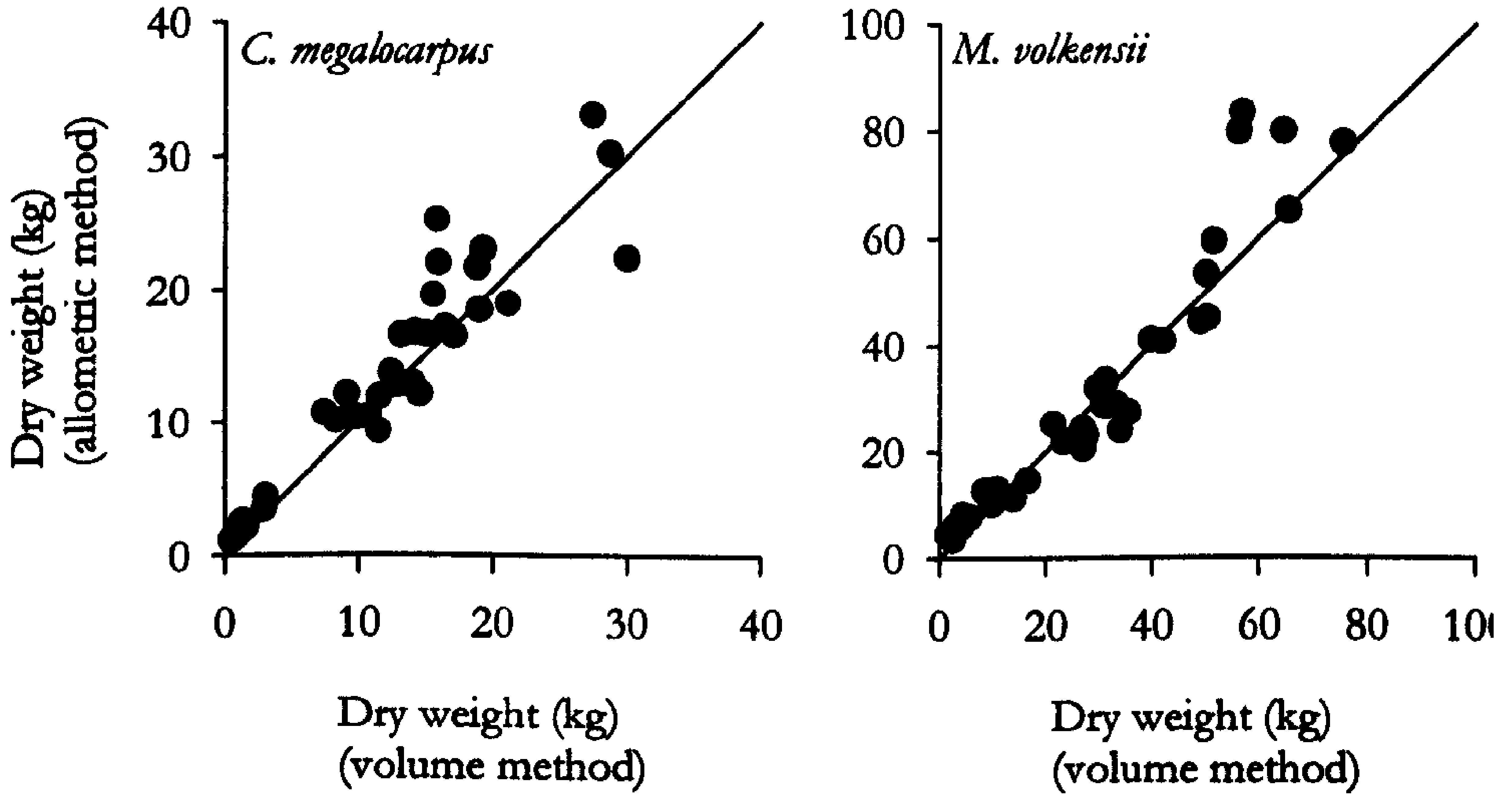


Figure 6.3. Dry weight as estimated by allometric and a modified volumetric method.

S. spectabilis and G. sepium

The relationships between trunk diameter c. 5 cm above ground level and dry weight for *S. spectabilis and G. sepium* and the slopes of the lines are shown in Figure 6.4 and Table 6.4 respectively. Although the data are extremely limited, the simple relationship showed a good fit to the points.

Table 6.4. Parameters for the relationships between the square of trunk diameter c. 5 cm above ground level (m^2) and above-ground woody dry weight (kg) for *S. spectabilis* and *G. sepium*: $B=ad^2$; a is a constant.

Species	n	a
S. spectabilis	2	1229.3 ± 1.45
G. sepium	2	1140.5 ± 52.97

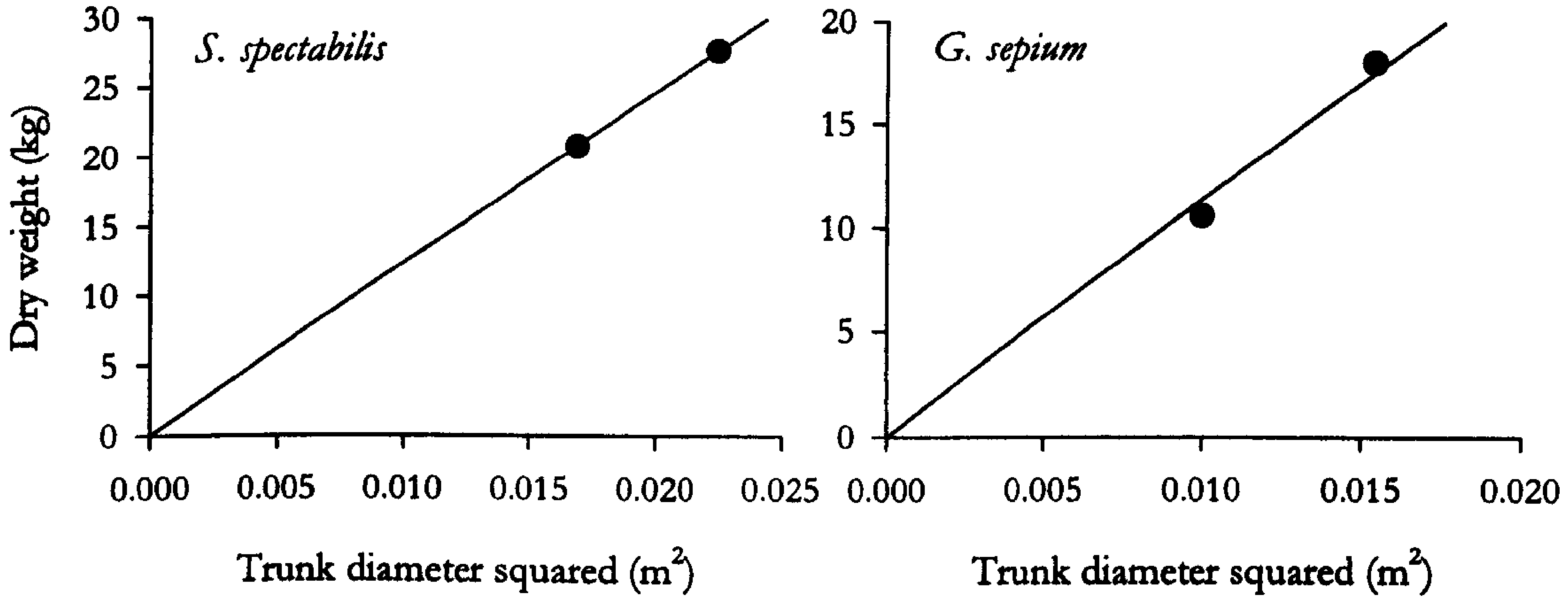


Figure 6.4. Relationship between dry weight and the square of trunk diameter c. 5 cm above ground level for *S. spectabilis* and *G. sepium*. Lines show the fitted relationship described in Table 6.4.

6.3.2 LEAF BIOMASS

Leaf dry weight was calculated from the corresponding estimates of leaf area (cf. Section 4.3.3). Due to the compound leaves of *M. volkensii*, two values were used to derive leaf dry weight from estimated leaf areas, specific leaf area (114.8 ± 7.42) and the ratio of leaflet dry weight to leaf dry weight (0.476 ± 0.020). In *C. megalocarpus*, only specific leaf area was required (142.0 ± 2.92). The seasonal trends for leaf dry weight per metre length of tree row are shown for both species at the same scale as woody dry weight in Figure 6.6. Leaf weight reached a maximum of 9.5 % of total above-ground dry weight towards the end of the 1997/98 short cropping season in *C. megalocarpus*. In *M. volkensii*, the corresponding peak of 16.7 % occurred during the 1997 long cropping season.

Assuming that leaf flushing and leaf fall were temporally discrete, the sum of the positive increments in leaf dry weight during each season provides an estimate of biomass production. As leaf fall in *C. megalocarpus* continued at a low level throughout the year, leaf biomass production determined in this way is likely to slightly underestimate the true values. Values for the three seasons during which estimates were made are shown in Table 6.5. Annual leaf biomass yield estimates over the three seasons were 1.2 and 4.0 t ha^{-1} for *C. megalocarpus* and *M. volkensii* respectively. The much greater production of leaf biomass in *M. volkensii*, with its high nutritional quality, is of great potential importance as a source of fodder for livestock (Milimo, 1994).

Table 6.5. Leaf biomass production (t ha^{-1}) during extended seasons which include the dry periods preceding crop planting at the onset of the ensuing rainy season.

Season	*C. megalocarpus*	*M. volkensii*
1996/97 short rains growing season	0.22	0.84
1997 long rains growing season	0.54	2.18
1997/98 short rains growing season	0.86	2.26

6.3.3 TREE GROWTH

Survival of all tree species examined was high, although a limited number of *S. spectabilis* trees had to be replaced during the establishment phase following attack by termites; termite resistance was good in all other species. Figure 6.5 shows mean trunk diameter c. 5 cm above ground level and height between December 1993 and February 1998. In all species, the overriding feature of the timecourses for diameter and especially height was the gradual decrease in the slope of the curve with time, an effect which may have been at least partly attributable to the general decrease in annual rainfall over most of this period (i.e. 1994, 810 mm; 1995, 666 mm; 1996, 450 mm; 1997, 704 mm). The decrease in net biomass production with increasing tree size (Kira, 1977) and the relatively small size of the species used in the present experiment are also likely to have played a part. As described in Section 2.5-2.8, maximum tree heights are typically 10-12 m *G. sepium*, ~15 m in *S. spectabilis* and 15-20 m in *M. volkensii*. Although *C. megalocarpus* may reach heights of 35 m in some areas, trees of more than half of this height were never observed in Machakos District.

Multi-purpose tree species trials at three sites in the Ugandan highlands (Okorio *et al.*, 1994) and two sites in Ethiopia (Abebe, 1994) provided contrasting results. Thus Okorio *et al.* (1994) reported that height and diameter increments decreased 3-4 years after planting, but a similar pattern was not apparent after 5 years in the results reported by Abebe (1994). This discrepancy may have resulted from the lower growth rates and smaller trees at the drier, lower altitude site in Ethiopia. The periodic surges in the trends for trunk diameter c. 5 cm above ground level and height apparent in the present study in 1994 and 1995 (Figure 6.5) resulted from the response of tree growth to rainfall at the beginning of the long rains following the preceding dry season. The absence of a similar pattern during the later stages of the observation period probably occurred because the larger trees accessed larger volumes of soil and deep water reserves within the profile.

The relatively small size of *C. megalocarpus* trees in the present experiment reflects the small annual height increments shown in Table 6.6, which were undoubtedly affected by the dryness of the climate in Machakos relative to the native range of this species. The high leaf areas during the relatively wet 1997/98 rains (cf. Figure 4.5) support this hypothesis. The much higher growth rates of *M. volkensii* reflect its comparatively high leaf areas and stomatal conductances (cf. Section 5.3.3), in combination with the necessary rooting attributes to supply sufficient water to support transpirational demand. *G. sepium* grew more slowly than expected for this high yielding provenance due to a combination of insect infestation, fungal attack, poor drought resistance (Shelton, 1994) and the reduced yield associated with the relatively cool conditions prevailing in Machakos District (Swasdiphanich, 1993). Heineman *et al.* (1997) recorded a mean height of 4.6 m and trunk diameter of 13.1 cm 21 months after planting the same provenance of *G. sepium* (Retalhuleu) in an area of western Kenya with an annual rainfall of 1678 mm; average height and diameter in the present study were 2.9 m and 5.7 cm at the same stage. Heineman *et al.* (1997) also reported that average height and stem diameter 21 months after planting were 4.8 m and 9.9 cm for three *S. spectabilis* provenances grown in western Kenya, whereas the equivalent values in the present experiment were 4.9 m and 6.2 cm; the differences were therefore smaller than for *G. sepium*, but again highlight the adverse effect of the lower rainfall at Machakos. Although *M. volkensii* had the greatest trunk diameter c. 5 cm above ground, *S. spectabilis* trees were taller; however, height growth slowed relative to *M. volkensii* towards the end of the period (Figure 6.5). Abebe (1994) observed comparable heights and trunk diameters for a range of multipurpose agroforestry trees planted at a density of 2500 trees ha^{-1} at two sites in Ethiopia at similar elevation and with similar rainfall to Machakos. The fastest growing species, *Acacia nilotica*, and *Eucalyptus camaldulensis*, attained mean annual height and trunk diameter increments of 1.10 m and 2.30 cm and 1.87 m and 2.55 cm respectively over a 5 year period. At 30 months after planting, the range of heights (1.7-4.5 m) and trunk diameters (3.8-7.0 cm) in the present experiment were at the lower end of those measured for several faster growing agroforestry species (height: 4.5-5.0 m, trunk diameter: 7-10 cm) at a wetter, lower elevation site in the Ugandan highlands (Okorio *et al.*, 1994). These two datasets indicate that *M. volkensii* and *S. spectabilis* were highly productive under the prevailing relatively dry climatic conditions in Machakos.

Table 6.6. Mean annual height (m) and trunk diameter c. 5 cm above ground (cm) increments over a four year period from the first measurement, made 6 months after planting.

	C. megalocarpus	*M. volkensii*	*S. spectabilis*	*G. sepium*
Diameter	0.023 ± 0.001	0.032 ± 0.001	0.030 ± 0.001	0.028 ± 0.001
Height	0.869 ± 0.021	1.345 ± 0.075	1.511 ± 0.062	1.052 ± 0.030

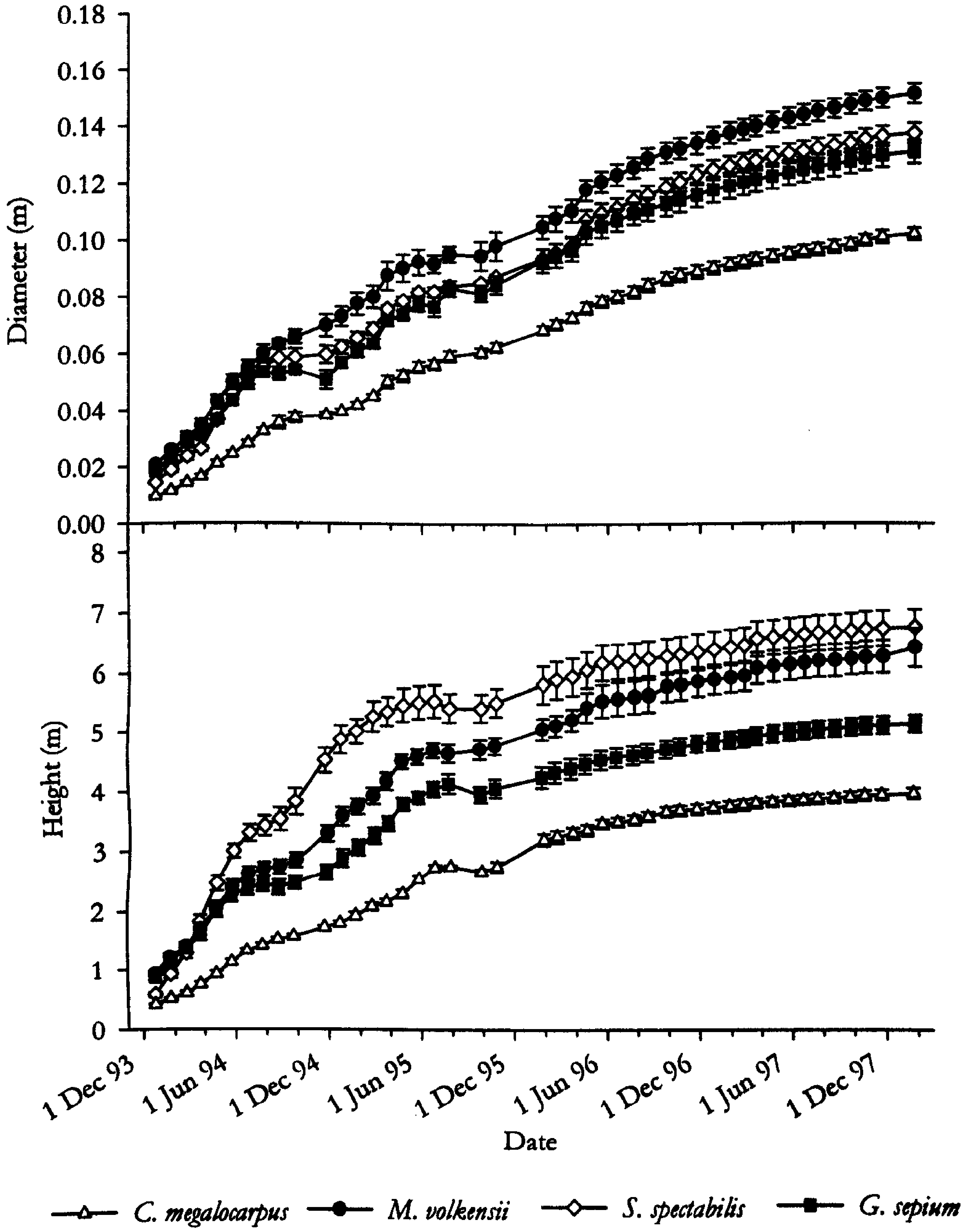


Figure 6.5 Trunk diameter c. 5cm above ground and height ± standard error for *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium* trees between December 1993 and February 1998. The trees were planted as seedlings in April 1993.

Figure 6.6 shows the timecourses for leaf and woody dry weight for the four species examined between January 1996 and February 1998; dry weight values are expressed in units of kilograms per tree and tonnes per hectare. As for height and trunk diameter, a dominant feature of the data for all species is the slowing of the rate of accumulation of woody biomass with time. One-way analysis of variance showed that woody dry weight was 79 % greater in *M. volkensii* than in *C. megalocarpus* (p=0.002) at the end of the measurement period in February 1998. There was no significant difference between *S. spectabilis* and *G. sepium* (p=0.177).

Figure 6.7 shows average daily dry weight increments expressed per tree for the four species examined during the cropping seasons and the dry periods between cropping seasons. Although only 98 mm (9.3 %) of rain was received outside the cropping seasons between 1 January 1996 and 1 January 1998, there is no evident difference between growth rates during the cropping seasons and the intervening dry periods. Lott *et al.* (2000a) found growth differences between the wet and dry seasons in *Grevillea robusta* trees growing at a nearby site, although the shallower, sandier and more freely drained soil is likely to have accentuated seasonal variations in water availability. In the present study, growth increments were greatest in *M. volkensii* followed by *S. spectabilis*, *G. sepium* and *C. megalocarpus* until the end of the 1997 long rains, after which the dry weight increments for *C. megalocarpus* exceeded those for *S. spectabilis* and *G. sepium*. Table 6.7 shows woody dry weight production during the extended seasons which include the dry period preceding the ensuing cropping season. Production decreased in all species between the first and second season as a result of the unusually low rainfall during the 1996/97 short rains. Thereafter, although growth increased during the 1997 long rains, the underlying trend of decreasing yield continued. These results suggest that, although rainfall affects tree growth, tree size is the more important factor notwithstanding the observed substantial variation in water supplies. The woody dry weight production of *M. volkensii*, the highest yielding tree, substantially exceeded that of *Grevillea robusta* grown at a nearby site, 4.5 years after planting by Lott *et al.* (2000a); the values for *G. robusta* and *M. volkensii* were c. 11.0 and 16.2 t ha^{-1}. However, the *G. robusta* trees were pruned more severely and grown on a sloping site with poorer soil.

Table 6.7. Above-ground woody dry weight production (t ha^{-1}) during extended seasons including the dry periods preceding crop planting at the onset of the following rainy season.

Season	*C. megalocarpus*	*M. volkensii*	*S. spectabilis*	*G. sepium*
1996 long growing season	4.35 ± 0.47	7.84 ± 0.39	6.78 ± 0.55	4.54 ± 0.28
1996/97 short growing season	1.75 ± 0.12	2.64 ± 0.22	2.10 ± 0.07	1.81 ± 0.08
1997 long growing season	2.34 ± 0.08	3.61 ± 0.10	2.43 ± 0.13	2.06 ± 0.14
1997/98 short growing season	0.93 ± 0.24	1.38 ± 0.33	0.86 ± 0.07	0.84 ± 0.08

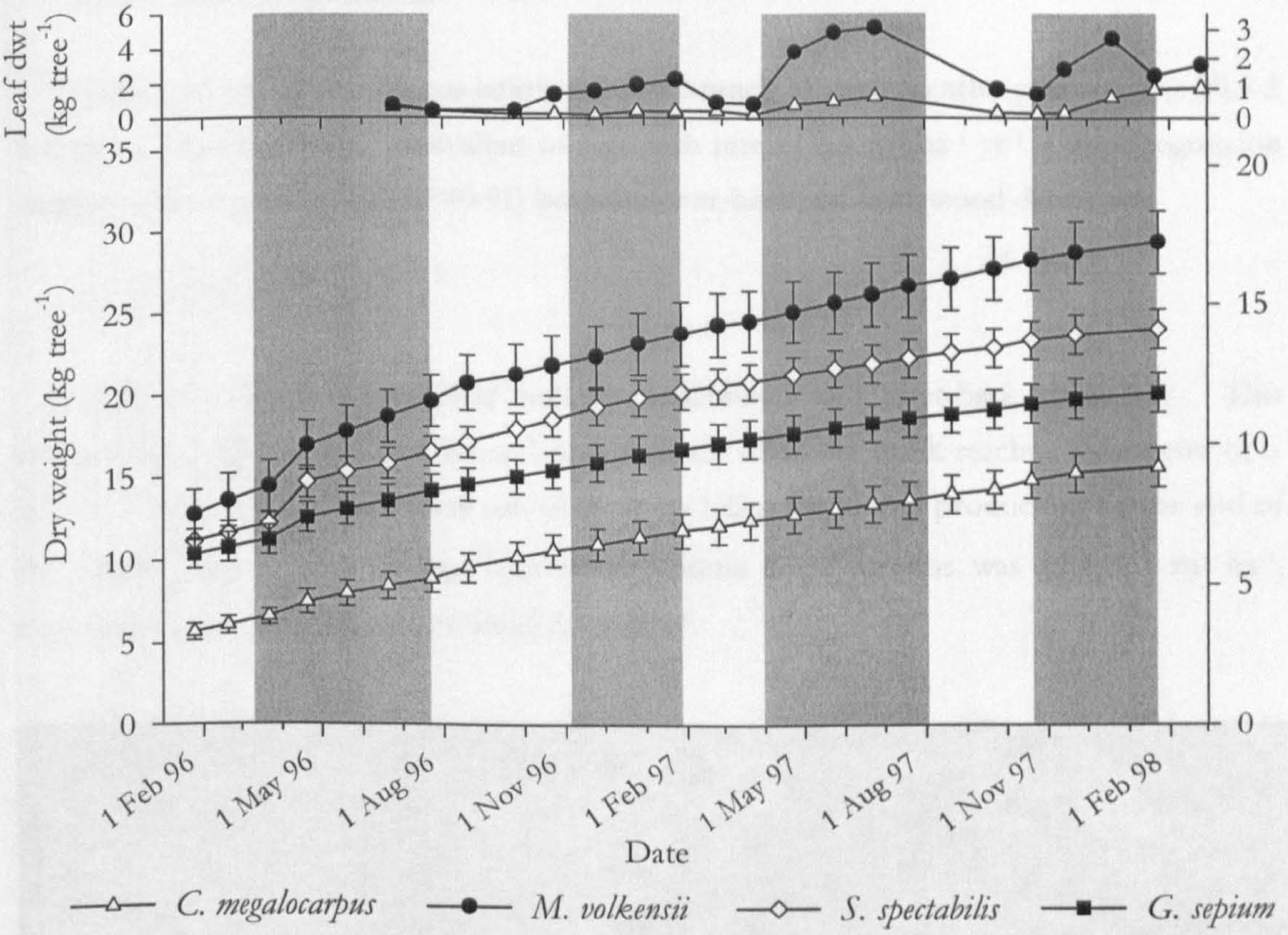


Figure 6.6. Estimated leaf dry weights ± standard errors for *C. megalocarpus* and *M. volkensii* and, on the same scale, estimated woody dry weights ± standard errors between January 1996 and February 1998 for *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium*.

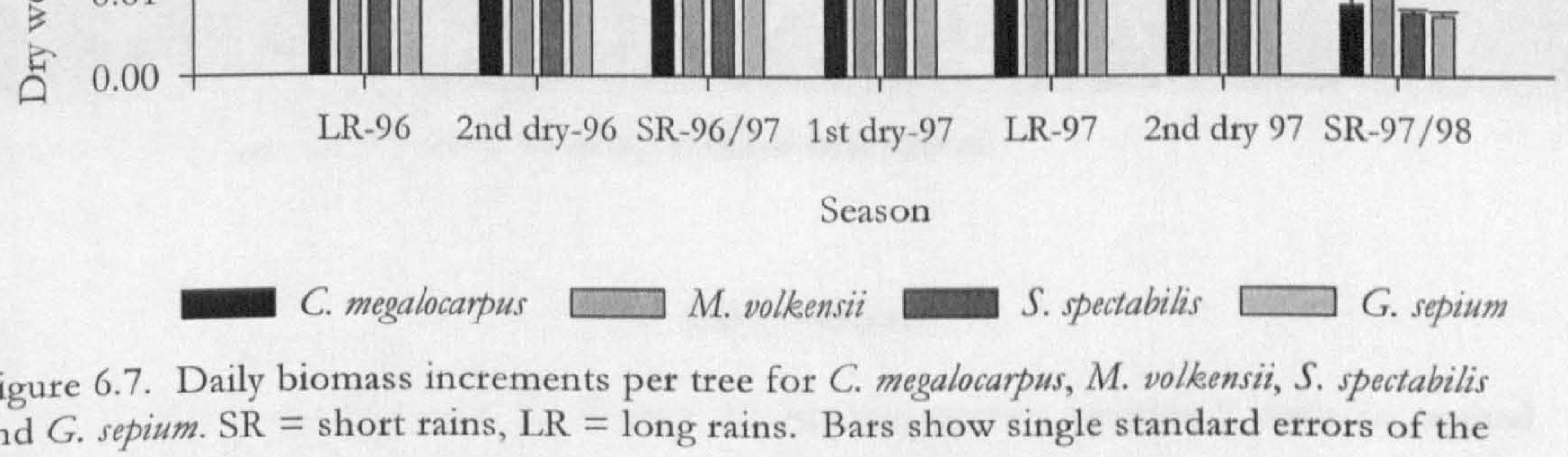


Figure 6.7. Daily biomass increments per tree for *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium*. SR = short rains, LR = long rains. Bars show single standard errors of the mean.

Estimated over-bark volume below the first branch 58 months after planting was 29.5 ± 4.8 $m^3\ ha^{-1}$ in *M. volkensii*, equivalent to a growth rate of 6.1 $m^3\ ha^{-1}\ yr^{-1}$. Linear regression showed a close relationship ($r^2=0.91$) between over-bark and heartwood diameters:

$$d_h = 0.756\ d - 3.16 \qquad [6.4]$$

where d_h and d respectively indicate heartwood and over-bark diameters. This relationship suggests that heartwood began to form when the trunk reached a diameter of c. 4.2 cm. Although the trees were too small to be felled for timber production by the end of the observation period, average heartwood volume at 58 months was 11.4±2.1 $m^3\ ha^{-1}$, equivalent to an annual production of 2.4 $m^3\ ha^{-1}$.

Plate 6.1. Cut *M. volkensii* trunk showing reddish heartwood.

6.4 DISCUSSION

M. volkensii was the most productive of the tree species examined, with an annual average production of 3.6 t ha^{-1} of above-ground woody biomass and 2.4 $m^3\ ha^{-1}$ of high value timber. Woody biomass yields were augmented by an estimated annual leaf dry weight production of 4.0 t ha^{-1} measured between 43 and 58 months after planting. The least productive species, *C. megalocarpus*, produced 1.9 t ha^{-1} year^{-1} of woody biomass and 1.2 t ha^{-1} year^{-1} of leaf biomass. *C. megalocarpus* is favoured predominantly for the shading it provides during the dry season, and for that reason will doubtless remain a favoured species for farmers in dryland areas. However, attack by caterpillars may, according to local experience, cause severe problems, as occurred during the 1997 long rains when trees almost denuded of leaves were observed around Machakos town. The superior performance of *M. volkensii* results not only from its greater leaf area, stomatal conductance and photosynthetic rate, but also its greater water use efficiency (cf. Section 5.3.4). The two exotic species, *S. spectabilis* and *G. sepium*, provided an average woody biomass production of 2.9 and 2.5 t ha^{-1} yr^{-1} respectively over the observation period; leaf dry weights were not determined for these species. Although *S. spectabilis* has not often been used in agroforestry, its uniform growth, straight stems and high productivity make it an attractive choice for the production of poles and timber for light construction. *G. sepium* is more commonly grown in alley cropping systems in the humid tropics, where it is used to provide mulch and fodder (Gutteridge and Shelton, 1994). Heineman *et al.* (1997) reported that the leaves of *G. sepium* improved soil nutrient status, whereas those of *S. spectabilis* had no effect compared to non-mulch control plots in western Kenya. The nitrogen-fixing species, *G. sepium*, is therefore more likely to be beneficial under nitrogen-limiting conditions.

Modelled daily net canopy assimilation rates increased over the three cropping seasons between the end of 1996 and the beginning of 1998 in both *C. megalocarpus* and *M. volkensii* (cf. Section 5.3.4), whereas above-ground woody biomass production decreased. This may have originated partly from increased allocation of assimilates to the roots as a result of the decreasing rainfall experienced over most of this period; however the increase in the maintenance respiration/growth respiration ratio as the proportion of non-photosynthetic tissue increased would also have restricted net biomass production (Kira, 1977). These observations suggest that the performance of agroforestry systems may be improved by using short duration tree species. However, the large and increasing production of leafy material of high nutritive quality for livestock observed in *M. volkensii* (Milimo, 1994) may serve to alleviate the decreases in woody biomass production and crop yields as the trees grow larger and competition increases.

The results presented in Chapter 7 show that all tree species depleted soil moisture to a greater extent than sole crops, so affecting crop growth. Ong *et al.* (1992) also found that overall water use was increased in a *Leucaena leucocephala*-based agroforestry system in India, but that severe competition reduced crop yield. Similar effects are also apparent in natural ecosystems such as the thorn scrub vegetation of the Sahel, where Nizinski, Morand and Fournier (1994) found that transpiration of trees and herbaceous vegetation in *Acacia tortilis* and *Balanites aegyptiaca* groves was consistently greater than in adjacent herbaceous zones. The effects of water use by trees on crop yield are likely to be less important in areas where the water table is accessible to tree roots or which receive greater off-season rainfall than the 98 mm (9.3 % of total rainfall) recorded in the present experiment between 1 January 1996 and 1 January 1998. The advantages of agroforestry were most apparent during the two short growing seasons when beans were grown. Thus during the 1996/97 season, the trees were still productive despite crop failure due to the low rainfall. During the 1997/98 season, when rainfall was particularly abundant, tree and crop production were both high as the trees were able to use water which was excess to crop requirements that would otherwise have been lost by deep drainage.

When considering the results, it must be remembered that the germplasm for *M. volkensii* and *C. megalocarpus* used in the present study came from unimproved stock, and that further selection based on form, phenology or competitiveness may provide more profitable alternatives. A possible avenue for long term exploration that may prove beneficial for agroforestry is the identification and transfer of genes controlling leafing phenology to enable the practical potential of the reverse phenology of *F. albida* to be assessed and applied in semi-arid subsistence agricultural environments. However, this would only be feasible if leaf fall and flushing are controlled by a limited number of gene loci and the natural phenological patterns in recipient species could be suppressed. In order to alleviate poverty and mitigate deforestation and land depletion, Leakey and Simons (1990) highlighted the need for the rapid domestication of valuable indigenous tree species and the development of suitable management strategies to allow important environmental services to be maintained, whilst moving the source of tree products away from natural forests. These aims need to go hand-in-hand with the introduction of policies favouring rural smallholders, as opposed to large scale monocultural producers, and the development of commercial markets and the awareness of farmers for marketing opportunities. Domestication and selection of *M. volkensii* is one of ICRAF's current activities (Sanchez, 1995).

7 CROP PERFORMANCE

7.1 INTRODUCTION

Crop performance in agroforestry systems is dependent upon the additive and interactive effects of seasonal climate and tree-related factors. The orientation of tree rows interacts with directionally discrete climatic effects to introduce systematic modifications in shading, wind and rainfall patterns around the trees depending on their canopy size, height, density and leafing phenology (Darnhofer *et al.*, 1989; Tournebize and Sinoquet, 1995; Brenner, 1995). As previous studies have shown that tree and crop roots predominantly occupy the same soil horizons (Jonsson *et al.*, 1988; Mwihomeke, 1992; Toky and Bisht, 1992; van Noordwijk *et al.*, 1996; Odhiambo *et al.*, 2000), transpiration by the tree component is likely to reduce the availability of water to support crop growth unless the water table is accessible to the tree roots (Smith, Jarvis and Odongo, 1997b). In semi-arid agroforestry systems, below-ground competition for water is the main cause of reductions in crop yield (Ong and Saharan, 1989; Malik and Sharma, 1990; Monteith Ong and Corlett, 1991; Singh, Dhanda and Ralhan, 1993; Singh, Howard *et al.*, 1995; Jones, Sinclair and Grime, 1998; Lott *et al.*, 2000b). However, as the quantity of water available to support crop growth increases, shade becomes increasingly important (Lawson and Kang, 1990; Okorio *et al.*, 1994; Osman, Emmingham and Sharrow, 1998). Thus, tree canopy characteristics which affect transpiration and rainfall interception and the horizontal rooting extent of the tree are of primary importance in determining crop performance in rainfed semi-arid agroforestry systems, whereas shading and above-ground microclimate modifications are of secondary importance (Ong *et al.*, 1991; Monteith; Ong and Corlett, 1991).

Tree phenology and canopy characteristics affecting transpiration are considered in Chapters 3 and 4 respectively. Rainfall interception by tree canopies decreases water inputs to the crop rooting zone, exacerbating the competitive effect of water extraction by tree roots. 10-15 % reductions in rainfall penetration to the soil beneath tree canopies have been reported depending on canopy density (Darnhofer *et al.*, 1989; Breman and Kessler, 1995). Measurements perpendicular to 12 m long rows of *Senna siamea* trees at Machakos Field Research Station showed that rainfall at ground level was primarily dependent on wind direction (Darnhofer *et al.*, 1989). The main effect was an 18 % reduction in rainfall within a distance of one tree height (~3.5 m) on the leeward side of the canopy, although small increases in rainfall due to runoff from the canopy occurred under both the windward and leeward edges of the canopy. The distribution of tree rooting densities and water extraction patterns with increasing distance from trees have seldom been quantified. Rooting density usually decreases with increasing distance from trees (van Noordwijk *et al.*, 1996), although measurements and predictions of the horizontal patterns of tree rooting and water extraction remain fraught with difficulty (Odhiambo *et al.*, 2000). Toky and Bisht (1992) reported that tree roots extended to a distance of 1.3 times the canopy spread in 6 year old *Prosopis cineararia* (3.3 m) and *Populus deltoides* (5.8 m) trees, although fine roots may well have extended further. Effects of water extraction by tree roots on crop performance have been measured at distances of up to 10 m from 3.5 year old *Eucalyptus tereicornis* trees (Malik and Sharma, 1990) and 8-10 m from fully grown *Acacia nilotica* trees (Yadav, Sharma and Khanna, 1993). However, substantial variation in rooting patterns may be induced by genotype*environment interactions (van Noordwijk *et al.*, 1996).

Although less extensive, and usually less important, than competition between trees and crops for water, reductions in photosynthetically active radiation (PAR) resulting from shading may adversely affect carbon assimilation by understorey crops (Caldwell, 1987). The relative effects of shading on C3 and C4 species differ due to the generally higher light saturation levels of C4 species, although differences between leaves produced under differing irradiances may be greater than those attributable to the intrinsic characteristics of the photosynthetic pathway (Jones, 1992). Thus, in the absence of other limiting factors, assimilation may be more affected by incident PAR than by photosynthetic pathway. Surprisingly, in agroforestry trials spanning a range of sub-humid sites in Uganda, Okorio *et al.* (1994) found that shading alone induced greater yield reductions in bean (*Phaseolus vulgaris*) than in maize (*Zea mays*). In trials at Machakos Research Station, the yields of maize grown under shade nets were little affected during drier seasons, but were reduced in seasons of higher rainfall (Lott *et al*, 2000b). At an adjacent site, Howard (1995) also found that the reductions in maize yield under shade nets were greater under irrigated than unirrigated conditions relative to unshaded control plots. These results suggest that light limitation may become increasingly important as water availability increases. Shading also influences surface radiative budgets and the energy balance of leaves, with the result that canopy temperature and transpiration rate are affected to an extent dependent on the spectral properties of the leaves and stomatal and boundary layer conductances. Reductions in radiative flux may protect plants from water stress (Allen *et al.*, 1976), permit increased seedling survival following germination by reducing soil temperature (Vandenbeldt and Williams, 1992), and alter crop duration (Corlett *et al.*, 1987). Corlett *et al.* (1992a) reported that leaf temperatures within the crop canopy were cooler by day and warmer at night in a *Leucaena leucocephala*/millet agroforestry system at a site in semi-arid India than in sole millet plots; the consequent small reduction in crop duration was considered to be unimportant, especially when water stress was taken into account (Corlett *et al.*, 1987). Lott *et al.* (2000b) reached a similar conclusion for a *Grevillea robusta*/maize agroforestry system at Machakos

Research Station.

Crop performance is also affected by shelter from wind, which produces a range of microclimatic modifications (Brenner, 1995) and appears to benefit plant growth when soil moisture is freely available, although results are less clear where water is limiting (Davis and Norman, 1988). The effects depend on the response of vegetation and vapour pressure deficit to increases in air temperature. However, controlled environment experiments to examine the interactive effects of soil moisture and evaporative demand (Berard and Thurtell, 1991) suggest that atmospheric conditions which favour high transpiration rates are much less important than soil moisture in causing reductions in maize yield resulting from decreases in photosynthetic rate.

Two crop species were examined in the present study (cf. Section 2.9), *Zea mays* (Katumani composite), a C4 species, and *Phaseolus vulgaris* (var. Rosecoco), a C3 species. Dry matter production is almost always greater in C4 than in C3 species (Kira and Kumura, 1983), as is water use efficiency (2.67-3.34 mg dry matter g^{-1} H_2O for maize and 1.33-1.76 mg dry matter g^{-1} H_2O for pulses (Jones, 1992)). Of the principal C4 cereal crops grown in the sub-humid tropics, maize has the highest production potential when water and nutrients are not limiting, but is also the most drought sensitive (Carberry *et al.*, 1989). In the absence of nutrient limitation, grain yield in Katumani composite maize is linearly correlated with evapotranspiration, with lower planting densities giving higher yields only under conditions where potential evaporation is low (Stewart, 1988). Several factors are involved in water-induced limitations of maize yield; these include reductions in net photosynthetic rate and stomatal conductance (Bethenod, Tardieu and Katerji, 1996) and decreases in green leaf area resulting from reductions in leaf growth and premature senescence (Bolanos *et al.*, 1993). The reproductive phase is also affected, as drought delays silking and reduces grain number due to increased asynchrony in flowering; pollen production is reduced during the receptive period of the silks, which are also exposed for a shorter period (Norman, Pearson and Searle, 1995).

Thus the temporal distribution of rainfall during the cropping season may have as great an effect as the seasonal total (Reshid and Getahun, 1987). Drought selection in maize has mainly been concerned with shortening crop duration, maintaining assimilation during drought and shortening the interval between anthesis and silking (Bolanos *et al.*, 1993; Edmeades *et al.*, 1993). Bean yields have been shown to increase linearly with evapotranspiration above a threshold, below which the increase in yield is more gradual (Stewart, 1988). Yield in *Phaseolus vulgaris* is most sensitive to drought during flowering and less sensitive during pod growth and grain filling (Monhouche, Ruget and Delecolle, 1998).

Morphologically, reductions in leaf area resulting from the production of fewer and smaller leaves and accelerated senescence is the most important response to drought (Schneider *et al.*, 1997). Foster, Pajarito and Acosta-Gallegos (1995) also observed that nitrogen mobilisation and water use efficiency decreased under severe moisture stress. Nitrogen fixation in *Phaseolus vulgaris* is commonly considered to be low and susceptible to soil drying, although there is wide genotypic variation, and its importance in drier regions results largely from its nitrogen fixing ability (Serraj and Sinclair, 1998).

The effects of trees on crop yield are usually less severe during the first 2-3 years after planting (Ralhan *et al.*, 1992; Rao, Ramakrishna, Singh and Chopra, 1993; Akyeampong *et al.*, 1995). In the present study, the effects of the trees on crop growth were modest during the first three years of the experiment. In 1995, two years after tree planting when rainfall was 302 mm (84 % of long term average), maize yields were most affected by *M. volkensii* and *G. sepium*; the effects of *C. megalocarpus* were intermediate and similar to *Grevillea robusta*, while *S. spectabilis* induced the smallest reduction in crop yield (Rao, Nair and Ong, 1997).

This chapter describes the effects of *C. megalocarpus*, *M. volkensii*, *S. spectabilis* and *G. sepium* on the yields of associated maize and bean crops relative to equivalent sole crops and examines the effects of available soil moisture. The distribution of photosynthetically active radiation within plots and canopy rainfall interception were examined in the *C. megalocarpus* and *M. volkensii* treatments. The treatment comparisons were designed to investigate the differing influence of trees between: (1) sole crop and agroforestry treatments; (2) indigenous and exotic tree species; (3) indigenous deciduous and evergreen species; (4) exotic nitrogen-fixing and non-leguminous species. The effects attributable to the side of the plot (northern or southern side of the tree row or central crop row in the sole crop plots) were also examined. Data describing the overall agroforestry system performance for both trees and crops are also presented.

7.2 METHODS

7.2.1 MEASUREMENT OF RAINFALL INTERCEPTION BY THE TREE CANOPY

It was noted during the 1996 long rains that the soil on the southern, more shaded side of the trees remained wet for longer following rainfall than on the northern, less shaded side. To investigate possible causes, rain gauges were constructed from two 50 cm long sections of 10 cm diameter PVC drain-pipe which were halved lengthways and joined end-to-end by an angled steel bracket as shown in Figure 7.1. Gauges were located 1.5 m to the north and south of the tree rows in all *C. megalocarpus* and *M. volkensii* plots to determine throughfall; a single gauge placed in the open was used as a reference. The gauges were orientated diagonally with respect to the tree rows to integrate rainfall over a range of distances from the row and reduce susceptibility to local variation attributable to individual branches located above the gauges. As the maize plants close to the trees were small during the 1997 long rains and the bean plants were compact, the crops did not overtop the gauges.

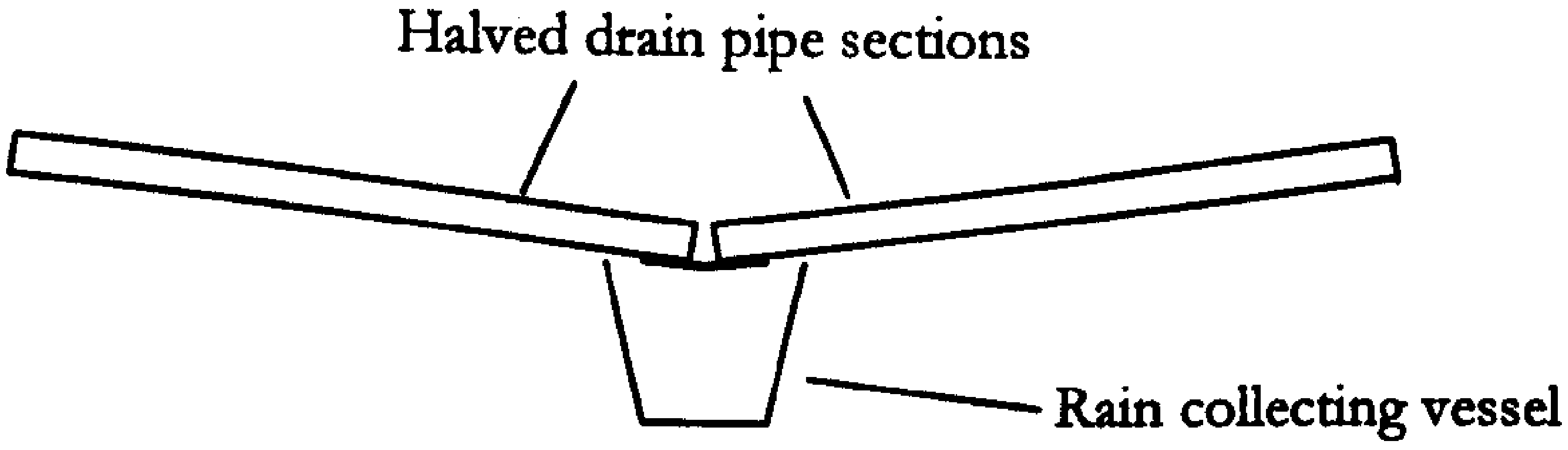


Figure 7.1 Rain gauge constructed for measurement of rainfall beneath tree canopies.

7.2.2 DETERMINATION OF SOIL MOISTURE

Soil moisture measurements were made at approximately weekly intervals using a Wallingford neutron probe (Bell, 1987) calibrated for the soil profile adjacent to the experimental site (Appendix 1). Aluminium access tubes were installed on the northern side of all plots in Replicates 1, 3 and 4 in 1993, in lines running north-south from the centre of the plot. The access tubes were located 1.0, 2.5, 4.0, 5.5, 7.0 and 8.5 m from the tree row in the agroforestry plots, and 1.0, 2.5 and 4.0 m from the centre of the sole crop plots. Measurements were made at 20 cm depth intervals between 20 and 160 cm where soil depth permitted. In Replicate 1, four of the six access tubes in the *M. volkensii* plot and one in the *C. megalocarpus* plot extended little deeper than 100 cm due to the presence of a relatively shallow murram layer.

Because of the observed differences in the wetness of the soil surface between the northern and southern sides of the tree rows, additional access tubes were installed on the southern side of the tree rows to allow north-south comparisons to be made. These were installed towards the end of the 1996/97 short rains at distances of 1 and 4 m from the tree rows in the *C. megalocarpus* and *M. volkensii* plots in Replicates 1, 3 and 4. Measurements are presented for the 1997 long and 1997/98 short rains.

In the present chapter, soil moisture is expressed as "available water", defined as the quantity of water above the permanent wilting point (-1.5 MPa) in the upper 1.1 m of the soil profile, in which the overwhelming majority of crop roots are generally found (Jonsson *et al.*, 1988; Squire, 1990; Odhiambo *et al.*, 2000). Values are expressed as the depth of water nominally available to support plant growth, although it is recognised that the permanent wilting point is a somewhat arbitrary measure and osmotic adjustment by plants grown under drought conditions may influence the quantity of extractable water (Jones, 1992). Percentage moisture content at the permanent wilting point for each neutron probe measurement depth (Table 7.1) was interpolated from the values determined by Kiepe (1995; cf. Table 3.2). Multiplication of these values by the depth of soil between the soil surface and midway between the first and second measurement point or midway between consecutive measurement points gives the available water content in each soil horizon. The sum of the values for each horizon provided estimates of available water content to a depth of 1.1 m. Soil water content was 315 mm at field capacity and 141 mm at the permanent wilting point, giving 174 mm available to support plant growth when the soil was at field capacity.

Table 7.1. Percentage soil moisture content at permanent wilting point and field capacity. The values for each depth are interpolated from the measurements of Kiepe (1995; cf. Table 3.2).

Depth (m)	Permanent wilting point (%)	Field capacity (%)
0.2	11	25
0.4	12	27
0.6	13	29
0.8	14	31
1.0	15	33

7.2.3 ESTIMATION OF PHOTOSYNTHETICALLY ACTIVE RADIATION (PAR)

The program MAESTEST (cf. Section 5.2.5) was used to estimate the patterns of photosynthetically active radiation across the *C. megalocarpus* and *M. volkensii* plots during three of the four cropping seasons examined. MAESTEST is companion program to MAESTRA and uses the same input files, but with an additional file "points.dat" (cf. Appendix 5) to specify the positions of the points for which incident PAR is calculated. Other input files contain data, including plot dimensions and orientation, tree crown positions, crown dimensions, leaf area and leaf spatial distribution. In the present study, individual tree canopies were defined as being box-shaped (i.e. six sided volumes with adjacent sides at 90° to one another), running contiguously along the centre of the plot in an east-west direction. The canopy of each tree within the row was assumed to have a similar leaf area, effectively creating a single homogeneous canopy. Leaves were assumed to be randomly distributed within the canopy, with elliptical leaf angle distributions being fitted to direct measurements (cf. Section 5.2.5). Full details are given in Section 5.2, and validation of the combined canopy measurements and calculations are presented in Section 5.3.4. PAR was calculated at 1 m intervals for transects along the centre of the plots extending from 9 m to the north to 9 m to the south of the tree rows.

7.2.4 MAIZE

Experiment layout and plot design are shown in Section 2.4.2. The soil was tilled prior to the onset of the rains and maize was sown during the long growing season in rows running parallel to the tree row with an inter-row spacing of 90 cm; within-row spacing was 25 cm, giving a population of 44444 plants ha^{-1}. Two or three seeds were sown at each point after the first significant rainfall of the season, and the seedlings were thinned 2-3 weeks after sowing to leave a single maize plant at each sowing point. Weeding was carried out by workers using local tools to scarify the soil surface when weed growth dictated. When the crop reached maturity, eight rows to the north and south of the tree rows were harvested in the 6 m wide central section of the plots (Figure 2.3); a single buffer row was left along the outer edges of the plots. The timing of events is shown in Table 7.2.

Plants were harvested separately from each row and their numbers recorded before separating the grain from the remainder of the shoot; the dry weight of each component was determined. In 1996, two sub-samples of grain and two for the remainder of the shoot were taken from rows 1-4 and 5-8 in each plot and dried to constant weight at 70 °C to establish fresh to dry weight conversion factors; sub-samples were taken from each row in 1997.

Table 7.2. Timing of events during maize cropping seasons. DAS denotes days after sowing.

Season	Sowing date	Thinning (DAS)	Weeding (DAS)	Harvest date	Season duration (d)
1996 Long rains	12 March 1996	20	13, 21	21 July 1996	131
1997 Long rains	1 April 1997	17	15, 56	2 August 1997	123

7.2.4.1 *Shade treatments*

To determine the effects of shading on crop growth, shade nets (Plate 7.1) with neutral spectral qualities (Lowes of Dundee, UK), nominally extinguishing 25 or 50 % of the incident shortwave radiation, were set up on the southern side of the sole crop plots in each replicate. Each net covered an area of 4 x 3 m. The nets were supported 80 cm above ground-level at the beginning of the season and raised periodically as plant height increased. The proportion of PAR excluded by the nets was measured using a Sunfleck ceptometer (Decagon Devices, Pullman, USA); 10 paired measurements were made under each net and in the open. PAR values under "50 %" and "25 %" shade netting were respectively 57.6±1.2 and 31.4±1.8 of the incident values. Four rain gauges were placed under each shade net in Replicate 3 to determine effects on rainfall; three gauges were placed at 1 m intervals along the centre of the long axis of the shade net enclosures (east-west) and the fourth was located 1 m to the south of the centre (Plate 7.1). As the open sides of the covered area allowed free air movement, modifications to crop microclimate resulting from factors other than reductions in incident radiation and rainfall were minimal (Lott *et al*, 2000b).

Plate 7.1 Shade nets in a sole crop plot during 1996/97 short rainy season.

Of the five crop rows beneath each net, only the plants in the three central rows were harvested, thereby excluding plants within 1 m of the edge of the nets. Equivalent areas were harvested between the two shade nets in each plot to provide unshaded control data for comparison. Plant number and the total dry weight for each plant were recorded after drying. In 1997, four randomly selected plants were harvested from the central three rows, again excluding plants within 1 m of the edge of the net. The dry weight of grain and the remainder of the shoot were recorded separately after drying to constant weight at 70 °C.

7.2.4.2 Leaf nitrogen content

During the 1997 season, the leaves of maize plants growing close to the tree rows began to yellow in early to mid-May. Leaf samples were taken for nitrogen analysis from all replicate plots in the *C. megalocarpus*, *M. volkensii* and *S. spectabilis* treatments on 6 June 1997, 66 days after sowing, when most plants located some distance from the tree rows had reached the silking stage. Flag leaves were sampled from five plants in each of six rows on both the northern and southern sides of plots; plants from adjacent rows were bulked to provide three samples for each side of the plot (i.e. rows 1+2, 4+5 and 7+8). In the sole crop plots, only rows 1 2, 4, and 5 were sampled. Nitrogen analysis was carried out at Machakos Research Station using the Kjeldahl method.

7.2.5 BEANS

Beans were grown during the short growing season after tilling the soil prior to the first rains. Inter-row spacing was 60 cm, with 15 cm spacing between plants within rows (c. 111111 plants ha^{-1}); two or three seeds were sown at each planting point following the first significant rainfall. The seedlings were thinned to leave one plant at each sowing point, except during the 1996/97 season when the crop was not thinned due to the dryness of the soil, as thinning under such conditions may severely affect the remaining plants. Weeding was carried out twice during the season when weed growth dictated. The timing of events is shown in Table 7.3.

The beans were harvested when the leaves had senesced and the pods had dried. Of the 15 rows on either side of the centre of each plot, 14 were harvested, leaving a guard row along the outside edge of the plot. Plant number per row and grain weight were recorded. No other weight measurements were made as most of the leaf material had desiccated and blown away by final harvest. The pods were harvested separately from each row and shelled on site. Sub-samples of the seed were bulked for rows 1-7 and 8-14 in 1996/97 and for individual rows in 1997/98 to determine dry to fresh weight conversion factors.

Table 7.3. Timing of events during bean cropping seasons. DAS denotes days after sowing.

	Sowing date	Thinning (DAS)	Weeding (DAS)	Harvest date	Season duration (d)
1996/97 short rains	5 November 1996	-	27, 35	27 January 1997	83
1997/98 short rains	22 October 1997	23	23, 48	21 January 1998	91

7.2.5.1 Shade treatments

Shade nets were again used to investigate the effects of shading on crop yield, as described in Section 7.2.4.1. However, as beans are much shorter than maize, there was no need to raise the nets; these were maintained at a constant height of 80 cm. Five rows of beans were grown beneath each net (Plate 7.1); the three central rows were harvested at maturity, leaving a 1 m discard at each end of the row. Equivalent areas of unshaded sole crops between the shaded areas were harvested for comparison. Plant number in each row and the dry weight of beans produced were recorded.

7.2.6 STATISTICAL ANALYSIS

Several spatial and temporal variables were involved in many of the analyses reported here. The randomised block experimental design (Figure 2.2) lends itself to analysis of variance to test for various effects. Split-plot analysis of variance was used to establish effects associated with location within the plots (north or south of the centre/tree row), with each side of the plot being designated as a sub-plot within the main plot. Similarly, the two seasons for which data were obtained for maize were included in a single split-plot Anova in which the seasons were designated as sub-plots; however, the two seasons for which data were obtained for beans were analysed separately as rainfall and yield differed greatly. To separate effects stemming from the presence of trees as opposed from those resulting from differences between tree treatments, a factor, named "control", was included to distinguish plots containing trees from those lacking trees. Another factor, "origin", was used to determine differences attributable to the origin of the tree species, i.e. indigenous or exotic. As the rows did not constitute independent factors, the slopes of the lines fitted to the row-by-row data by linear regression were analysed to test for significant trends across the plots. Anova model structures are shown in each analysis section, but the following example, used for analysis of data for maize yield, is presented here to explain the syntax used to denote treatment and blocking structures:

Treatment: side*control/treatment*season

Blocks: replicate/plot/side of row/season

The crossing operator (*) is used to specify factorial structures where the main effects of each factor and the interaction between factors are determined. The nesting operator (/) specifies that the effects of the first factor in the equation and interactions between the first and second factor are sought, but not the main effects of the second factor. In the above blocking structure, the plot-within-replicate, side-within-plot-within-replicate and season-within-side-within-plot-within-replicate effects are determined. All analyses were performed using Genstat 5, Release 4.1 for Windows (Lawes Agricultural Trust, UK).

7.3 RESULTS

7.3.1 CANOPY RAINFALL INTERCEPTION

This section examines rainfall interception by the tree canopies during the maize and bean cropping seasons. In agreement with Darnhofer *et al.* (1989), rainfall interception was highly variable between individual events; thus in all three seasons examined, there were events when rainfall totals under the tree canopies were greater and less than those recorded in the open. Figure 7.2 shows percentage differences between seasonal rainfall totals under the tree canopies and in the open for the three cropping seasons when measurements were made. Although there were small differences between the northern and southern sides of the trees during the 1996/97 short rains, rainfall totals under the tree canopies were comparable to the incident values shown in Table 7.4. Rainfall was approximately 12 % lower under the trees than in the open during the 1997 long rainy season and 4 % lower during the 1997/98 short rains, again with small differences between the north and south sides of the canopies. Data for one major rain event during the 1997/98 short rains (14 January 1998) were lost because gauges overflowed. The small differences between the rainfall receipts beneath the tree canopies and in the open during the 1996/97 short growing season were probably a reflection of the low canopy density at a time when the trees were still relatively small. However, it is not clear why interception was lower during the 1997/98 short rains than during the 1997 long rains as leaf area was greater in *C. megalocarpus* during the former season and similar during both seasons in *M. volkensii* (Figure 4.5). A possible explanation is the slightly greater mean daily rainfall intensity during the 1997/98 short growing season; thus rainfall occurred at an average intensity of 6.4 mm d^{-1} on 49 days during the 1997 long rains as compared to 7.9 mm d^{-1} on 77 days during the 1997/98 short rains.

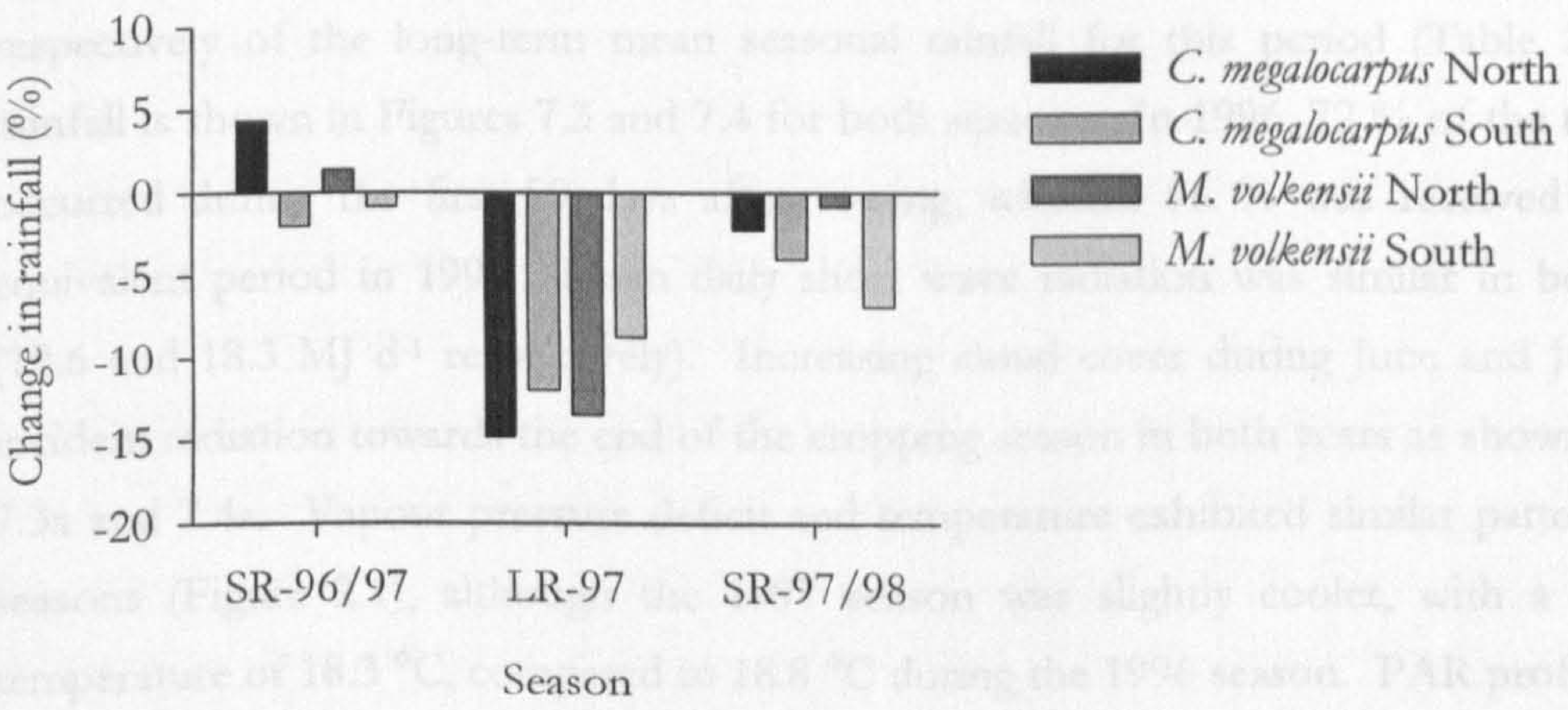


Figure 7.2. Percentage difference between total seasonal rainfall under the tree canopies to the north and south of the tree rows and incident rainfall during the 1996/97 short rains (SR-97/97), 1997 long rains (LR-97) and 1997/98 short rains (SR-97/98).

Analysis of wind direction during hours when rain fell showed that easterly winds prevailed in all four seasons, the modal direction being 90-120°, with only a small proportion of rain falling when wind direction was between 150-360°. The orientation of the tree rows parallel to the prevailing wind accounted for the small difference in rainfall between the two sides of the tree canopy. Split-plot analysis of variance of seasonal total rainfall on the northern and southern sides of the trees (Treatment: side*species*season, Blocks: replicate/plot/side/season) demonstrated significant seasonal effects (p=<0.001) but no significant effect of side-of-tree row or side*season interaction. Over the three cropping seasons examined, the tree canopies intercepted only 5 % of rainfall, some of which may subsequently have reached the ground by stem flow (Wallace, 1996).

Table 7.4. Total rainfall (mm) beneath the tree canopies and in the open during three cropping seasons (values include two days prior to sowing except during the 1996/97 short rains when gauges were not installed until five days after sowing).

Season	*C. megalocarpus*	*M. volkensii*	Open
1996/97 short rains	144.9 ± 5.1	143.6 ± 3.6	143.2
1997 long rains	276.5 ± 11.5	283.9 ± 9.0	319.3
1997/98 short rains	665.9 ± 17.3	660.8 ± 15.6	687.5

7.3.2 MAIZE CROPPING SEASONS (LONG RAINS)

This section describes available soil water content, PAR receipts and crop yields during both maize cropping seasons. Total rainfall during the 1996 and 1997 long growing seasons (defined here as the period between 1 March-31 July) was 223 and 316 mm, 62 and 88 % respectively of the long-term mean seasonal rainfall for this period (Table 2.2). Daily rainfall is shown in Figures 7.3 and 7.4 for both seasons. In 1996, 72 % of the total rainfall occurred during the first 50 days after sowing, whereas 96 % was received during the equivalent period in 1997. Mean daily short wave radiation was similar in both seasons (18.6 and 18.3 MJ d^{-1} respectively). Increasing cloud cover during June and July reduced incident radiation towards the end of the cropping season in both years as shown in Figures 7.3a and 7.4a. Vapour pressure deficit and temperature exhibited similar patterns in both seasons (Figure 2.1), although the 1997 season was slightly cooler, with a daily mean temperature of 18.3 °C, compared to 18.8 °C during the 1996 season. PAR profiles and soil moisture in the experimental plots are described in Sections 7.3.2.1 and 7.3.2.2, while crop yields in the agroforestry and sole crop treatments are presented in Section 7.3.2.3.

7.3.2.1 Available soil water

1996 long rains

Figure 7.3 shows mean values for available soil water content on the northern side of the plots. The seasonal means were tested for control effects (tree *vs.* non-tree plots) by Anova (Treatments: control/treatment, Blocks: replicate). Soil water contents were significantly lower in the agroforestry treatments than in the sole crops (p=0.038) and were consistently ordered throughout the season. Thus, among the agroforestry treatments, seasonal mean available soil water content was greatest for *C. megalocarpus* (80 % of that in sole maize), followed sequentially by *S. spectabilis* (71 %), *G. sepium* (62 %) and *M. volkensii*, in which the equivalent value was 54 % of that in sole maize.

The gradients for the correlation between available soil water and distance from the tree rows (defined here as "slope") indicate the effects of water uptake by the trees, which resulted in positive slopes being obtained for most seasons (Figure 7.3c). The slopes increased after rainfall in all treatments before levelling off. The slopes for *S. spectabilis* declined most sharply during the early part of the season, but were similar to *C. megalocarpus* during the later stages; the steeper slopes and higher soil water contents are indicative of the less extensive rooting system and lower transpiration rates relative to *G. sepium* and *M. volkensii*. The average slope for *M. volkensii* was close to zero for most of the season, with a maximum difference in available soil water between the tree row and the edge of the plot of only 16 mm. Anova showed that there were no significant differences between treatments containing exotic and indigenous trees, or between *C. megalocarpus* and *M. volkensii* or between *S. spectabilis* and *G. sepium* with regard to seasonal mean soil water content or the average slope of soil water content with distance from the tree rows.

1997 long rains

The situation was less clear during the 1997 long rains than in 1996. Plots containing *M. volkensii* consistently had the lowest available soil water content, followed by *G. sepium* and *S. spectabilis* (Figure 7.4). The values for sole maize were comparable to those for the *C. megalocarpus* treatment between ~10 and 50 days after sowing, but were higher at other times. This effect resulted partly from the low leaf area of *C. megalocarpus* at the beginning of the season, and its relatively low transpiration rate (Figure 5.22). There was no significant difference in seasonal mean available water content between the agroforestry and sole crop treatments (p=0.16), largely because of the high variance for the sole maize treatment, in which the values ranged from 51.8 mm in Replicate 3 to 98.7 mm in Replicate 4. However, when expressed as a percentage of the corresponding value for sole maize, mean available water content was 93 % in the *C. megalocarpus* treatment, 81 % for *S. spectabilis* and *G. sepium*, and 66 % for *M. volkensii*. There were no significant differences between treatments containing the exotic and indigenous tree species, *S. spectabilis* and *G. sepium*, but water availability was 41 % greater in the *C. megalocarpus* system than in the *M. volkensii* treatment (p=0.03). The slopes for the correlations between available soil water and location within plots were generally greater than in 1996, but were much closer to zero at the beginning of the season, possibly reflecting low tree root activity during the preceding 1996/97 short rains, when rainfall was 45 % of the long term average. The slopes were greatest for *S. spectabilis* and smallest in *G. sepium* for much of the season, although variance between replicates was generally high. There were no significant effects of geographic origin (indigenous *vs.* exotic) or significant differences between the two exotic species or the two indigenous species in the slopes of the correlations for available soil water.

Rainfall interception differed little between the northern and southern sides of the *C. megalocarpus* and *M. volkensii* tree rows during the 1997 long rains (Figure 7.2), although soil water contents were consistently higher on the southern side of both treatments (Figure 7.5). These differences reflect the higher radiation receipts on the northern sides of the tree rows (Figure 7.6). Jackson and Wallace (1999) showed that the mean rate of soil evaporation during two long growing seasons at Machakos Field Station was 24 % lower under *Grevillea robusta* than from bare soil, whereas soil evaporation was reduced by only 8 % beneath the maize canopy. Split-plot Anova (Treatment: side*treatment, Blocks:

replicate/treatment/side) confirmed these results by showing that available soil moisture content was significantly greater on the southern side of the tree rows ($p<0.001$) and 34 % greater in the *C. megalocarpus* than *M. volkensii* treatment ($p=0.037$); thus seasonal mean available soil water contents were 11 and 16 mm greater on the southern as opposed to the northern side of the tree rows in the *C. megalocarpus* and *M. volkensii* treatments. The slopes for the relationship between available soil water and distance from the tree rows show that, although there was substantial variance, the tendency was for positive slopes to be obtained to the north and negative slopes to the south of the tree rows. However, statistical analysis showed that the seasonal mean slopes for the relationship between available soil moisture and location did not differ significantly between the side of the tree row or treatments.

The decrease in mean available soil water content during the season at locations 2 and 4 m from trees on both sides of the tree rows was c. 4 mm greater under *C. megalocarpus* than in the *M. volkensii* treatment although the difference was not significant ($p=0.295$). The model prediction that transpiration was 26 % higher in *M. volkensii* than in *C. megalocarpus* (Table 5.10) is therefore likely to have resulted either from greater extraction from soil horizons below 1.1 m or from relative reductions in crop transpiration and/or soil evaporation in this treatment. Of these, the most important factor is likely to have been a reduction in crop transpiration, given that crop yields were significantly lower in treatments containing *M. volkensii* ($p=0.008$, cf. Section 7.3.2.3).

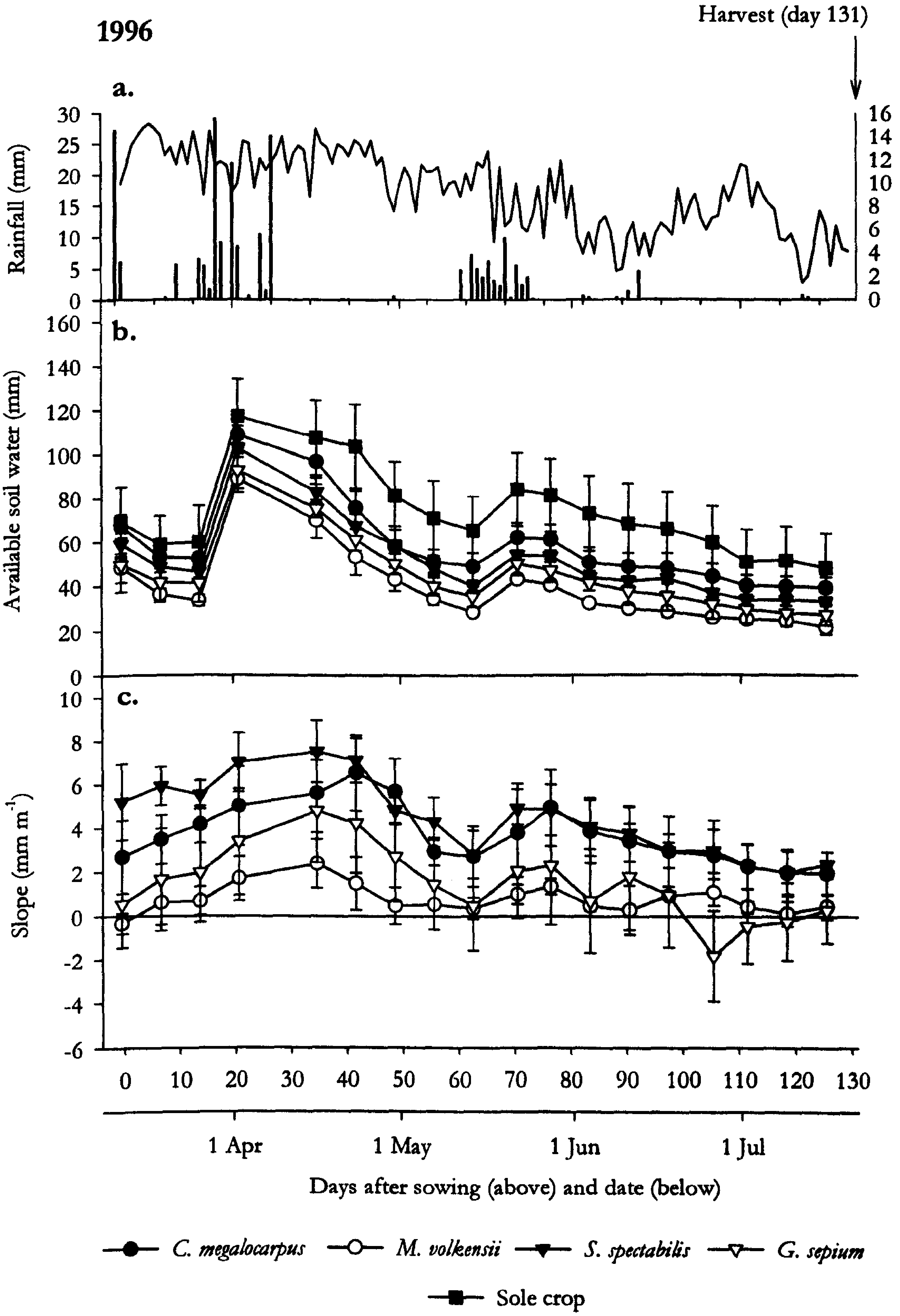


Figure 7.3. a) daily total rainfall (bars) and PAR receipts (line) during the 1996 long rains; b) available soil water content (±SE) to a depth of 1.1 m; c) slope (±SE) for the correlation between available soil water content and distance from the tree row.

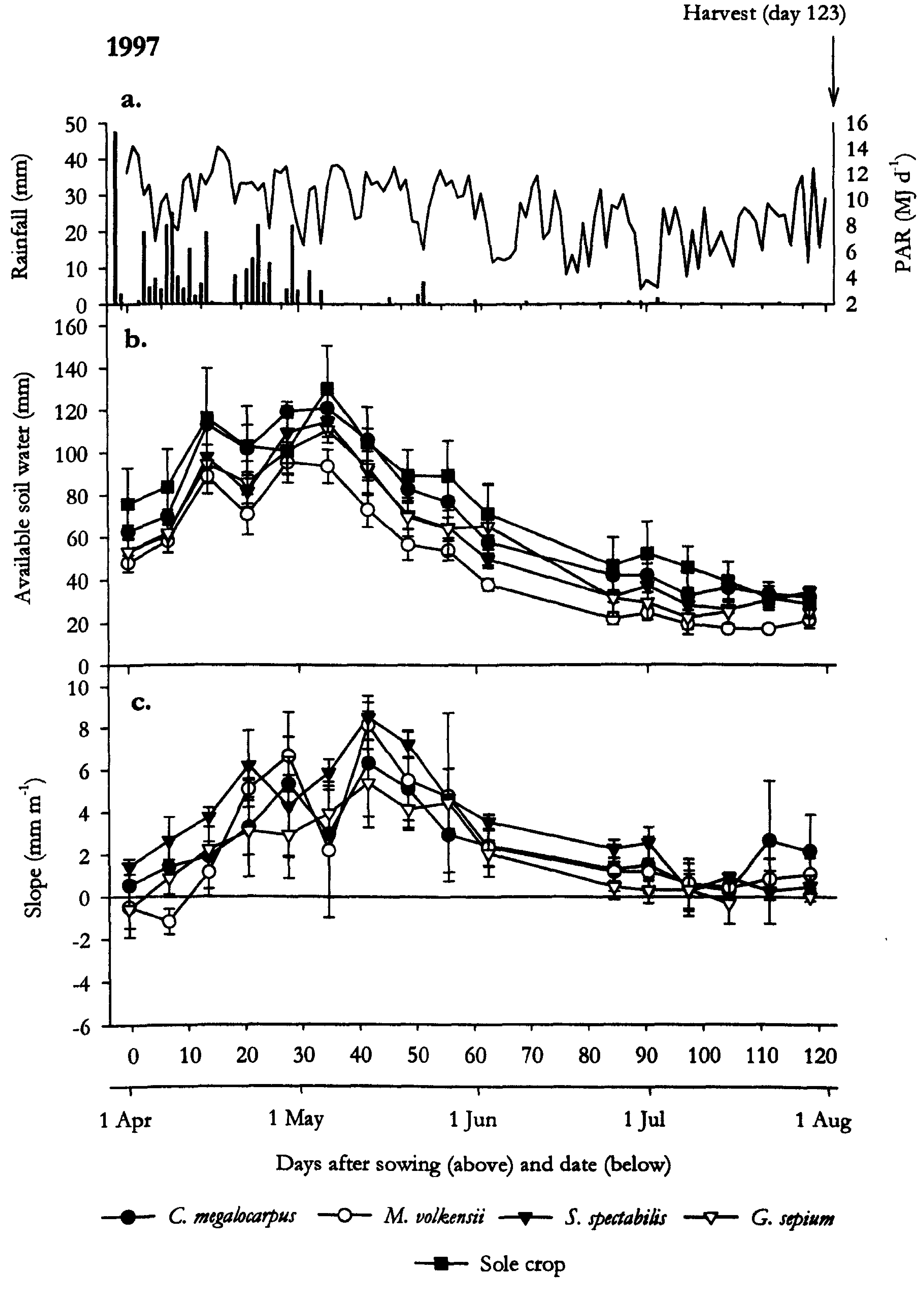


Figure 7.4. a) daily total rainfall (bars) and PAR receipts (line) during the 1997 long rains; b) available soil water content (±SE) to a depth of 1.1 m; c) slope (±SE) for the correlation between available soil water content and distance from the tree row.

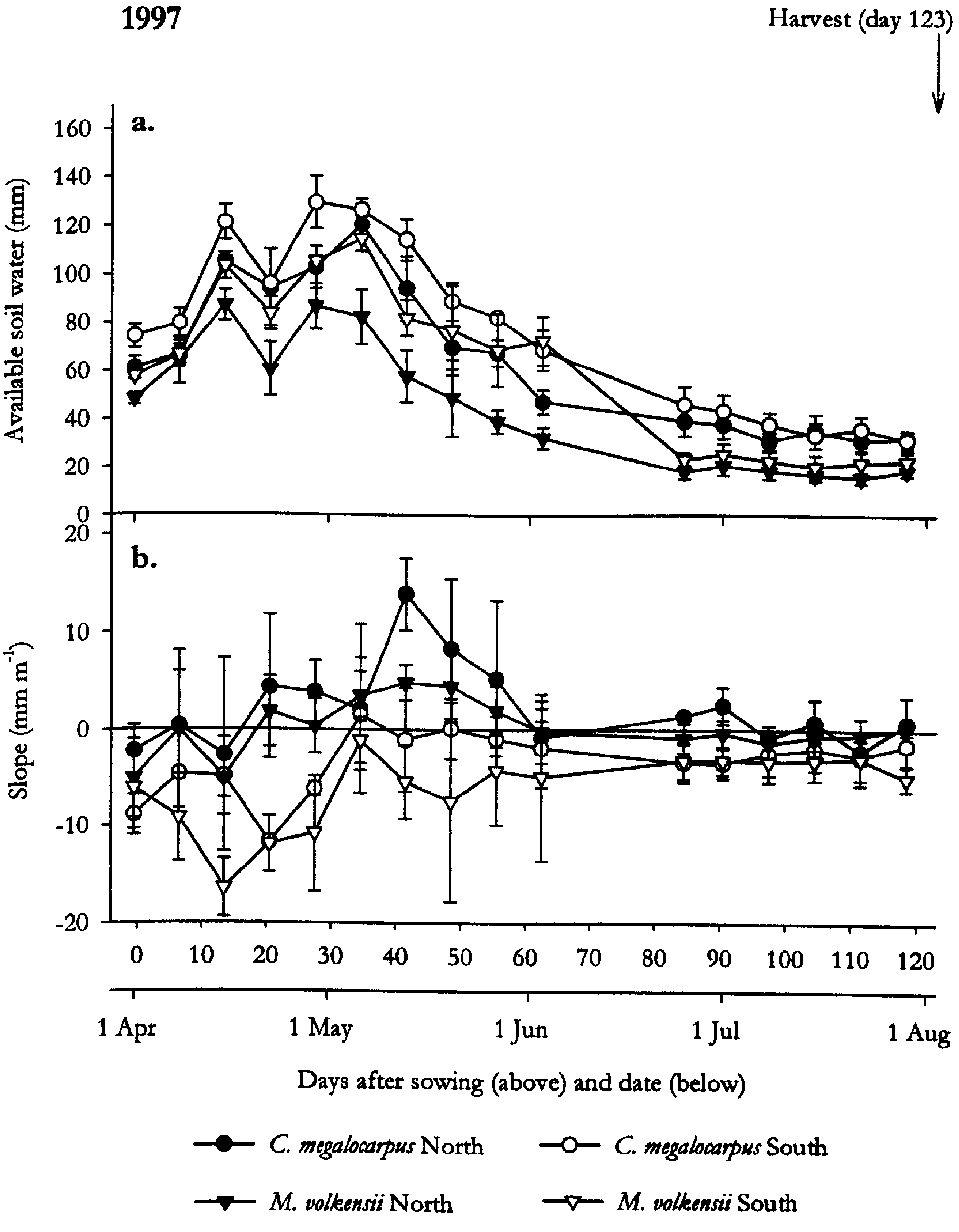


Figure 7.5. a) available soil water content (±SE) to a depth of 1.1 m on the northern and southern sides of the tree rows in the *M. volkensii* and *C. megalocarpus* treatments during the 1997 long rains; b) Slopes (±SE) for the correlations between available soil water content and distance from the tree row.

7.3.2.2 Incident PAR

Daily mean PAR receipts and seasonal patterns were comparable in both seasons (Figures 7.3 and 7.4). PAR transects across the *C. megalocarpus* and *M. volkensii* plots calculated using MAETEST for the 1997 long growing season are shown in Figure 7.6. The lower PAR values to the south of the tree rows reflect the sun's position to the north of the site during the period between approximately five days before the spring equinox (21 March) and five days after the autumn equinox (22 September). The reduced radiation to the north of the tree rows relative to the incident level is attributable to a decrease in diffuse radiation receipts caused because the trees obscured a fraction of the sky, rather than resulting from shading from direct light. The greater horizontal extent of the PAR reduction on the southern side of the *M. volkensii* plots reflects their larger canopies.

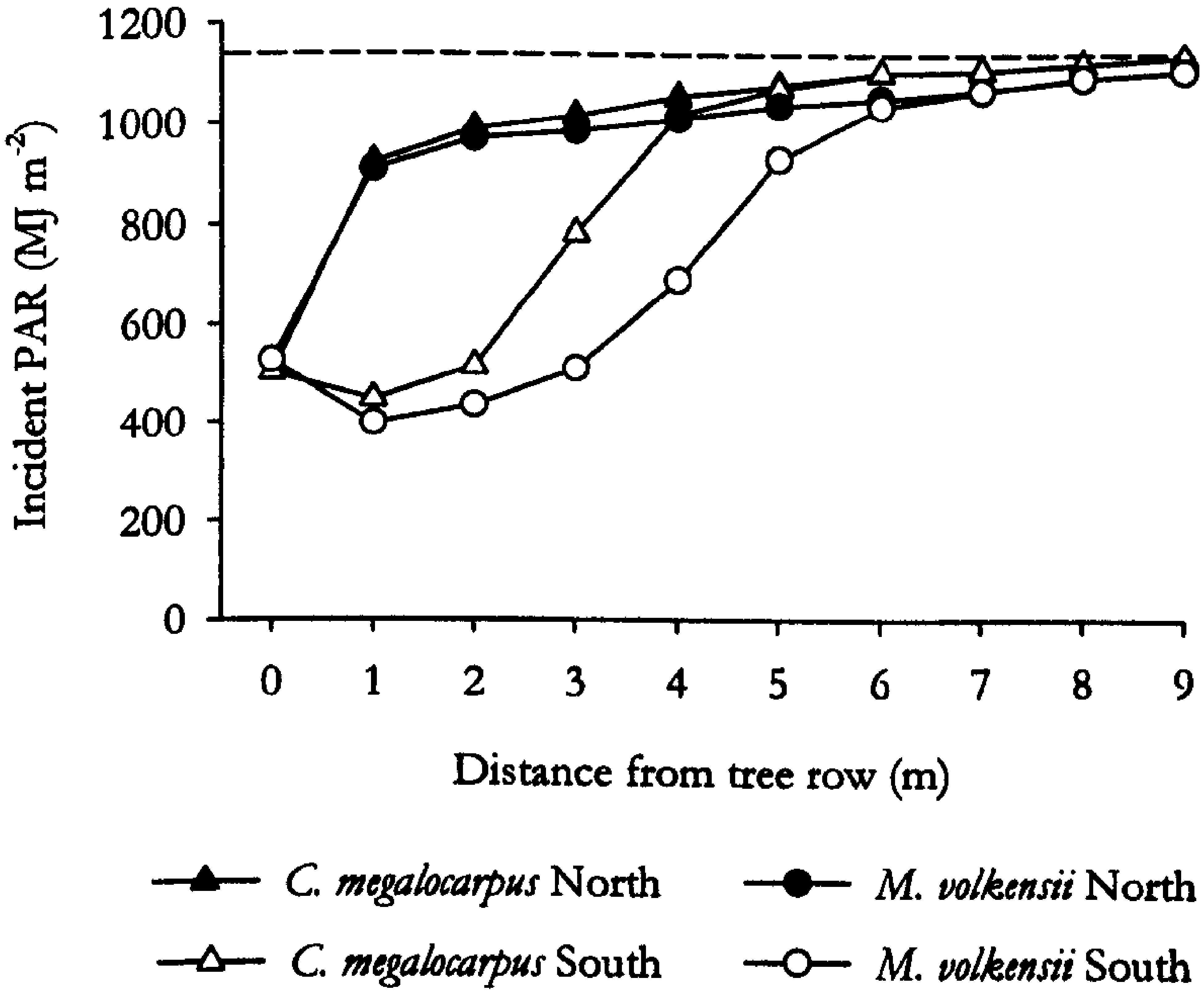


Figure 7.6. Total seasonal PAR receipts along a north-south transect across plots containing *C. megalocarpus* and *M. volkensii* trees during the 1997 long rains. The estimates were obtained using the MAESTEST program. The dashed line represents PAR in the open.

Table 7.5 shows the percentage of incident PAR calculated using MAETEST reaching understorey crops in different areas of the *C. megalocarpus* and *M. volkensii* treatments. The largest reductions were close to the trees on the southern side of the plots, although reductions close to the trees on the northern side of the tree rows were also considerable. In the outer halves the plots, PAR receipts approached those obtained in the open.

Table 7.5. PAR incident on the understorey crops on the northern and southern side of the tree rows expressed as a percentage of that in the open during the 1997 long rains.

	North of tree row		South of tree row	
Species	0-4.5 m	4.5-9.0 m	0-4.5 m	4.5-9.0 m
C. megalocarpus	79	97	57	97
M. volkensii	77	94	45	92

7.3.2.3 Maize crop yields

Figure 7.7 shows total above-ground dry weight and grain dry weight at final harvest for crops growing on both sides of the tree rows during the 1996 and 1997 long rains. The grain yields are comparable with those reported by Stewart (1988) for Katumani composite grown under high level management and at optimum planting densities (1 t ha^{-1} with 200 mm of rainfall, rising to 3 t ha^{-1} with 300 mm). Lott *et al.* (2000b) reported lower grain yields for a *Grevillea robusta* agroforestry system at an adjacent site on sloping land, although the stocking density of the trees was higher and the soil was both shallower and more sandy. Grain yields for sole maize were 66 % greater in 1997 than 1996 ($p<0.001$), when rainfall was 93 mm lower. No significant difference between the northern and southern sides of the tree rows was apparent in either year despite the higher soil water content and reduced PAR receipts to the south of the *C. megalocarpus* and *M. volkensii* tree rows during the 1997 short rains. Table 7.6 shows grain yields for each treatment expressed as a percentage of those for sole maize. In both years, grain yields were greatest in sole maize, followed by *C. megalocarpus*, *G. sepium*, *S. spectabilis* and *M. volkensii*. This sequence relates closely to the ranking of water availability in both 1996 (Figure 7.3) and 1997 (Figure 7.4), although it should be remembered that soil moisture measurements only provide "snapshot" estimates for the dynamic system linking crop yield and water availability, in which negative feedback occurs between two important factors. Firstly, under conditions where water is the primary factor limiting growth, drought limits plant size; secondly, smaller plants are likely to transpire less, so depleting available soil water more slowly than the larger plants produced in wetter areas. The resulting negative feedback may be expected to decrease the range of soil moisture contents obtained across a cline of water availability, thereby weakening correlations between crop yield and available water.

Table 7.6. Grain yields for maize in the agroforestry treatments expressed as a percentage of those for sole maize during the 1996 and 1997 long rains

	Season	
Treatment	1996 long rains	1997 long rains
C. megalocarpus	70.4	47.9
M. volkensii	27.8	29.6
S. spectabilis	44.5	37.8
G. sepium	57.9	46.2

Figures 7.8 and 7.9 show total above-ground dry weight, grain dry weight and harvest index at maturity for each harvested row (6 m length) on either side of the tree rows during the 1996 and 1997 long growing seasons. The absence of significant differences between the northern and southern sides of the tree rows in the agroforestry treatments suggests that the lower water availability to the north of the trees (Figure 7.5) and the lower PAR levels to the south in the *C. megalocarpus* and *M. volkensii* treatments (Figure 7.6) limited crop yield. However, nitrogen deficiency may also have contributed in 1997 (cf. Section 7.3.2.5). Figure 7.10 shows the numbers of plants and cobs per row in both years. The slopes for the correlation between cob number and distance from the tree row were greater than those for plant number in all agroforestry treatments, indicating the greater sensitivity of reproductive growth to drought stress. There was again no significant difference between the northern and southern sides of the tree rows. The results of the statistical analyses are presented below.

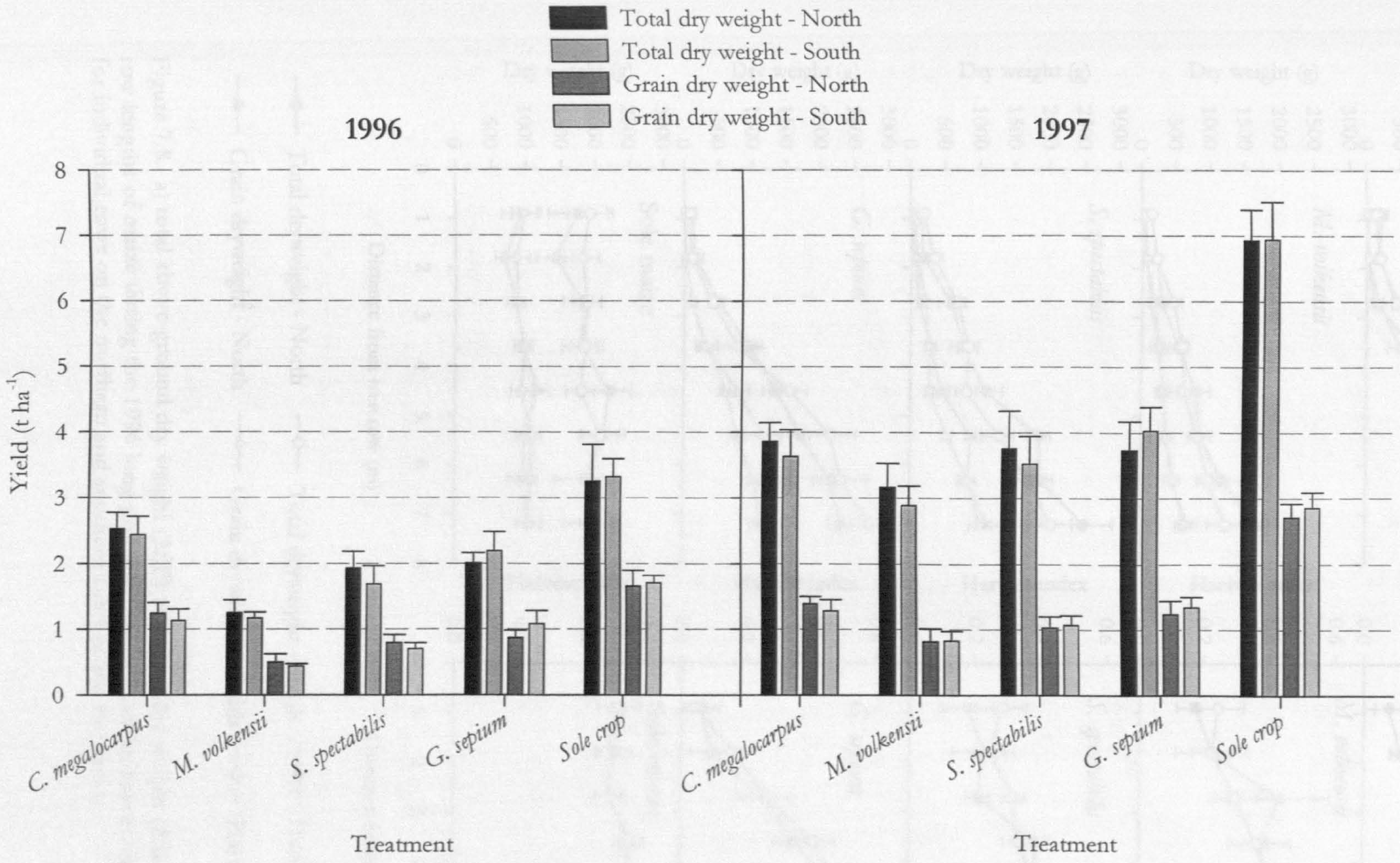


Figure 7.7. Total above-ground dry weight (±SE) and grain dry weight (±SE) at final harvest on the northern and southern sides of the tree rows during the 1996 and 1997 long rains.

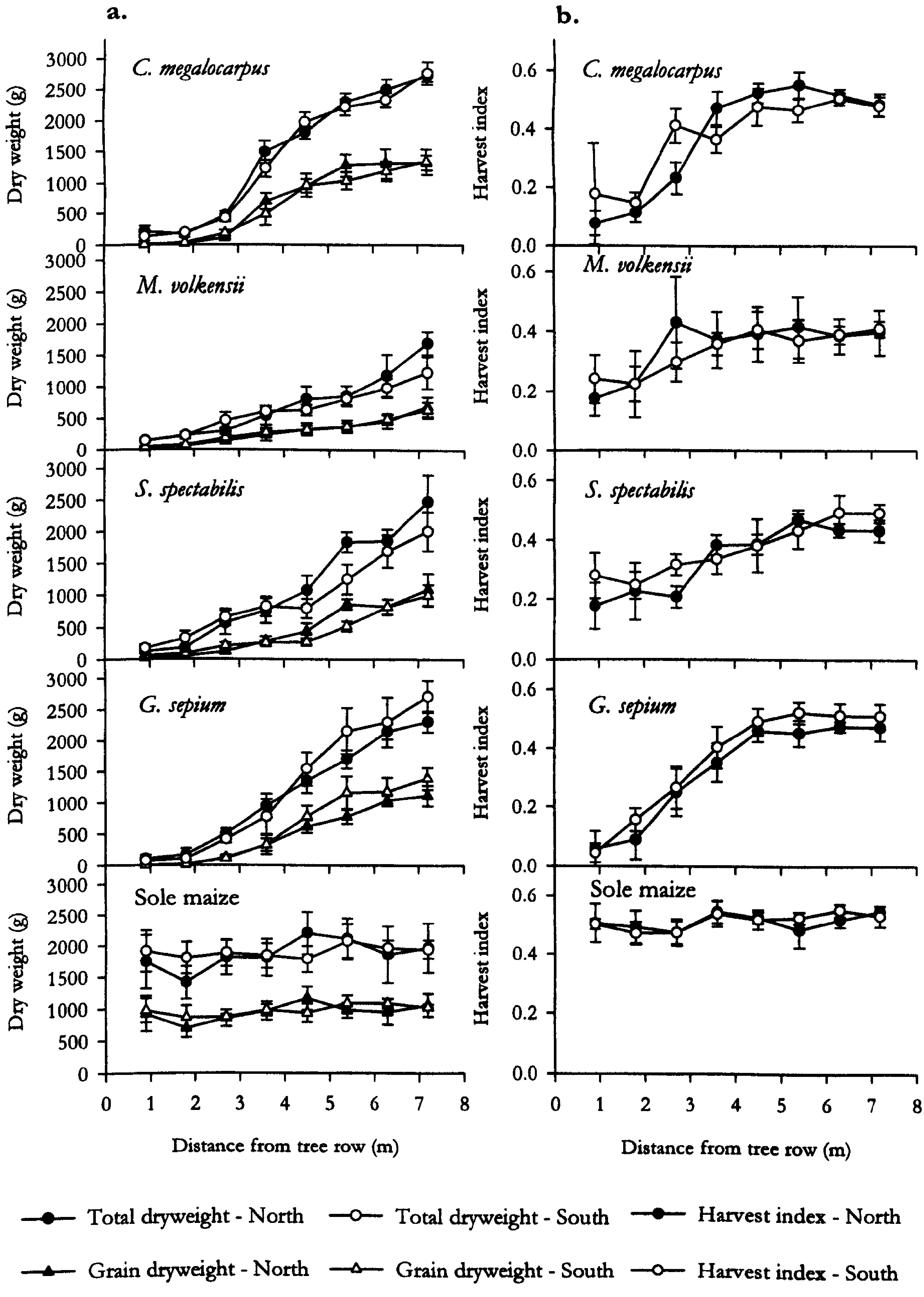


Figure 7.8. a) total above-ground dry weight (±SE) and grain dry weight (±SE) for 6 m row lengths of maize during the 1996 long growing season; b) mean harvest index (±SE) for individual rows on the northern and southern sides of the tree rows.

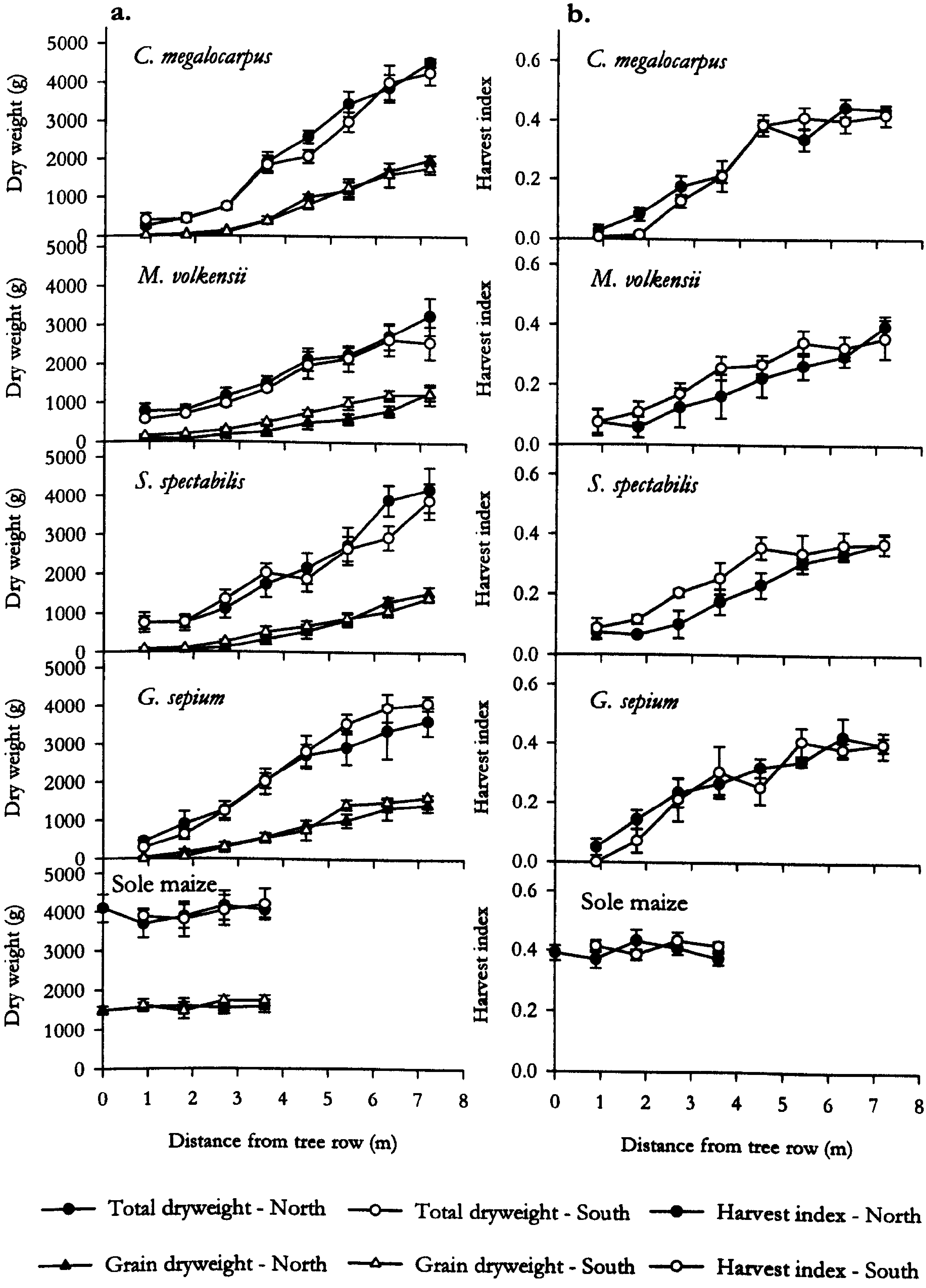


Figure 7.9 a) total above-ground dry weight (±SE) and grain dry weight (±SE) for 6 m row lengths of maize during the 1997 long growing season; b) mean harvest index (±SE) for individual rows on the northern and southern sides of the tree rows.

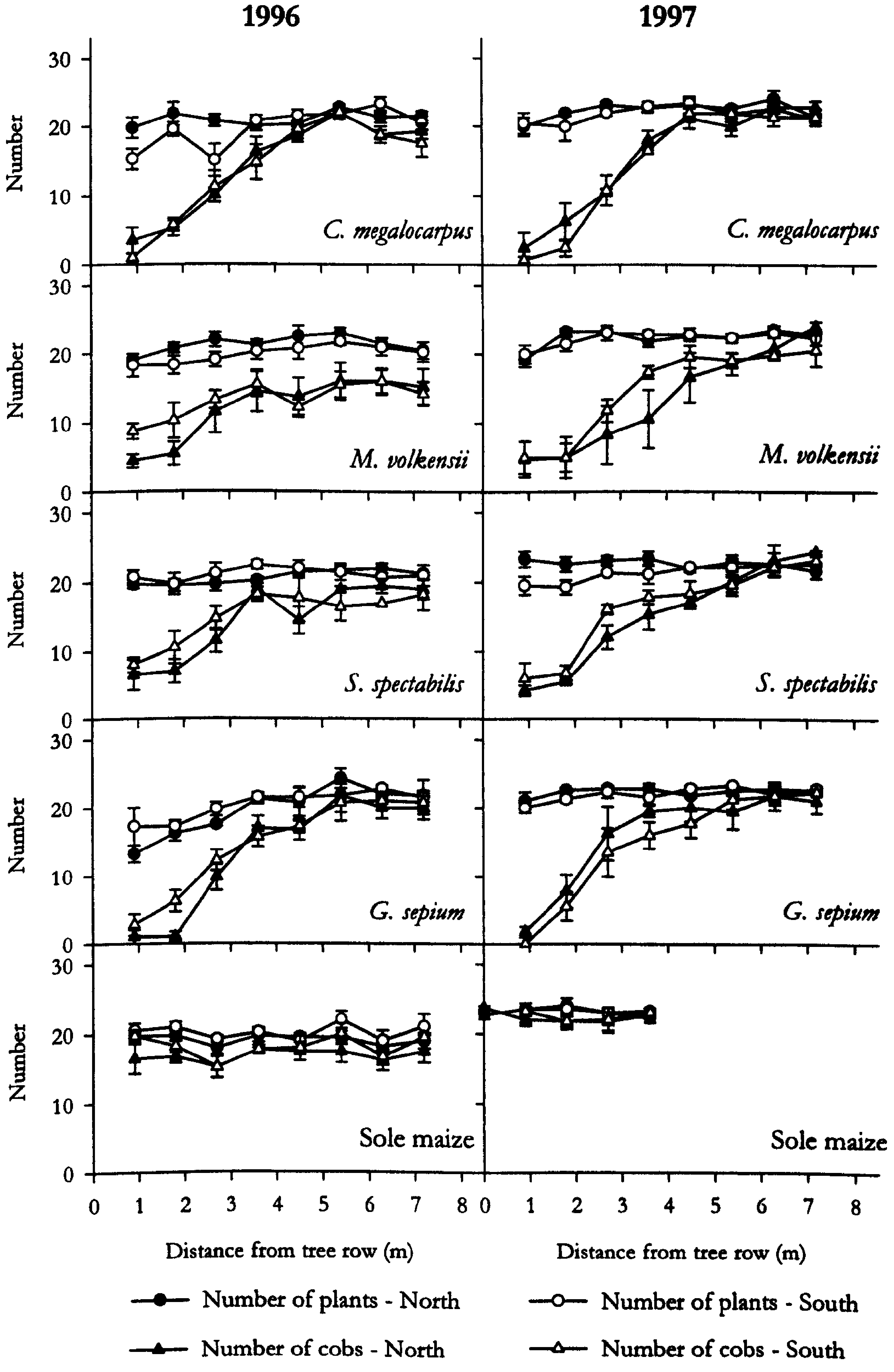


Figure 7.10. Plant and cob numbers (±SE) for 6 m row lengths harvested on the northern and southern sides of the tree rows and in sole maize in 1996 and 1997.

Effects of trees on crop yield variates

Several components of maize yield were analysed using variates determined for the northern and southern sides of each plot; these included total above-ground dry weight, grain dry weight, harvest index and plant and cob numbers. In addition, the slopes for the correlations between several variates and distance from the trees were established by linear regression analysis and analysed in the same way; these included total above-ground dry weight, grain dry weight, plant number and harvest index. Tables showing the values for these variates for each side of the plot and season are presented in Appendix 7.

Output from split-plot analysis of variance (Treatments: side*control/treatment*season, Blocks: replicate/plot/side/season) combining both seasons, and for separate seasons where significant interaction terms were detected, is shown in Table 7.7. The control factor has two levels denoting whether the plot contained trees. Analysis of total above-ground dry weight showed a significant season*control interaction ($p<0.001$), reflecting the smaller dry weight difference between 1996 and 1997 in the tree treatments than in the sole maize treatment. Total above-ground dry weight for sole maize was 111 % greater during the wetter 1997 season ($p<0.001$), whereas yields in the agroforestry treatments were on average only 88 % higher ($p<0.001$). The difference was probably a result of higher tree leaf area although Odhiambo, *et al.* (in press) measured lower root length densities in 1997 in the *Grevillea robusta* and *G. sepium* treatments. This is thought to have resulted from the low rainfall during the months preceding the 1997 long rains (158 mm in 6 months). The fact that the reduced root length density did not lessen the impact on crops suggests that the trees were able to withdraw sufficient water with fewer fine roots resulting in relatively lower crop yields than sole cropping but higher absolute yield than in 1996. As the season*control interaction may have concealed significant factor effects at higher levels in the table, the two seasons were analysed separately. The results for both seasons showed significant control effects; the significant control*treatment interaction in 1996 occurred because total above-ground dry weights varied widely between the various agroforestry treatments. Analysis of grain yield provided similar results, with highly significant control and season effects and a season*control interaction being obtained ($p<0.001$). The grain yield for sole maize was 66 % higher in 1997 than in 1996, and the corresponding values for the agroforestry treatments were on average 34 % greater. Analysis of the 1996 data again revealed a significant control*treatment interaction ($p=0.019$), showing that grain yield differed widely between the various agroforestry treatments.

Harvest index showed highly significant control and seasonal effects ($p<0.001$), although the control*treatment interaction was not significant. Averaged over all treatments, harvest index was 40 % greater in 1996, even though yields were lower than in 1997. When the data for both seasons were combined, harvest index was 35 % lower in the agroforestry treatments than in sole maize. Lott *et al.* (2000b) reported that harvest index in Katumani composite maize is positively correlated with grain yield and rainfall, suggesting that the higher harvest index obtained in 1996 in the present study is likely to have been attributable to the occurrence of significant rainfall between 60 and 75 days after sowing (Figure 7.3), during the reproductive and early grain filling phases of growth. Lower water availability *per se* did not increase harvest index, as shown by the lower values obtained for the agroforestry treatments.

Plant number did not differ significantly between the sole maize and agroforestry treatments (Table 7.7), indicating that plant survival was not an important determinant of yield. However, averaged over all treatments, 9 % more plants survived to maturity in 1997 (p<0.001). The significant season*control interaction resulted from the absence of significant treatment effects on plant number in 1996 and the presence of 5 % more plants in the sole crop treatment (p=0.001) in 1997. Overall, cob number at maturity was 13 % greater in 1997 (p<0.001). The significant season*control interaction (p=0.005) reflects the observation that cob number was 21 % lower in the agroforestry treatments than in sole maize in 1996 and 33 % lower in 1997.

The slopes of the correlations with distance from the trees showed significant control effects for all variates examined and significant control*treatment interactions when the pooled data for both years were analysed (Table 7.7). As the occurrence of significant high level interactions for all variates examined indicated that the responses in the agroforestry and sole crop treatments differed between seasons, these were analysed separately. The analyses showed that there were significant control effects and control*treatment interactions for all variates except the slope of plant number in 1997. Thus, the tree rows significantly affected crop growth, resulting in steeper slopes in the agroforestry treatments (cf. Figures 7.8-7.10) this shows the effects of tree water extraction and alteration in incident PAR on crop growth. Further comparisons of the agroforestry treatments are presented below.

Effects of geographic origin of the tree species on crop yield variates

The two exotic tree species, *S. spectabilis* and *G. sepium*, were compared with the indigenous species, *C. megalocarpus* and *M. volkensii*, by setting origin as a main factor and determining treatment effects nested within origin effects (Blocks: replicate/plot/side/season, Treatments: side*origin/treatment*season). There were no significant origin effects on any of the variates (Table 7.8), but there were significant season*origin*treatment, side*season*origin and season*origin interactions. Further analysis of the separate seasons provided no evidence that there was any difference between the effects of indigenous and exotic tree species on maize yield. Further analysis is presented for the two indigenous and exotic species below.

Effects of M. volkensii and C. megalocarpus on crop yield variates

The treatments containing indigenous tree species were compared using split-plot Anova (Blocks: replicate/plot/side/season; Treatments: side*treatment*season). Analysis of above-ground dry weight at final harvest demonstrated significant effects of treatment and season, but no significant side-of-row effect or interactions (Table 7.10). Above-ground crop dry weight at maturity was 47 % greater under *C. megalocarpus* than in the *M. volkensii* treatment (p=0.008), and was 83 % higher in 1997 than in 1996 across both treatments (p<0.001). The yield increase between 1996 and 1997 despite the larger size of the trees is a result of the higher rainfall combined with the lower tree rooting densities as outlined above. The season*treatment interaction approached significance (p=0.076) as above-ground dry weight was 106 % greater under *C. megalocarpus* than in the *M. volkensii* treatment in 1996, but was only 24 % greater in 1997. These observations suggest that the difference between treatments was decreased in wetter years. The relatively high leaf area of *C. megalocarpus* and the lower leaf area of *M. volkensii* when rainfall was abundant during the 1997/98 short rains (Figure 4.5) suggest that adaptation to the local climate may increase competition with understorey crops.

The lack of significant side-of-row effects despite higher PAR receipts on the northern side of the tree rows (Figure 7.6) and higher available soil water and leaf nitrogen contents on the southern side of the tree rows in 1997 (Sections 7.3.2.1 and 1.2.2.5) may have resulted from the occurrence of differing growth-limiting factors with similar effects on crop performance either side of the tree rows. In 1996, there was no evidence of nitrogen deficiency and the smaller tree canopies would have been expected to have had less effect on soil water content and PAR incident upon the understorey crops; water limitation may therefore have been the most important limiting factor on both sides of the tree rows. In 1997, the greater foliar nitrogen content of crops on the southern side of the tree rows reflected the higher soil water content, suggesting that these plants were light-limited relative to those grown on the northern side of the tree rows, which were predominantly water-limited.

Table 7.7. F-probabilities from Anova for control, side-of-plot, and season effects on maize yield parameters. * and ** denote significance at $p<0.05$ and $p<0.01$.

		Above-ground dry weight	Grain dry weight	Plant number	Cob number	Harvest index	Slope for total dry weight	Slope for grain dry weight	Slope for plant number	Slope for harvest index
1996 and 1997 combined	Replicate*plot stratum									
	Control	<0.001**	<0.001**	0.553	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**
	Control*treatment	0.169	0.056	0.695	0.423	0.737	<0.001**	<0.001**	0.016*	0.015*
	Replicate*plot*side stratum									
	Side	0.647	0.711	0.131	0.264	0.189	0.882	0.885	0.311	0.808
	Side*control	0.710	0.435	0.014*	0.686	0.845	0.387	0.351	0.847	0.511
	Side*control*treatment	0.651	0.393	0.153	0.398	0.525	0.102	0.200	0.459	0.708
	Replicate*plot*side*season stratum									
	Season	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	0.006**	0.448
	Side*season	0.783	0.675	0.476	0.476	0.962	0.292	0.429	0.517	0.362
	Season*control	<0.001**	<0.001**	0.006**	0.005**	0.93	<0.001**	0.011*	0.335	0.322
	Side*season*control	0.994	0.764	0.633	0.817	0.781	0.085	0.135	0.583	0.706
	Season*control*treatment	0.188	0.501	0.502	0.981	0.689	0.665	0.393	0.05*	0.031*
1996 only	Replicate*plot stratum									
	Control	<0.001**	<0.001**	0.156	0.004**	N/A	<0.001**	<0.001**	0.006**	<0.001**
	Control*treatment	0.035*	0.019*	0.528	0.441	N/A	<0.001**	<0.001**	0.014*	0.012*
	Replicate*plot*side stratum									
	Side	0.748	0.995	0.827	0.104	N/A	0.396	0.71	0.685	0.494
	Side*control	0.649	0.677	0.113	0.565	N/A	0.694	0.893	0.79	0.509
	Side*control*treatment	0.632	0.333	0.119	0.67	N/A	0.245	0.318	0.015*	0.562
1997 only	Replicate*plot stratum									
	Control	<0.001**	<0.001**	0.001**	<0.001**	N/A	<0.001**	<0.001**	0.010**	<0.001**
	Control*treatment	0.449	0.208	0.716	0.815	N/A	0.004**	0.008**	0.867	0.045*
	Replicate*plot*side stratum									
	Side	0.683	0.553	0.092	0.936	N/A	0.648	0.577	0.196	0.621
	Side*control	0.815	0.406	0.201	0.961	N/A	0.131	0.126	0.574	0.749
	Side*control*treatment	0.805	0.720	0.441	0.412	N/A	0.185	0.376	0.308	0.689

Table 7.8. F-probabilities obtained from Anova for origin, side-of-plot and seasonal effects on maize yield parameters. * and ** denote significance at $p<0.05$ and $p<0.01$.

		Above-ground dry weight	Grain dry weight	Plant number	Cob number	Harvest index	Slope for total dry weight	Slope for grain dry weight	Slope for plant number	Slope for harvest index
1996 and 1997 combined	Replicate*plot stratum									
	Origin	0.386	0.66	0.720	0.294	0.961	0.313	0.575	0.321	0.681
	Origin*treatment	0.064	0.025*	0.601	0.596	0.609	<0.001**	0.001**	<0.001**	0.011*
	Replicate*plot*side stratum									
	Side	0.599	0.985	0.013*	0.450	0.217	0.630	0.778	0.268	0.618
	Side*origin	0.607	0.266	0.043*	0.864	0.355	0.551	0.396	0.305	0.561
	Side*origin*treatment	0.581	0.464	0.366	0.307	0.529	0.088	0.169	0.341	0.618
	Replicate*plot*side*season stratum									
	Season	<0.001**	<0.001**	<0.001**	0.052	<0.001**	<0.001**	<0.001**	<0.001**	0.263
	Side*season	0.804	0.817	0.633	0.611	0.941	0.853	0.974	0.307	0.325
	Season*origin	0.221	0.605	0.700	0.868	0.515	0.448	0.114	0.136	0.032*
	Side*season*origin	0.591	0.958	0.022*	0.736	0.625	0.609	0.959	<0.001**	0.549
	Season*origin*treatment	0.197	0.387	0.255	0.937	0.673	0.472	0.620	0.01**	0.101
1996 only	Replicate*plot stratum									
	Origin	N/A	N/A	1.000	N/A	N/A	N/A	N/A	0.209	0.252
	Origin*treatment	N/A	N/A	0.356	N/A	N/A	N/A	N/A	0.006**	0.022*
	Replicate*plot*side stratum									
	Side	N/A	N/A	0.255	N/A	N/A	N/A	N/A	0.772	0.412
	Side*origin	N/A	N/A	0.007**	N/A	N/A	N/A	N/A	0.001**	0.499
	Side*origin*treatment	N/A	N/A	0.933	N/A	N/A	N/A	N/A	0.206	0.542
1997 only	Replicate*plot stratum									
	Origin	N/A	N/A	0.399	N/A	N/A	N/A	N/A	0.464	0.194
	Origin*treatment	N/A	N/A	0.712	N/A	N/A	N/A	N/A	0.825	0.009**
	Replicate*plot*side stratum									
	Side	N/A	N/A	0.053	N/A	N/A	N/A	N/A	0.132	0.697
	Side*origin	N/A	N/A	0.404	N/A	N/A	N/A	N/A	0.097	0.909
	Side*origin*treatment	N/A	N/A	0.406	N/A	N/A	N/A	N/A	0.484	0.317

Treatment effects on grain dry weight at final harvest were greater than those for total dry weight, as grain yield was 95 % greater under *C. megalocarpus* than in the *M. volkensii* treatment (*p*=0.008). Grain yield averaged over both treatments was 31 % greater in 1997 than in 1996 (*p*=0.008). There was no significant season*treatment interaction or side-of-row effect. Harvest index was not significantly affected either by the treatment or side of the tree row, but was 52 % greater overall during the relatively low rainfall 1996 season (*p*<0.001). The observation that harvest index was higher during the drier 1996 season, but increased with distance from the tree rows in both seasons suggests that harvest index was dependent on the timing rather than the quantity of rainfall. Plant number showed no significant treatment effect, although there were 4 % more plants on the less shaded northern side of the tree rows (*p*=0.004), and 8 % more plants during the wetter 1997 season (*p*=<0.001). There was no significant effect on cob numbers.

The slopes for the correlations between above-ground dry weight and distance from the tree rows did not differ significantly between the northern and southern sides of the tree rows but, when averaged across seasons, were significantly higher for *C. megalocarpus* than *M. volkensii* (*p*=0.006; Figures 7.8 and 7.9), reflecting the greater ability of the latter to extract water over substantial distances from the tree rows (cf. Figures 7.3 and 7.4). The slopes were significantly greater in 1997 (*p*<0.001) which, in view of the higher above-ground dry weight yields, suggests that the extraction of water was greater close to the trees than from the outer areas of the plots. The slopes for grain dry weight exhibited a similar pattern, being greater in *C. megalocarpus* than in *M. volkensii* (*p*=0.007) and in 1997 than in 1996 (*p*<0.001). The smaller increase in the slope for grain dry weight than for total dry weight between 1996 and 1997 provides an explanation for the 52 % greater harvest index in the former season. The slope for harvest index was 28 % higher in 1997 than in 1996 (*p*=0.039), reflecting the greater water availability towards the margins of the plots in 1997. There was no significant treatment effect on the relationship between plant number and distance from the tree row (Table 7.10).

Effects of S. spectabilis and G. sepium on crop yield variates

There were no significant treatment or side-of-row effects on either total above-ground or grain dry weight, although the values were respectively 93 and 36 % greater in 1997; mean plant number for both treatments was 7 % higher in 1997 (*p*=0.002). Harvest index was 41 % higher in 1996, but there was no significant seasonal effect on cob numbers. Analyses of crop yield variates in the *S. spectabilis* and *G. sepium* agroforestry treatments (Table 7.11) showed significant treatment effects only for the slope of plant number against distance from the tree rows; however, as the interaction term proved significant, the data for the two seasons were analysed separately. Significant treatment effects were not detected in either season.

The slope for the correlation between above-ground dry weight and distance from the tree row was 49 % greater in 1997 than in 1996; which, together with the higher total yields in 1997 demonstrates the same pattern as the results for the *C. megalocarpus* and *M. volkensii* treatments. The slopes for grain yield were 13 % greater in 1997 than in 1996 and, as for total above-ground dry weight, exhibited a significant side-of-row*species interaction (p=0.012), but no significant side-of-row or treatment effect.

Although the nitrogen contents of maize leaves were not measured in the *G. sepium* treatment, the absence of significant differences in crop yield between the *S. spectabilis* and *G. sepium* treatments suggests that nitrogen was not highly limiting in the *S. spectabilis* treatment as nitrogen fixation by *G. sepium* would be expected to increase soil nitrogen pools and reduce any crop deficiency. However, there is some controversy concerning the importance of nitrogen fixation in *G. sepium*. For instance, Liyanage, Danso and Jayasundara (1994) reported that this species can fix substantial quantities of nitrogen, while Heineman *et al.* (1997) observed that mulch from *G. sepium* improved soil fertility and maize yields at a nitrogen-limited site in western Kenya. However, in a modelling analysis of the soil nutrient balance in the East African Highlands, Shepherd *et al.* (1996) concluded that, although nitrogen levels were improved, the tree roots removed most of the fixed nitrogen and agroforestry systems did not significantly reduce nitrogen deficits unless a large proportion of the pruned biomass was returned to the soil.

7.3.2.4 Shade treatments

Seasonal rainfall under the shade nets and in the open is shown in Table 7.9. Seasonal rainfall under the nominal 25% shade (light shade) and 50 % shade (intense shade) treatments was 91 and 98 % respectively of that in the open in 1996, and 94 and 81 % in 1997. The substantial difference between years in rainfall in the nominal 50 % shade net treatment may have resulted from differences in the positioning of the rain gauges beneath the nets, which were prone to sag between the supporting poles.

Table 7.9. Rainfall beneath the shade nets during the 1996 and 1997 long growing seasons. Standard errors of the mean are shown.

Season	Open	light Shade	intense shade
1996 long rains	138 ± 4.5	125 ± 2.5	134 ± 9.2
1997 long rains	264 ± 2.3	248 ± 8.4	213 ± 9.8

Table 7.10. F-probabilities obtained from analysis of variance of season, side-of-row and treatment (*M. volkensii* and *C. megalocarpus*) effects on maize yield variates during both cropping seasons. * and ** denote significance at $p<0.05$ and $p<0.01$.

1996 and 1997	Above ground dry weight	Grain dry weight	Plant number	Cob number	Harvest index	Slope for total dry weight	Slope for grain dry weight	Slope for plant number	Slope for harvest index
Replicate*plot stratum									
Treatment	0.008**	0.008**	0.676	0.412	0.461	0.006**	0.007**	0.105	0.093
Replicate*plot*side stratum									
Side	0.562	0.548	0.004**	0.744	0.829	0.581	0.547	0.282	0.535
Side*treatment	0.973	0.698	0.61	0.286	0.635	0.858	0.986	0.515	0.748
Replicate*plot*side*season stratum									
Season	<0.001**	0.008**	<0.001**	0.083	<0.001**	<0.001**	<0.001**	0.019	0.039*
Side*season	0.567	0.856	0.162	0.884	0.764	0.806	0.951	0.004**	0.295
Season*treatment	0.076	0.223	0.764	0.814	0.908	0.277	0.865	0.096	0.371
Side*season*treatment	0.927	0.81	0.695	0.832	0.399	0.408	0.775	0.1	0.192
1996									
Replicate*plot stratum									
Treatment	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.072	N/A
Replicate*plot*side stratum									
Side	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.054	N/A
Side*treatment	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.243	N/A
1997									
Replicate*plot stratum									
Treatment	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.75	N/A
Replicate*plot*side stratum									
Side	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.911	N/A
Side*treatment	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.97	N/A

Table 7.11. F-probabilities obtained from analysis of variance of season, side-of-row and treatment (*S. spectabilis*/*G. sepium*) effects on maize yield variates during both cropping seasons. * and ** denote significance at $p<0.05$ and $p<0.01$.

1996 and 1997	Above ground dry weight	Grain dry weight	Plant number	Cob number	Harvest index	Slope for total dry weight	Slope for grain dry weight	Slope for plant number	Slope for harvest index
Replicate*plot stratum									
Treatment	0.525	0.333	0.381	0.499	0.784	0.156	0.153	0.035*	0.087
Replicate*plot*side stratum									
Side	0.991	0.167	0.698	0.341	0.133	0.854	0.49	0.896	0.939
Side*treatment	0.177	0.065	0.267	0.341	0.307	0.001**	0.012*	0.039*	0.273
Replicate*plot.side*season stratum									
Season	<0.001**	<0.001**	0.002**	0.289	<0.001**	<0.001**	0.007**	0.013*	0.424
Side*season	0.857	0.895	0.091	0.621	0.709	0.657	0.99	0.017*	0.774
Season*treatment	0.879	0.95	0.163	0.804	0.416	0.567	0.399	0.032*	0.056
Side*season*treatment	0.902	0.399	0.675	0.498	0.420	0.529	0.935	0.77	0.913
1996									
Replicate*plot stratum									
Treatment	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.061	N/A
Replicate*plot*side stratum									
Side	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.002**	N/A
Side*treatment	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.161	N/A
1997									
Replicate*plot stratum									
Treatment	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.54	N/A
Replicate*plot*side stratum									
Side	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.035*	N/A
Side*treatment	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.213	N/A

Figure 7.11 shows values for total above-ground dry weight at maturity for maize in both cropping seasons and grain yield in 1997. The yields were analysed by one way Anova using a split-plot blocking structure to account for the two seasons (Blocks: replicate/season Treatments: shade*season). As the shade treatments were not randomly positioned within plots due to their relatively small size, it was assumed that there were no systematic east-west trends across the plots for factors which might have affected maize growth. The analysis demonstrated a significant effect of the shade nets (*p*=0.016), but no significant seasonal effect (*p*=0.319) on total yield. The yields obtained under light shade were 74 and 99 % of those for the unshaded sole crop in 1996 and 1997 respectively; the corresponding values for intense shade were 69 and 65 %. The grain yield data for 1997 showed a significant effect of shade (*p*=0.002), with yield under light and intense shade being 50 and 35 % of that obtained from unshaded plants. The significant effect of shade seen in the shade net experiments was not apparent in response to the reduced radiation levels recorded on the southern side of the tree rows, although PAR was reduced to a similar extent (Figure 7.6). Table 7.5 shows that the modelled incident PAR receipts close to the trees on the southern side of the *C. megalocarpus* and *M. volkensii* rows were 57 and 45 % respectively of those in the open in 1997, whereas PAR levels in the nominal 25 and 50 % shade net treatments were 68 and 42 % of those in the open.

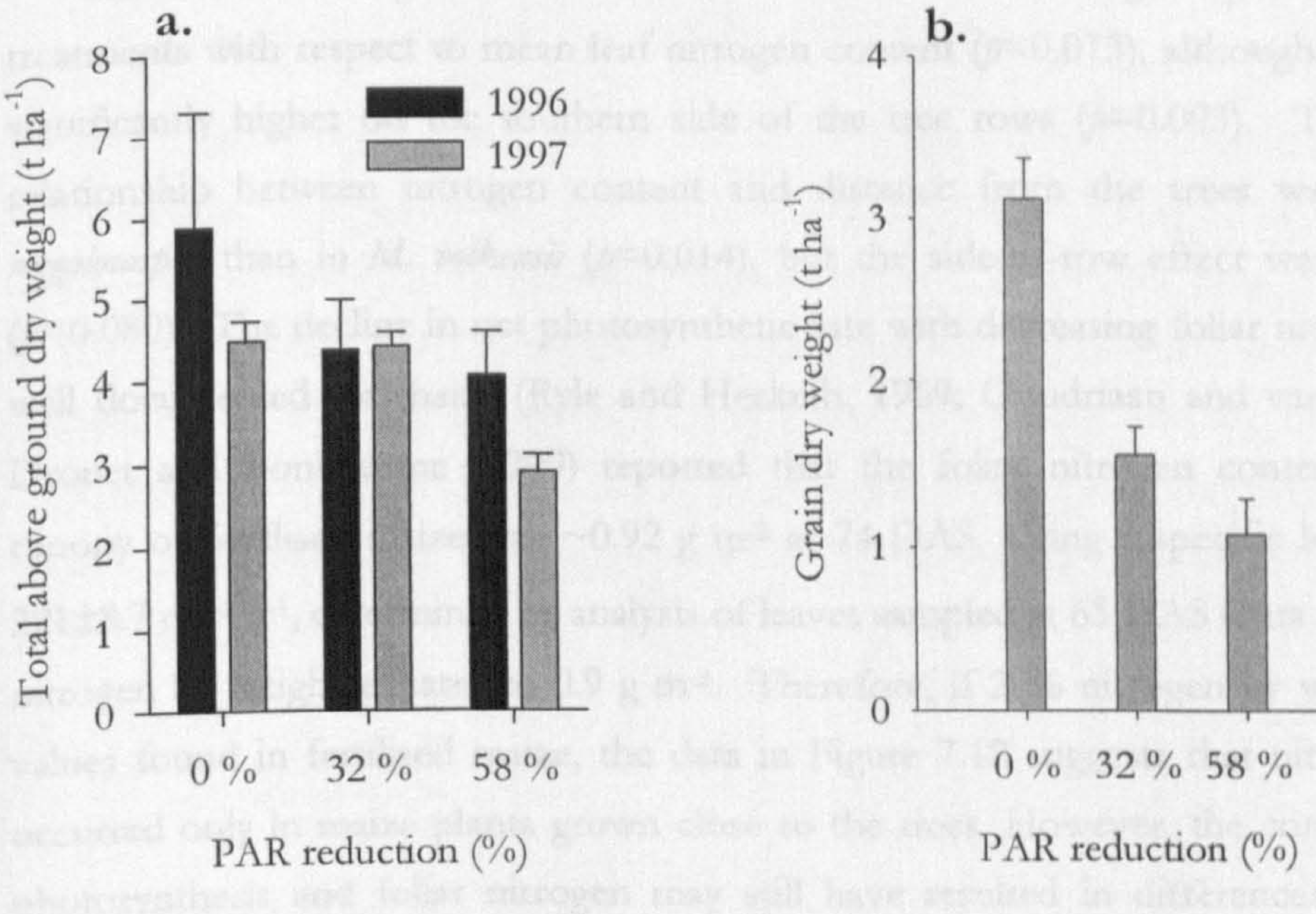


Figure 7.11. a) total above-ground dry weight (±SE) at maturity in shade net treatments of maize during the 1996 and 1997 long rains; b) grain dry weight (±SE) at maturity in shade net treatments during the 1997 long rains.

These results demonstrate that light limitation in agroforestry systems is more important when water availability is relatively high (cf. Section 7.1). Lott *et al.* (2000b) reported that the performance of maize under shade nets at an adjacent site was improved when rainfall was low, probably due to the alleviation of stress resulting from the reduced evaporative demand. The fact that this effect was not seen here even though rainfall was below the long term average in both seasons suggests that it may only occur under more severe drought.

7.3.2.5 Leaf nitrogen content

Figure 7.12 shows the percentage nitrogen contents of the flag leaves of maize plants sampled 66 days after sowing, when the plants furthest from the trees had entered the silking stage. Statistical analysis of treatment averages by split-plot Anova (Blocks: replicate/plot/side-of-row; Treatments: control/treatment*side) showed that nitrogen content was greater in sole crops than in the agroforestry treatments (p<0.001), and on the southern side of the tree rows (p<0.001). However, the control*treatment interaction (p<0.001) and side-of-row*control*treatment interaction (p=0.037) were highly significant, indicating that the responses of the agroforestry and sole crop treatments to the side-of-row and control factors differed.

There was no significant difference between the *C. megalocarpus* and *M. volkensii* treatments with respect to mean leaf nitrogen content (p=0.073), although the values were significantly higher on the southern side of the tree rows (p=0.003). The slope of the relationship between nitrogen content and distance from the trees was greater in *C. megalocarpus* than in *M. volkensii* (p=0.014), but the side-of-row effect was not significant (p=0.080). The decline in net photosynthetic rate with decreasing foliar nitrogen content is well documented for maize (Ryle and Hesketh, 1969; Goudriaan and van Keulan, 1979). Drouet and Bonhomme (1999) reported that the foliar nitrogen content in the upper canopy of fertilised maize was ~0.92 g m^{-2} at 74 DAS. Using a specific leaf area value of 221±8.7 cm^{-2} g^{-1}, determined by analysis of leaves sampled at 65 DAS (data not shown), 2 % nitrogen by weight equates to 0.9 g m^{-2}. Therefore, if 2 % nitrogen by weight represents values found in fertilised maize, the data in Figure 7.12 suggests that nitrogen deficiency occurred only in maize plants grown close to the trees. However, the correlation between photosynthesis and foliar nitrogen may still have resulted in differences in growth rate depending on distance from the tree row. Nitrogen deficiency may have originated partly from the failure of the bean crop and the consequent lack of nitrogen input to the soil during the 1996/97 short rains.

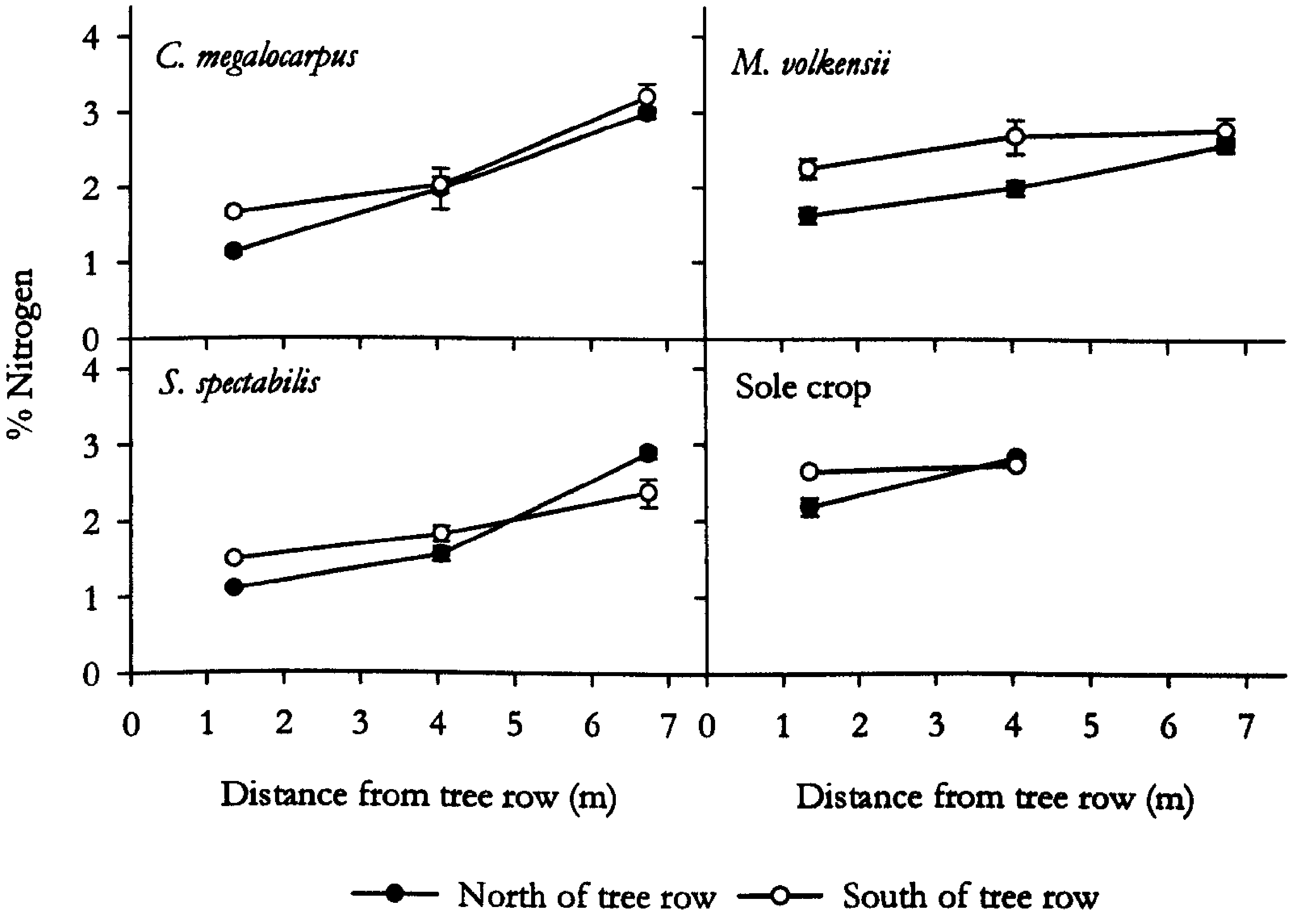


Figure 7.12. Percentage nitrogen content (±SE) expressed on a gravimetric basis for the flag leaves of maize at 66 days after sowing (early silking).

7.3.3 BEAN CROPPING SEASONS (SHORT RAINS)

Total rainfall during the 1996/97 and 1997/98 short rains (1 October-28 February) was 158 and 608 mm respectively. The 1996/97 total was only 45 % the long term average (cf. Table 2.2), whereas that for the 1997/98 season was 174 % of the long term average, with 734 mm received in total during the cropping period. Mean daily short wave radiation receipts for the 1996/97 season (22.6 MJ d^{-1}) were 18 % higher than in 1997/98 (19.2 MJ d^{-1}), while vapour pressure deficit and air temperature were lower during the 1997/98 season (Figure 2.1). Mean daily temperature was 19.5 °C during the 1996/97 season, compared to 18.8 °C in 1997/98.

7.3.3.1 Available soil water

1996/97 short rains

Figure 7.13 shows daily rainfall, PAR receipts, average available soil water content and the slope of the relationship between available soil water and distance from the trees on the northern side of the tree rows during the 1996/97 short rains. The treatments followed a consistent ranking throughout the season whereby available water content was greatest in the sole crop for most of the season, followed by *C. megalocarpus*, in which available soil moisture was 90 % of that in the sole crop, *G. sepium* (81 %), *S. spectabilis* (77 %) and *M. volkensii* (65 %). Thus, the leaflessness of *G. sepium* at the beginning of the season (Figure 3.4) did not result in higher soil water availability on the northern side of the tree row as a result of reduced water extraction by the trees. Instead it is likely that the lack of shade cast by the leafless *G. sepium* canopies resulted in increased evaporation from the soil surface compared with *C. megalocarpus* next to which soil moisture contents were higher despite a more fully developed canopy (cf. Figures 3.1 and 3.4). Analysis of variance (Blocks: replicates; Treatments: control/treatment) showed no significant difference between the sole crop and agroforestry treatments with respect to seasonal water availability (p=0.131). Nor were there any significant differences between the treatments containing indigenous or exotic tree species (p=0.796), or between *S. spectabilis* or *G. sepium* (p=0.816). However, the mean quantity of water available to support crop growth was 40 % greater under *C. megalocarpus* than under *M. volkensii* (p=0.05). The slopes of the relationship between available water content and distance from the trees shown in Figure 7.13 were initially close to zero, but generally became increasingly positive during the second half of the season as the soil dried. The shallower or negative slopes at the beginning of the season are a result of shading close to the trees on the northern side of the tree rows, which would have decreased evaporative demand. The slopes for both *C. megalocarpus* and *S. spectabilis* were positive, whereas those for *M. volkensii* and *G. sepium* were generally negative, indicating the greater importance of shading relative to water extraction by the trees. There were, however, no significant differences in the seasonal mean slopes for the relationship between available soil water and distance from the trees between the indigenous and exotic tree species (p=0.709), neither were there significant differences between *C. megalocarpus* and *M. volkensii* (p=0.340) or between *S. spectabilis* and *G. sepium* (p=0.278).

1997/98 short rains

Daily rainfall, PAR receipts, mean available soil water content and the slope of available water content with distance from the trees are shown in Figure 7.14 for measurements made on the northern side of the tree rows during the 1997/98 short rains. Heavy rainfall throughout the season caused a continued increase in available water content. There was little difference between treatments with respect to available soil moisture content, although the values were frequently greater in the *C. megalocarpus* treatment than in the sole crop, suggesting that reduced soil evaporation resulting from shading by the tree canopy was important. *G. sepium* differed little from the other treatments with regard to water availability on the northern side of the tree rows despite the marked differences in canopy phenology (Figure 3.4). This is likely to have been due to the a relative lack of shade at the beginning of the season resulting in higher evaporation from the soil surface as was also the case during the 1996/97 short rains. The seasonal mean available soil water content in the *C. megalocarpus* treatment was 105 % of that in the sole crop stand, whereas the corresponding values for *S. spectabilis*, *G. sepium* and *M. volkensii* were respectively 99, 97 and 91 %. The differences between agroforestry treatments were therefore small. Anova showed that there were no significant differences between the sole crop and agroforestry treatments (p=0.763), between treatments containing exotic and indigenous tree species (p=0.868), or between *S. spectabilis* and *G. sepium* (p=0.771). However, the seasonal mean available soil water content was 15 % greater for *C. megalocarpus* than in the *M. volkensii* treatment (p=0.044).

The slopes for available soil water content with increasing distance from the trees (Figure 7.14) were generally positive for *S. spectabilis* and negative for *G. sepium*, but approached zero for most of the season in *C. megalocarpus* and *M. volkensii*. There were no significant differences in the slopes for seasonal mean soil water content between the sole crop and agroforestry treatments (p=0.162), between exotic and indigenous tree species (p=0.983), between *S. spectabilis* and *G. sepium* (p=0.256), or between *C. megalocarpus* and *M. volkensii* (p=0.756).

Mean values and the slopes for available soil water content 1 and 4 m from the trees on the northern and southern sides of the tree rows in the *C. megalocarpus* and *M. volkensii* treatments are shown in Figure 7.15. Available soil water content was generally lower on the less shaded southern side of the plots and lower in the *M. volkensii* treatment. However, Anova showed that there was no significant difference in seasonal mean available water content between the northern and southern sides of the tree rows (p=0.386) or between these two treatments (p=0.090), although modelled transpiration for *M. volkensii* was 30 % greater than that for *C. megalocarpus* (Table 5.10). The slopes for water availability were lower or negative on the southern sides of the tree rows in both treatments, although there were again no significant treatment (p=0.410) or side-of-plot effects (p=0.162).

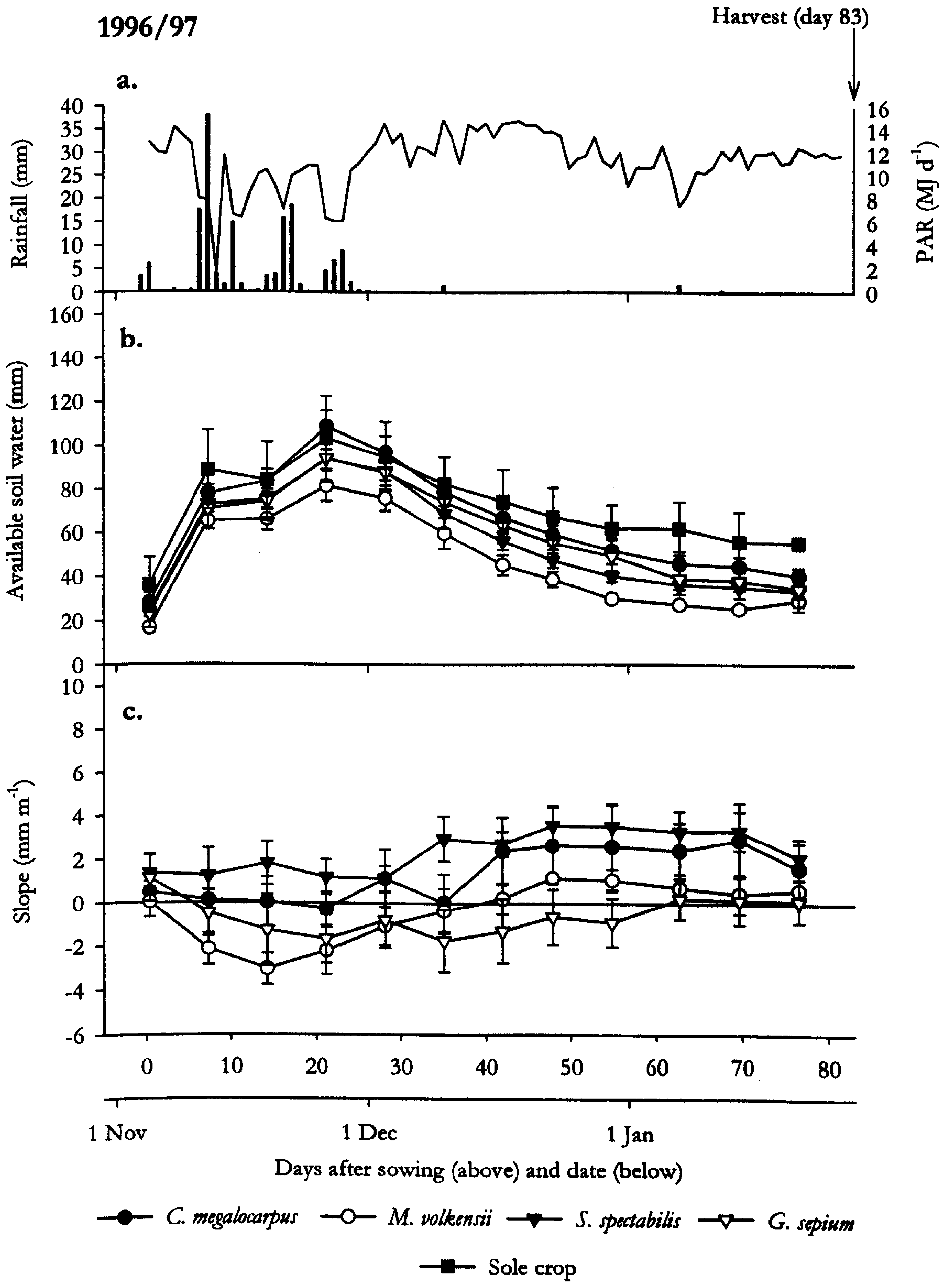


Figure 7.13. a) daily total rainfall (bars) and PAR (line) during the 1996/97 short rains; b) available soil water content (±SE) to a depth of 1.1 m; c) slope (±SE) of available soil water content with distance from the tree row.

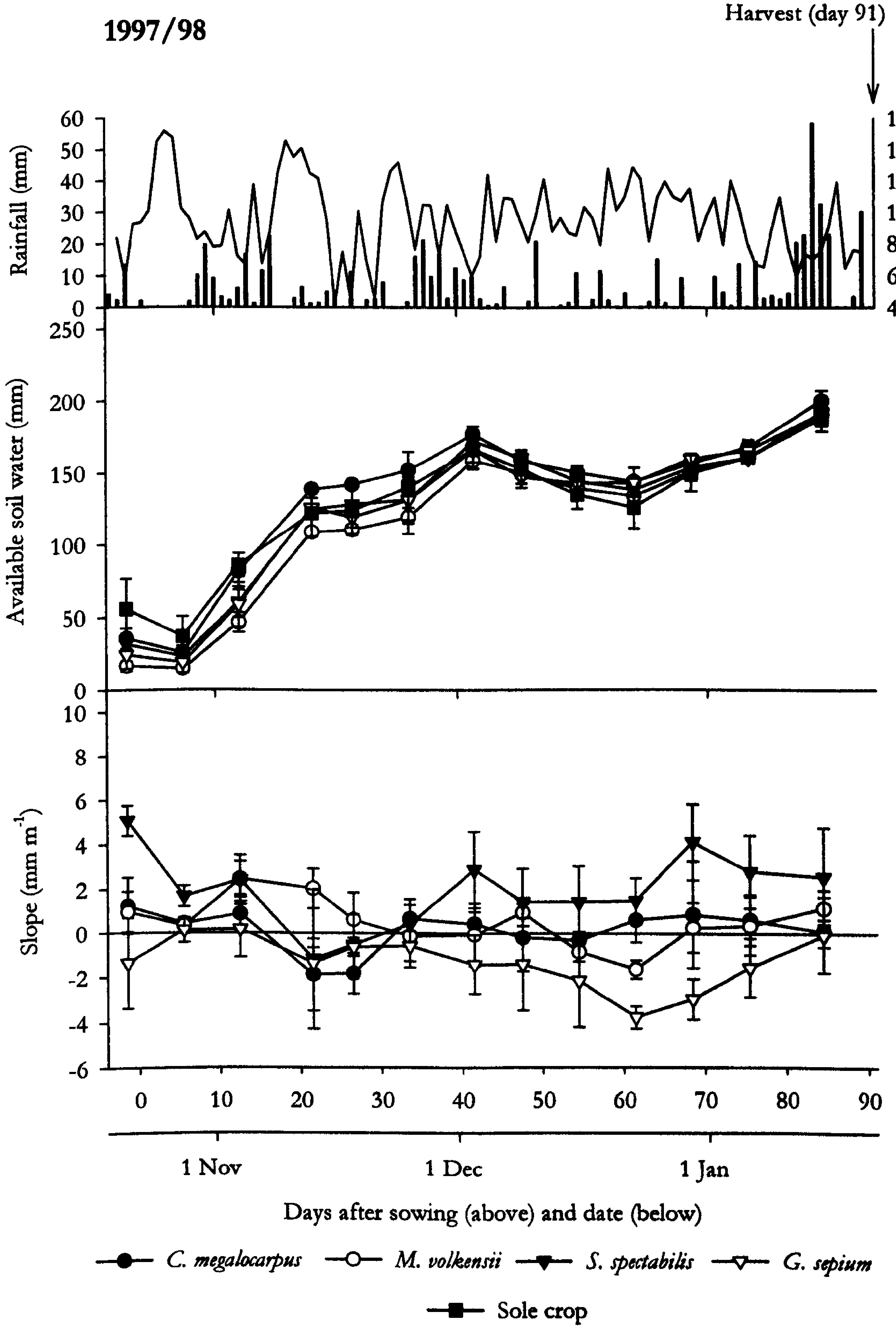


Figure 7.14. a) daily total rainfall (bars) and PAR (line) during the 1997/98 short rains; b) available soil water content (±SE) to a depth of 1.1 m; c) slope (±SE) of available soil water content with distance from the tree row.

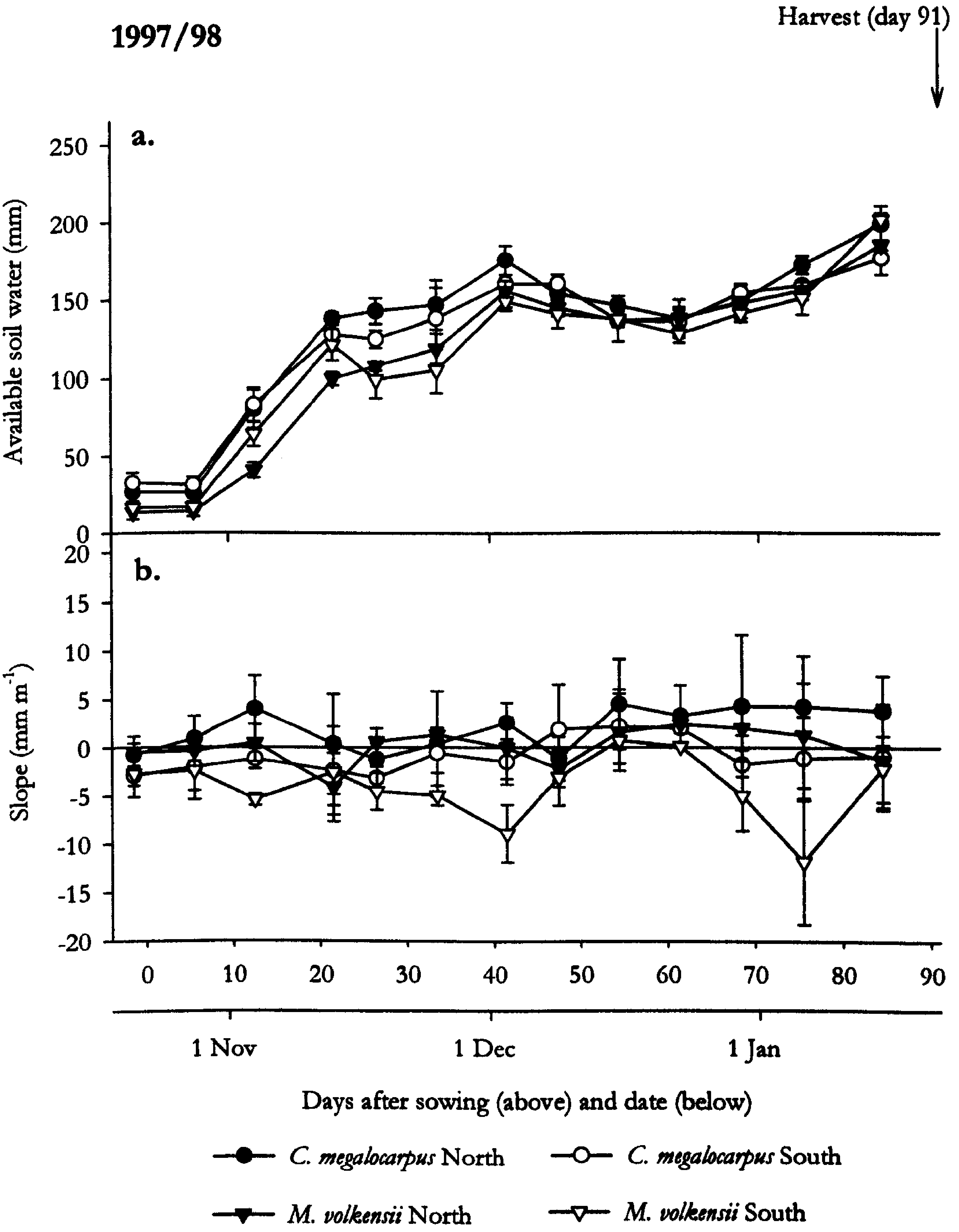


Figure 7.15. a) available soil water content (±SE) to a depth of 1.1 m at distances of 1 and 4 m on the northern and southern sides of the *C. megalocarpus* and *M. volkensii* tree rows; b) slope of available soil water content (±SE) with distance from the tree row on the northern and southern sides of the tree rows.

7.3.3.2 *Incident PAR*

Daily PAR receipts and rainfall are shown in Figures 7.13 and 7.14. The greater cloud cover associated with the higher rainfall during the 1997/98 short rains caused the short wave radiation receipts to be lower than in 1996/97 (cf. Section 2.4.1). The modelled PAR profiles across the *C. megalocarpus* and *M. volkensii* plots are shown in Figure 7.16 for both short rainy seasons.

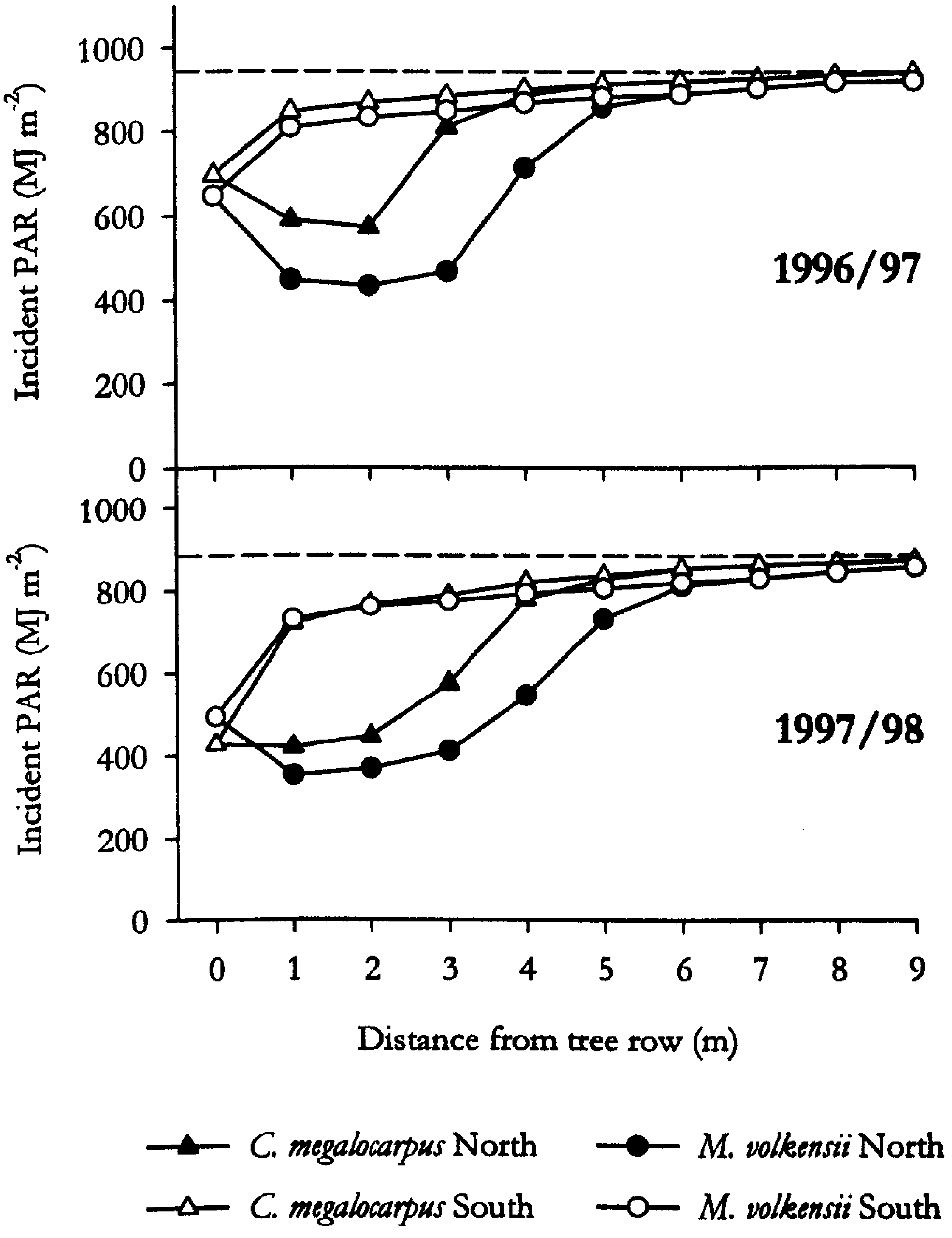


Figure 7.16. Total seasonal PAR receipts at intervals along north-south transects across the *C. megalocarpus* and *M. volkensii* treatments during the 1996/9 and 1997/98 long rains. Calculations were made using MAESTEST. The dashed line represents PAR in the open.

The lower PAR levels on the northern side of the tree rows resulted from the sun's position to the south of the site between approximately five days after the autumn equinox (22 September) and five days before the spring equinox (21 March), while the lower radiation levels on the southern side of the rows relative to those in the open occurred because the trees obscured a fraction of the sky, thereby decreasing the quantity of diffuse radiation received, rather than providing shade from direct radiation.

Table 7.12 shows modelled values for incident PAR to the north and south of the tree rows expressed as a percentage of that in the open. In both years, PAR receipts were lowest close to *M. volkensii* trees, although the difference between treatments was much smaller during the wetter 1997/98 rains due to the greater leaf area of *C. megalocarpus* (cf. Figure 4.5). Percentage interception varied much less between species and seasons on the southern side of the trees and on the outermost section of the plots to the north of the tree rows.

Table 7.12. Incident PAR expressed as a percentage of that in the open for areas of plots to the north and south of the tree rows in the *C. megalocarpus M. volkensii* treatments during the 1996/97 and 1997/98 short rains.

		North of tree row		South of tree row	
Season	Species	0-4.5 m	4.5-9 m	0-4.5 m	4.5-9 m
1996/97 short rains	*C. megalocarpus*	76	99	85	96
	M. volkensii	58	95	89	99
1997/98 short rains	*C. megalocarpus*	60	97	80	94
	M. volkensii	49	92	80	97

7.3.3.3 Bean crop yields

Bean yields were substantially greater during the 1997/98 short rains than in 1996/97, reflecting the substantial difference in rainfall. Production of *Phaseolus vulgaris* in East Africa is most successful when 300-400 mm of rain is received during the main growing period and seed maturation occurs during dry weather (Kay, 1979); although heavy rainfall may lead to disease (Norman *et al.*, 1995), the crop was not affected in the present study. Figure 7.17 shows bean yields on the northern and southern sides of the plots for both seasons; the y-axis scale used for the 1996/97 data is ten times greater than that used in 1997/98 as the sole crop yield in the former season was only 5.5 % of that in 1997/98. The cause of the large standard error for the sole crop data in 1996/97 is discussed below. Treatment yields in 1996/97 followed the same ranking as water availability to the north of the tree rows (Figure 7.17), being greatest in the *G. sepium* treatment, followed by *C. megalocarpus*, *S. spectabilis* and *M. volkensii*. However, no correlation was detected during the 1997/98 season, suggesting that water was not an important limiting factor due to the abundant rainfall. Bean yields in the agroforestry treatments expressed as a percentage of the sole crop yield are presented in Table 7.13. Bean yield in the agroforestry treatments was lowest in the *M. volkensii* treatment in the 1996/97, but highest in 1997/98, although the ranking of treatments was otherwise identical in both years. The fact that *M. volkensii* is adapted to more arid habitats than the other species examined (cf. Section 2.5-2.8) provides an ecological explanation for its greater competitiveness with associated crops during the relatively dry 1996/97 season compared to the wetter 1997/98 season. Bean yields in the agroforestry treatments were greatest in the *G. sepium* treatment in 1996/97 and a close second in 1997/98; these observations may be partially be explained at least partly by the phenological differences (Section 3.3.2). The yields for specific treatments are discussed further below.

Table 7.13. Bean yields expressed as percentage of sole crop yield.

	Season	
Treatment	1996/97	1997/98
C. megalocarpus	48.5	76.1
M. volkensii	24.6	87.3
S. spectabilis	39.9	71.0
G. sepium	53.6	86.5

Yields in the agroforestry treatments were higher on the northern side of the tree rows in 1996/97 but lower in 1997/98, reflecting the reversed effect of shading on crop yield between the two seasons. In 1996/97, mean daily incident PAR in the open receipts were greater and total rainfall was much lower than in 1997/98. These results suggest that shading was beneficial for crop yield under water-limiting conditions, but detrimental under non-limiting conditions.

The large standard errors for the row yields in the sole crop plots are primarily attributable to the high yield obtained for Replicate 2, which was 6.9 times greater than the average for the other three replicates. As soil moisture content was not determined in Replicate 2, the data for the other replicates were examined in search of an explanation. There was little variability in soil water content between the remaining three replicates (data not shown) and no correlation with yield. The origin of the much higher yield in Replicate 2 is therefore unclear, and the possibility that soil water content was higher than in the other replicates cannot be ruled out. Incident PAR on the crops was comparable for all replicates and nutrients are unlikely to have been limiting as yield in Replicate 2 was third highest of the four replicates during the 1997/98 season when water was not limiting, suggesting that differences in soil conditions were not responsible.

Plant numbers and above-ground dry weights for each 6 m row length at final harvest are shown in Figure 7.18 and 7.19 for both cropping seasons. The spatial variation within plots varied greatly between seasons, with higher yields being obtained to the north of the tree rows in 1996/97 and to the south in 1997/98. The differences in plant number were smaller, indicating that plant survival did not have a major role in determining yield differences between plots or seasons. The yield profiles on the northern side of the tree rows exhibited distinctive peaks close to the trees in all treatments in the 1996/97 short rains, an effect which may have been attributable to a reduction in evaporative demand resulting from shading. The observed effects in *M. volkensii* and *C. megalocarpus* correspond to the horizontal extent of the tree canopies and the consequent percentage reduction in PAR incident on the crops (Figure 7.16). The yield reduction on the northern side of the plots in 1997/98 again corresponded to the intensity and pattern of shading, which extended ~6 m from the tree rows in *M. volkensii* and ~4 m in *C. megalocarpus*. During the 1996/97 season, the *G. sepium* treatment showed the most pronounced maximum in crop yield on the southern side of the tree rows, an effect which resulted from a combination of the negative slope of water availability on the northern side of the plots and the high mean available soil water relative to the other agroforestry treatments (Figure 7.13). The lack of full leaf cover in *G. sepium* during the first half of the season (Figure 3.4), when most rainfall occurred would have limited transpiration by the trees and increased drainage losses; however, as the tree canopy developed later in the season, shading would have increasingly reduced the evaporative demand experienced by the associated crops as the soil profile dried. In common with the 1996/97 short rains, but resulting from different processes, the relatively high crop yield obtained in the *G. sepium* treatment is likely to have resulted from a combination of increased PAR receipts during the early part of the season when tree leaf cover was low, and increased shading later in the season, which would have reduced soil drying, as evidenced by the negative slope for water availability with increasing distance from the tree rows later in the season (Figure 7.14).

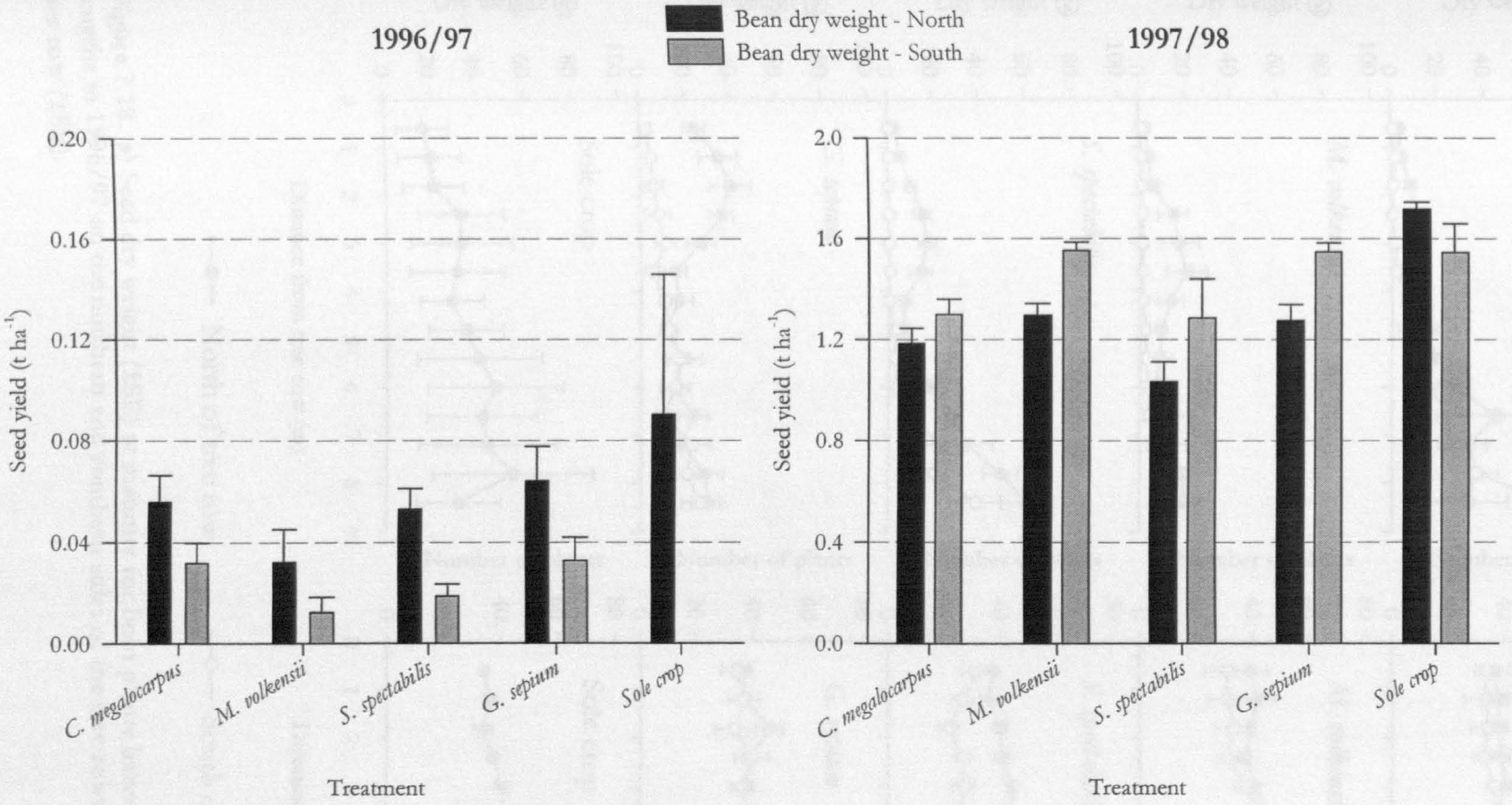


Figure 7.17. Seed dry weight (±SE) at maturity for beans grown on the northern or southern side of the tree rows during the 1996/97 and 1997/98 short rains.

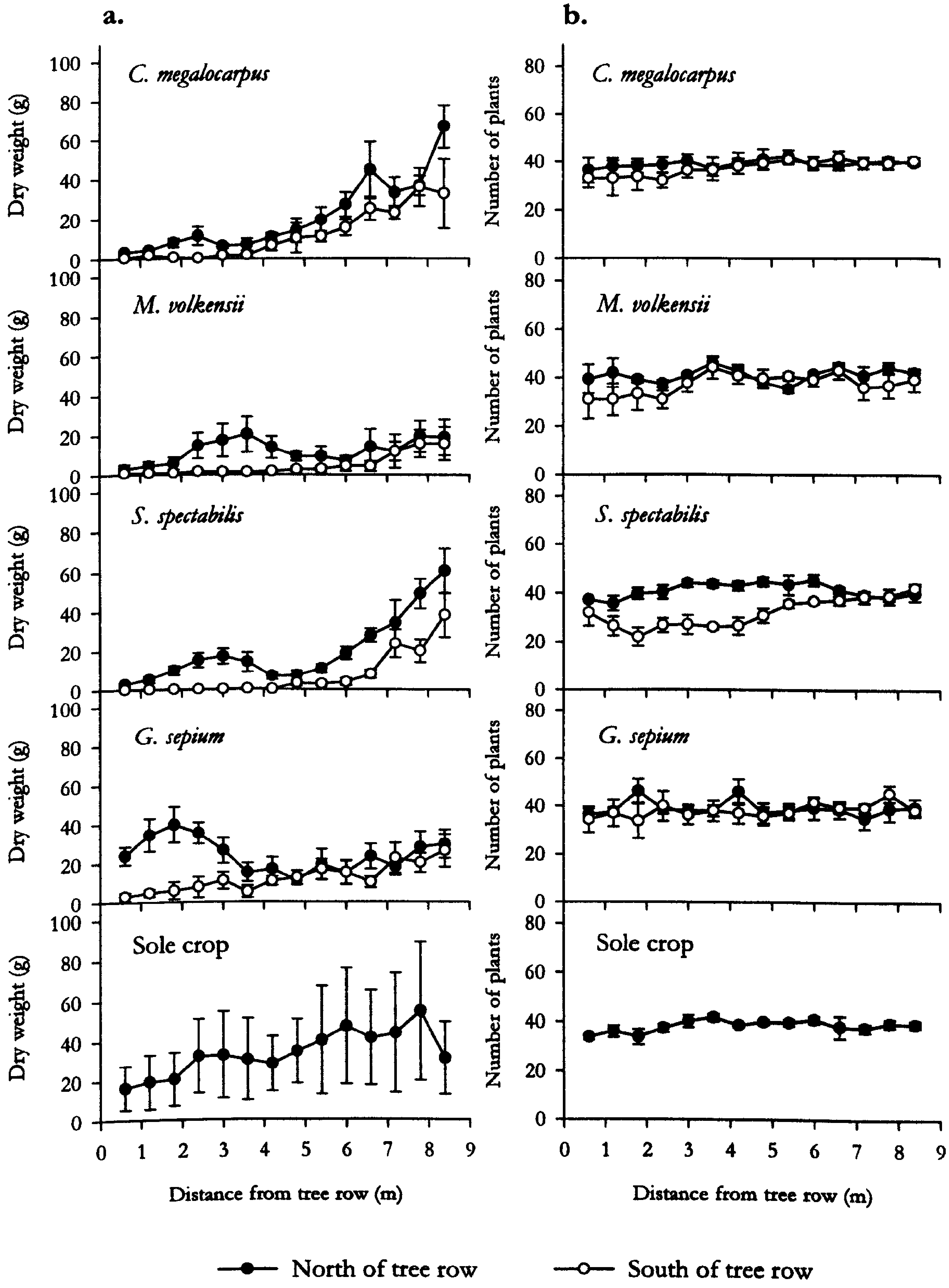


Figure 7.18. a) Seed dry weight (±SE) at maturity for bean plants harvested from 6 m row lengths in 1996/97 on the northern and southern sides of the tree rows; b) plant number per row (±SE).

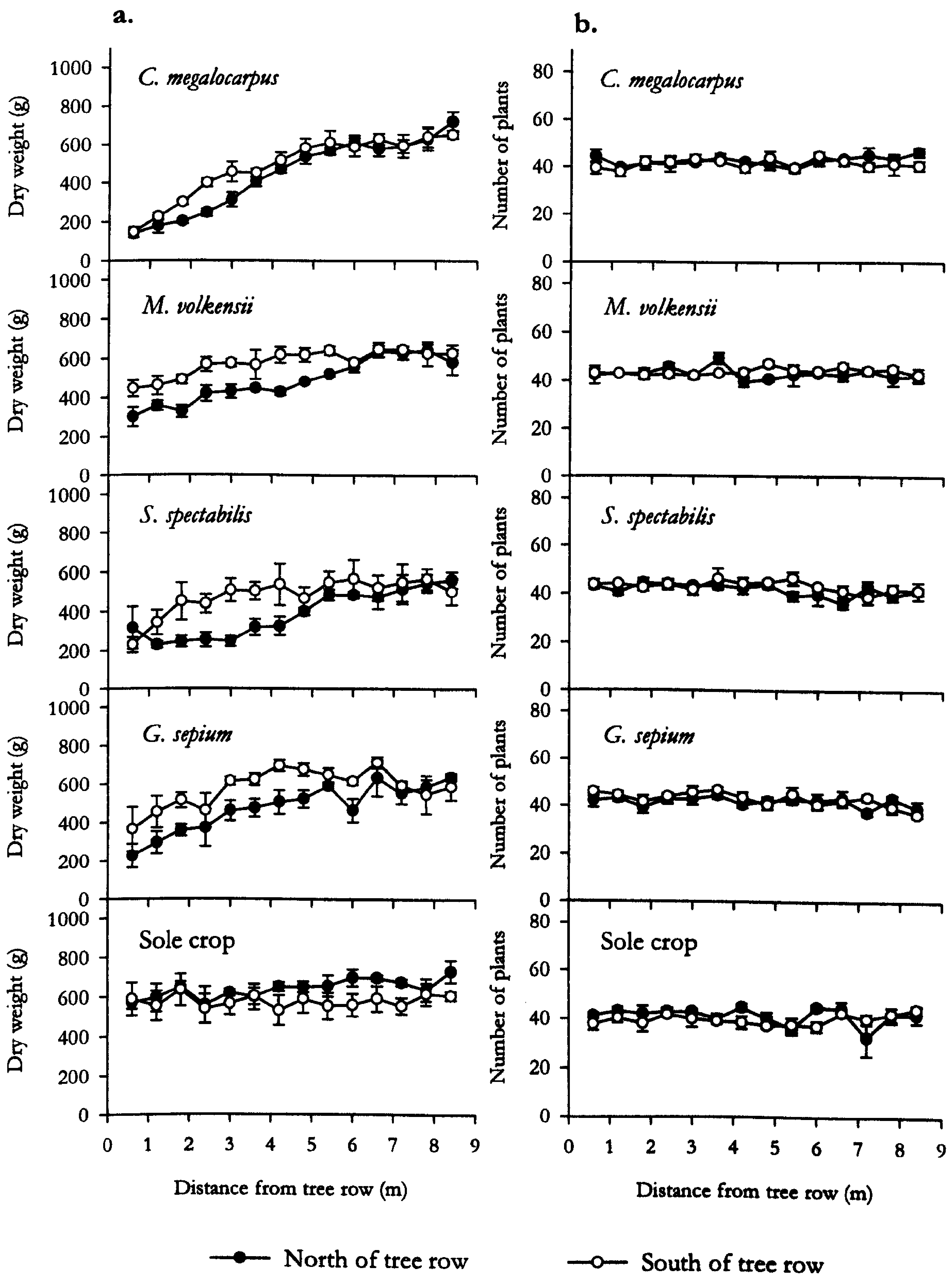


Figure 7.19. a) Seed dry weight (±SE) at maturity for bean plants harvested from 6 m row lengths on the northern and southern sides of the tree rows in 1997/98; b) plant number per row (±SE).

Effects of trees on crop yield variates

As the rainfall and yield patterns differed greatly between seasons, the data for each season were analysed separately. Tests for significant effects of the trees were carried out by split-plot Anova (Treatments: side-of-row*control/treatment, Blocks: replicate/ plot/side). However, as data were not collected for the southern side of the tree rows in 1996/97, analysis of differences between the sole crop and agroforestry treatments was limited to data from the northern side of the plots.

During the 1996/97 short cropping season, bean yields on the northern side of the plots did not differ significantly between the agroforestry and sole crop treatments (p=0.216; Table 7.14). Thus, crop productivity in the agroforestry treatments rivalled that obtained from sole cropping, suggesting that shading by the tree canopy countered the adverse effect of below-ground competition for water. However, the fact that near crop failure occurred during this season decreases the importance of the result. The slope for the correlation between crop yield and distance from the trees showed no significant control effect, although there was a significant control*treatment interaction, indicating that the slopes for the various agroforestry treatments were not parallel (cf. Figure 7.18). Plant number and the slope of plant number with distance from the centre of the plots did not differ significantly between the agroforestry and sole crops, indicating that the differences in yield did not result from differences in plant survival.

Crop yield during the 1997/98 season was 25 % higher in the sole crop than the mean for all agroforestry treatments (p=0.002; Table 7.14), an effect which probably resulted from the observed reductions in PAR levels as water availability was often greater in the *C. megalocarpus* treatment than in the sole crop (Figure 7.14). The significant side-of-plot*control interaction (p<0.001) indicates that yield was 11 % higher on the northern side than on the southern side of sole crop plots, and was 16 % lower to the north of the tree rows in the agroforestry treatments. The higher yield obtained on the northern side of the sole crop plots and the steeper slope of the relationship between bean yield and distance from the tree row (see below), may be attributed to chance, as there is no apparent physiological explanation. However, the lower yields on the northern side of the agroforestry plots are probably attributable to reductions in PAR incident on the crops (Figure 7.16). There were significant side-of-tree-row effects on the slopes for bean yield in all treatments (Table 7.14). The slope of the relationship between bean yield and distance from the tree row (Figure 7.19) was significantly higher on the northern than on the southern side of the plots (p<0.001); the significant control*treatment interaction (p=0.041) results from the large variation in slopes between the agroforestry treatments, while the significant control effect ($p=0.003$) indicates that the slopes for the agroforestry treatments were steeper than in the sole crop plots, demonstrating the effect of the presence of trees. The non-significant side-of-row*control interaction ($p=0.657$) indicates that differences between the slopes for bean yield on the northern and southern sides of the plots were not attributable to the presence of trees. This is illustrated by Figure 7.19, in which the slopes for yield are steeper on the northern side of the plots in all treatments, including the sole crop. This is partly the result of analysing simplified linear yield trends across the plots, and partly due to the wide range of slopes in the agroforestry treatments. However the reason for the steeper slope on the northern side of the sole crop plots is unclear. Plant number and the slope for plant number were not significantly affected by any of the main factors (Table 7.14), indicating that plant survival was unaffected by the presence of trees.

Table 7.14. F-probabilities determined by analysis of variance for control effects (tree *Vs* non-tree) on variates of bean yield during the 1996/97 short rains, and for control and side-of-row effects during the 1997/98 short rains. * and ** denote significance at $p<0.05$ and $p<0.01$ respectively.

1996/97 North side of plots only	Bean dry weight	Slope for bean dry weight	Plant number	Slope for plant number
Replicate*plot stratum				
Control	0.216	0.758	0.290	0.508
Control*treatment	0.853	0.003**	0.746	0.712
1997/98 Both sides of plots				
Replicate*plot stratum				
Control	0.002**	0.003**	0.063	0.351
Control*treatment	0.060	0.041*	0.761	0.010**
Replicate*plot*side stratum				
Side	<0.001**	<0.001**	0.858	0.537
Side*control	<0.001**	0.657	0.097	0.111
Side*control*treatment	0.400	0.878	0.347	0.395

Effects of tree species origin on crop yield variates

The geographical origin of the tree species examined had no significant effect on the variates of bean yield measured during the 1996/97 season (Table 7.15). However, bean yields averaged over all agroforestry treatments were 114 % higher on the northern, more shaded side of the trees ($p<0.001$), an effect which was partially attributable to the 11 % greater plant population ($p=0.021$). The slope for mean plant number was significantly greater on the less shaded southern side of the trees ($p=0.009$), suggesting that survival close to the trees was reduced by competition for water.

There were again no significant effects of tree origin on the variates of bean yield during the 1997/98 short rains. However, in contrast to 1996/97, mean yield for all agroforestry treatments was 19 % higher on the less shaded southern side of the tree rows, ($p<0.001$), suggesting that the lower incident PAR levels may have limited crop yield on the more shaded northern side of the tree rows. The significant origin*treatment interaction occurred because yields in the two agroforestry treatments containing indigenous trees spanned those obtained for the two treatments containing exotic tree species. Again in contrast to 1996/97, the slopes for crop yield with distance from the trees were higher to the north of the tree rows, reflecting the lower PAR receipts (Figure 7.16) and crop production (Figure 7.19). As plant number showed no significant effect, little importance is attached to the significantly higher slope for plant number in the indigenous tree treatments during the 1997/98 short rains.

Table 7.15. F-probabilities determined by analysis of variance for origin and side-of-row effects on the variates of bean yield during the 1996/97 and 1997/98 short rains. * and ** denote significance at $p<0.05$ and $p<0.01$ respectively.

1996/97	Bean dry weight	Slope for bean dry weight	Plant number	Slope for plant number
Replicate*plot stratum				
Origin	0.325	0.195	0.402	0.995
Origin*treatment	0.191	<0.001**	0.527	0.384
Replicate*plot*side stratum				
Side	<0.001**	0.839	0.021*	0.009**
Side*origin	0.258	0.241	0.424	0.361
Side*origin*treatment	0.926	0.015*	0.167	0.670
1997/98				
Replicate*plot stratum				
Origin	0.537	0.081	0.676	0.003**
Origin*treatment	0.047*	0.035*	0.645	0.536
Replicate*plot*side stratum				
Side	<0.001**	<0.001**	0.388	0.810
Side*origin	0.206	0.805	0.241	0.344
Side*origin*treatment	0.250	0.760	0.466	0.163

Effects of M. volkensii and C. megalocarpus on crop yield variates

Neither above-ground yield nor plant number differed significantly between the *C. megalocarpus* and *M. volkensii* treatments during the 1996/97 season (Table 7.16), even though the mean available soil water content on the more shaded northern side of the plots was 40 % greater under *C. megalocarpus* than *M. volkensii* (Section 7.3.3.1) and the modelled transpiration for *M. volkensii* was 47 % higher than for *C. megalocarpus* (Table 5.10).

These results suggest that the microclimatic effects resulting from the lower PAR receipts on the northern side of the *M. volkensii* plots as compared with the *C. megalocarpus* plots (Figure 7.16) countered the effect of the higher transpiration in *M. volkensii*. When averaged over both treatments, yield to the north of the trees was double that to the south (p=0.034), indicating that the greater yield on the northern side of the trees is likely to have resulted from the lower PAR receipts (Figure 7.16) and associated decrease in radiative flux. The slope of bean yield with distance from the trees was significantly greater for *C. megalocarpus* (p=0.026), but there was no significant side-of-row effect. The smaller increase in yield with distance from the trees in the *M. volkensii* treatment (Figure 7.18) probably reflects a more extensive tree rooting system; the lack of a side-of-row effect despite the differing yield patterns between treatments resulted from the variation in the slopes. There was again no significant treatment effect on plant number.

Bean yields in 1997/98 were 15 % higher in the *M. volkensii* treatment than in *C. megalocarpus* (p=0.038). The side*treatment interaction was significant (p<0.001); yield on the less shaded southern side of the *M. volkensii* treatment was 20 % greater than on the northern side, whereas the corresponding difference for *C. megalocarpus* was only 10 % (Figure 7.19). This difference may have resulted from the later development of the canopy in *M. volkensii* (Figure 4.5), which would have increased incident PAR receipts and hence crop yield even though available soil water content was lower throughout the season (Figure 7.14). Alternatively yield reductions in *C. megalocarpus* may have resulted from temporary waterlogging of the surface soil layers in the shade of the *C. megalocarpus* trees due to lower rates of tree water extraction compared to the other species. The latter appears more plausible as yields on the southern side of the tree rows were lower for *C. megalocarpus* than for *M. volkensii*, even though incident PAR levels were comparable (Figure 7.16). Temporary waterlogging is also thought to have induced premature tree leaf abscission during the 1997/98 short rains (Section 3.3.5). When averaged over both treatments, the slope for bean yield was significantly greater to the north than to the south of the tree rows (p=0.006), thereby demonstrating the effect of the lower PAR receipts on the northern side of the trees. The slopes for bean yield (Figure 7.19) were significantly greater in the *C. megalocarpus* treatment (p=0.008), demonstrating the effect of the postulated temporary flooding close to the trees and their more limited agroforestry spread of roots. There were no significant differences for plant number or the slope of plant number between treatments or sides of the plot.

Table 7.16. F-probabilities from analysis of variance for treatment (*C. megalocarpus* and *M. volkensii*) and side-of-row effects on the variates of bean yield during the 1996/97 and 1997/98 short rains. * and ** denote significance at p<0.05 and p<0.01 respectively.

1996/97	Bean dry weight	Slope for bean dry weight	Plant number	Slope for plant number
Replicate*plot stratum				
Treatment	0.136	0.026*	0.809	0.835
Replicate*plot*side stratum				
Side	0.034*	0.559	0.252	0.069
Side*treatment	0.797	0.277	0.668	0.848
1997/98				
Replicate*plot stratum				
Treatment	0.038*	0.008**	0.343	0.424
Replicate*plot*side stratum				
Side	<0.001**	0.006**	0.827	0.661
Side*treatment	<0.001**	0.437	0.274	0.247

Effects of S. spectabilis and G. sepium on crop yield variates

During the 1996/97 season, neither bean yield at maturity nor plant numbers differed significantly between the *S. spectabilis* and *G. sepium* treatments. Yields close to the trees in the *G. sepium* treatment were higher than under *S. spectabilis* (Figure 7.18) as a result of the phenological differences discussed above (cf. Figure 3.4), but were lower in the outer crop rows presumably due to greater competition for water at distance from the trees in the *G. sepium* treatment. Overall, yield on the northern side of the tree rows was 127 % greater (p<0.001) than on the southern side and plant number was 15 % higher (p=0.047). The slope for bean yield was significantly greater in the *S. spectabilis* treatment, demonstrating the higher relative yields at distance from the tree probably resulting from less severe competition for water. The significant side-of-row*treatment interaction (p=0.007) resulted because the slope on the northern side of the *G. sepium* tree rows was negative because higher yields were obtained close to the trees as a result of their phenology, as discussed above. The slopes for plant number showed no significant treatment effect.

There were no significant treatment effects during the 1997/98 season for any of the yield variates examined (Table 7.17). Bean yield was 23 % higher on the southern side of the plots (p=0.003) due to the reduced incident PAR receipts on the northern side of the tree rows. The slope for bean yield was 76 % greater on the northern side of the plots (p=0.037), again as a result of the reduced PAR receipts. There were no significant side-of-row effect on plant number or the slope of plant number with distance from the tree rows.

Table 7.17. F-probabilities obtained from analysis of variance for treatment (*S. spectabilis* and *G. sepium*) and side-of-row effects on the variates of bean yield examined during the 1996/97 and 1997/98 short rains. * and ** denote significance at $p<0.05$ and $p<0.01$ respectively.

1996/97	Above-ground dry weight	Slope for bean dry weight	Plant number	Slope for plant number
Replicate*plot stratum				
Treatment	0.472	0.017*	0.330	0.341
Replicate*plot*side stratum				
Side	<0.001**	0.245	0.047*	0.059
Side*treatment	0.765	0.007**	0.090	0.493
1997/98				
Replicate*plot stratum				
Treatment	0.057	0.894	0.958	0.743
Replicate*plot*side stratum				
Side	0.003**	0.037*	0.166	0.343
Side*treatment	0.858	0.713	0.820	0.136

7.3.3.4 Shade treatments

Table 7.18 shows rainfall beneath the shade nets. Seasonal rainfall under the nominal 25 % shade nets (light shade) was 85 and 93 % of that in the open during the 1996/97 and 1997/98 seasons respectively; the equivalent values for the nominal 50 % shade treatment (intense shade) were 61 and 106 %. The seasonal differences may have resulted from the higher mean daily rainfall (including only days on which rain fell) of 7.8 mm d^{-1} during the 1997/98 season compared to 5.6 mm d^{-1} during the 1996/97 season. The observation that rainfall under the 50 % shade treatment was slightly greater than in the open in 1997/98 may have occurred because low points in the nets were located above the rain gauges.

Table 7.18. Seasonal rainfall receipts under shade nets and in the open during the 1996/97 and 1997/98 short rains.

Season	open	light shade	intense shade
1996/97 short rains	134 ± 0.3	114 ± 2.4	82 ± 10.9
1997/98 short rains	664 ± 4.1	620 ± 57.2	705 ± 71.5

Despite the reduced rainfall beneath the nets, yield increased with shading intensity during the 1996/97 short rains (Figure 7.20), probably because evaporative demand was decreased as a result of the reduced incident radiation. However, statistical analysis did not show a significant effect of shade for either bean yield (p=0.096) or plant number at final harvest ($p=0.697$). These effects were reversed during the 1997/98 season when yield increased significantly with increasing PAR ($p<0.001$); yields under light and intense shade were respectively 50 and 33 % of that in the open. There was also a significant effect of shade on plant numbers ($p=0.001$), which were respectively 69 and 58 % greater in the light and intense shade treatments than in the open. The observed yield differences between shading treatments during both seasons reflect those observed in the agroforestry treatments, providing further confirmation that the higher yields obtained on the northern side of the tree rows during the 1996/97 season and the lower yields during the 1997/98 season resulted largely from shading effects.

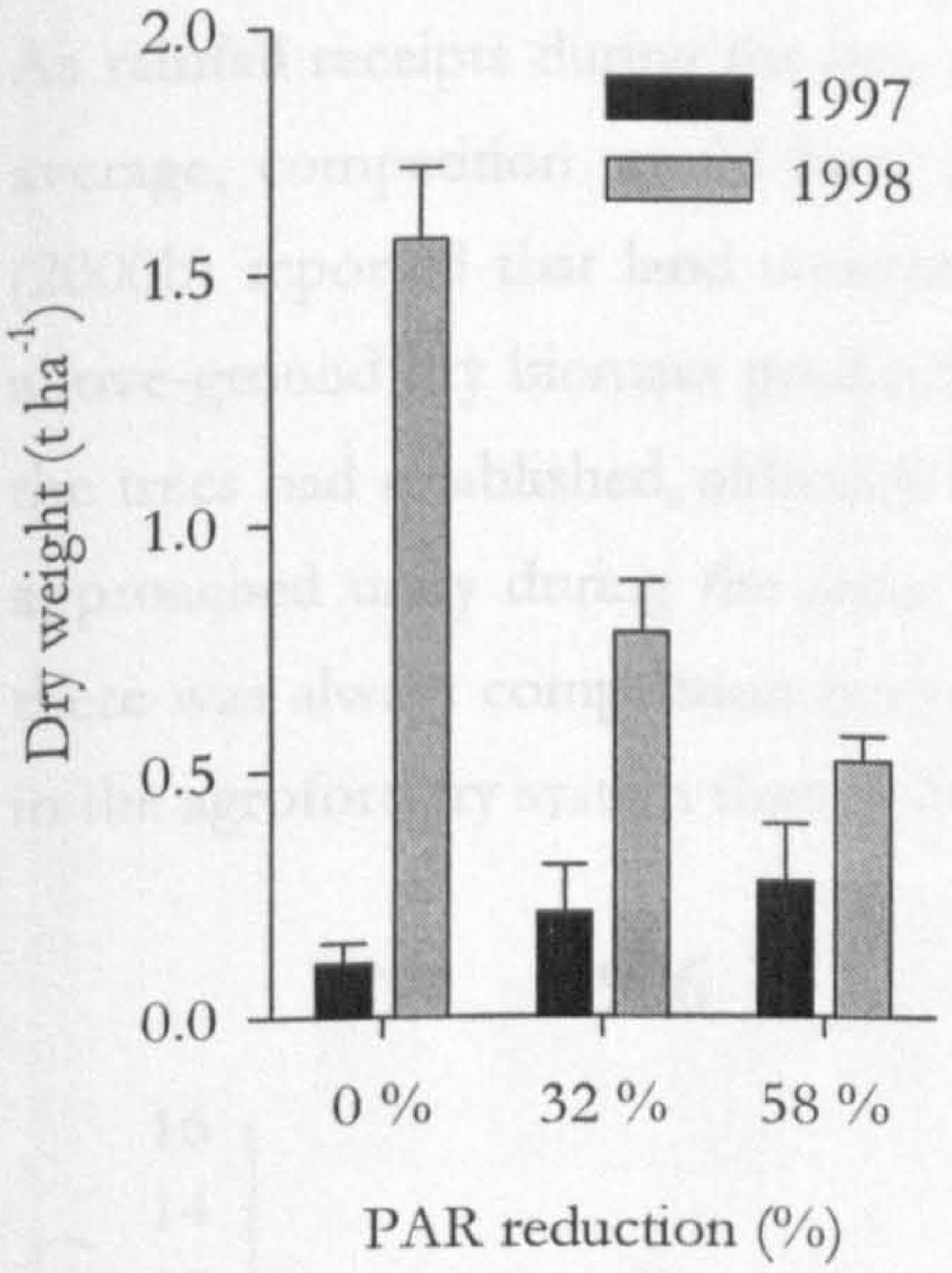


Figure 7.20. Seed dry weight yields (±SE) for beans grown in artificial shade treatments during the 1996/97 and 1997/98 short rains.

7.3.4 SYSTEM PERFORMANCE

Figure 7.21 shows above-ground dry weight production for the agroforestry treatments and sole maize during the 1996 and 1997 long rains; tree leaf biomass production was not included as values were only estimated for *C. megalocarpus* and *M. volkensii.* The woody yields include the period up to the sowing date for the subsequent cropping season. Grain yields were greatest in sole maize in both seasons, although productivity was higher in the agroforestry treatments than in sole maize during the drier 1996 season, when the trees were younger and net biomass productivity was higher (Section 6.3.3). The lower net biomass production of the trees in 1997 may have resulted partly because of lower tree root densities than in 1996 which were measured in the *Grevillea robusta* and *G. sepium* treatments

(Odhiambo *et al.*, 2000). However, the reduction in net biomass productivity with increasing tree size (Kira, 1975) is likely to have been the main cause. The greater yield of the sole maize compared to the maize yields in the agroforestry treatments in 1997 compared to 1996 is probably the result of greater competition from the larger trees. Inclusion of leaf dry weight production during the 1997 season by *C. megalocarpus* and *M. volkensii* (0.5 and 2.2 t ha^{-1} respectively, cf. Table 6.5) would not have changed the relative performance of the agroforestry and sole crop treatments greatly. Although data limited to only two seasons cannot be used to establish a clear temporal pattern, it appears likely, given the decreasing net biomass production as trees mature, that the productivity of the agroforestry treatments would have decreased as the trees aged, as is discussed in Chapter 6. As rainfall receipts during the two maize seasons were only 62 and 88 % of the long term average, competition would have been expected to be greater than normal. Lott *et al.* (2000b) reported that land equivalent ratios were consistently above 1 for total seasonal above-ground dry biomass production by the trees and crops in agroforestry systems once the trees had established, although the performance ratios of the trees or crops never both approached unity during the same season; these observations clearly show that, although there was always competition between the trees and crops, overall productivity was higher in the agroforestry system than in the sole stands.

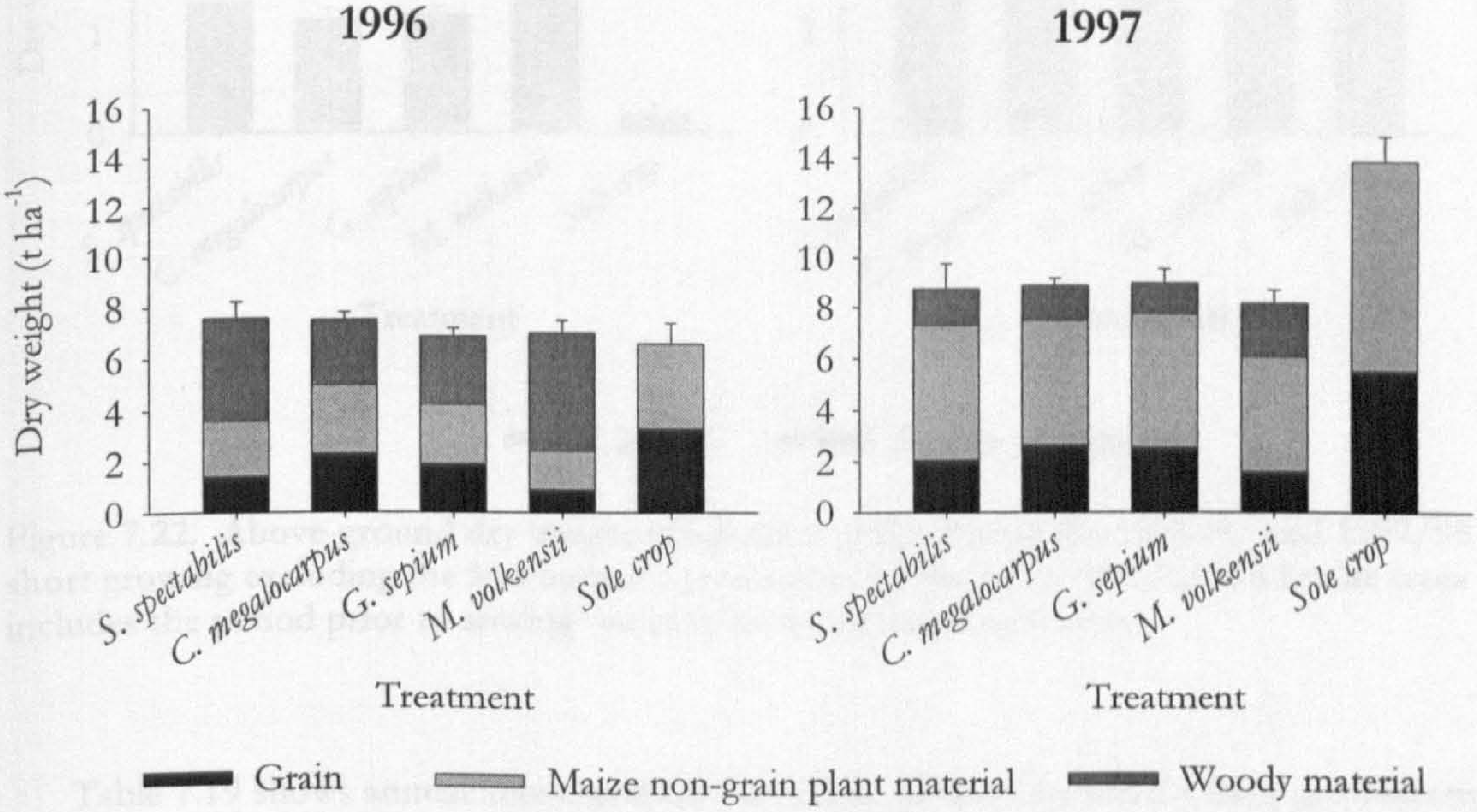


Figure 7.21. Above-ground dry weight production (±SE) during the 1996 and 1997 long growing seasons excluding leaf biomass production by the trees. Tree biomass values include the period prior to sowing the crop during the subsequent season.

Figure 7.22 shows above-ground dry weight production for the agroforestry treatments and sole bean crops during the 1996/97 and 1997/98 short rains. As for the long growing seasons, the woody yields include the period up to the crop sowing date for the subsequent cropping season. The productivity of the agroforestry treatments was higher than that of the sole crops during the 1996/97 season and for all except *S. spectabilis* and *C. megalocarpus* in the 1997/98 short rains. However, these results reflect the extreme nature of the two seasons, as low rainfall caused almost total crop failure in 1996/97, whereas the abundant rainfall in 1997/98 minimised tree-crop competition. Inclusion of leaf dry weight production by the trees (0.2 and 0.9 t ha^{-1} for *C. megalocarpus* and 0.9 and 2.3 t ha^{-1} for *M. volkensii* in 1996/97 and 1997/98 respectively cf. Table 6.5) further accentuates the productivity of the both agroforestry systems as well as increasing the productivity of the *C. megalocarpus* system above that of the sole crop in the 1997/98 season.

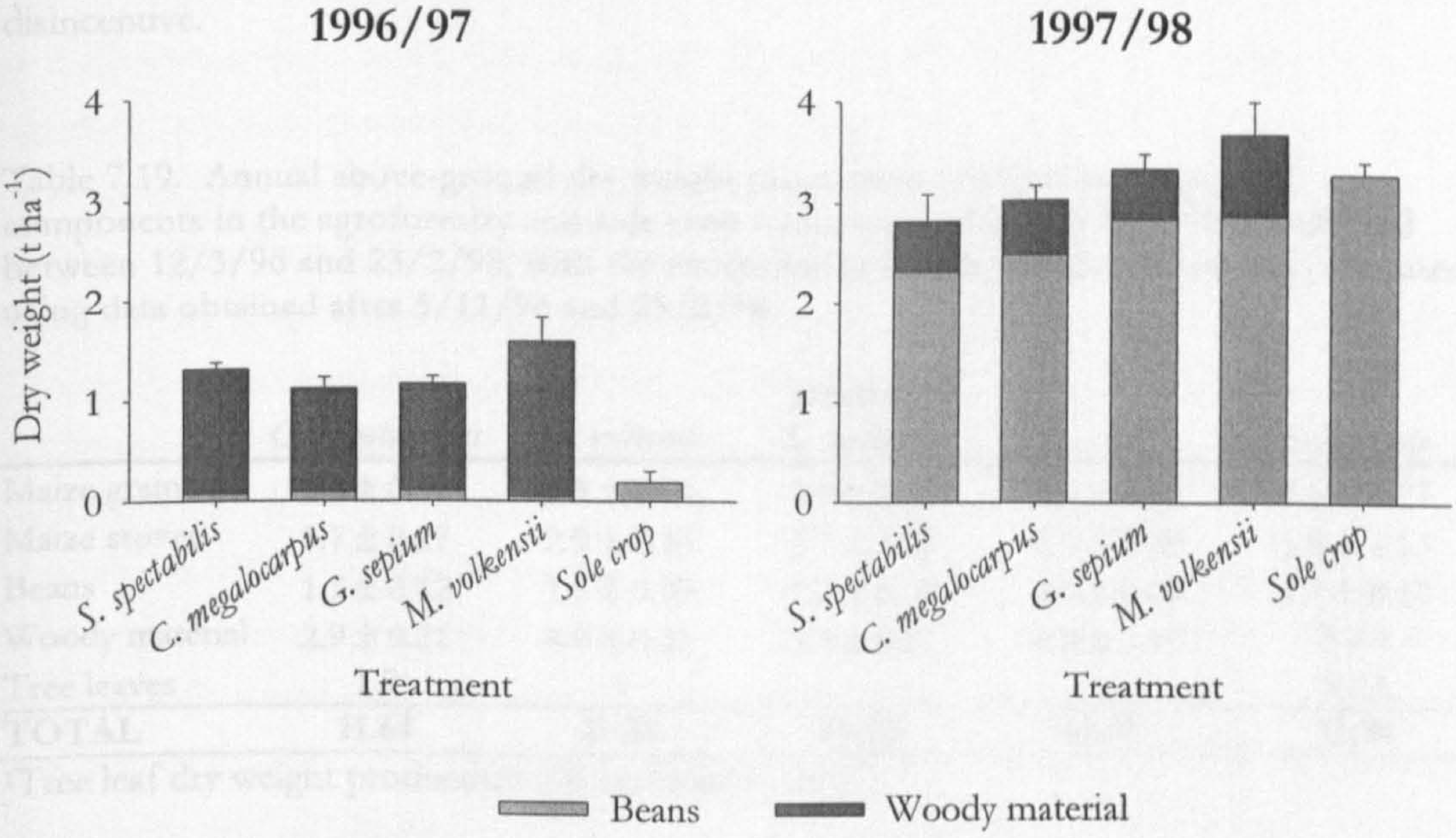


Figure 7.22. Above-ground dry weight production (±SE) during the 1996/97 and 1997/98 short growing excluding the leaf biomass production by the trees. Production by the trees includes the period prior to sowing the crop in the subsequent season.

Table 7.19 shows annual above-ground dry weight production for the four agroforestry treatments and the sole crop. Leaf biomass production by *S. spectabilis* and *G. sepium* was not included as no measurements were made. The *M. volkensii* treatment was the only one to exceed that of the sole crop stand in terms of total production although, if leaf dry weight production for *S. spectabilis* and *G. sepium* were included, total production would probably have been at least equal to that of the sole crop in view of the leaf biomass production recorded for *C. megalocarpus* and *M. volkensii*. The crop yield data suggest that the competitive influence of the roots of *M. volkensii* extended to the edge of the harvested area (~8 m from the tree row) in all except the 1997/98 short rains, when effects were not evident due to the high rainfall. This observation suggests that the yield reductions measured adjacent to *M. volkensii* may have been slightly underestimated in comparison with the other treatments. Decisions based on the observations made in the present study would depend on the needs and requirements of the farmer and the relative value of each of the products. Thus food yields (i.e. maize grain and beans) were greatest in systems containing *C. megalocarpus* or *G. sepium*, whilst wood production was highest with *M. volkensii*. *S. spectabilis* appears less attractive as crop yields and woody biomass production were lower than with *M. volkensii*. As far as livestock fodder production is concerned, the production of maize stover and leafy tree biomass were greater in the *M. volkensii* treatment than with *C. megalocarpus*. The high value timber produced by *M. volkensii* may be the main attraction of this species, as the slightly greater yield loss relative to the other tree species may not be a disincentive.

Table 7.19. Annual above-ground dry weight production (±SE) (t ha^{-1}) for yield components in the agroforestry and sole crop treatments calculated from data collected between 12/3/96 and 23/2/98, with the exception of leaf dry weight which was calculated using data obtained after 5/11/96 and 25/2/98.

	Treatment				
	C. megalocarpus	*M. volkensii*	*S. spectabilis*	*G. sepium*	Sole crop
Maize grain	2.5 ± 0.42	1.3 ± 0.38	1.8 ± 0.45	2.3 ± 0.62	4.5 ± 0.77
Maize stover	3.7 ± 0.27	2.9 ± 0.33	3.7 ± 1.02	3.7 ± 0.38	5.8 ± 1.13
Beans	1.3 ± 0.12	1.5 ± 0.09	1.2 ± 0.22	1.5 ± 0.09	1.7 ± 0.17
Woody material	2.9 ± 0.21	4.9 ± 0.21	3.8 ± 0.21	2.8 ± 0.09	N/A
Tree leaves	1.2	4	-	-	N/A
TOTAL	**11.64**	**14.54**	**10.43**[1]	**10.31**[1]	**11.94**

[1] Tree leaf dry weight production not included in total.

7.4 DISCUSSION

In agreement with previous agroforestry studies in the semi-arid tropics (cf. Section 7.1), water was found to be the primary limiting factor for plant growth in the present study. Limitation of growth in understorey maize and bean crops resulting from reduced availability of light was only apparent during seasons when water supplies were less limiting. This only occurred under artificial shade where there was no tree root influence and during the 1997/98 short rains when, owing to the high rainfall, bean yields were significantly lower on the shaded side of the trees. Alleviation of water stress as a result of reduced incident radiation was important only during the 1996/97 short rains when bean yields were increased in tree shade. The lack of a significant effect of tree shade on maize yield was surprising as shading was expected to be more important in maize than in beans owing to C4 and C3 photosynthetic pathways. Although the effect of shade on the yield of beans may have resulted partly from the extremes of rainfall experienced during the short rainy seasons, Okorio *et al.* (1994) reported that shading by trees induced greater yield reductions in beans than in maize when tree roots were excluded, suggesting that maize may be better able to acclimatise to shading.

Factors influencing maize yields in the 1996 and 1997 long rains were more subtle and difficult to interpret. Maize yields differed between seasons as a result of rainfall totals, rainfall temporal distribution, root competition and differences in nitrogen availability. In 1997, maize yields in the agroforestry treatments were increased both by higher rainfall and lower tree rooting densities than in 1996. Rooting densities were measured in the *G. sepium* and *Grevillea robusta* treatments (Odhiambo *et al.*, in press) and are thought to have declined in 1997 in response to the low rainfall in the preceding 1996/97 short rains. The four agroforestry treatments studied here showed significantly lower yields relative to the sole crop in 1997 than 1996, suggesting that lower tree rooting density was not sufficient to outweigh the effects of the higher leaf areas of the larger trees. The temporal distribution of rainfall in the two maize cropping seasons was also important in determining the final yields. During the 1996 long rains, yields were disproportionately increased relative to the 1997 season by rainfall during the reproductive and grain filling phases, resulting in a significant increase in harvest index. Low leaf nitrogen concentrations in maize plants close to the tree rows during 1997 also played a part in reducing differences between the seasons. This may have resulted from insufficient soil nitrogen supplies for the crops, especially where there was tree root competition, due to poor bean performance in the previous season. However, this may well have been exacerbated by drought and, as leaf nitrogen contents were not excessively low (cf. Section 7.3.2.5), it is proposed that water limitation was the most important factor.

Rainfall interception by the tree canopy, although highly variable between rainfall events and seasons, reduced seasonal water input to the soil beneath the tree canopies by a maximum of 15 % (cf. Figure 7.2). If, as postulated by Wallace, Jackson and Ong (1998), increases in rainfall interception by the tree canopy and decreases in soil evaporation are of similar magnitude, their combined effect on crop growth would be minimal. However, the east-west orientation of the tree rows in the present experiment meant that shade from direct sunlight was restricted to one side of the tree row or the other depending on the season. This effect resulted in soil moisture contents being higher on the shaded side of the tree rows during the 1997 long rains and 1997/98 short rains, although the difference in the latter season was not significant. These results demonstrate that the distribution of rainfall and evapotranspiration are independent around tree rows and that reduced evapotranspiration in tree shade is not necessarily offset by increased water extraction by the trees, as hypothesised by Kessler and Bremen (1991).

The patterns of shading and rainfall adjacent to tree canopies may be expected to change with the orientation of the tree rows which, in practice, is more likely to be governed by farm layout than by ecophysiological considerations. At the present experimental site, where the trees were planted in east-west rows, shading patterns varied little within seasons, with one side of the trees being in direct sunlight and the other in shade throughout the day. However, when the tree rows are oriented in a north-south direction, shading is much more variable within the day, as shown by Reifsnyder (1989); thus shade is cast to the west of the tree row during the morning and to the east in the afternoon, with little annual variability. Previous studies have not demonstrated consistent side-of-row effects in row orientation experiments in the semi-arid tropics (e.g. Rao, Sharma and Ong, 1991; Huxley, 1994), although Chirko *et al.* (1996) found that increased incident PAR during critical developmental stages on the eastern side of north-south rows of *Paulownia* sp. trees improved wheat yields relative to yields to the north and west of the trees. Nygren and Jimenez (1993) asserted that, as shading is likely to be less extreme, north-south rows are preferable to east-west rows in agroforestry systems. Alteration of rainfall patterns are likely to be greatest when the tree rows are perpendicular to the prevailing winds as Darnhofer *et al.* (1989) found that alterations in rainfall were greatest downwind of the trees. At the experimental site, the tree rows were oriented parallel to the prevailing wind and significant differences in rainfall between the north and south sides of the tree rows were not apparent.

Crop yields differed between agroforestry treatments but were never higher than under sole cropping. During both maize cropping seasons, sole crop yields exceeded those in the agroforestry treatments, which were consistently ranked according to soil water availability. In the agroforestry treatments, crop yields were greatest for *C. megalocarpus* and lowest for *M. volkensii*, whilst the treatments containing the two exotic species, *S. spectabilis* and *G. sepium*, produced intermediate yields that were not significantly different. Sole bean yields also exceeded those in the agroforestry treatments, although the difference was not significant during the 1996/97 cropping season, when tree shade had a beneficial influence. Within the agroforestry treatments, bean yield was lowest in the *M. volkensii* treatment during the 1996/97 cropping season due to intense competition for water, but highest during the 1997/98 season due to postulated temporary flooding close to the trees in the other agroforestry treatments in which soil moisture contents were higher. Bean yield was greatest in the *G. sepium* treatment in 1996/97 and in the *S. spectabilis* treatment during the 1997/98 short rains. The leafing phenology of *G. sepium*, which provided limited leaf cover during the short rains (Figure 3.4), produced the highest bean yields of all agroforestry treatments in 1996/97 and a close second in 1997/98. However, yields were lower than those provided by sole crops, indicating that competition was not entirely alleviated. It is likely that under less extreme rainfall conditions than in the two seasons examined (45 and 174 % of long term average rainfall), the leafing pattern of *G. sepium* would result in a more pronounced relative yield increase as the importance of below-ground competition for water would be increased.

Mean annual dry matter production in the *M. volkensii* treatment was 22 % greater than in the sole crop treatment, but was 3 % lower in the *C. megalocarpus* treatment (cf. Table 7.19). The greater dry matter production in the *M. volkensii* treatment occurred at the expense of crop yield and therefore resulted mainly from the longer growing period of the trees, although the higher water use efficiency of *M. volkensii* also contributed (cf. Section 5.3.4). System performance is thus likely to be greater when more off-season rainfall is received than in the present study (9.3 % over two years) or when rainfall exceeds crop requirements, as occurred during the 1997/98 short rains when soil moisture levels exceeded field capacity. Dry weight production in the *C. megalocarpus* treatment was similar to that of the sole crop, suggesting that slower growing tree species, although transpiring less, are less likely to improve overall productivity. Overall productivity in the *S. spectabilis* and *G. sepium* treatments were comparable, although the balance of yield was in favour of the trees in the former. Direct comparison of system performance of all four agroforestry treatments was only possible when tree leaf biomass was excluded as no estimates were made for *S. spectabilis* and *G. sepium*. The treatments involving the two indigenous species, *M. volkensii* and *C. megalocarpus*, were the highest yielding, followed by *S. spectabilis* and *G. sepium*. Inclusion of leaf biomass production in these comparisons would probably reduce the ranking of the *C. megalocarpus* treatment due to their lower leaf turnover. The indigenous or exotic origin of the tree species had no significant effect on crop or system performance and is therefore unlikely to provide any prediction of performance in agroforestry systems.

Agroforestry in semi-arid areas has generally been found to affect crop yields adversely, although the extent to which system productivity is influenced varies depends on, amongst other factors, tree planting density, rainfall and tree size. Cannell, Mobbs and Lawson (1998), using an agroforestry model parameterised for sorghum and a generic broad-leaved tree species, claimed that the sum of grain yield and tree productivity in agroforestry systems would be exceeded by the grain yield of sole crop in areas with less than c. 800 mm annual rainfall, even though the capture of light and water resources is greater in the former system. If it is assumed that plant dry weight comprises c. 50 % carbon and the roots constitute

c. 50 % of tree dry weight, an approximate comparison may be made with the results obtained in the present study, in which total rainfall was 450 and 704 mm in 1996 and 1997 respectively. In both years, the sum of grain and tree dry weight, excluding leaves, in the agroforestry treatments exceeded the sum of grain dry weights for the sole crops in all seasons except the 1997 long rains and for *C. megalocarpus* and *S. spectabilis* in the 1997/98 short rains (cf. Figures 7.21 and 7.22). However, when the leaf biomass production of the trees was included (cf. Table 6.5), total production for the 1997 long rains in the *M. volkensii* treatment exceeded that of the sole crop, and likewise in the 1997/98 short rains sole crop productivity was exceeded by that of the *C. megalocarpus* treatment. Although below-ground dry weight is highly variable and carbon allocation to roots may be higher than that to above ground tissues (Van Noordwijk *et al*, 1996), the results obtained in the present study suggest that agroforestry may be more profitable in terms of overall biomass production than sole cropping systems under considerably drier conditions than suggested by Cannell, Mobbs and Lawson (1998).

Although the increased frequency of crop failure in semi-arid agroforestry systems has led researchers to consider separate planting of trees and crops, (Ong, Odongo, Marshall and Black, 1992; Lott *et al.*, 1998), boundary plantings constitute a distinct scenario where trees are of necessity planted adjacent to crops. Thus, when crop yields are of primary importance, adverse effects may be alleviated by altering tree planting densities, as suggested by Ong *et al.* (1991). Lott *et al.* (2000b) suggested that branch and/or root pruning of the trees may be used at the beginning of the cropping season to minimise below-ground competition for water; however, Sanchez (1995) cited excessive management requirements as one of the reasons for the failure of alley cropping, suggesting that such measures may not be universally applicable. Furthermore, with high value tree products such as timber the premise that tree production is less important than crop yield does not hold and management practices which undermine tree productivity may be ill advised. Alternatively, Payne *et al.* (1998) proposed making use of environmental changes near trees through diversification of crop species. This may prove useful where more drought resistant species may be substituted for the main crop, although, now that global climate is becoming increasingly understood and El Niño forecasts are available in advance of cropping seasons (cf. Section 2.2.1), overall improvements in production may be achieved by substituting higher yielding varieties when increased rainfall is expected. Other issues, such as farmer priorities, seed costs, market status and the time until tree value can be realised must also be considered (Hoekstra, 1994), although the fact that farmers already favour border planting suggests that impediments are few and that increased use of tree species yielding high value product holds considerable potential for the alleviation of poverty.

8 FINAL DISCUSSION AND CONCLUSIONS

8.1 PROSPECTS FOR AGROFORESTRY IN THE SEMI-ARID TROPICS

Agroforestry systems have only recently begun to be quantified in terms of the nature and intensity of biophysical interactions between trees and crops (Nair, 1997; Rao, Nair and Ong, 1997). Efforts have focussed on the exploration of interactions beneficial to crop growth and the means by which the resource use patterns of trees and crops may be spatially or temporally separated to reduce the adverse effect of competition on crop growth. The precedent set by intercropping, in which combinations of C3 and C4 species with dissimilar stature and growth patterns provide yield improvements (Marshall and Willey, 1983), had an important formative influence on the development of these aims and in shaping agroforestry research (Sanchez, 1995; Ong, 1996). However, similar yield advantages are uncommon in agroforestry, for which both the present investigation and previous studies in the semi-arid tropics have shown that reductions in crop yield adjacent to trees are common. These observations are not surprising as the high degree of seasonality and limited supply of water in the semi-arid tropics limit the potential for niche differentiation, while the stature and perennial nature of trees confers competitive dominance. Perhaps more surprising are the serendipitous instances where tree-crop interactions harmonise to promote increases in crop yield adjacent to trees. The most notable examples involve systems containing *Faidherbia albida*, in which several factors, including nitrogen fixation by the trees, their reverse phenology and ability to access deep water tables, combine to increase crop yield (Poschen, 1986; Sanchez, 1995; Roupsard *et al.*, 1999). Similar situations have proved difficult to reproduce experimentally due to the unique nature of the *F. albida* system and the domination of tree-crop interactions by competition for water (Ong and Black, 1994; Ong *et al.*, 1996). Similarly, efforts to improve soil fertility using nitrogen-fixing trees have often failed due to the adverse impact of water extraction by the trees on crop growth (Rao, Nair and Ong, 1997).

Such observations have stimulated exploration of the concept that reductions in crop yield may be offset by values arising either directly or indirectly from the presence of the tree component (e.g. tree products, soil improvement and erosion control). For instance, Gill (1992) concluded that a compromise may have to be sought in the semi-arid tropics between providing tree products and the associated benefits of agroforestry and avoiding excessive reductions in crop yield. The nature of the compromise depends on the relative value of the tree and crop components, the severity of competition, and the availability of land for the establishment of separate woodlots in instances where crop yield is severely reduced. The substantial yield reductions observed for maize and cowpea in a *Grevillea robusta* agroforestry system at ICRAF's Machakos Research Station once the trees had established (Lott *et al.*, 2000b) led the authors to conclude that tree planting densities should either be reduced or the trees and crops grown separately. Growing trees separately is often impossible due to the small farm sizes and the need to maximise crop production. However, boundary and dispersed plantings of trees offer several advantages which may help to resolve some of the problems encountered and provide the opportunity to expand agroforestry into areas where market development or increased demand for tree products dictate. The preference for boundary planting reflects several factors, including the reduced aerial extent of the tree-crop interface and decreased management inputs, which can largely be confined to the dry seasons (Ong *et al.*, 1996), and the requirement to demarcate field boundaries and stabilise hillslopes and terraces (Malik and Sharma, 1990; Verma, 1990; Rao, Nair and Ong 1997). Less obvious benefits of agroforestry such as soil improvement and erosion control are also likely (Young, 1989; van Noordwijk *et al.*, 1996).

Although several agroforestry systems, including those examined here, have been shown to exceed the productivity of sole cropping systems in terms of dry matter production (Corlett *et al.*, 1992b; Ong, 1996; Lott *et al.*, 2000b), equating value with productivity is less useful where the tree component contributes benefits not necessarily associated directly with productivity. Under such circumstances, the *value* of the tree component should be balanced against the *yield* of the crop when determining optimal performance. Estimation of the overall productivity of farm boundary planting systems using results from experimental plots may be done by scaling up results to represent a situation similar to that found in practice. Table 8.1 shows yields for the components of the agroforestry systems studied here estimated using a scenario adapted from that suggested by Rao, Nair and Ong (1997) whereby a 1 ha farm is planted with a 100 m row of trees which reduces crop yield on both sides of the row. Values were calculated using average yields from the two maize and two bean harvests between 1996 and 1998 assuming that crop yields within 8.5 m of the tree rows corresponded to those in the agroforestry treatments and at greater distances corresponded to the yields obtained for sole crops. The values obtained suggest that the effects of boundary planting on crop yield would be limited, as maize yields were reduced by a maximum of 12 % under *M. volkensii* and a minimum of 7 % under *C. megalocarpus.* Bean yields were even less affected, with a maximum reduction of 5 % being predicted under *S. spectabilis* and a minimum of 3 % under *M. volkensii* and *G. sepium.* Although the value of the additional leaf and woody dry weight and other potential indirect benefits provided by the trees referred to previously are likely to offset the negative effect of the relatively small reductions in crop yield where the tree component has proven value, the economic viability of agroforestry systems requires further evaluation by analysis of farmer priorities and practical constraints to adoption.

Table 8.1. Estimated yield components (t ha^{-1} yr^{-1}) in agroforestry systems containing various indigenous and exotic tree species assuming that crop yield was reduced within 8.5 m on either side a 100 m tree row planted on a 1 ha plot (see text for details). N/A, not applicable.

	C. megalocarpus	*M. volkensii*	*S. spectabilis*	*G. sepium*	sole crop
Maize grain	4.13	3.92	4.01	4.09	4.46
Bean seed	1.65	1.67	1.63	1.68	1.72
Woody dry weight	0.50	0.83	0.65	0.49	N/A
Tree leaves	0.20	0.68	-	-	N/A

8.1.1 WIDER APPLICABILITY OF THE RESULTS OBTAINED

The wider applicability the preceding results can be evaluated by assessment of important experimental factors which were not randomly assigned, such as seasonal climate, tree age, row orientation of the trees, and soil-related factors. Total rainfall during the 1996 and 1997 maize cropping seasons was 62 and 88 % of the long term average. The increase in crop yield during the season of greater rainfall was proportionally lower in the agroforestry treatments than under sole cropping due to the higher leaf areas of the trees; thus, average grain yield in the agroforestry treatments was 50 % of that in the sole crop plots in 1996, and 40 % in 1997 (cf. Table 7.6). Odhiambo *et al.* (2000) reported that tree rooting densities for *Gliricidia sepium* and *Grevillea robusta* were lower during the higher rainfall 1997 season, probably reflecting the low rainfall during the preceding 1996/97 short rains. The lower crop yields in the agroforestry treatments relative to sole crops suggest that the observed reduction in tree rooting densities did not reduce competition. These observations suggest that rainfall and tree canopy size are the main determinants of competition with understorey crops but that, due to the observed effects on tree rooting density, information on responses to rainfall during previous seasons may be required for reliable estimation of crop yield. As both maize cropping seasons received below average rainfall, it is difficult to assess how crop yields in the agroforestry treatments differed from sole crops. However, the fact that yields were reduced by artificial shade but were largely unaffected by variation in shade adjacent to the trees suggests that the importance of light limitation increases with soil water content (cf. Section 7.3.2.4, Lott *et al.*, 2000b; Howard, 1995). The effect of shade adjacent to trees might therefore be expected to increase with rainfall, although crop yield might also be expected to increase due to relief of water stress.

During the two seasons when beans were grown (short rains 1996/97 and 1997/98), seasonal rainfall comprised 45 and 174 % of the long-term average. Bean yields in the agroforestry treatments were not significantly different from sole crops during the low rainfall season, but were, on average, 25 % higher during the wetter season (Table 7.13). During the high rainfall 1997/98 season, although the dominant effect was still competition for water, reductions in PAR resulting from shading decreased crop yield adjacent to the trees, whereas during the low rainfall 1996/97 season shading reduced the adverse effect of soil water deficits resulting from competition for water. During seasons when rainfall is closer to the long-term average, lower vapour pressure deficits and higher soil water availability may be expected to reduce the ameliorative effect of shading observed during the 1996/97 low rainfall season, but without neutralising the adverse effect of water extraction by the trees to the extent apparent during the high rainfall 1997/98 season. Thus, crop yields in the agroforestry treatments would be expected to comprise a smaller proportion of those provided by sole crops in seasons when rainfall is closer to the long term average. Therefore the two seasons studied may give a positively biased estimate of bean yield in the agroforestry treatments as compared with sole cropping.

The location of the experiment close to the equator and the east-west orientation of the tree rows resulted in shading pattern which varied more between seasons than within days (cf. Sections 7.3.2.2, 7.3.3.2). During the short rains (October-February), crops to the north of the tree rows were shaded from direct sunlight, whilst during the long rains (March-July), shade was cast to the south of the trees. With north-south tree rows, the shading patterns would vary less between seasons, but the area of shade would move from the west of the tree rows before midday to the eastern side in the afternoon. Available soil water content was higher on the shaded side of the trees in the two seasons when soil moisture measurements were made on both sides of the tree row (Figures 7.5 and 7.15). The combined effects of shading and higher soil moisture levels had no significant effect on maize yields adjacent to trees during the 1997 long rains cropping season (Section 7.3.2.3), suggesting that tree row orientation may have little effect unless rainfall is abundant and light limitation for understorey crops becomes important. Under such conditions, an east-west orientation would produce greater yield differences between the sides of the tree row than a north-south orientation due to the seasonal permanence of the shading patterns induced. The greater effect of shade on bean yields resulted from the unusually high and low rainfall during the two seasons examined, and demonstrated yield differences between sides of the trees close the full extent possible under any row orientation as a result of the high contrast in light microclimate between sides of the east-west tree rows and the opposing effects of shade in the two seasons. As outlined above, tree shade reduced crop yield relative to the unshaded side of the tree row during the high rainfall 1997/98 season, but increased yield during the low rainfall 1996/97 season. The higher soil water content on the shaded side of the tree rows in the former season were not reflected by increases in crop yield as a result of concomitant reductions in PAR availability (Section 7.3.3.3). With north-south rows, yield differences between the sides of the tree rows would be smaller due to the more even distribution of PAR receipts and evaporation rates. Over the whole plot, yields are unlikely to differ greatly as a result of tree orientation. No significant differences in rainfall interception by the tree canopy were found between the northern and southern sides of the tree rows (Section 7.3.1). The lack of difference was partly because the tree rows were aligned parallel to the prevailing wind; larger effects may be anticipated when the tree rows are oriented perpendicular to the prevailing wind. Rainfall interception by the tree canopy reached a maximum of 15 % of the total seasonal rainfall during the 1997 long rains (Figure 7.2), although substantial variability was apparent between seasons and specific rainfall events. Although larger canopies would intercept a greater proportion of the incident rainfall, the effects on crop yield in semi-arid areas where trees are generally small and leaf areas are low, are likely to be unimportant relative to below-ground competition for water.

The patterns of leafing phenology for the four species examined exhibited a general trend for leaf cover to be high during the rainy seasons and for leaf fall to occur during the long dry season (July-October). *S. spectabilis* and *G. sepium* showed limited reductions in leaf cover during the brief dry period between the short and long rainy seasons relative to the indigenous species (Figures 3.1-3.4). The evergreen *C. megalocarpus*, although flushing after the onset of the rains, exhibited a similar phenological pattern to *M. volkensii*, but with a smaller amplitude in the fluctuation of leaf cover. *G. sepium* showed the most unusual leafing phenology in that leaf cover remained low until the beginning of the short rains and only increased slowly to full cover towards the end of the cropping season. This pattern contributed to the relatively high bean yields obtained in both seasons, although during seasons with rainfall closer to the long term average, the leafing pattern would probably result in higher yields relative to sole crops than observed. Such an effect would result from a reduction in the ameliorative effects of shading, evident in the 1996/97 low rainfall season, and increased benefits of lower tree water extraction than evident in the 1997/98 high rainfall season. *G. sepium*, *M. volkensii* and *S. spectabilis* all flushed prior to the beginning of the rains, although this tendency was much less pronounced in *G. sepium*. Such patterns are likely to increase competition with crops and it was partly because of the slow development of leaf cover during the short rains in *C. megalocarpus* that competition was less intense. However, the relatively low stomatal conductances in this species were probably the most important contributory factor in limiting competition for water. Thus, unless a specific tree species exhibits a reverse phenological pattern, leafing phenology may be less important than leaf area and stomatal conductance in influencing crop production as a result of the sensitivity of crop yields to water deficits during reproductive development (Norman, Pearson and Searle, 1995; Monhouche, Ruget and Delecolle, 1998). The fact that soil moisture contents in the agroforestry treatments were lower than in the sole crop plots shows that a developing tree canopy drawing water from the soil may reduce crop yield by imposing a soil water deficit during the reproductive phase of crop growth. However, once its root system is fully developed, the crop may be better able to compete for water; further research is required to test this hypothesis.

Modelling of gas exchange by *M. volkensii* and *C. megalocarpus* over three cropping and three dry seasons indicated that, overall, assimilation and transpiration were respectively 49 and 11 % greater in *M. volkensii* than in *C. megalocarpus* (Section 5.3.4). The differences between species were smaller during the dry seasons than during the cropping periods due to the greater increase in leaf area in *M. volkensii*. However, towards the end of the 1997/98 short rains, when high rainfall promoted larger increases in the leaf area of *C. megalocarpus* and induced leaf fall in *M. volkensii*, the differences in daily assimilation decreased and daily total transpiration was greater in *C. megalocarpus* than in *M. volkensii*. These results show that the relative competitiveness of the two species may be reversed in high rainfall areas, for which *M. volkensii* may be unsuitable due to its apparent lack of adaptation to wetter soil conditions. Although trees are unlikely to be selected for use in agroforestry systems solely on the basis of water use efficiency, the 35 % higher modelled canopy value for *M. volkensii* is an attractive attribute which may influence overall system productivity without affecting crop yield. As no estimates of growth and maintenance respiration rates of tree roots, stems or branches were made, estimation of the net productivity of the trees was not possible. However, the decreasing growth rates of the trees with time showed that, although assimilation increases with tree size and leaf area, productivity decreased as the trees aged.

The influence of tree age and size on system productivity results from the decreasing ratio of growth respiration to maintenance respiration as tree size increases (Kira, 1975). The outcome is a reduction in net tree productivity despite concurrent increases in gross productivity, although competition with crops continues to increase due to increased shading and extraction of soil water. Pruning, by reducing the standing volume of respiring tree biomass and containing competition with crops, may represent the most effective means of reducing the importance of these effects; future studies should include pruning treatments and longer established agroforestry systems to establish their effects on system productivity and economic viability. These objectives may also be partly addressed using modelling approaches, which should include some estimation of the optimum rotation length for maximising profits by determining the point when the current and mean annual growth increments of trees become equal under different management strategies.

The location of the present experiment on deep, relatively nutrient rich soil inevitably imposes some limitations on the scope of the findings. Soils which are shallower, have a lower water holding capacity, or are on sloping sites will generally support lower levels of plant productivity, and competition with trees for limited soil water supplies may result in disproportionately greater reductions in crop yield. However, productivity benefits associated with reductions in deep drainage, runoff and evaporation (Young, 1989; Wallace, 1996) should outweigh the negative effects, especially where valuable trees are planted at low density or along field boundaries. In poorer soils, nutrient extraction by trees and reduced proliferation of crop roots close to the trees will exacerbate deficiencies; however, in semi-arid regions, although overall productivity will be reduced, nutrient deficiencies are likely to be important only during high rainfall seasons when competition for water is reduced.

When considering the wider applicability of the results, the data shown in Table 8.1 provide the basis for decisions to be made depending on whether the productivity and value of the trees are sufficient to offset associated reductions in crop yield. The decision may depend partly on the length of time required to realise the benefits from newly planted trees (Hoekstra, 1994). David (1995) concluded that, although farmers appeared to be convinced of the benefits of hedgerow intercropping, most were deterred by the reductions in crop productivity and did not recognise the long term benefits. This obstacle to adoption may be partially surmounted by fodder production from trees, although reduced initial planting densities would provide a more definitive method for lessening the impact of trees. Several other factors need to be addressed to facilitate the adoption of agroforestry in semi-arid areas, although the spontaneity of tree planting in some parts of Kenya (Stewart and Blomley, 1994; Hoekstra, 1994) suggests that the barriers to adoption are not insurmountable. Hoekstra (1994) identified government policy concerning the prices of fertiliser, tree seedlings and food commodities, limitations imposed by the management capabilities of farmers, and the labour costs involved in establishing and maintaining the system as important constraints influencing the adoption and economic viability of agroforestry. Scherr (1992) outlined the importance of increasing awareness and confidence in agroforestry, improving market access, encouraging market development and matching extension methods to local circumstances by understanding the needs of households and the strengths and weaknesses of community resources.

8.1.2 SELECTION OF SUITABLE TREE SPECIES

The tree species examined here represented a range of growth rates, phenological patterns and nutritional strategies and included both commonly used exotics and less well known indigenous species. The results showed that there was no significant difference in crop yields between agroforestry treatments containing indigenous and exotic tree species (Sections 7.3.2.3, 7.3.3.3), suggesting that the geographic or climatic origin of individual tree species cannot be used to predict their suitability for specific systems, although climate in a species' native habitat may provide guidance on the range of climates most suitable for planting. The leaf fall observed in *M. volkensii* under unusually wet conditions would have less effect on competition for water with associated crops than leaf fall during drier conditions, although consequent reductions in the extent of shading may nevertheless have contributed to an increase crop yield. The introduction of deciduous exotic species from unimodal rainfall areas to bimodal areas may produce phenological responses which alleviate competition with crops, as was the case with *G. sepium*; however, speculative trials may not be worthwhile unless the tree species under consideration offer other proven values.

The evergreen *C. megalocarpus* is commonly planted to provide shade, fuelwood, poles and mulch in East Africa. Its relatively mild competitive impact on associated crops, resulting from the occurrence of leaf flushing after the onset of the rains and its relatively low stomatal conductance, make this species ideal for such purposes where the relatively low value of the products means that larger reductions in crop yield may be economically unsustainable. Observations of larger trees in wetter climatic zones and the rapid increase in leaf area with high rainfall during the 1997/98 short growing season (Figure 4.5) showed that this species is better adapted to areas of higher rainfall, where productivity is likely to be increased. Selection for single-stemmed, straight-boled genotypes would increase the value and viability of the species for use in agroforestry.

The success of the other indigenous species, *M. volkensii*, has already been documented for the semi-arid areas of eastern Kenya (Stewart and Blomley, 1994; Tedd, 1997), where farmers have been planting this species in dispersed arrangements within crops at spacings of 10-15 m and along boundaries for at least 30-40 years. Crown thinning is widely practised to maintain a clear bole and limit competition with crops, probably primarily for water rather than light (Stewart and Blomley, 1994). Problems remain with mass propagation, although several methods have been adopted locally to improve seed germination (Stewart and Blomley, 1994). The timber value of *M. volkensii* has been the main impetus for its adoption by farmers, with a value of $15 for a mature standing tree (c. 20 years) being reported by Stewart and Blomley (1994). However, economic value varies from region to region and may be difficult to ascertain due to the variety of forms in which the products may be sold (Tedd, 1997). The high productivity and fodder quality of leaves and new growth of *M. volkensii* have largely gone unrecognised (Milimo, 1994), but can only increase the value of the species during the period between planting and felling to realise the economic potential of the timber.

Although the uniformity and straight stems of *S. spectabilis* are likely to enhance its economic potential, there are no recorded estimates of its economic value in Kenya, where it is not widely planted other than as an ornamental species. Its competitiveness would necessitate realisation of a high economic value relative to the other tree species examined to offset consequent reductions in crop yield. Further investigation of the suitability of this species to meet farmers' requirements is therefore desirable. The other exotic species examined, *G. sepium*, is used for several purposes, including the production of fuelwood, charcoal, timber, poles, mulch, green manure and fodder (ICRAF, 1992), so increasing the likelihood that the relatively small reductions in the yields of associated crops may be offset. As a leguminous species, nitrogen fixation may further its potential in areas where the soil is nitrogen-deficient and labour is available to manage the system for nutrient benefits (Shepherd, 1996). In the present experiment, tree form was poor and the trees were subject to constant attack by insects and fungal pathogens; the effects on tree productivity were not investigated but, if repeated more widely, these problems may severely limit the popularity of this species.

The best opportunity for agroforestry to succeed in the semi-arid tropics is to use trees which provide high value products, so minimising the importance of reductions in crop yield. Economic value and the existence of local markets are highly variable and, although some species may prove universally useful, the promotion of existing locally important species will reduce sociological and anthropological impediments to the adoption of agroforestry.

8.2 FUTURE DIRECTIONS

The acceptance that agroforestry in the semi-arid tropics will, in most cases, reduce crop yields requires that research be focussed on offsetting these reductions against direct and indirect values associated with agroforestry. Lack of off-season rainfall, absence of a water table, and the invariability of tree leafing phenology limit the possibility for spatial or temporal complementarity. Similarly, efforts to determine ways by which system productivity may be increased relative to sole crops generally do not take account of the fact that tree and crop yields are not interchangeable other than through trade. These factors suggest that economic value rather than the biological productivity of the system should be the focus of future research. It is proposed that research efforts should be directed towards improvement and optimisation of boundary and scattered tree planting systems with potential for fulfilling farmers' needs and providing environmental services. This may be achieved either by encouraging the adoption of recognised species or through domestication of indigenous species by a process of germplasm collection and genetic improvement (Leakey and Simons, 1997). These activities need to be linked to market creation and expansion and improvement of management techniques with emphasis on pruning to reduce competition with crops where necessary and increase clear bole length for timber production.

The importance of economic assessment of agroforestry is increased where the value of the trees is a deciding factor. Determination of tree growth rates and the extent and severity of competition with crops in systems containing older and larger trees are crucial for determining economic viability and would ideally include assessment of profit-maximising planting densities and rotation lengths, as outlined above. Burley (1982) has referred to the need to continue trials over a number of years at various locations in Kenya and other areas where rainfall is erratic and there is a high degree of climatic heterogeneity which precludes extensive extrapolation of results from a single or limited number of sites. These objectives may be partly achieved through modelling, although concurrent field trials are generally required as existing models are often not widely validated due to the lack of appropriate experimental datasets providing the parameters required as model input. Models offer a rapid and efficient means of testing hypotheses and scenarios in agroforestry, and their use should become more widespread as they become easier to use and more reliable following further validation.

Recent attempts to develop techniques which allow rapid determination of the extent of below-ground competition by assessing rooting patterns have encountered difficulties (Odhiambo *et al.*, 2000) resulting from a lack of correlation between fine rooting density and lateral root dimensions and the unpredictability of rooting phenology. However, such studies are still in their infancy and there is great potential to expand below-ground theory to match that developed to describe canopy function. The numerous observations that tree root densities are greatest in the surface soil horizons suggest that measurements of stomatal conductance and leaf area may provide the best opportunity for rapid assessment of the competitiveness of trees. However, assessment of the leaf area of isolated trees remains problematic and a low cost, rapid method would greatly simplify efforts. The observations of leafing phenology reported here suggest that a wide range of tree species are likely to flush before the beginning of the cropping season. A rapid method for assessing competitiveness might therefore be achieved on the basis of phenological observations made around the end of the dry season.

8.3 CONCLUSIONS

- Soil water availability is the most important constraint on plant growth and by far the most important determinant of competition between trees and crops in agroforestry systems in the semi-arid tropics.

- Biomass production on agricultural land in the semi-arid tropics may be increased by implementation of agroforestry.

- Crop yields are almost invariably reduced adjacent to trees; in practice, the primary determining factors are the leaf area and stomatal conductance of the trees.

- Maize yields were reduced by 30-72 % and bean yields by 13-75 % within 8.5 m of trees during the fourth and fifth years after tree planting; crop yields were greatest in the *C. megalocarpus* treatment, followed by *G. sepium*, *S. spectabilis* and *M. volkensii.*

- Mean woody biomass yields for the fourth and fifth years after tree planting were greatest for *M. volkensii*, followed by *S. spectabilis*, *C. megalocarpus* and *G. sepium.*

- Leaf flushing subsequent to the beginning of cropping seasons reduces competition between trees and crops; where this does not occur naturally, pruning may provide a similar effect.

- The evergreen or deciduous leafing patterns of trees cannot be used in isolation to infer competitiveness.

- Similarly, the exotic or indigenous origin of tree species cannot be used to infer competitiveness or growth rate.

- The influence of rainfall interception by the tree canopy is small relative to water deficits resulting from uptake of soil water by the trees.

- Future research should focus on valuable tree species which offset losses of system value resulting from reductions in crop yield. Improvement of species already favoured by farmers, such *M. volkensii*, offers greater potential due to the reduced importance of sociological and anthropological constraints to adoption.

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1. NEUTRON PROBE CALIBRATION

The neutron probe (Institute of Hydrology, Wallingford, UK), used for measuring soil water content, was calibrated with gravimetric measurements of the water content in soils samples taken from the same depths at which neutron probe measurements were made in the experimental plots. Eight neutron probe access tubes were installed in two replicates of four tubes, one replicate adjacent to the east and one to the west of the experimental plots (cf. Figure 2.2). The tubes were left for several weeks to allow the soil around them to settle before water was applied to the soil surface, over the course of a week. Water was applied at three intensities around three of the four access tubes in each replicate to provide a range of soil water contents including a single tube in each replicate around which no water was applied. As on all occasions when neutron probe measurements were made, three water counts (i.e. number of reflected neutrons detected in 100% water) were first taken using an access tube supported in the centre of an oil drum filled with water. (N.B. Division of neutron probe counts made in the field by the water count removes variation related to the strength of the neutron source). Measurements were then taken at 20 cm depth intervals between 20 cm and 120 cm below the soil surface. Following these measurements an area around each tube was excavated and three soil samples were taken at each depth using open ended tubes of known volume. The soil from each sample was placed in an air tight steel tin, returned to the laboratory and weighed. The open tins were then placed in an oven and the soil dried at 90 °C to constant weight before being re-weighing. Water content was given by the wet minus the dry weight.

Figure A1 shows the correlation between weight by volume percent water content and scaled neutron probe count (soil measurement count/water count). Analysis of variance of counts per % water content showed a non-significant effect due to the level of water application (p=0.294), a non-significant depth effect (p=0.147) and a non-significant treatment*depth interaction (p=0.973). Therefore all measurements were combined to provide a regression equation to convert neutron probe measurements into soil water contents as follows:

$$\%\ \text{water content} = 73.01 \times \left(\frac{\text{count}}{\text{water count}}\right) - 1.65$$

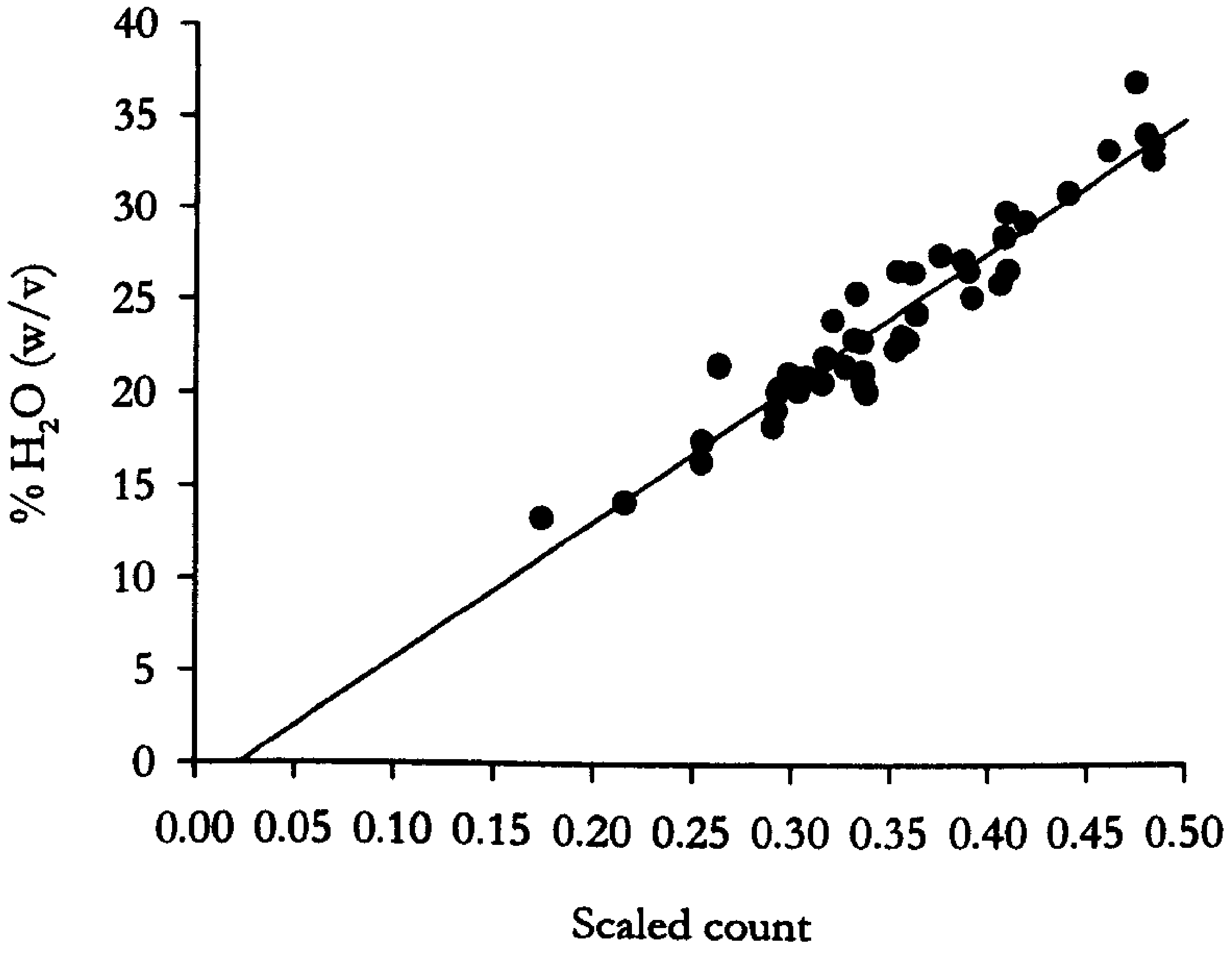


Figure A1. Percent water content (weight/volume) against scaled count (neutron probe soil count/water count). $r^2 = 0.91$

2. PHENOPHASE DIFFERENCES BETWEEN REPLICATES

Table A1. *P* values from Kruskal-Wallis tests for the significance of replicate differences in phenophase scores for each scoring occasion. * and ** indicate significance at $p<0.05$ and $p<0.01$; ns indicates a non-significant difference.

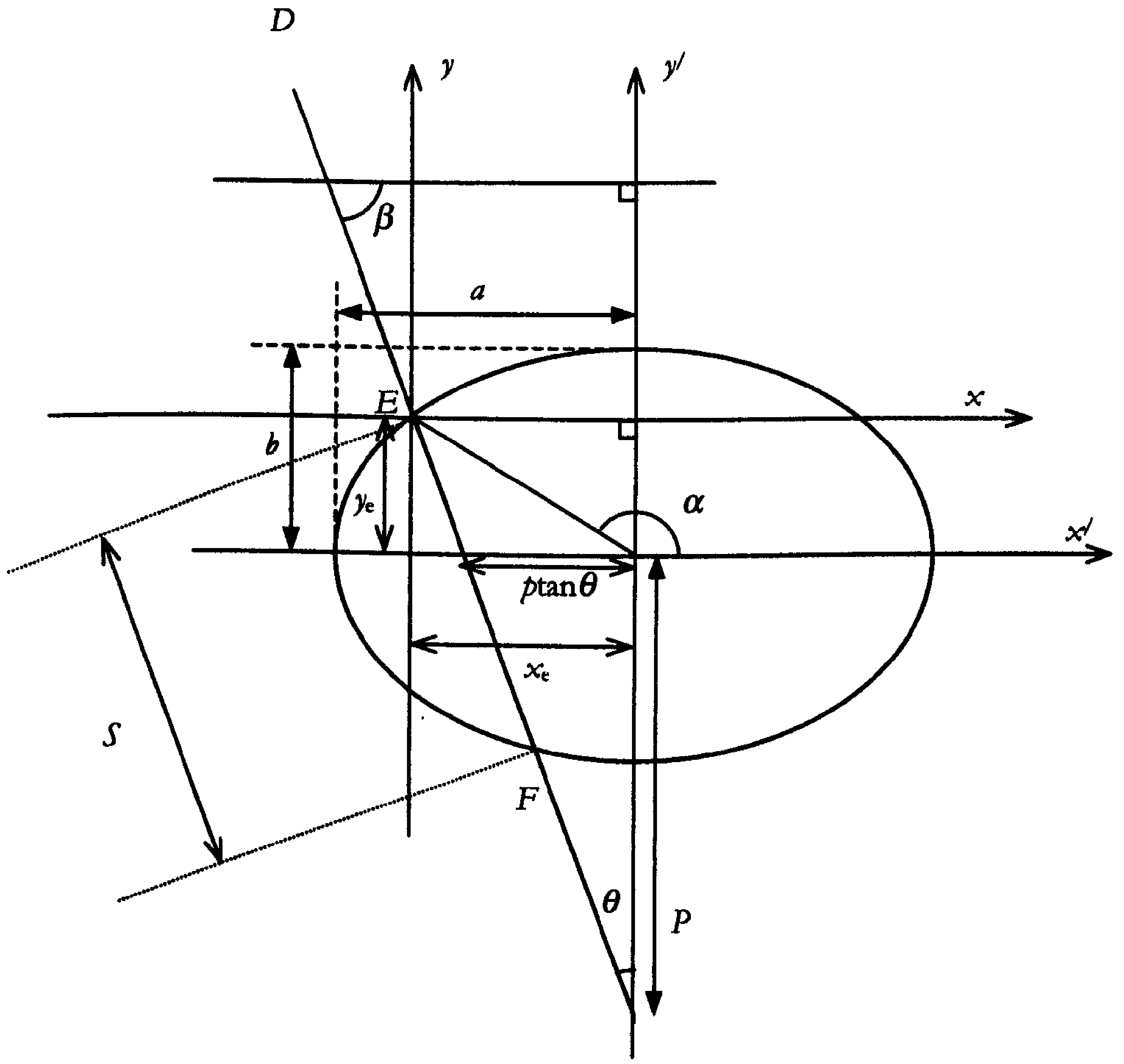
	C. megalocarpus			*M. volkensii*			*S. spectabilis*			*G. sepium*		
Date	leaf cover	leaf flushing	leaf fall	leaf cover	leaf flushing	leaf fall	leaf cover	leaf flushing	leaf fall	leaf cover	leaf flushing	leaf fall
11/03/96	0.56 (ns)	<0.01 (**)	0.01 (*)	0.31 (ns)	0.12 (ns)	0.06 (ns)	0.04 (*)	0.76 ((ns))	0.92 (ns)	0.01 (*)	0.09 (ns)	0.39 (ns)
27/03/96	ns	ns	<0.01 (**)	0.54 (ns)	0.14 (ns)	0.04 (*)	0.5 (ns)	0.22 (ns)	ns	<0.01 (**)	0.16 (ns)	ns
15/04/96	0.1 (ns)	ns	0.39 (ns)	0.52 (ns)	<0.01 (**)	0.12 (ns)	0.1 (ns)	0.01 (*)	<0.01 (**)	0.24 (ns)	<0.01 (**)	<0.01 (**)
29/04/96	<0.01 (**)	<0.01 (**)	ns	0.28 (ns)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	0.56 (ns)	0.09 (ns)	<0.01 (**)
13/05/96	ns	ns	ns	0.01 (*)	<0.01 (**)	0.39 (ns)	0.01 (*)	0.28 (ns)	0.39 (ns)	0.23 (ns)	0.3 (ns)	ns
03/06/96	ns	ns	ns	0.01 (*)	<0.01 (**)	0.39 (ns)						
17/06/96	ns	<0.01 (**)	ns	<0.01 (**)	<0.01 (**)	<0.01 (**)	0.01 (*)	<0.01 (**)	<0.01 (**)	0.28 (ns)	<0.01 (**)	0.28 (ns)
01/07/96	ns	ns	ns	<0.01 (**)	0.01 (*)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	0.02 (*)	0.03 (*)	ns
15/07/96	ns	ns	ns	0.45 (ns)	0.04 (*)	0.03 (*)	0.02 (*)	<0.01 (**)	0.01 (*)	0.09 (ns)	0.11 (ns)	0.1 (ns)
29/07/96	ns	<0.01 (**)	ns	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)
19/08/96	ns	ns	ns	0.55 (ns)	0.56 (ns)	<0.01 (**)	ns	ns	ns	0.46 (ns)	0.03 (*)	<0.01 (**)
28/08/96	ns	ns	ns	0.4 (ns)	0.14 (ns)	0.08 (ns)	<0.01 (**)	<0.01 (**)	0.1 (ns)	0.67 (ns)	<0.01 (**)	0.29 (ns)
19/09/96	ns	<0.01 (**)	ns	0.74 (ns)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	<0.01 (**)	0.12 (ns)	<0.01 (**)	<0.01 (**)
24/10/96	ns	ns	<0.01 (**)	0.16 (ns)	<0.01 (**)	0.39 (ns)	ns	ns	0.1 (ns)	0.14 (ns)	0.02 (*)	0.42 (ns)
15/11/96	0.01 (*)	<0.01 (**)	ns	ns	ns	<0.01 (**)	ns	ns	ns	0.19 (ns)	0.03 (*)	0.11 (ns)
25/11/96	<0.01 (**)	<0.01 (**)	ns	ns	ns	ns	ns	<0.01 (**)	<0.01 (**)	0.09 (ns)	<0.01 (**)	<0.01 (**)
27/12/96	ns	ns	ns	ns	ns	<0.01 (**)	0.1 (ns)	<0.01 (**)	<0.01 (**)	<0.01 (**)	ns	<0.01 (**)
13/01/97	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.39 (ns)	ns	ns
30/01/97	ns	<0.01 (**)	ns	<0.01 (**)	<0.01 (**)	<0.01 (**)	ns	ns	ns			
17/02/97	ns	ns	ns	0.54 (ns)	<0.01 (**)	<0.01 (**)	ns	<0.01 (**)	ns	ns	<0.01 (**)	ns
03/03/97	<0.01 (**)	0.28 (ns)	<0.01 (**)	0.39 (ns)	<0.01 (**)	<0.01 (**)	0.56 (ns)	ns	ns	0.02 (*)	<0.01 (**)	ns

continued overleaf

	C. megalocarpus			*M. volkensii*			*S. spectabilis*			*G. sepium*		
Date	leaf cover	leaf flushing	leaf fall	leaf cover	leaf flushing	leaf fall	leaf cover	leaf flushing	leaf fall	leaf cover	leaf flushing	leaf fall
14/03/97	0.56 (ns)	ns	ns	0.45 (ns)	0.49 (ns)	0.21 (ns)	<0.01 (**)	ns	ns	0.01 (*)	ns	ns
04/04/97	0.19 (ns)	ns	0.09 (ns)	0.01 (*)	0.28 (ns)	<0.01 (**)	0.28 (ns)	ns	ns	0.17 (ns)	ns	ns
15/04/97	ns	ns	ns	ns	ns	ns	<0.01 (**)	<0.01 (**)	ns	ns	ns	ns
28/04/97	ns	ns	ns	ns	ns	0.01 (*)	<0.01 (**)	0.11 (ns)	ns	ns	ns	ns
12/05/97	ns	ns	ns	ns	ns	ns	<0.01 (**)	0.15 (ns)	ns	ns	ns	ns
30/05/97	ns	ns	0.39 (ns)	0.1 (ns)	0.1 (ns)	0.1 (ns)	<0.01 (**)	0.56 (ns)	ns	0.39 (ns)	0.1 (ns)	<0.01 (**)
15/06/97	ns	ns	ns	ns	ns	ns	ns	0.51 (ns)	ns	ns	ns	ns
30/06/97	ns	ns	0.39 (ns)	ns	0.23 (ns)	ns	<0.01 (**)	0.1 (ns)	ns	0.39 (ns)	0.1 (ns)	<0.01 (**)
15/07/97	ns	0.39 (ns)	ns	0.02 (*)	0.01 (*)	<0.01 (**)	<0.01 (**)	0.02 (*)	<0.01 (**)	0.12 (ns)	<0.01 (**)	<0.01 (**)
01/08/97	ns	ns	ns	<0.01 (**)	0.03 (*)	<0.01 (**)	0.02 (*)	<0.01 (**)	<0.01 (**)	0.12 (ns)	0.02 (*)	<0.01 (**)
15/08/97	ns	0.09 (ns)	ns	0.15 (ns)	0.19 (ns)	<0.01 (**)	0.02 (*)	ns	0.02 (*)	<0.01 (**)	<0.01 (**)	<0.01 (**)
01/09/97	0.39 (ns)	0.39 (ns)	0.27 (ns)	0.1 (ns)	0.11 (ns)	<0.01 (**)	<0.01 (**)	<0.01 (**)	0.1 (ns)	0.01 (*)	0.05 (ns)	0.23 (ns)
15/09/97	ns	ns	ns	<0.01 (**)	0.39 (ns)	<0.01 (**)	0.02 (*)	ns	0.39 (ns)	<0.01 (**)	<0.01 (**)	0.2 (ns)
01/10/97	ns	ns	ns	0.21 (ns)	0.29 (ns)	<0.01 (**)	0.02 (*)	0.39 (ns)	0.39 (ns)	0.96 (ns)	0.01 (*)	0.96 (ns)
15/10/97	<0.01 (**)	ns	<0.01 (**)	0.39 (ns)	<0.01 (**)	0.49 (ns)	<0.01 (**)	0.39 (ns)	ns	0.04 (*)	0.26 (ns)	ns
01/11/97	<0.01 (**)	ns	<0.01 (**)	<0.01 (**)	<0.01 (**)	0.04 (*)	ns	ns	ns	0.1 (ns)	0.39 (ns)	ns
15/11/97	<0.01 (**)	0.02 (*)	0.01 (*)	0.1 (ns)	ns	<0.01 (**)	ns	ns	ns	0.02 (*)	<0.01 (**)	ns
30/11/97	ns	ns	0.02 (*)	ns	ns	ns	ns	ns	ns	0.05 (ns)	ns	ns
01/01/98	ns	ns	ns	ns	ns	<0.01 (**)	ns	ns	ns	<0.01 (**)	0.39 (ns)	ns
23/01/98	ns	ns	ns	0.39 (ns)	ns	<0.01 (**)	ns	ns	<0.01 (**)	ns	ns	ns

3. RAY PATH LENGTH CALCULATION

Derivation of formula to determine ray path length, S, through a tree canopy with elliptical cross section.



S – path length
D – notional ray
E – entry point of notional ray into canopy
F – exit point of notional ray from canopy
P – distance between sensor and centre of canopy
a – ellipse semi-axis length (distance of edge of canopy from tree row)
b – ellipse semi-axis length (½ (canopy top height – canopy bottom height))
θ – zenith angle (ring view angle)
β – 90° minus θ
α – angle between horizontal at canopy centre and E
x_e and y_e are co-ordinates relating E the Cartesian origin to the ellipsoid origin $x^{/},y^{/} = (0,0)$

Figure A2. Ellipse defined from canopy measurements to calculate path length, S. Solid headed arrows represent dimensions taken from tree measurements. Open headed arrows represent calculated dimensions.

The position of *E*, the entry point of a notional ray of angle θ from the vertical, is found in terms of α, from the measured dimensions *P*, *a* and *b*. *P* is the distance of the canopy analyser sensor below the centre of the canopy and a and b are defined by canopy dimensions.

$$x_e = a\cos\alpha \qquad \text{A 1.1}$$

$$y_e = b\sin\alpha \qquad \text{A 1.2}$$

$$x_e - p\tan\theta = \tan\theta y_e \qquad \text{A 1.3}$$

$$a\cos\alpha - p\tan\theta = \tan\theta \cdot b\sin\alpha \qquad \text{A 1.4}$$

$$\tan\theta = \frac{a\cos\alpha}{b\sin\alpha + p} \qquad \text{A 1.5}$$

rearranging and squaring both sides

$$\tan^2\theta(b\sin\alpha + p)^2 = a^2\cos^2\alpha \qquad \text{A 1.6}$$

and by De Moivres theorem:

$$1 = \sin^2\alpha + \cos^2\alpha \qquad \text{A 1.7}$$

$$p^2\tan^2\theta + 2pb\sin\alpha\tan^2\theta + \tan^2\theta b^2\sin^2\alpha = a^2(1-\sin\alpha)^2 \qquad \text{A 1.8}$$

$$= a^2 - a^2\sin^2\alpha \qquad \text{A 1.9}$$

rearranging gives

$$\sin^2\alpha(a^2 + b^2\tan^2\theta) + \sin\alpha 2pb\tan^2\theta + (p^2\tan^2\theta - a^2) = 0 \qquad \text{A 1.10}$$

the solves to

$$\alpha = \sin^{-1}\left(\frac{-pb\tan^2\theta \pm a(a^2 + \tan^2\theta(b^2 - p^2))^{1/2}}{a^2 + b^2\tan^2\theta}\right) \qquad \text{A 1.11}$$

both positive and negative solutions give correct path length although the latter is negative.

To find *S* from β and *E*. *E*, defined as the centre of Cartesian origin (0, 0) is related to ellipsoid co-ordinates x' and y' by

$$x' - x_e = x \qquad \text{A 1.12}$$

$$y' - y_e = y \qquad \text{A 1.13}$$

and

$$x_e = a\cos\alpha \qquad \text{A 1.14}$$

$$y_e = b\sin\alpha \qquad \text{A 1.15}$$

the straight line *D* has an intercept equal to zero as the line is defined as passing through the Cartesian origin therefore

$$y = \tan\beta x \qquad \text{A 1.16}$$

for an ellipse

$$\frac{x^2}{a^2} + \frac{y^2}{b^2} = 1 \qquad \text{A 1.17}$$

and for this ellipse

$$\frac{x'^2}{a^2} + \frac{y'^2}{b^2} = 1 \qquad \text{A 1.18}$$

substituting x' and y'

$$\left(\frac{x + x_e}{a}\right)^2 + \left(\frac{y + y_e}{b}\right)^2 = 1 \qquad \text{A 1.19}$$

combining equations A 1.16 and A 1.19

$$\left(\frac{x + x_e}{a}\right)^2 + \left(\frac{\tan\beta x + y_e}{b}\right)^2 = 1 \qquad \text{A 1.20}$$

The solutions to this quadratic are 0 and

$$x = \frac{-(b^2 2x_e + a^2 2y_e \tan\theta)}{(b^2 + a^2 \tan^2\theta)} \qquad \text{A 1.21}$$

therefore, from equation A 1.16

$$y = \tan\beta\left(\frac{-(b^2 2x_e + a^2 2y_e \tan\theta)}{(b^2 + a^2 \tan^2\theta)}\right) \qquad \text{A 1.22}$$

by Pythagoras' theorem

$$S^2 = x^2 + y^2 \qquad \text{A 1.23}$$

$$S = \frac{2ab(b\cos\alpha + a\sin\alpha\tan\beta)}{\cos\beta(b^2 + a^2\tan^2\beta)} \qquad \text{A 1.24}$$

4. CALIBRATION OF CIRAS-1 PORTABLE PHOTOSYNTHESIS SYSTEM

Infra-red gas analysers.

Calibration of the carbon dioxide measurement function of the infra-red gas analysers (IRGAs) was done by attaching an air source of known carbon dioxide concentration to the reference inlet pipe of the CIRAS-1 and following the calibration routines contained in the software and detailed in the CIRAS-1 manual (PP systems, 1994). The calibration gas, supplied by Cryoservice (Blackpole Road, Worcester, UK) was of certified concentration 341.9 ppm ± 2%.

Calibration of the IRGAs in their water vapour measuring capacity was done following the method given by the manufacturers. This involved bubbling air through water, the temperature of which was measured using a mercury thermometer. An air stone, available from pet shops and aquarium specialists, was used to diffuse the air bubbles and facilitate saturation of the air with water vapour. The air was then passed into the CIRAS-1 and the calibration performed by the instrument software.

Leaf boundary layer resistance within Parkinson leaf cuvette

Boundary layer resistance of a surface within the cuvette is necessary for calculation of stomatal conductance and may vary between cuvettes depending on the effectiveness of the stirring fan within the cuvette head. Measurement of boundary layer resistance in the narrow Parkinson leaf cuvette, used for all measurements here, was performed by the method recommended by PP Systems (1994). This involved suspending a strip of wet filter paper, with an exposed area of 2cm^2, across the width of the closed cuvette and following the keypad inputs for the CIRUS-1 to perform the necessary calculation.

PAR sensor

The PAR sensor was calibrated under a range of daylight conditions against a recently calibrated Quantum sensor (Skye Instruments, Llandrindod Wells, UK) attached to a Campbell 21x data logger (Campbell Scientific, Shepshed, UK). Linear regression was used determine calibration factors which were subsequently applied to the measured values.

Temperature sensors

The air and leaf temperature thermistors were not calibrated as the manufacturers state that they should not require recalibration even if sensors are replaced.

5. MAESTRA INPUT PARAMETERS

Namelists are given in bold in the left-hand column followed by the parameter name.

confile.dat

NAMELIST PARAMETER	VALUE	DESCRIPTION
CONTROL		
IOHRLY	1	Flag indicating hourly output required
IOTUTD	1	Flag indicating diffuse transmittances to be calculated daily
IORESP	0	Flag indicating no respiration flux output required
IOHIST	0	Flag indicating no PAR histogram required
MODEL		
MODELGS	0	Flag to indicate use of Jarvis stomatal conductance model
MODELRD	0	Flag to indicate how RD0 parameters should be read in (not used)
MODELJM	0	Flag to indicate how JMAX and VCMAX parameters should be read in (not used)
ITERMAX	0	Number of iterations to find leaf temperature. 0 → leaf temperature = air temperature
MODELSS	0	Flag to indicate that photosynthesis calculations to be done for sun and shade leaves separately
TREESCON		
NOTREES	18	Number of trees considered in calculating shading of the target tree
NOTARGET	10	Target tree number
DATES		
START	'01/06/97' *	Starting date for simulation
END	'31/12/97' *	End date for the simulation
DIFFANG		
NOLAY	6	Number of layers in the crown assumed when calculating radiation interception
NZEN	5	Number of zenith angles for which diffuse transmittances are calculated
NAZ	11	Number of azimuth angles for which diffuse transmittances are calculated

* figures included as example

met.dat

NAMELIST PARAMETER	VALUE	DESCRIPTION
ENVIRON		
PRESS	86900	Atmospheric pressure (Pa)
CA	345	Atmospheric CO_2 concentration μmol mol^{-1}
DIFSKY	0	Controls distribution of diffuse radiation incident from the sky. Uniform = 0
LATLONG		
LATHEM	'S'	Hemisphere (N/S)
LAT	01 33 0	Latitude
LONHEM	'E'	Hemisphere (W/E)
LONG	37 14 0	Longitude
TZLONG	45	Longitude of the meridian of the time zone
FORMAT		
DAYORHR	1	Flag indicating met file data is hourly
START	'01/01/97'*	Start date of the met data
END	'31/12/97'*	End date of the met data
NOCOLUMNS	7	Number of columns of meteorological data
COLUMNS		list of names describing the contents of each column in following table
	'DATE'	Date (DD/MM/YY)
	'TIME'	Hour (HH:MM)
	'WIND'	windspeed above the canopy (m s^{-1})
	'TAIR'	Air temperature (°C)
	'TSOIL'	Soil temperature (°C)
	'VPD'	Vapour pressure deficit (Pa)
	'PAR'	Hourly incident photosynthetically active radiation (μmol m^{-2} s^{-1})

* figures included as example

phy.dat

NAMELIST	VALUE		DESCRIPTION
PARAMETER	*C. megalocarpus*	*M. volkensii*	
ABSORP			
NOLAYERS	1	1	Number of crown layers for which reflectance and transmittance are specified
RHOSOL	0.10 0.30 0.05	0.10 0.30 0.05	Soil reflectance in three wavebands (PAR, NIR, thermal). Estimated (Monteith and Unsworth, 1990)
ATAU	0.02 0.32 0.01	0.02 0.32 0.01	Leaf transmittance in three wavebands (PAR and NIR measured in four Sahelian species (Levy, 1995), thermal estimated (Monteith and Unsworth, 1990))
ARHO	0.05 0.45 0.05	0.05 0.45 0.05	Leaf reflectance in three wavebands (measured in four Sahelian species (Levy, 1995) , thermal estimated (Monteith and Unsworth, 1990))
JARGS			
GSREF	0.3433	0.481	Maximum stomatal conductance to CO^2 (mol m^{-2} s^{-1})
GSMIN	0.004	0.002	Minimum stomatal conductance to CO^2 (mol m^{-2} s^{-1})
PAR0	371.94	574.42	Parameter relating stomatal conductance to PAR
D0	6.57	2.823	Parameter relating stomatal conductance to VPD
GSJA	0	0	Slope of straight line relating CO$_2$ concentration to stomatal conductance
T0	not used		parameters for stomatal response to temperature
TREF	not used		
TMAX	not used		
WLEAF	0.069	0.022	Leaf width for calculating boundary layer conductance
NSIDES	1	1	Number of sides of the leaf with stomata
JMAXCON			Parameters for Farquhar and von Caemmerer (1982) model
NOLAYERS	not used		
NOAGES	not used		
NODATES	not used		
JMAX			
DATES	not used		
VALUES	not used		
VCMAXCON			
NOLAYERS	not used		
NOAGES	not used		
NODATES	not used		
VCMAX			
DATES	not used		
VALUES	not used		
JMAXPARS			
THETA	not used		
EAVJ	not used		
EDVJ	not used		
DELSJ	not used		
VCMAXPARS			
EAVC	not used		

continued overleaf

RDPARS		Leaf respiration parameters
RTEMP	not used	
Q10F	not used	
DAYRESP	not used	
TBELOW	not used	
SLACON		Specific leaf area for calculating foliage growth respiration
NODATES	not used	
NOLAYERS	not used	
NOAGES	not used	
SLA		
DATES	not used	
VALUES	*not used*	
WRESP		Stem respiration rate parameters
EFFY	not used	
RM	not used	
Q10W	not used	
RTEMP	not used	
BRESP		Branch respiration rate parameters
RMB	not used	
Q10B	not used	
RTEMPB	not used	
RRESP		Root respiration rate parameters
RMFR	not used	
RMCR	not used	
Q10R	not used	
RTEMPR	not used	

str.dat

NAMELIST	VALUE		DESCRIPTION
PARAMETER	*C. megalocarpus*	*M. volkensii*	
LADD			
JLEAF	0	0	Flag indicating uniform leaf area density throughout the canopy
NOAGEC	1	1	Number of leaf age classes to be considered in distribution of leaf area density
RANDOM	1	1	Ration of projected shoot area to projected leaf area
CANOPY			
CSHAPE	'BOX'	'BOX'	Canopy shape
LIA			
ELP	0.807	1.18	Parameter of the ellipsoidal leaf angle distribution (fitted to measurements shown in Section 4.3.2)
NALPHA	5	5	Number of leaf angle classes
AERO			
EXTWIND	0	0	Exponential coefficient describing the decrease in windspeed with depth in the canopy
ALLOM			Coefficients used to describe allometric relationships between diameter and biomass for stem branches and roots for use in calculation of woody biomass respiration rates
COEFFT	Not used		
EXPONT	Not used		
WINTERC	Not used		
ALLOMB			
BCOEFFT	Not used		
BEXPONT	Not used		
BINTERC	Not used		
ALLOMR			
RCOEFFT	Not used		
REXPONT	Not used		
RINTERC	Not used		

trees.dat

NAMELIST	VALUE		DESCRIPTION
PARAMETER	*C. megalocarpus*	*M. volkensii*	
PLOT			
XMAX	20	20	Length of plot in the X direction (m)
YMAX	20	20	Length of plot in the Y direction (m)
XSLOPE	0	0	Slope of the plot in the X direction
YSLOPE	0	0	Slope of the plot in the Y direction
BEARING	90	90	Bearing of the X axis from south (degrees)
NOTREES	19	19	Total number of trees in the plot
AERODYN			
ZPD	not used	not used	Zero plane displacement (m)
Z0HT	not used	not used	Roughness length (m)
ZHT	not used	not used	Measurement height (m)
XY			
XYCOORDS	1 10	1 10	X and Y co-ordinates of each tree
	2 10	2 10	
	3 10	3 10	
	4 10	4 10	
	5 10	5 10	
	6 10	6 10	
	7 10	7 10	
	8 10	8 10	
	9 10	9 10	
	10 10	10 10	
	11 10	11 10	
	12 10	12 10	
	13 10	13 10	
	14 10	14 10	
	15 10	15 10	
	16 10	16 10	
	17 10	17 10	
	18 10	18 10	
	19 10	19 10	
ALLRADX			
NODATES	1	1	Number of dates on which crown radii in X direction specified
DATES	'01/09/96'	'01/09/96'	Date on which crown radii in X direction specified
VALUES	0.5	0.5	Crown radii in X direction (m)
ALLRADY			
NODATES	4	4	Number of dates on which crown radii specified
DATES	'21/12/96'	'04/01/97'	Date on which crown radii in Y direction specified
	'24/06/97'	'24/06/97'	
	'22/10/97'	'22/10/97'	
	'13/01/98'	'23/12/97'	
VALUES	1.22	1.43	Crown radii in Y direction (m). Figures correspond respectively to dates above
	1.47	1.65	
	1.35	1.46	
	1.72	1.72	

continued overleaf

ALLHTCROWN			
NODATES	4	4	Number of dates on which crown specified
DATES	‘21/12/96’	‘04/01/97’	Dates on which crown height specified.
	‘24/06/97’	‘24/06/97’	
	‘22/10/97’	‘22/10/97’	
	‘13/01/98’	‘23/12/97’	
VALUES	2.04	4.23	Crown height (m). Figures correspond in order to dates given above
	2.1	4.77	
	2.19	4.62	
	2.84	4.99	
ALLHTTRUNK			
NODATES	4	4	Number of dates on which trunk height specified
DATES	‘21/12/96’	‘04/01/97’	Dates on which trunk height specified
	‘24/06/97’	‘24/06/97’	
	‘22/10/97’	‘22/10/97’	
	‘13/01/98’	‘23/12/97'	
VALUES	2.11	2.61	Trunk height (vertical distance between base of trunk and bottom of canopy) (m). Figures correspond in order to dates given above
	2.09	2.53	
	2.08	2.87	
	1.81	2.75	
ALLLAREA			
NODATES	18	18	Number of dates on which leaf area specified
DATES	'25/06/96'	'25/06/96'	Dates on which leaf area specified
	'25/07/96'	'25/07/96'	
	'25/09/96'	'25/09/96'	
	'25/10/96'	'25/10/96'	
	'25/11/96'	'25/11/96'	
	'27/12/96'	'27/12/96'	
	'25/01/97'	'25/01/97'	
	'25/02/97'	'25/02/97'	
	'25/03/97'	'25/03/97'	
	'25/04/97'	'25/04/97'	
	'25/05/97'	'25/05/97'	
	'25/06/97'	'25/06/97'	
	'25/09/97'	'25/09/97'	
	'22/10/97'	'22/10/97'	
	'14/11/97'	'14/11/97'	
	'20/12/97'	'20/12/97'	
	'21/01/98'	'21/01/98'	
	'25/02/98'	'25/02/98'	

VALUES	9.88	3.82	Leaf area per tree (m²). Figures correspond in order to dates given above
	6.47	2.32	
	4.22	2.72	
	3.18	7.46	
	2.39	9.10	
	5.58	10.60	
	6.24	11.86	
	5.40	5.31	
	3.11	4.84	
	11.63	21.35	
	14.49	28.12	
	17.57	28.8	
	4.05	8.12	
	3.20	7.46	
	4.37	14.54	
	17.12	25.23	
	23.41	12.58	
	25.28	16.35	

points.dat (Input file for MAESTEST)

NAMELIST PARAMETER	VALUE	DESCRIPTION
CONTROL		
NOPOINTS	18	number of points at which incident PAR calculated
XYZ		
COORDS	10.0 10.0 2.1	X, Y and Z co-ordinates of points at which PAR calculated
	10.0 10.0 2.4	
	10.0 10.4 2.1	
	10.0 10.4 2.4	
	10.0 10.5 2.1	
	10.0 10.5 2.4	
	10.0 10.6 2.1	
	10.0 10.6 2.4	
	10.0 10.7 2.1	
	10.0 10.7 2.4	
	10.0 9.3 2.1	
	10.0 9.3 2.4	
	10.0 9.4 2.1	
	10.0 9.4 2.4	
	10.0 9.5 2.1	
	10.0 9.5 2.4	
	10.0 9.6 2.1	
	10.0 9.6 2.4	

6. DRY WEIGHT REMOVED DURING PRUNING

Table A2. Dry weight (kg) removed from trees in each replicate on all pruning occasions.

Season	Replicate	*C. megalocarpus*	*M. volkensii*	*S. spectabilis*	*G. sepium*
pre long rains 96	1	2.69	13.27	9.70	6.13
(March)	2	4.78	9.45	0.24	9.26
	3	4.69	8.45	0.49	6.95
	4	3.38	9.96	0.73	10.62
pre short rains 96	1	0.07	14.94	0.49	0.84
(October)	2	2.62	15.75	0.10	4.73
	3	0.55	3.97	-	1.87
	4	6.66	8.27	0.10	1.46
pre long rains 97	1	-	12.00	-	-
(March)	2	2.48	18.67	-	-
	3	4.11	10.76	-	-
	4	6.00	20.61	-	-
pre short rains 97	1	-	3.74	-	-
(October)	2	-	6.83	-	-
	3	-	10.85	-	-
	4	-	15.56	-	-

7. CROP YIELD PARAMETERS

Table A3. Maize yield parameters for 1996 long rains for north and south sides of plots (multiplying by 2.179×10^{-4} converts values to t ha^{-1}).

Treatment	Side	Total dry weight (g)	Grain dry weight (g)	No. plants	No. cobs	Harvest index	Slope of total dwt (g row^{-1})	Slope of grain dwt (g row^{-1})	Slope of no. plants (row^{-1})	Slope of harvest index (row^{-1})
S. spectabilis	**N**	8870.3	3657.0	165.8	116.0	0.33	346.7	163.3	0.36	0.043
		± 1150.2	± 542.0	± 2.2	± 8.9	± 0.03	± 37.7	± 24.6	± 0.10	± 0.015
	S	7716.3	3201.7	169.5	121.0	0.37	256.9	133.0	0.08	0.037
		± 1311.8	± 427.7	± 7.2	± 5.8	± 0.03	± 32.4	± 20.8	± 0.17	± 0.011
C. megalocarpus	**N**	11622.0	5667.5	168.0	113.5	0.37	416.9	229.2	0.19	0.070
		± 1122.4	± 785.0	± 2.3	± 4.3	± 0.02	± 31.2	± 29.6	± 0.12	± 0.006
	S	11216.3	5183.7	157.5	110.5	0.38	420.2	215.4	0.91	0.049
		± 1265.7	± 787.8	± 3.3	± 7.4	± 0.02	± 45.7	± 29.0	± 0.17	± 0.019
G. sepium	**N**	9211.9	3978.2	157.0	107.3	0.33	348.5	179.5	1.29	0.066
		± 697.7	± 511.8	± 6.1	± 11.3	± 0.04	± 29.6	± 18.9	± 0.30	± 0.009
	S	10059.4	4943.9	163.3	116.8	0.36	421.1	226.6	0.75	0.070
		± 1343.3	± 912.4	± 1.4	± 7.6	± 0.04	± 49.5	± 33.7	± 0.26	± 0.003
M. volkensii	**N**	5714.5	2278.6	170.5	97.0	0.35	208.6	87.6	0.22	0.028
		± 927.5	± 568.5	± 4.0	± 13.2	± 0.08	± 41.4	± 21.0	± 0.06	± 0.015
	S	5346.5	2007.7	159.5	105.8	0.34	153.3	67.6	0.44	0.027
		± 409.7	± 157.2	± 5.5	± 7.1	± 0.04	± 33.9	± 15.5	± 0.24	± 0.008
Sole crop	**N**	14941.0	7586.1	153.5	135.0	0.51	62.2	33.1	-0.10	0.005
		± 2572.4	± 1120.8	± 5.4	± 7.9	± 0.02	± 28.5	± 8.1	± 0.12	± 0.008
	S	15231.3	7820.9	162.0	145.3	0.51	19.2	24.1	0.01	0.009
		± 1284.6	± 523.3	± 5.8	± 5.6	± 0.02	± 44.6	± 27.3	± 0.30	± 0.003

Table A4. Maize yield parameters for 1997 long rains for north and south sides of plots (multiplying by 2.179×10^{-4} converts values to t ha^{-1}).

Treatment	Side	Total dry weight (g)	Grain dry weight (g)	No. plants	No. cobs	Harvest index	Slope of total dwt (g row^{-1})	Slope of grain dwt (g row^{-1})	Slope of no. plants (row^{-1})	Slope of harvest index (row^{-1})
S. spectabilis	**N**	17262.5	4730.2	180.5	121.3	0.21	535.9	223.2	-0.17	0.049
		± 2642.3	± 768.4	± 3.3	± 6.1	± 0.01	± 49.4	± 22.6	± 0.19	± 0.007
	S	16200.4	4926.5	169.8	129.3	0.26	436.0	190.2	0.47	0.044
		± 1911.3	± 659.0	± 2.5	± 6.0	± 0.02	± 44.1	± 16.4	± 0.17	± 0.004
C. megalocarpus	**N**	17727.2	6385.7	179.8	124.5	0.26	662.1	305.5	0.25	0.064
		± 1338.4	± 496.6	± 3.0	± 3.8	± 0.01	± 43.8	± 19.5	± 0.19	± 0.003
	S	16659.9	5856.9	175.0	117.5	0.25	615.7	286.0	0.23	0.070
		± 1876.3	± 809.9	± 1.7	± 7.2	± 0.01	± 75.6	± 39.5	± 0.22	± 0.006
G. sepium	**N**	17162.2	5658.0	178.5	127.5	0.27	472.6	212.3	0.12	0.050
		± 2025.4	± 969.6	± 3.2	± 14.3	± 0.03	± 57.2	± 28.7	± 0.07	± 0.003
	S	18497.3	6145.6	175.8	118.0	0.25	603.3	261.3	0.32	0.058
		± 1667.1	± 758.8	± 2.7	± 11.1	± 0.03	± 18.9	± 11.8	± 0.10	± 0.006
M. volkensii	**N**	14541.8	3763.2	178.5	108.3	0.20	364.3	161.0	0.28	0.047
		± 1696.1	± 897.2	± 2.7	± 19.9	± 0.05	± 48.7	± 19.3	± 0.07	± 0.005
	S	13260.7	3811.1	177.5	117.8	0.24	336.1	149.6	0.25	0.043
		± 1366.3	± 655.7	± 3.6	± 9.7	± 0.03	± 67.3	± 34.2	± 0.17	± 0.006
Sole crop	**N**	31791.2	12452.4	184.8	179.2	0.40	0.9	1.1	-0.15	0.000
		± 2161.6	± 963.4	± 3.0	± 3.3	± 0.02	± 56.2	± 11.9	± 0.09	± 0.003
	S	31849.0	13111.3	186.5	180.0	0.41	121.0	59.8	-0.13	0.005
		± 2663.5	± 1100.9	± 1.5	± 5.0	± 0.00	± 54.4	± 44.5	± 0.38	± 0.015

Table A5. Yield parameters for 1996/97 short rains bean harvest for north and south sides of plots (multiplying by 1.916×10^{-4} converts values to t ha^{-1})

Treatment	Side	No. plant	Grain dry weight (g)	Slope of no. plants	Slope of grain dry weight (g row^{-1})
S. spectabilis	N	570.3 ± 7.1	277.2 ± 41.9	0.13 ± 0.10	3.4 ± 0.5
	S	441.5 ± 17.4	98.7 ± 24.0	1.22 ± 0.51	2.2 ± 0.6
C. megalocarpus	N	547.5 ± 32.9	291.8 ± 55.6	0.21 ± 0.36	3.9 ± 0.8
	S	523.5 ± 34.8	165.9 ± 42.2	0.69 ± 0.34	2.8 ± 0.8
G. sepium	N	545.8 ± 42.3	334.8 ± 70.0	-0.12 ± 0.21	-0.7 ± 0.3
	S	532.3 ± 43.3	170.6 ± 47.9	0.45 ± 0.45	1.5 ± 0.3
M. volkensii	N	571.5 ± 18.8	167.9 ± 67.8	0.19 ± 0.21	0.7 ± 0.5
	S	521.0 ± 53.4	64.5 ± 32.1	0.59 ± 0.26	1.1 ± 0.6
Sole crop	N	531.8 ± 17.5	471.5 ± 289.1	0.27 ± 0.09	2.1 ± 1.2
	S	-	-	-	-

Table A6. Yield parameters for 1997/98 short rains bean harvest for north and south sides of plots (multiplying by 1.916×10^{-4} converts values to t ha^{-1}).

Treatment	Side	No. plant	Grain dry weight (g)	Slope of no. plants	Slope of grain dry weight (g row^{-1})
S. spectabilis	N	580.5 ± 8.1	5388.1 ± 419.7	-0.29 ± 0.09	27.0 ± 6.0
	S	600.5 ± 19.7	6705.6 ± 805.7	-0.21 ± 0.10	17.0 ± 2.8
C. megalocarpus	N	596.8 ± 12.7	6176.3 ± 321.5	0.23 ± 0.21	44.8 ± 2.5
	S	579.5 ± 19.4	6781.9 ± 308.9	0.10 ± 0.14	36.5 ± 4.4
G. sepium	N	584.3 ± 14.1	6652.6 ± 331.4	-0.12 ± 0.11	27.2 ± 4.4
	S	599.0 ± 11.5	8078.7 ± 181.	-0.43 ± 0.14	13.9 ± 9.3
M. volkensii	N	598.5 ± 16.3	6762.9 ± 239.7	-0.11 ± 0.11	26.2 ± 3.1
	S	610.3 ± 5.1	8104.3 ± 173.9	0.15 ± 0.08	13.8 ± 3.2
Sole crop	N	578.5 ± 15.6	8962.4 ± 144.1	-0.21 ± 0.22	9.2 ± 4.3
	S	555.5 ± 12.7	8063.7 ± 591.8	0.23 ± 0.23	0.6 ± 7.9