

Optimising nutrition for productive and sustainable farm forestry systems

-pasture legumes under shade

A report for the RIRDC/
Land & Water Australia/
FWPRDC
MDBC
Joint Venture Agroforestry Program

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October 2003

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ISBN 0642 58679 9 ISSN 1440-6845

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Published in October 2003
Printed on environmentally friendly paper by Canprint

Foreword

With the closure of North Queensland rainforests to logging following World Heritage Listing, timber plantations are being established on degraded and other agricultural land. Experimental evidence indicates that current fertiliser regimes produce suboptimal growth in many species, particularly on the less fertile soils. Further there is public concern about the possibility of fertilisers in agricultural runoff having adverse effects on the downstream environment. Added to this, fertilisers are a significant economic cost to the landowner that affects returns from farm forestry enterprises.

Significant acceptance of silvo-pastoral (tree plantation-pasture) systems has been impeded by the belief that productive pasture cannot be maintained under tree canopies. The benefits of raising livestock in conjunction with tree plantations include increased and diversified income, better use of land resources, soil stabilisation, and the potential for higher plantation crop yield through better weed control, nutrient cycling and nitrogen accretion. The chief aim of this research was to identify a suite of pasture legumes that can be used to improve pasture quality in agroforestry systems under differing rainfall regimes. Nitrogen fixed by these legumes is also likely to benefit tree growth.

This project was funded by three R&D Corporations — RIRDC, LWA and FWPRDC together with the Murray Darlin Basin Commission, through the Joint Venture Agroforestry Program. These Corporations are funded principally by the Australian Government.

This report, a new addition to RIRDC's diverse range of over 900 research publications, forms part of our Agroforestry and Farm Forestry R&D program, which aims to integrate sustainable and productive agroforestry within Australian farming systems.

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Dr Simon Hearn

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Acknowledgements

We gratefully acknowledge the funding support provided by the Joint Venture Agroforestry Program and the Community Rainforest Reforestation Program (CRRP).

We would also like to acknowledge the generosity of Mr Errol Wiles (Babinda) and the Burdekin Agricultural College in allowing us access to the their tree plantations for our field studies.

Our colleagues Dr Joe Holtum (ecophysiology), Mr Chris Gardiner (forage legumes), Associate Professor Ross Coventry (soils), Adjunct Professor Peter Brownell (plant nutrition), and Ms Cherie Stafford (research assistance) provided much valued advice and assistance with various parts of this project.

Dr Bruce Cook (QDPI), Dr Arthur Cameron (DPIF - NT), Dr Harry Bishop (QDPI) and the Genetic Resources Centre (CSIRO Cunningham Laboratory) generously provided seed of suitable legume accessions. We are also obligated to Jeff Corfield (CSIRO Davies Laboratory) for his advice on pasture sampling technique and data analysis.

We thank Rod Collins, Gary Sexton and Sue Vize of the North Queensland Afforestation Association for their support.

We also thank Professor Richard Pearson, Head of the School of Tropical Biology, James Cook University, who made laboratory, office and shade-house space available, and the staff of the Research Office, James Cook University, who provided extremely valuable assistance with the financial management of this project.

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Executive Summary

Significant acceptance of tree plantation-pasture systems has been impeded by the belief that productive pasture cannot be maintained under tree canopies. The benefits of raising livestock in conjunction with tree plantations include increased and diversified income, better use of land resources, soil stabilisation, and the potential for higher plantation crop yield through better weed control, nutrient cycling and nitrogen accretion. This project identified a suite of pasture legumes that can be used to improve pasture quality in agroforestry systems under differing rainfall regimes in the tropics. Nitrogen fixed by these legumes is also likely to benefit tree growth.

The major thrust of the research was to identify pasture legume species which are able to tolerate different levels of shading under tree plantations in the Australian tropics - providing improved forage quality and productivity for grazing in agroforestry situations, and improving soil fertility and reducing fertiliser costs through nitrogen fixation. The benefits to tree growers include enhanced tree growth, weed suppression (reduced costs for herbicides), and reduced erosion on steep or degraded sites (due to mixed ground cover).

A total of 35 species and cultivars of tropical pasture legumes were tested for shade tolerance beneath four levels of shade under shadehouse conditions. A range of agronomic and ecophysiological parameters were measured, including biomass production, root:shoot ratio, root nodulation, foliar nutrient content, time to flowering, seed production, and light response curves.

Above- and below-ground biomass were both depressed by shading, although species were affected to different degrees. The most promising species tended to yield well under the control treatment and also beneath shade treatments, indicating they may also be suitable for use beneath young plantations where shade levels are relatively low, in addition to older, more heavily shaded plantations. Root nodulation was greatly decreased or entirely absent beneath shaded treatments, implying that fixation of atmospheric nitrogen may be lower under shade than open conditions, however fertilization of pots in this trial was a complicating factor. The concentration of leaf N was affected by shading, with increased concentrations found under shade treatments compared to the control. However no similar changes were discernible in leaf P. Vegetative growth appears to be prolonged in many species by shading, with the time taken to the production of the first flower often increased in plants grown under shade. The yield of seeds was greatly reduced under shade, however seed size appears to have been maintained at the expense of seed number. The seed of several species had an increased fraction of readily germinable seed, speed of seed germination and lower levels of hard seed when grown under shade. Light response curves were not always correlated with the results for dry matter production, with several species that appear to be shade tolerant when viewing dry matter production and relative yields, producing light curves that suggest otherwise.

Growth and performance of 15 species/cultivars were also examined under *Khaya senegalensis* and *Eucalyptus pellita* / mixed rainforest species plantations. *Arachis pintoi* was clearly the best performing of six species/accessions of legume tested beneath a five-year-old *Eucalyptus pellita* / mixed rainforest species plantation. *Clitoria ternatea* and *Centrosema brasilianum* proved to be the best performing species beneath both a conventional stand and a Nelder wheel comprised of *Khaya senegalensis*, however legume growth beneath trees was depressed compared to growth in more open conditions. The production of pasture decreased exponentially with increasing tree density beneath the Nelder wheel plantation. Both *Clitoria ternatea* and *Centrosema brasilianum* were observed to climb trees during the trial, highlighting the potential smothering of young or small trees by vigorous climbing species. Due to this, sowing of either species is not recommended in very young plantations, or if they are, then additional management will be required to control climbers. Trees were also found to decrease soil moisture content as planting density increased, suggesting light may not always be the only limiting factor to pasture production beneath trees in seasonally dry areas, which comprise much of the Australian tropical region.

This study identified 16 species of potentially useful, shade-tolerant, pasture legume species that show promise for use under trees in farm forestry situations in both the wet and the seasonally dry tropics. The most promising species for the wet tropics were *Desmodium intortum*, *Calopogonium mucunoides*, *Arachis pintoi*, *D. ovalifolium*, *D. canum*, *Centrosema acutifolium*, *Pueraria phaseoloides*, *D. heterophyllum*, *C. pubescens*, *D. uncinatum* and *C. macrocarpum*. *Clitoria ternatea*, *Arachis stenosperma*, *Macroptilium lathyroides*, *M. atropurpureum* and *Centrosema brasilianum* were the most successful of the species suited for seasonally dry tropical regions.

However, many of the species identified as shade tolerant, or being relatively productive under shaded conditions, have a climbing/twining habit that can cause concern in tree plantations, particularly in respect to potential smothering of small trees. When the climbing species are removed the remaining species recommended for the wet tropics are *D. intortum*, *A. pintoi*, *D. ovalifolium*, *D. canum*, *D. heterophyllum* and *D. uncinatum*, while *A. stenosperma* shows potential for the seasonally dry tropics. Nevertheless climbing species may still be useful beneath older plantations, or where a higher level of pasture management is acceptable in order to help prevent smothering of trees through controlling the frequency and intensity of grazing.

Further research should examine the possibility of controlling climbing legumes in tree plantations through grazing management in order to broaden the range of legume species available for use. Research is also required to examine the longer-term persistence and productivity of the species identified in this study, as tree plantations age and shade levels increase. Compatibility with shade tolerant grasses is an important aspect of pasture production beneath tree plantations, which has seen relatively little research and will have an important effect upon the persistence and productivity of both the grass and legume components of the pasture.

Introduction

Over the past decade there has been increasing interest in the potential for farm forestry and private plantations in north-east Queensland. With the closure of rainforests to logging following World Heritage Listing in 1988, some timber plantations were established in the wet tropics on degraded agricultural land under the Community Rainforest Reforestation Program (CRRP) and Private Plantations Initiative (PPI) schemes. Many landholders in the more seasonal tropics are also becoming interested in the potential of growing timber trees to diversify incomes, with several plantations of African Mahogany (*Khaya senegalensis*), in particular, being established in areas such as Alligator Creek (south of Townsville) and around Charters Towers. As well as helping farm incomes and Australia's negative balance of trade in forest products, such plantations provide several environmental services. Returning trees to cleared agricultural land may help soil and water conservation, mitigate climate change (growing trees take up more CO₂ than mature forest), and add to local biodiversity (Fisher & Cruz 1994; Keenan *et al.* 1997; Lugo 1992; Myers 1988; Parrotta 1992).

A disincentive to farm forestry is the long lead time until income can be earned from harvested timber, especially in the case of the slow-growing, high value cabinet timber species. Such tree crops may be more attractive if the land can be used for other purposes, such as grazing livestock, while the trees are growing. While agroforestry is widely practised overseas, it is not widely established in Australia. Such a strategy requires the ability to grow productive pasture under the trees for a substantial portion of the plantation's life. This can be achieved through the use of pasture species that are tolerant of some degree of shading, and through the optimal spacing and thinning of trees to allow sufficient light to reach the ground. Hence there is a need to identify a suite of grass and legume species that will tolerate levels of shading found in a range of plantations with different rainfall regimes and soil types. Legumes are particularly important in raising the protein content of forage for livestock.

Some very useful research has previously examined the shade tolerance of a large variety of legumes under plantations in south-east Asia (Reynolds 1995; Shelton 1991; Wong *et al.* 1985a). However, few studies have examined the shade-tolerance, agronomic and ecophysiological performance of legumes under controlled conditions, and potential for use in plantations in tropical Australia – especially for those regions with a prolonged dry season.

The role of legumes in nitrogen cycling also can provide benefits for farm forestry. Experimental evidence indicates that current fertiliser regimes produce suboptimal growth in many plantation tree species, particularly on the less fertile soils (Adams 1995; Chonglu & Reddell 1992; Webb *et al.* 1997). Further there is public concern about the possibility of fertilisers in agricultural runoff having adverse effects on the downstream environment (Hunter *et al.* 1996; Yellowlees 1991). Added to this, fertilisers are a significant economic cost to the landowner, which affects returns from agroforestry enterprises.

Much of the arable land in the wet tropics is now being used to cultivate traditional wet tropical crops, such as sugarcane and bananas. These areas are expanding into traditional beef cattle grazing areas, thus pushing out the grazing industry from these wet tropical environments. Like the grazing industry, tree plantations and agroforestry are unlikely to be farmed on the better arable crop areas. This trend means that agroforestry and grazing will be conducted on the less arable, poorer fertility soils, and on steep sites. The combination of plantations, pastures and grazing in a silvo-pastoral system is a sustainable method of maximising land-use in such areas. However, a completely new suite of pasture plants adapted to these specific conditions (low and changing light regimes, poor soil fertility, steep and erodable landscapes and defoliation) will need to be sought. Native pastures under plantations are usually dominated by grasses of low productivity and quality, and by weed species (Shelton & Stür 1991). Replacement of weeds with improved pastures can improve ruminant live weight gains by up to 250% (Mullen 1994). Introduction of legume cover crops into plantations can

reduce erosion, shade the soil in the early establishment phase, increase soil organic matter and soil biological activity, improve soil structure and fertility, and increase the growth rate of trees (Jayasinghe 1991; Lal *et al.* 1979).

The grazing of cattle under tree plantations can result in several benefits, including increased and diversified income, soil stabilisation, and higher plantation crop yield through better weed control and nutrient cycling, including nitrogen accretion (Shelton 1991). Significant acceptance of tree plantation-pasture systems in tropical Australia has been impeded by the belief that productive pasture cannot be maintained under tree canopies. Research has identified several pasture legumes that grow well under tree canopies in the dry tropics (Amar 1996; Amar *et al.* 1996), and there are others which are likely to grow well under trees in the wet tropics (Wong 1991). Further research will identify a suite of pasture legumes that can be used to improve pasture quality in agroforestry systems under differing rainfall regimes. Nitrogen fixed by these legumes is also likely to benefit tree growth.

An ideal legume for silvo-pastoral systems would:

- be adapted to low and changing light levels,
- be productive,
- be persistent,
- be palatable and nutritious to stock,
- control weeds,
- not compete with trees,
- fix significant quantities of atmospheric nitrogen.

The aims of this study were to:

- identify suitable legume species for use over a range of light levels;
- quantify the effects of shade on production, persistence and nutrient content of selected pasture legumes; and
- provide recommendations for legume species use over a range of light levels (tree ages and densities).

Agronomic performance of forage legumes under shade

2.1 Introduction

The major constraint to pasture growth under tree plantations is the low light transmission that reaches the understorey vegetation after filtering by the tree canopy. The main constraint on the use of plantation lands for forage and ruminant production was indicated by Wong *et al.* (1985b) to be the fast changing light environment under the plantation canopy.

In the past, research on shade-tolerant plants has tended to focus upon legume and grass species, suited to the wet tropics in particular. Very little information could be found relating to the shade tolerance of species of grass and legume suited to the seasonally dry tropics. With the large areas of relatively cheap land available to the west of Townsville around Charters Towers, where the tree species *Khaya senegalensis* (African Mahogany) is displaying promise as a fast growing timber species in the semi-arid zone, coupled with an increased interest in establishing timber plantations, identification of shade-tolerant pasture species suited to the conditions present will be essential if any viable silvopastoral systems are to be established.

Generally plants that occupy sunny habitats (sun plants) are capable of higher photosynthetic rates at high quantum flux densities than plants restricted to shaded environments (Bjorkman 1981). The light beneath vegetation canopies is composed of two components: unfiltered solar radiation both direct and diffuse, which has passed through gaps in the vegetation, and filtered radiation which has passed through vegetation and been modified by absorption, reflection and scattering (Smith 1982). After passing through the canopy, filtered light will have had its spectrum altered and specifically the proportion of light in the red (approximately 660 nm) and the far-red (approximately 730 nm) wavelengths (Durr 1997). The red:far-red ratio (R:FR) is lowered by tree canopies through the selective absorption by leaf pigments. It is the combination of these two components, in differing proportions depending upon the nature of the vegetation, that determines the below-canopy spectrum (Smith 1982). The quantity of light beneath vegetation canopies is determined basically by two factors: the light incident upon the top of the canopy and the degree of transmission through the canopy (Durr 1997).

Adaptations by plants to differing light environments include:

- under low light, leaves tend to be thinner, with thinner cuticles and larger leaves than plants adapted to high light;
- leaves on shade-adapted species tend to have greater longevity than those in high light environments in order to increase lifetime carbon gain;
- the orientation of leaves under shaded conditions tends to be horizontal as opposed to vertical on plants in high light;
- cells of sun plants tend to be large while those of shade plants are small;
- chloroplasts are smaller in sun than shade plants;
- there is a high chlorophyll a/b ratio in sun plants while the ratio in shade plants is low;
- a decrease in root to shoot ratio under shade;
- an increase in leaf area ratio with shading:
- a higher photosynthetic capacity under high light than under shaded conditions;
- lower compensation point under shaded conditions;
- plants adapted to high-light have a lower quantum yield, a higher light compensation point, a higher light saturation point and a higher light saturated photosynthetic rate than plants adapted to low light levels

(Atwell et al. 1999; Bjorkman 1981; Nilsen & Orcutt 1996; Shelton et al. 1987; Smith 1982).

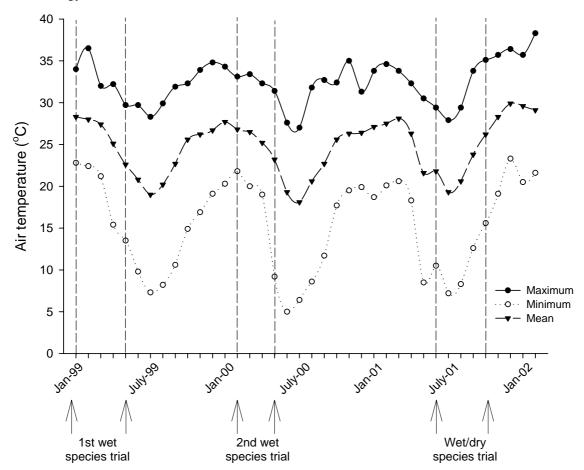
In addition to the testing of legume species suited to the wet tropics, an extra pot trial was conducted examining a selection of legumes suited to the seasonally dry tropics, to address the lack of information on shade-tolerant legumes for farm forestry in these regions. All species were examined for a range of qualities, both agronomic and physiological, in order to determine the potential suitability of species for use under timber plantations.

2.2 Materials and Methods

2.2.1 Trial Establishment

The experiment was conducted as a pot trial at the School of Tropical Biology, James Cook University, Townsville (19° 16' S, 146° 48' E). Townsville has a seasonally dry tropical climate with the majority of rainfall falling between December-March. Air temperatures during the trial periods are shown in Figure 2.1.

Figure 2.1 Maximum, minimum and mean air temperatures during trial period. Species tested are shown in Table 2.1. Graph constructed from data obtained from the Australian Bureau of Meteorology.



Experimental Design.

Legume species were grown beneath four shade levels in a shade-house with a clear plastic roof (Laserlite, with a light transmittance of approximately 0.60) - control (no shade), 63, 76 and 84% shade. The shade levels used in this study were medium (60%) to very heavy (84%). Shade was provided by Sarlon shade-cloth, with the shade levels determined by grades of shade cloth

commercially available. Light levels were measured using both a hand-held LI-COR Quantum/Radiometer and a LI-COR 1000 data logger. Each species was replicated five (first wet tropical species trial) or four times (second wet and wet/dry tropical species trials) at each shade level to give a total of 140, 224 and 224 pots respectively. Species tested are shown in Table 2.1.

The following characteristics were recorded for each species; days to flowering, days to first pod, above-ground biomass, below-ground biomass, total biomass, root nodulation level, root:shoot ratio, leaf biomass, stem biomass, stem:leaf ratio, leaf nitrogen and phosphorus content, number of pods produced, total number of seeds produced, average number of seeds per pod, average seed weight, seed germination characteristics, light response curves, estimated quantum efficiency, compensation point and light saturation level.

Seed and Soil Preparation.

The soil used in the trial was a loamy sand, commercial 'potting mix' supplied by Flintstones Pty. Ltd. of Townsville (Table 2.2).

Table 2.2 Major nutrients in the fine earth fraction (<2mm) of the soil used in shade house pot trials.

Property	Concentration	SE	n
Organic carbon (%)	1.09	0.11	5
Total nitrogen (%)	0.291	0.020	15
Total phosphorus (%)	0.063	0.018	15
pН	5.44	0.06	15
Electrical conductivity (dS m ⁻¹)	0.517	0.019	15

Organic carbon was determined by Heanes (1984) method (Rayment & Higginson 1992), total nitrogen and phosphorus after wet oxidation with sulphuric acid and hydrogen peroxide as described by Anderson & Ingram (1989), and soil pH and electrical conductivity on a 1:5 soil/water suspension (Rayment & Higginson 1992).

The soil was passed through a 2 mm sieve in order to mix the soil and remove any coarse material such as stones, twigs and leaf litter. Pots (6.3 litre capacity) were lined with paper towel in order to prevent any loss of soil from pot drainage holes. Pots were then filled with 3.6 kg of air-dry soil and watered daily for approximately a week to allow germination of weed seeds, which were removed. There was no treatment of the legume seeds prior to planting as sufficient germinants were obtained without it.

Planting and maintenance.

Seeds of each species were planted directly into the pots at varying numbers, depending on seed availability. Seedlings were thinned to leave the most vigorous seedling in each pot after the first two weeks. Seedlings were inoculated where necessary, as indicated by (Mannetje & Jones 1992), after two weeks with the appropriate strain of inoculum. Inoculant was applied by mixing with water and watering onto the soil. Water and nutrients were not limiting in this experiment. Plants were watered daily and fertilised once every two weeks with a complete soluble fertilizer ("Thrive", Yates Australia) at the rate of 8 g per 4.5 litres of water, with 300 mL applied per pot. Climbing plants were supported by placing a one-metre stake in the pot.

(a)

First wet tropical species	Cultivar/Accession
tested	
Arachis pintoi	cv. Amarillo
Calopogonium mucunoides	CPI 43428
Desmodium canum	CQ 1781
Desmodium intortum	cv. Greenleaf
Desmodium ovalifolium	Q8194
Macrotyloma axillare	cv. Archer
Vigna luteola	cv. Dalrymple

(b)

Second wet tropical species	Cultivar/Accession
tested	
Aeschynomene americana	Lee
Aeschynomene villosa	CPI 37235
Aeschynomene villosa	Kretschmer
Arachis kretschmeri	-
Centrosema acutifolium	CPI 95562
Centrosema macrocarpum	CPI 95531
Centrosema pubescens	Cardillo
Desmodium heterophyllum	Johnstone
Desmodium triflorum	CPI 49341
Desmodium uncinatum	Silverleaf
Flemingia congesta	P4435
Neonotonia wightii	Tinaroo
Pueraria phaseoloides	CQ 3613
Stylosanthes guianensis	Cook

Table 2.1 cont. (c)

Wet/dry tropical species tested	Cultivar/Accession
Arachis paraguariensis	ssp. paraguariensis 91419
Arachis stenosperma	ATF 377
Centrosema brasilianum	Ooloo
Centrosema pascuorum	Cavalcade
Chamaecrista rotundifolia	Wynn
Clitoria ternatea	Milgarra
Desmanthus virgatus	cv. Jaribu*
Desmodium scorpiurus	CPI 81346
Macroptilium atropurpureum	Aztec Atro
Macroptilium lathyroides	L11-94 cv. Murray
Macroptilium martii	CPI 49780
Rhynchosia minima	Nuda
Stylosanthes hamata	Verano
Stylosanthes scabra	Seca

^{*} Cultivar Jaribu was later found to be composed from a mix of the species Desmanthus pubescens, D. virgatus and D. leptophyllus.

Planting and harvesting dates for each trial were as follows:

- First wet tropical species trial 17th Jan 2000 to 2nd May 2000 (107 days).
- Second wet tropical species trial 16th Feb 2001 to 30th May 2001 (103 days).
- Wet/dry tropical species trial 22nd June 2001 to 29th October 2001 (119 days).

2.1.2 Measurement of Agronomic Properties

Time to first flower and first pod.

Times to opening of first flowers (flowers opening) and the production of first pods (pods visible) were recorded and expressed as days after planting (DAP).

Above and below ground dry matter, root nodulation, root:shoot ratio and leaf:stem ratio.

Planting day was considered as day 0. Plant herbage was harvested at ground level at the end of each trial. Root material was collected by washing away soil on a 2 mm sieve and nodulation level scored according to Sykes *et al.* (1988). All plant material was dried at 70°C in a forced draught oven for 3 days to a constant weight and then weighed. The root:shoot ratio was determined (root mass divided by total above-ground biomass). Above-ground plant material was then separated into stem and leaf components and the leaf:stem ratio determined.

Leaf nitrogen and phosphorus content

Leaf material (lamina and petiole) was hammer-milled through a 2 mm sieve and analysed for nitrogen and phosphorus using the methods of Anderson & Ingram (1989). This involved wet oxidation with sulphuric acid and hydrogen peroxide, and a selenium catalyst. Nitrogen was determined colorimetrically by the salicylate-hypochlorite method of Baethgen & Alley (1989), and phosphorus by an adaptation of Murphy & Riley's (1962) single solution method (Anderson & Ingram 1989).

Number of seeds produced, average seed weight, average number of seeds per pod, number of pods per plant and seed germinability

Seeds and pods were collected from each plant as each pod began to mature. Seeds were separated from their pods, where possible and the number of seeds per pod recorded. Seeds were then air-dried in order to maintain their viability for later germination tests, counted and weighed. Seed-pods were oven-dried and included in the above-ground biomass. Seed germination tests were conducted in a growth cabinet at the School of Tropical Biology at James Cook University, Townsville. The treatments consisted of two factors, the first being the legume genotype and the second the level of shade under which the seeds were produced. Seeds were germinated under a 12 hour day/night cycle with temperatures between 32 -34°C and 26 - 28°C respectively. Seeds were placed upon filter paper in petri dishes and watered daily with deionised water. The number of seeds tested varied according to the amount of seed produced (Table 2.3), making it impossible to follow the standard procedure of the International Seed Testing Association (1999).

Table 2.3. Total number of seeds used for each species, under each shade treatment in the germination test.

	Shade treatment				
Species	Control (0%)	63%	76%	84%	
Centrosema brasilianum	400	400	400	96	
Centrosema pascuorum	400	52	280	80	
Chamaecrista rotundifolia	400	40	200	-	
Desmanthus virgatus	400	40	40	-	
Macroptilium atropurpureum	400	340	360	140	
Macroptilium lathyroides	400	400	400	-	
Macroptilium martii	400	280	400	40	
Rhynchosia minima	400	28	-	-	

Seed from each species, under each light treatment, was pooled and then divided into five replicates. Dishes were arranged in a randomised complete block design within the cabinet and randomly moved every day to minimise microclimate effects. The number of germinated seeds was recorded daily at midday and the germinated seeds removed. A seed was considered to have germinated when a radicle 3 mm long or more had been produced. Germination was recorded for 28 days due to the hard-seeded nature of some of the legume species tested. After 28 days any seeds that had not germinated had an incision made in their seed coats with a scalpel at the opposite end to the embryo. Germination was then recorded for another 10 days. At the end of this period any ungerminated seeds were considered to be non-viable. Seeds were then classified as being either readily germinable (germinated in the first 28 days), hard (germinated after scarification of the seed coat) or non-viable (seeds that did not germinate by the end of the experiment). The time to 50% germination of the total number of readily germinable seeds (T50) was estimated using the formula given by Coolbear *et al.* (1984):

$$T50 = t_i + \{0.5(N+1) - n_i\}\{t_j - t_i\} / (n_j - n_i)$$

Where: T50 is time to 50% germination,

N is the final number of readily germinable seeds,

' n_i ' and ' n_j ' are the number of readily germinable seeds between two adjacent counts at time ' t_i ' and ' t_i ' where " $n_i < 0.5(N+1) < n_i$ ".

Data for seed germination, seed production, size and number of seeds per pod were obtained only for the wet/dry tropical species trial as this was the only trial where sufficient amounts of seed was produced under more than one shade treatment.

2.1.3 Statistical analysis

Data were analysed by analysis of variance (ANOVA) and means compared by the method of least significant difference (LSD, P<0.05), using the computer programs Statistix Version 2 (Analytical Software, 1998) and SPSS Release 8 (SPSS Inc., 1998). The shoot:root data was transformed by taking the log of the value in order to meet the requirements for analysis of variance.

2.3 Results

Detailed results for all parameters will not be presented here, as they are very extensive and covered in the PhD thesis by Addison (2003). The effects of shade on total biomass are provided below, and a summary of the main results for the other parameters.

2.3.1 Summary of Results

Highly significant (P<0.0001) effects for shade, species and shade x species interaction were found in all plant attributes with the exceptions of the species and interaction effect on root:shoot ratio, but these were still found to be significant (Table 2.4). Number of days to first flower was the other plant attribute that was not strongly affected in all categories. No shade or interaction effects were detected, while plant species was found to have a highly significant effect.

2.3.2 Total Plant Biomass

a) Effects of shade level

The above-ground and root biomass were summed in order to determine the total plant biomass produced by each species under the shade treatments. Statistical analysis found highly significant (P<0.001) shade and species effects in addition to a highly significant shade by species interaction. Overall total plant biomass production, as would be expected, displayed similar results as above-ground and root biomass. The control treatment clearly produced the greatest yielding plants, with total plant biomass falling with increased shade levels (Table 2.5).

Table 2.5 Means, standard errors and LSD groupings of the overall production of total biomass by 7 and 14 species of wet tropical and 14 species of wet/dry tropical forage legume grown beneath four shade levels, harvested 107, 103 and 119 days after planting respectively (n = 35, 56 and 56 respectively). Means in a column followed by the same letter are not significantly different.

	1 st Trial	2 nd Trial	Wet/dry Species Trial
	Mean Total Biomass	Mean Total Biomass	Mean Total Biomass
Shade	(g/pot)	(g/pot)	(g/pot)
Control	40.11 ± 3.03 a	57.2 ± 3.8 a	27.4 ± 2.5 a
63%	$18.99 \pm 2.22 \text{ b}$	$18.1 \pm 2.0 \text{ b}$	$9.5 \pm 1.3 \text{ b}$
76%	$7.08 \pm 0.92 \text{ c}$	$12.8 \pm 1.5 \text{ bc}$	$8.7 \pm 1.3 \text{ b c}$
84%	6.27 ± 0.81 c	$8.2 \pm 0.8 \text{ c}$	$3.3 \pm 0.5 \text{ c}$
Probability	< 0.001	< 0.001	< 0.001

b) Effects of legume genotype

First wet tropical species trial

Overall, *V. luteola* produced the greatest biomass, although it was not statistically different from *D. intortum* or *C. mucunoides*. *Desmodium canum* produced the lowest overall biomass, which was approximately one-third of the biomass produced by *V. luteola*, with *A. pintoi* yielding only slightly more (Table 2.6a).

Second wet tropical species trial

P. phaseoloides produced the greatest average total biomass followed by *C. acutifolium>D. heterophyllum>A. americana>D. uncinatum*, all of which were not significantly different from one another (Table 2.6b). *Flemingia congesta* and *D. triflorum* yielded particularly low levels of biomass production and overall were the two poorest producing species, with the exception of *A. kretschmeri* which will be explained later (see discussion). The lowest yielding statistical grouping contained a large range of yields (22.7 to 3.8 g per pot) with a total of eight species.

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Table 2.4 Statistical summary of three shade-house trials examining effects of shade on a range of properties in 35 accessions of tropical forage legume.

	1 st Wet Species Trial			2 nd Wet Species Trial			Wet/Dry Species Trial		ies Trial
Plant Attribute	Shade	Species	Interaction	Shade	Species	Interaction	Shade	Species	Interaction
Above-ground biomass	***	***	***	***	***	***	***	***	***
Root biomass	***	***	***	***	***	***	***	***	***
Total biomass	***	***	***	***	***	***	***	***	***
Root: shoot ratio	***	**	*	***	***	n.s.	***	***	n.s.
Root nodulation	***	***	***	***	***	*	***	***	***
Leaf N content	***	***	***	***	***	***	***	***	***
Leaf P content	***	***	***	***	***	***	***	***	n.s.
Days to first flower	n.s.	***	n.s.	*	***	*	***	***	***

n.s. = no significant effect); * = 0.05 > P > 0.01; ** = 0.01 > P > 0.001; *** = P < 0.001.

Wet/dry tropical species trial

Clitoria ternatea was clearly the greatest producer of biomass across all light levels, with 75% more biomass than A. stenosperma, the second highest yielding species. It was also the only species in the first statistical grouping (Table 2.6c). Other species that yielded high levels of dry matter include A. stenosperma>M. lathyroides>D. scorpiurus>C. rotundifolia>S. hamata>M. atropurpureum>R. minima. The poorest overall yielding species was found to be D. virgatus, which yielded only marginally less than S. scabra. Statistically D. virgatus and S. scabra were not found to be significantly different from eight other species (C. rotundifolia>S. hamata>M. atropurpureum>R. minima>C. pascuorum>C. brasilianum> A. paraguariensis>M. martii).

c) Interaction effects

First wet tropical species trial

Table 2.7 shows total plant biomass of each species under the four shade treatments. Beneath full sunlight *V. luteola* was clearly the most productive species tested, producing an average total biomass 23.7 g per pot (or 38.2%) more than *D. intortum*, the second greatest total biomass producer. *Macrotyloma axillare, C. mucunoides* and *D. ovalifolium* all produced intermediate yields of biomass while *D. ovalifolium* and *A. pintoi* were the lowest yielding species.

Vigna luteola remained the greatest producer of biomass under 63% shade, however its higher relative production to other species was greatly reduced, with the second and third greatest yielding species being C. mucunoides and D. intortum, respectively. Statistically there was no significant difference between these species at this shade level, whereas under full light V. luteola was statistically distinct from the other species. Desmodium canum and A. pintoi remained the lowest yielding species, but were not statistically different from D. ovalifolium and M. axillare.

Calopogonium mucunoides yielded the greatest quantity of biomass beneath 76% shade but was not statistically different from *D. intortum* or *V. luteola*. In addition to *D. intortum* and *V. luteola* all remaining species were not statistically separate despite large differences in biomass production. *Macrotyloma axillare* suffered a large reduction in biomass production beneath 76% shade compared with 63% shade and full sun.

The highest yielding group beneath 84% shade was composed of *C. mucunoides* and *V. luteola*. *Desmodium intortum, D. ovalifolium, A. pintoi* and *D. canum* all produced similar amounts of biomass while *M. axillare* remained the lowest yielding species, producing only 23.5% of the second lowest yielding species, *D. canum*.

Within species the control treatment was always found to be the only shade treatment in the highest yielding LSD grouping (Table 2.7). *Arachis pintoi*, *D. canum*, *D. ovalifolium* and *M. axillare* all displayed no statistical difference between the 63%, 76% and 84% shade treatments, although the trend of decreasing biomass with shade was still clearly evident.

Second wet tropical species trial

Shade by species interaction effects on total plant biomass are shown in Table 2.8. Seven statistical groupings in which the means were significantly different from one another were found among plants grown in full light. *Pueraria phaseoloides* yielded the greatest biomass under full sun, but was not statistically separate from *A. americana* and *C. acutifolium*, the second and third highest yielding species respectively. The large number of LSD groupings makes it difficult to separate species into clearly defined groups. Instead there appears to be a gradual reduction in yields between species, with nearly all species belonging to two or three LSD groupings. Only the highest and lowest yielding species, *P. phaseoloides* and *A. kretschmeri*, were contained in only one LSD grouping. *Arachis kretschmeri* was clearly the least productive of the species tested under full light, however, statistically, it was not different from *F. congesta* and *A. villosa* both of which had substantially larger means than *A. kretschmeri*.

Table 2.6 Means, standard errors and LSD groupings of total plant biomass (g per pot, oven dried at 70°C) production by (a) 7, (b) 14 and (c) 14 legume species grown under 4 shade levels, harvested 107, 103 and 119 days after planting respectively (n = 20, 16 and 16 respectively). Means in a column followed by the same letter are not significantly different.

(a) 1 st Trial		(b) 2 nd Trial		(c) 3 rd Trial	
Species	Mean total biomass	Species	Mean Total biomass	Species	Mean total biomass
	(g per pot)		(g per pot)		(g per pot)
V. luteola	27.4 ± 5.38 a	P. phaseoloides	$43.1 \pm 8.8 \text{ a}$	C. ternatea	$35.4 \pm 7.6 a$
D. intortum	23.6 ± 4.77 a	C. acutifolium	$35.1 \pm 7.5 \text{ ab}$	A. stenosperma	20.4 ± 5.4 b
C. mucunoides	23.5 ± 3.01 a	D. heterophyllum	$34.0 \pm 6.3 \text{ abc}$	M. lathyroides	$19.3 \pm 2.9 \text{ b}$
M. axillare	18.4 ± 5.41 b	A. americana	$33.1 \pm 9.9 \text{ abcd}$	D. scorpiurus	$18.1 \pm 6.6 \text{ bc}$
D. ovalifolium	14.3 ± 3.53 bc	D. uncinatum	$33.1 \pm 5.6 \text{ abcd}$	C. rotundifolia	$14.3 \pm 4.9 \text{ bcd}$
A. pintoi	10.1 ± 2.43 cd	C. pubescens	$32.9 \pm 5.8 \text{ bcd}$	S. hamata	$13.1 \pm 4.7 \text{ bcd}$
D. canum	$9.73 \pm 2.05 \text{ d}$	C. macrocarpum	22.7 ± 6.5 bcde	M. atropurpureum	$12.2 \pm 1.9 \text{ bcd}$
Probability	< 0.001	N. wightii	22.7 ± 3.6 bcde	R. minima	$11.4 \pm 2.7 \text{ bcd}$
		S. guianensis	$16.3 \pm 6.7 \text{ cde}$	C. pascuorum	$9.5 \pm 3.3 \text{ cd}$
		A. villosa	$14.7 \pm 9.0 \text{ de}$	C. brasilianum	$9.3 \pm 1.5 \text{ cd}$
		A. villosa cv. Kret	$14.6 \pm 5.3 \text{ de}$	A. paraguariensis	$8.4 \pm 2.5 \text{ cd}$
		D. triflorum	$12.6 \pm 3.7e$	M. martii	$8.2 \pm 2.8 \text{ cd}$
		F. congesta	$7.1 \pm 2.8 \text{ e}$	S. scabra	$6.6 \pm 2.3 \text{ cd}$
		A. kretschmeri	3.8 ± 1.2 e	D. virgatus	$6.3 \pm 1.3 \text{ d}$
		Probability	< 0.004	Probability	< 0.0001

Shading of 63% substantially reduced yields of all species, however *P. phaseoloides* remained the greatest producer. *Desmodium uncinatum* was the second greatest yielding species under this shade level followed by *C. pubescens*, *D. heterophyllum* and *C. acutifolium*. All of these species were contained in the highest yielding LSD grouping and were not statistically separate. *Stylosanthes guianensis* and *A. villosa* cv. Kretschmer underwent large decreases in production in relation to other species, becoming the second and third lowest yielding species respectively, whereas under full sunlight they had been the eighth and ninth ranked producers. No plants of *A. villosa* survived under 63% shade until the harvest date. The overall statistical results were not as complicated as found under full light, but there were five LSD groupings found with most species contained in two or more groupings.

The LSD groupings under 76% shade were much clearer than the control or 63% shade. Only two groupings were found and no species overlapped groups. *Pueraria phaseoloides* remained the most productive species, however *C. macrocarpum* had become the second highest yielding species, followed by *D. heterophyllum. Centrosema macrocarpum* was unique in this trial as its yield of total biomass was greater under 76% shade than 63% shade. The two LSD groupings detected could be viewed as containing high and low yielding species with no intermediates as the lowest yielding species in the high yielding group, *N. wightii*, produced an average of 18.5 g per pot, while the highest yielding species in the low yielding group, *A. americana*, averaged only 7.4 g per pot. There were no surviving plants of *A. kretschmeri* at the time of harvest.

At the 84% level of shading the six highest yielding species, the highest yielding LSD group, all produced within 3 g per pot of one another. *Desmodium heterophyllum* replaced *P. phaseoloides* as the highest yielding species, with *C. pubescens* the second highest yielding. Differences between these species were small with only 0.6 g per pot between *D. heterophyllum* and *P. phaseoloides*. The lowest yielding group comprised six species with *A. villosa*, the lowest yielding of these. Neither *A. kretschmeri* nor *A. villosa* cv. Kretschmer had any surviving plants under 84% shade by the time of harvest.

Interaction effects within species (Table 2.8) typically displayed the control treatment to be significantly different from the other shade treatments. The three shaded treatments were typically all contained in a second grouping (A. americana, D. triflorum, D. uncinatum, F. congesta, N. wightii and S guianensis), or as a two further groups with the 76% shade treatment belonging to both of these groups (C. acutifolium, C. pubescens and D. heterophyllum). It was clear in all species, including those in which no significant differences were detected, that the production of total plant biomass was greatly reduced with increasing levels of shade.

Wet/dry tropical species trial

A total of six statistical groupings were found with *C. ternatea*, the highest yielding species, significantly different from all other species (Table 2.9). Other species, which performed well under full light include *A. stenosperma>D. scorpiurus>C. rotundifolia>M. lathyroides*. The poorest performing species was *D. virgatus*, which produced only 60% of the dry matter of the second lowest yielding species (*S. hamata*).

Clitoria ternatea continued to be the most productive species beneath 63% shade, with 71% more dry matter than the second most productive species, *M. lathyroides*. It remained the only species in the highest yielding statistical grouping. *Macroptilium lathyroides* and *A. stenosperma* performed well with both species forming the second highest yielding statistical grouping. A group with more intermediate yields was comprised of the species *A. stenosperma>R. minima>M. atropurpureum>C. rotundifolia>C. brasilianum*. The grouping with the lowest yields contained a total of 10 species, with the lowest yielding of these being *S. hamata*, of which only one plant survived at the time of harvest.

C. ternatea remained the most productive species and the only species in the highest yielding statistical grouping beneath shading of 76%. However the margin between C. ternatea and the second highest yielding species, M. lathyroides, was much smaller than found under the previous shade treatments, 3 g as opposed to 17.4 g and 13 g beneath the control and 63% shade treatments respectively. Despite being more productive than the remaining species, M. lathyroides remained statistically grouped with other, clearly less productive species, M. lathyroides>M. atropurpureum>A. stenosperma>C. brasilianum>C. rotundifolia>M. martii>A. paraguariensis>D. scorpiurus>D. virgatus>R. minima. The lowest yield by a surviving species was by S. scabra, which was not found to be statistically different from any species up to and including M. atropurpureum (Table 2.9). No plants of S. hamata survived until the time of harvest.

No statistical differences were found between the species under 84% shade (P = 0.1946). The best yields under this shade level were given by the species M. lathyroides>M. atropurpureum>A. stenosperma>C. ternatea>C. brasilianum. Very little plant material was produced by M. martii, the lowest yielding species, and again S. hamata had no surviving plants by the end of the trial.

For species in which a significant difference was detected, the control treatment was always significantly different from the three shaded treatments (Table 2.9). The 63%, 76% and 84% shade treatments were always grouped together in the second statistical grouping. This statistical grouping of shaded treatments together often happened in spite of large differences. The most notable example of this was found in *C. ternatea*, with a difference between the 63% and 84% shade treatments of 27.1 g per pot. Four species (*D. virgatus*, *M. martii*, *R. minima* and *S. hamata*) were found not to have any significant differences between shade treatments.

2.3.2 Summary Of Results For Other Parameters

Total and root biomass

Total plant and root biomass were influenced in all species by shading, with the production of material lowered by shading following a pattern similar to above-ground biomass. Species that yielded high amounts of total/root biomass under full light, tended to have higher yields of plant material beneath the shade treatments. A decrease in the size of root systems may make the plant more susceptible to water stress and being pulled out of the ground by grazing animals The allocation of assimilate to plant organs was altered by shade as shown in the shoot:root ratio of plants.

Root Nodulation

Nodulation was clearly shown to decrease under shade, with nodulation beneath 84% shade almost completely absent in all three pot trials. Possible reasons for this may include the supply of soil and fertiliser N relative to plant growth, as the greatest levels of root nodulation were found under the control treatment where the growth of plants was greater than beneath the shaded treatments. As a result plants may have increased nodulation in order to meet increased N demands resulting from greater levels of growth. A second factor which may have contributed to this is increased mineralisation of soil organic N in shaded pots, resulting from lower soil temperatures and better soil moisture levels than found in pots beneath full sun. The conditions would provide a more favourable environment for microbial activity and mineralisation of N from soil organic matter. This effect has been observed in the past, usually in tropical grasses grown where N is limiting (Eriksen & Whitney 1981; Ludlow 1980; Shelton et al. 1987; Wilson et al. 1986; Wilson & Wild 1995). Reduction in nodulation and N fixation in legumes when grown in shade has also been noted before (Bacanamwo & Harper 1997; Chu & Robertson 1974; Eriksen & Whitney 1982; Lie 1974; Sundram et al. 1986; Wong & Wilson 1980). Fixation of N has been found to be directly related to the supply of surplus assimilate to nodules (Humphreys 1991; Othman et al. 1988), and therefore it can be expected that shading will decrease the overall production of assimilate and result in its diversion to shoots rather than roots, hence decreasing nodulation and N fixation. The reduction of root nodulation by shade

Table 2.7 Means, standard errors and LSD groupings of total plant biomass produced by seven wet tropical forage legume species grown under four different shade levels (n = 5). Means in a column followed by the same lowercase letter and means in the same row followed by the same uppercase letter do not differ significantly.

	Total plant biomass (g per pot)					
Species	Control	63% Shade	76% Shade	84% Shade	Probability	
V. luteola	$85.7 \pm 11.2 \text{ aA}$	$40.3 \pm 1.9 \text{ aB}$	$8.9 \pm 2.7 \text{ abC}$	$10.8 \pm 2.7 \text{ abC}$	< 0.0001	
D. intortum	$62.0 \pm 9.5 \text{ bA}$	$28.1 \pm 3.1 \text{ abB}$	$12.3 \pm 3.1 \text{ abBC}$	$6.6 \pm 1.8 \ bcC$	< 0.0001	
M. axillare	$56.1 \pm 0.8 \text{ bcA}$	$20.0 \pm 6.9 \text{ bcB}$	$1.8 \pm 0.5 \text{ bB}$	$1.2 \pm 0.4 \text{ cB}$	< 0.0001	
C. mucunoides	$52.2 \pm 6.8 \text{ bcA}$	$36.3 \pm 4.9 \text{ aB}$	$17.0 \pm 2.6 \text{ aC}$	$15.5 \pm 2.4 \text{ aC}$	< 0.0001	
D. ovalifolium	$45.4 \pm 5.2 \text{ bcdA}$	$9.35 \pm 0.6 \text{ cB}$	$5.8 \pm 1.3 \text{ bB}$	$5.9 \pm 1.1 \text{ bcB}$	< 0.0001	
D. canum	$29.7 \pm 3.4 \text{ cdA}$	$7.5 \pm 0.6 \text{ cB}$	$5.9 \pm 0.8 \text{ bB}$	$5.1 \pm 1.3 \text{ bcB}$	< 0.0001	
A. pintoi	$28.9 \pm 6.1 \text{ dA}$	$7.7 \pm 2.5 \text{ cB}$	$4.9 \pm 1.1 \text{ bB}$	5.4 ± 1.6 bcB	0.0170	
Probability	< 0.0001	< 0.0001	0.003	< 0.0001		

Table 2.8 Means, standard errors and LSD groupings of total plant biomass production (g per pot, oven dried at 70° c) by 14 wet tropical forage legume species grown under 0 (control), 63, 76 and 84% shade (n = 4), harvested 103 days after planting. Means in a column followed by the same lowercase letter and means in a row followed by the same uppercase letter do not differ significantly.

Species	Control	63 % Shade	76% Shade	84% Shade	Probability
P. phaseoloides	95.6 ± 11.4 aA	$38.5 \pm 9.4 \text{ aB}$	$26.0 \pm 1.4 \text{ aBC}$	$12.3 \pm 2.5 \text{ aC}$	< 0.0001
A. americana	$88.3 \pm 5.7 \text{ abA}$	$17.6 \pm 4.3 \text{ bcdB}$	$7.4 \pm 3.8 \text{ bB}$	$5.1 \pm 1.0 \text{ bcB}$	< 0.0001
C. acutifolium	$82.7 \pm 6.7 \text{ abcA}$	$27.3 \pm 4.5 \text{ abB}$	$20.6 \pm 4.3 \text{ aBC}$	$10.0 \pm 1.7 \text{ abC}$	< 0.0001
D. heterophyllum	$72.3 \pm 8.2 \text{ bcdA}$	$28.9 \pm 2.1 \text{ abB}$	$21.7 \pm 3.3 \text{ aBC}$	$12.9 \pm 2.8 \text{ aC}$	< 0.0001
C. pubescens	$68.4 \pm 8.2 \text{ bcdA}$	$29.1 \pm 3.5 \text{ abB}$	$21.4 \pm 1.8 \text{ aBC}$	$12.6 \pm 1.8 \text{ aC}$	< 0.0001
N. wightii	$67.9 \pm 12.5 \text{ bcdA}$	$11.4 \pm 0.9 \text{ cdeB}$	$18.5 \pm 2.7 \text{ aB}$	$4.3 \pm 0.9 \text{ cB}$	< 0.0001
D. uncinatum	$62.7 \pm 0.87 \text{ cdA}$	$35.8 \pm 6.0~aB$	$20.8 \pm 4.7 \text{ aC}$	$10.0 \pm 2.2 \text{ abC}$	< 0.0001
S. guianensis	$53.5 \pm 7.2 \text{ deA}$	$2.1 \pm 0.8 \text{ eB}$	$1.0 \pm 0.4 \text{ bB}$	$0.8 \pm 0.3 \text{ cB}$	< 0.0001
A. villosa cv. Kretschmer	$39.0 \pm 3.0 \text{ efA}$	$3.5 \pm 1.2 \text{ eB}$	$1.4 \pm 0.3 \text{ bB}$	-	< 0.0001
C. macrocarpum	$37.7 \pm 7.3 \text{ ef}$	$18.4 \pm 7.5 \text{ bc}$	$23.0 \pm 5.8 \text{ a}$	$11.8 \pm 0.9 \text{ a}$	0.0562
D. triflorum	$35.3 \pm 5.6 \text{ efA}$	$10.6 \pm 2.4 \text{ cdeB}$	$2.6 \pm 0.9 \text{ bB}$	$1.9 \pm 0.4 \text{ cB}$	< 0.0001
A. villosa	$32.2 \pm 17.5 \text{ efg}$	-	$2.0 \pm 0.9 \text{ b}$	$0.6 \pm - c$	0.2865
F. congesta	$22.4 \pm 6.4 \text{ fgA}$	$4.1 \pm 2.5 \text{ deB}$	$2.1 \pm 0.4 \text{ bB}$	$1.5 \pm 0.6 \text{ cB}$	0.0039
A. kretschmeri	$5.2 \pm 0.75 \text{ g}$	$4.0 \pm 2.0 \text{ e}$	$0.2 \pm - b$	-	n.r.
Probability	< 0.0001	<0.0001	< 0.0001	< 0.0001	

Table 2.9 Means, standard errors and LSD groupings of total plant biomass (g per pot, oven dried at 70° c) produced by 14 forage legume species grown under 0 (control), 63, 76 and 82% shade (n = 4), harvested 119 days after planting. Means in a column followed by the same lowercase letter and means in a row followed by the same uppercase letter do not differ significantly.

Species	Control	63% Shade	76% Shade	84% Shade
C. ternatea	$65.0 \pm 9.6 \text{ aA}$	$31.2 \pm 6.8 \text{ aB}$	$21.0 \pm 5.2 \text{ aB}$	4.1 ± 2.2 B
A. stenosperma	$47.6 \pm 8.7 \text{ bA}$	$14.9 \pm 1.4 \text{ bcB}$	$9.1 \pm 1.7 \text{ bcB}$	$5.7 \pm 1.6~\mathrm{B}$
D. scorpiurus	$40.5 \pm 6.8 \text{ bcA}$	$1.6 \pm 0.9 \text{ dB}$	$6.2 \pm 0.6 \text{ bcB}$	$1.8\pm0.6~\mathrm{B}$
C. rotundifolia	$34.2 \pm 11.3 \text{ bcdA}$	$8.4 \pm 2.5 \text{ cdB}$	$7.2 \pm 2.0 \text{ bcB}$	1.0 ± - B
M. lathyroides	$31.1 \pm 1.0 \text{ cdeA}$	$18.2\pm1.9~\mathrm{bB}$	$18.2 \pm 7.4 \text{ bB}$	$6.6 \pm 2.8 \; \mathrm{B}$
C. pascuorum	$26.5 \pm 1.9 \text{ cdeA}$	$2.9 \pm 1.1 \text{ dB}$	$1.8 \pm 0.6 \text{ cB}$	$1.4 \pm 0.9 \text{ B}$
A. paraguariensis	$20.9 \pm 5.2~\mathrm{defA}$	$4.3 \pm 1.0 \text{ dB}$	$6.3 \pm 2.7 \text{ bcB}$	$2.8 \pm 0.9 B$
M. atropurpureum	$19.5 \pm 3.5 \text{ defA}$	$9.4 \pm 1.7 \text{ cdB}$	$9.9 \pm 2.0 \text{ bcB}$	$6.1 \pm 2.3 \text{ B}$
R. minima	$17.3 \pm 2.1 \text{ ef}$	$11.5 \pm 1.9 \text{ c}$	$2.8 \pm$ - bc	2.1 ± -
C. brasilianum	$17.0 \pm 1.6 \text{ efA}$	$8.0 \pm 1.3 \text{ cdB}$	$8.5 \pm 2.9 \text{ bcB}$	$3.6 \pm 1.0 \text{ B}$
S. scabra	$16.5 \pm 2.9 \text{ efA}$	$2.4 \pm 0.7 \text{ dB}$	$1.0 \pm 0.005 \text{ cB}$	$1.0\pm0.9~\mathrm{B}$
M. martii	$16.4 \pm 1.3 \text{ ef}$	$1.4 \pm 1.1 d$	$6.5 \pm 6.1 \text{ bc}$	0.3 ± -
S. hamata	$16.2 \pm 4.6 \text{ efA}$	$0.9 \pm - B$	-	-
D. virgatus	$9.8 \pm 2.9 \; \mathrm{f}$	$7.4 \pm 2.0 \ d$	$5.5 \pm 2.9 \text{ bc}$	1.2 ± -
Probability	<0.0001	< 0.0001	0.0484	0.1946

has the potential to undermine the usefulness of legumes in such situations and to make them less effective fixers of N than in open pastures.

Leaf N

N content in leaf material of plants was consistently greater beneath shade treatments than under the control. Typically there was a substantial increase in leaf N upon shading of 63% when compared to the control. However increased shading to 76 and 84% gave small increases in leaf N, but not to the previous extent. The N content of plant material grown under shade has generally been found to increase (Humphreys 1994; Wilson et al. 1986; Wong & Wilson 1980). It is known that, when grown under shaded conditions, tropical grasses may undergo an increase in N content and dry matter yield if soil N is limiting to growth under full light. This effect was shown to reside in the soil by Wilson & Wild (1991), as it did not occur in plants grown in solution culture. The effect was a result of a more favourable environment for microbial activity in the soil due to reduced soil moisture decline in dry periods, and to lower soil temperatures at the litter-soil interface (Wilson & Wild 1991). This effect is thought to be limited to the soil surface where soil temperatures fluctuate to a much greater extent than at depth. It is hypothesised that the effect of reducing soil temperatures under shade leading to greater soil N availability would be prominent in these pot trials due to the surface area of soil exposed. The soil surface and the sides of each pot were exposed and able to absorb light/heat (pots were made of black plastic), with the likely result that pots under the control treatment would have had substantially greater soil temperatures than those beneath shade.

Leaf P

The effects of shade upon levels of leaf phosphorus were less clearly defined than those of nitrogen. In the second wet species and the wet/dry species trial, overall levels of leaf P were greater under the shade treatments, however the first wet species trial displayed the greatest levels of leaf P under the control, although there was no statistical difference found between treatments. Interaction effects were only present in the 1st and 2nd wet tropical species trials, which did not appear to display any clear relationship, with nine species not having significant differences between shade treatments. In species where differences were detected some displayed an increase in leaf P with shading (C. pubescens, D. uncinatum, F. congesta, N. wightii and S. guianensis), while others were found to have the greatest concentrations of leaf P under the control treatment (C. mucunoides, D. intortum and D. heterophyllum). In several species (A. americana and V. luteola) significant differences were detected, however no pattern was discernible. Within the wet/dry species tested, results were also mixed, with P concentrations in some species increasing with shade (C. rotundifolia, A. stenosperma, S. scabra, M. lathyroides, C. ternatea and D. virgatus), and others decreasing (C. brasilianum and D. scorpiurus). Despite an overall increase in leaf P concentrations, the effects of shade are inconsistent between species and do not suggest any clear relationship with shade. Norton et al. (1991) examined the P content of tropical grasses and concluded that the effects of shading on the P content of the grasses were small and inconsistent between species.

Time to first flower

Shade generally caused an increase in the time to first flower, however it was not always statistically significant. The species in which flowering was significantly delayed by shading include *D. triflorum, C. ternatea, M. atropurpureum* and *S. hamata*. This suggests that shading can cause some of the legume genotypes to prolong vegetative growth under shaded conditions. This may have implications for seed production, with earlier flowering cultivars/accessions desirable in certain situations in order produce seed before unfavourable conditions can affect seed production. As a result the delay in flowering present in some species, may be of importance to persistence through its potential effect upon seed production. It was noted by Tang *et al.* (1997) that plants acclimating to low light environments have a decreased allocation to reproduction. Amar (1996) also found that the times to first flower of the species *S. hamata* cv. Verano and *D. virgatus* CPI 79653 were significantly increased by shading of 78%, while no effect was found in *A. paraguariensis* or *A. triseminalis*.

Production of seed and seed characteristics

The production of seed was clearly decreased under the shaded treatments. The largest difference within each species was between the control and the 63% shade treatment, with much smaller differences between the three shade treatments. The decrease in seed production was not unexpected, due to the decrease previously observed in plant biomass production beneath shade treatments. Smaller plants beneath the shade treatments would not have had the same amount of photosynthate allocated to seed production as plants beneath the control treatment, due to lower total leaf area and less PAR. The delay in flowering of some species caused by shading suggested that reproductive growth may be delayed or take longer beneath shade and, as a result of this, plants beneath the shaded treatments may have had the potential seed production underestimated due to the delay. It is possible that if seed had been collected until all plants had finished flowering, the difference between seed production may have been smaller than found in this trial. However it would not be expected that shaded plants would produce similar amounts of seed as plants under the control treatment due to the reasons mentioned previously.

Seed weight was generally not affected by shading. When viewed in conjunction with the amount of seed produced, it appears that that the shaded plants may produce fewer seeds, however the weight of the seeds was similar to those produced in full light. This suggests that under shaded conditions available assimilate is used to produce fewer seeds but they are of similar size to those produced by plants beneath full light.

Seed production has been found to be decreased by shading during the reproductive stage in cereals such as rice (Venkateswarlu & Maddulety 1976), cotton seed (Eaton & Ergle 1954), grain legumes such as Peas (Meadly & Milbourn 1971) and Cowpea (Summerfield et al. 1976), grasses (de Oliveira & Humphreys 1986), and in forage legumes such as Subterranean Clover (Collins et al. 1978). In cereals subject to pre- and post-anthesis shading, shade was found to influence chiefly the number of ears per unit area and grain weight (Fisher 1975; Gifford et al. 1973). Similarly de Oliveira & Humphreys (1986) found that shading the tropical grass Panicum maximum cv. Gatton at 25 and 54% resulted in decreased yields of seed and a slight reduction in the hundred-seed-weight. Yields of seed produced by Subterranean Clover (Trifolium subterraneum) were invariably reduced by growth under 30 and 55% of full daylight (Collins et al. 1978). Seed size was not found to decrease beneath shade treatments, with seed size maintained at the expense of seed number, as appears to have been the case in this study. It was suggested that a shortage of photosynthate was the key factor limiting seed production under shade treatments. Any effects upon seed production and seed size are likely to have an impact upon the long-term persistence of a species beneath shaded conditions, with decreases in the amount of seed produced likely to diminish the ability of the species to build seed bank reserves from hard seed and to recruit new plants.

The amount of readily germinable seed was increased in some species when produced under shaded conditions (*M. atropurpureum* and *M. lathyroides*). Similarly the time to 50% germination was increased by shading, although in different species (*C. rotundifolia* and *M. martii*). Production of hard seed was also reduced in the species *M. atropurpureum* and *M. lathyroides*. The potential increase in the amount of readily germinable seed and the speed of seed germination may make species, in which this occurs, more vulnerable to unfavourable conditions after initial seed germination, with fewer reserves of hard seed left in the soil and readily germinable seeds germinating within a short time of one another. Shading produced no discernible pattern in the levels of non-viable seed produced.

Shoot:root ratio

The shoot:root ratio was increased by shade, a known effect which has been observed many times in the past (Amar 1996; Atwell *et al.* 1999; Lange *et al.* 1981; Ludlow *et al.* 1974; Samarakoon *et al.* 1990; Wilson & Ludlow 1991; Wong *et al.* 1985b; c). The increases in the proportion of shoot material came at the expense of the root system. An excessive allocation of resources from the roots to the shoots, may lead to problems where plants are subjected to periodic water stress and intensive grazing. Overly reduced root systems in these situations could lead to depression of dry matter

production and longer recovery periods in plants where regrowth after defoliation is related to carbohydrate and mineral reserves located in the crown and roots (Wilson & Ludlow 1991). Under full light, regrowth after defoliation has been found to be more dependent upon residual leaf area than upon stored reserves (Humphreys & Robinson 1966), but Wilson & Ludlow (1991) suggest that beneath shade this situation may be reversed due to other morphological responses such as increased stem elongation and reduced branching which may cause fewer axillary buds and little leaf area to remain after grazing. Also the vulnerability of plants to uprooting by stock, cattle in particular due to their style of grazing, may be increased due to smaller root systems less effectively anchoring the plants in the ground.

2.4 Discussion

2.4.1 Species adapted to wet tropical areas

Overall the level of shading under which legumes were grown greatly affected the production of above-ground biomass. Yield was invariably reduced as shade increased. Highly significant shade by species interactions indicated the differing performance of legume species. The reduction in the yield of dry matter due to shading was not unexpected, having been found by many workers in the past (Amar 1996; Chen 1993; Devkota *et al.* 2001; Eriksen & Whitney 1981; Peri *et al.* 2001; Varella *et al.* 2001).

The concept of shade tolerance is usually associated with the growth of plants in shade relative to that of full sun as influenced by regular defoliation (Wong 1991). When the production of aboveground dry matter is expressed as a percentage of production under the control, the potential shade tolerance of species is easier to ascertain (Tables 2.10). The species which produced approximately one-fifth or more of their yield under the control treatment beneath 84% shade were C. macrocarpum, C. mucunoides, D. uncinatum, A. pintoi, D. heterophyllum and C. pubescens (wet tropical species) and M. atropurpureum, C. brasilianum and M. lathyroides (wet/dry tropical species). However there were several other species, which still produced relatively large amounts of dry matter in comparison to other species. When the absolute production of dry matter is examined, species with greater yields beneath 84% shade include D. intortum, D. ovalifolium, C. mucunoides, D. heterophyllum, D. uncinatum, C. pubescens, P. phaseoloides, C. macrocarpum and C. acutifolium (wet tropical species), and C. ternatea, A. stenosperma, M. lathyroides, M. atropurpureum and C. brasilianum (wet/dry tropical species). Typically, species that yielded well relative to other species beneath 84% shade also yielded well under the other shade treatments. The data and corresponding light curves (see Chapter 3), indicate a difference between "shade tolerance" and "shade production". Where production of forage for livestock is desired the concept of shade production may be of greater importance than that of shade tolerance or shade adaptation.

Calopogonium mucunoides was the highest yielding species beneath 76% and 84% shade treatments in the first wet tropical species trial, while also producing the second greatest yield under 63% shade. Under the 84% shade treatment its yield relative to full sun was the second greatest of all species examined, approximately one third that of full light. These results, in addition to the photosynthetic light response curves (see Chapter 3), suggest that *C. mucunoides* is shade-tolerant and also shade productive. Other workers have found inconsistent results for *C. mucunoides*. Watson & Whiteman (1981) found it to persist well under moderate grazing pressure at 60% light transmission (40% shade). In a trial examining 84 legume species and accessions, Stur (1990) found *C. mucunoides* to be the seventh and eleventh most productive legume beneath 20% light (80% shade) and 50% light (50% shade) respectively. Wong (1991) indicated *C. mucunoides* as having a moderate shade tolerance, while Chen & Aminah (1992) state that *C. mucunoides* is poorly adapted to shade with nodulation, top and root growth all declining markedly with decreasing light intensity, and attribute this to the non-plasticity of leaves under shade in comparison to other shade-tolerant species.

Desmodium intortum is a promising species for fodder production under shaded conditions as it yielded very well under all shade levels including full sun, where it produced the second greatest yield of dry matter. The results suggest that it has the ability to yield well over a range of light levels, from full sun to heavy shade, and as a result has the potential for use in young plantations where light levels are still relatively high, yet still remain a relatively good producer of dry matter as the plantation ages and light levels decrease. Previous studies have described *D. intortum* as varying from shade-tolerant (Pengelly 1992a) to fairly shade-tolerant (Reynolds 1995), to very shade-tolerant (Ludlow 1980), however no reference to *D. intortum* as shade intolerant has been found. According to Whiteman *et al.* (1974) it performed well under 50% shade, and Stur (1990) ranked it as one of the best yielding legume species beneath 20 and 50% light transmission (80 and 50% shade respectively). Similarly Rika *et al.* (1990) and Kaligis & Sumolang (1990) found *D. intortum* to consistently be one of the best yielding of 35 and 40 species of legume (respectively) tested beneath mature coconut stands in Bali and Sulawesi.

Arachis pintoi, although not producing large levels of dry matter beneath the shade treatments or the control, displayed an adaptation to shade, maintaining just under a quarter of its yield beneath full light when grown under 84% shade. However, what is not reflected in the results is the condition of the plants. Plants of A. pintoi grown under shaded conditions appeared to be in a much healthier condition than those under full sun. Leaves of plants grown under any of the shade treatments were much greener than those of plants from the full sun treatment. In addition to the lighter colour of the leaves under the control treatment, chlorotic patches were present often turning into patches of necrosis with time. This phenomenon was not attributed to the suspected lower levels of nitrogen available to plants in full sun, as discussed elsewhere, due to its presence on new and old leaves alike, but possibly due to photoinhibition as A. pintoi has in the past been reported to be a shadeadapted plant and in some cases to perform better under light to moderate shading than under full sun. Fisher & Cruz (1994) noted that A. pintoi appeared to grow better under shaded conditions than under full sun and later confirmed this in a pot trial where A. pintoi grown under 70%, 50% and 30% of full sun produced larger amounts of dry matter than plants in full sun. The species may also have potential as a ground cover, being a shade-tolerant, stoloniferous, perennial herb not becoming much greater in height than 20 cm. Arachis pintoi is generally regarded as being shade-tolerant (Cook 1992; Fisher & Cruz 1994; Humphreys 1994; Mendra et al. 1995; Reynolds 1995), and its persistence under shaded conditions with defoliation has been found to be good but often production is not particularly high (Kaligis & Sumolang 1990; Kaligis et al. 1994b; Ng 1990; Rika et al. 1990; Stur 1990). Arachis pintoi's high degree of shade tolerance and hence usefulness as a ground cover in orchards was one of the main reasons for its commercial release 1987 (Cook et al. 1993).

Both Desmodium ovalifolium and D. canum yielded reasonably similar amounts of dry matter under the three shaded treatments, while under full sun D. ovalifolium produced approximately 58% more than D. canum. As a result D. canum had slightly greater production relative to full sun under shaded conditions, but under shade the species were relatively close in both relative and actual yields. However the relative yields of both species were not great enough to suggest shade tolerance and the shade production of dry matter was not particularly high. These results, when coupled with the light response curves (Chapter 3), suggest that neither species would be suited for the production of forage under shaded conditions. These results tend to contradict work done in the past, which has indicated that D. ovalifolium in particular is a very shade-tolerant species. Schultze-Kraft (1992a) noted that D. ovalifolium is often used as ground cover in plantations in southeast Asia with a mixture with Centrosema pubescens, Pueraria. phaseoloides, Calopogonium caeruleum and C. mucunoides of which it will be the most persistent as it is the most shade-tolerant. Satjipanon (1991) indicated that D. ovalifolium was shade-tolerant and is widely distributed under rubber trees in the south of Thailand. Its production was noted by Reynolds (1995) to be good under shaded conditions, however in a trial conducted by Rika et al. (1990), examining 35 species of legume under a stand of old coconut trees with a shade level of 42%, D. ovalifolium gave a moderate yield of dry matter in comparison to other legume species. In a similar trial under mature coconut trees, where shade was estimated at 27%, Kaligis & Sumolang (1990) noted that among other legume species D. ovalifolium

had slightly lower yields of dry matter than many other species but showed good persistence and regrowth.

In the past *D. canum* has been reported to perform well under 30% shade (Eriksen & Whitney 1982), and Skerman *et al.* (1988) described it as being quite shade-tolerant. It has been noted to occur naturally under coconuts in the Solomon Islands (Wahananiu *et al.* 1993), and was said to be more shade-tolerant than Siratro (*Macroptilium atropurpureum*) and Stylo (Ludlow 1980). However Reynolds (1995) found that its growth beneath coconuts in Western Samoa and Zanzibar was poor.

Macrotyloma axillare and Vigna luteola were the second and third greatest yielding species beneath full sun in the first wet tropical species trial, however, both species showed a great reduction in dry matter production with shading. The yield of dry matter by V. luteola was relatively high under the shade treatments when compared to most species, however the condition of the plants beneath full sun is not reflected in the yield of dry matter. Plants of V. luteola under the more heavily shaded treatments, 84% shade in particular, had few leaves, with most of those displaying patches of necrosis. Plants appeared sickly and weak, and composed mainly of stem material, indicating that nutritive value to stock and persistence, in particular, may be serious problems under shaded conditions. M. axillare was one of the worst affected species by shade, with dry matter production declining to very low levels beneath 76% and 84% shade. M. axillare had the second lowest relative yield of any species examined that survived beneath 84% shade. When the effect of shade upon production is examined in addition to the light response curves (Chapter 3), it is apparent that both species appear to being neither shade-tolerant nor shade-productive. According to Reynolds (1995), little is known about the shade tolerance of V. luteola, and it was not recommended for use beneath coconut plantations, although it yielded well under 50% and 20% light transmission in a trial undertaken by Stur (1990). M. axillare is reported by Staples (1992b) to have a moderate shade tolerance, and was found to give average to below average yields beneath coconuts in Bali (Rika et al. 1990), while in Sulawesi beneath coconuts it performed very poorly (Kaligis & Sumolang 1990). In a trial examining the performance of six grasses and six legume species sown into a layered, open Eucalypt forest near Gympie with an estimated minimum light penetration of 72%, Cook & Grimes (1977) found *M. axillare* to be the best performing legume species, yielding even greater amounts of dry matter than D. intortum. However the relatively good performance of M. axillare in the study was suspected to have resulted from the extremely dry conditions, as M. axillare is highly tolerant of drought, while D. intortum is not. Greater levels of production by D. intortum in moister gullies supported the theory that water may have been the limiting factor in the trial, not light.

Although it did not produce large quantities of dry matter under full light, *Centrosema macrocarpum* was one of the best yielding species beneath each of the three shaded treatments. Beneath 84% shade it was out-yielded by only three other species (*D. heterophyllum*, *D. uncinatum* and *P. phaseoloides*). *C. macrocarpum* maintained the greatest proportion of its yield under full light than any other species, save *C. mucunoides* under 63% shade. However the species' light response curve suggests that it is not a shade-tolerant plant, with a large difference between plants grown in the sun and 84% shade. The results obtained in this study do not allow a conclusion to be drawn regarding *C. macrocarpum* as to whether it is a shade-tolerator or a shade-producer. What is clear, however is that the species has the potential for use in shaded situations, provided its climbing, vine-like habit does not become a problem. Previous work examining the shade tolerance of *C. macrocarpum* is scarce, but Schultze-Kraft (1992b) stated that it tolerates moderate shade while Reyes *et al.* (1990) noted that it displayed good adaptation under coconut and *Pinus* plantations, and it tolerated light-restricted conditions in an oil-palm plantation. Horne & Stur (1999) indicated that it had potential as a cover crop beneath trees.

Silverleaf Desmodium (*Desmodium uncinatum*) had good actual and relative yields under all treatments, indicating that it has the potential for use in both open and shaded conditions. The production of dry matter under full light was not particularly high compared to some species, but under 63 and 84% shade it was the second greatest yielding species. The closeness of the light response curves obtained under 84% shade and the control also indicate *D. intortum* is a shade-

tolerant species. This is not surprising as the two species are closely related (Hacker 1992). Desmodium uncinatum has been reported to be more shade-tolerant than D. intortum and M. atropurpureum (Reynolds 1995). However Humphreys (1994) indicated that D. intortum and A. pintoi were more shade-tolerant than D. uncinatum. Beneath the canopies of both exotic (Pinus elliottii, P. taeda and P. caribaea) and native (Araucaria cunninghammii and Agathis robusta) pines, Desmodium intortum was found by Richards & Bevege (1967) to grow vigorously, however by the third season the stands of legume began to decline under the denser canopies of the plots containing Pinus spp.

The species Desmodium heterophyllum and Centrosema pubescens both produced very similar relative and actual yields with the greatest differences between the species being 1.5% and 5.7 g respectively. The yields of both species were very good under all shade treatments, especially the heavily shaded 84% treatment, where D. heterophyllum had the greatest yield of any species. The yield of both species under full sun was also good, indicating that they can be used over a range of shade levels from full sun to heavy shade. The relative yields were higher than average beneath 84% shade, although there was a substantial difference between D. heterophyllum and C. pubescens and the two species with the greatest relative yields, Centrosema macrocarpum and Calopogonium mucunoides (a difference of over 13%). The light response curves obtained in Chapter 3, in contrast to the relative yields, did not suggest shade tolerance. Desmodium heterophyllum is said to be shadetolerant by a number of sources (Reynolds 1995; Schultze-Kraft 1986; Skerman et al. 1988; Stur 1990; Wong 1991), with Hacker & Teitzel (1992) suggesting that it is one of the most shade-tolerant legumes. Kaligis & Sumolang (1991) found that D. heterophyllum, along with some other low growing species, initially gave low yields of dry matter with greater yields in later harvests when planted under coconuts with an estimated PAR of 73%. In a trial conducted by Gutteridge & Whiteman (1978), D. heterophyllum was found to maintain a strong presence in the pasture and even to invade other plots when grown with Para grass (Brachiaria mutica) under young coconut palms (50% light transmission).

Several species produced very little above-ground dry matter under the shaded treatments (*A. americana, S. guianensis, D. triflorum* and *F. congesta*), with no plants of the accessions *A. villosa* or *A. villosa* cv. Kretschmer surviving under the 84% shade treatment at the time of harvest. *Aeschynomene americana, S. guianensis* and *N. wightii* all yielded well under full light, however under 63% shade the yield of the species fell substantially. Higher levels of shade led to lower production, especially under 84% shade. Reports on the performance of *S. guianensis* under shade in the literature are mixed, with Gregor (1972) reporting *S. guianensis* as a shade-tolerant species and Mannetje (1992) recommending its use as a cover crop beneath plantations. Steel & Humphreys (1974) found the growth of *S. guianensis* beneath light transmission levels of 77 – 80% in a coconut plantation to be satisfactory. However other workers have found *S. guianensis* to perform poorly under shade (Eriksen & Whitney 1982; Ludlow 1980), with Gutteridge & Whiteman (1978) noting that it behaved more as a short-term pioneer species.

Aeschynomene americana produced high levels of biomass under the control treatment, having the second greatest yield of all species, however it performed poorly under shaded conditions, with severely depressed yields under the two heaviest shade treatments (76 and 84% shade). Relative yields were also low beneath these treatments, indicating that A. americana is neither shade-adapted nor shade-tolerant. Light response curves for the species further support these results with a large difference present between the curves of plants grown under the control treatment and 84% shade. In the past A. americana has not been found to perform well under shade. Beneath 50% light, A. americana cv. Glenn and CPI 56283 gave the two greatest yields of 84 legume species examined (Stur 1991). However when light was reduced to 20%, both A. americana cv. Glenn and CPI 56283 had much lower yield rankings. Beneath light transmission of 73% PAR A. americana initial yields were found by Kaligis & Sumolang (1991) to be the greatest given by 40 species of legume. However in the subsequent harvests, taken every two months, yields declined to low levels. Under a lower light level of 58% PAR beneath a stand of old coconuts in Bali, A. americana did not perform

as well, with a moderate initial yield followed by subsequent declines in yield as time progressed (Rika et al. 1991).

Both *A. villosa* cv. Kretschmer and CPI 37235 gave low yields of dry matter under the control treatment compared to other species. Both accessions suffered substantial decreases in their already low yield with shading of 63%. Further shading continued to reduce the yield of above-ground biomass to insignificant levels, with no plants of either accession surviving until the date of harvest under 84% shade. Relative yields were also very low for both accessions, with both producing less than a tenth of their yield under the control treatment beneath 63% shade, where the mean relative production was 38%. When these results are viewed with those obtained in Chapter 3, it is apparent that neither *A. villosa* cv. Kretschmer or *A. villosa* CPI 37235 display any adaptation or tolerance to shade, and hence little potential for use in shaded situations. There appears to be little literature detailing the performance of *A. villosa* under shaded conditions although Macfarlane (1993) indicated that, among other species, *A. villosa* displayed promising research results.

Neonotonia wightii gave a low yield under 63% shade but experienced a high yield beneath 76% shade (approximately twice that of 63% shade), which was comparable to that produced by *C. pubescens, C. acutifolium* and *D. uncinatum*, however under 84% shade the yield fell once gain to very low levels. Neonotonia wightii has been noted to have the potential to become a weed beneath tree crops (Pengelly & Benjamin 1992; Sexton pers comm.). Reports of its performance beneath plantations are somewhat mixed, with (Ludlow 1980) ranking its shade tolerance after that of *D. intortum* and *C. pubescens*. (Reynolds 1995) also indicated *N. wightii's* shade tolerance to be fair. However (Eriksen & Whitney 1982) found production to decline substantially below 45% light, while it was found to grow better under less shaded conditions by (Bazill 1987).

Production of dry matter by *Desmodium triflorum* was low under all treatments compared to other species, as were the yields relative to the control. However, despite the low production of dry matter, plants of *D. triflorum* appeared healthy beneath all treatments. The light response curves suggest *D. triflorum* is a shade plant with the light response curves showing little difference. The data suggest that *D. triflorum* is a shade tolerating species due to its similar light response curves beneath the control and 84% shade treatments and its ability to produce yields of dry matter under the control treatment that are relatively much greater than those under shade. If the species were shade-adapted, then greater yields of dry matter under the control treatment would not be expected as shade-adapted plants are unable to adapt to high light levels with an increase in photosynthesis (Wilson & Ludlow 1991). It has been observed to be naturalised in many coconut growing areas and found in native pastures beneath coconuts in Vanuatu (Reynolds 1995). *D. triflorum* is not a productive species, yielding little dry matter (Pengelly 1992b; Reynolds 1995), however it is resistant to heavy grazing and, with a mat-forming habit, it may be suitable for use as a ground-cover where the production of herbage is not of primary importance.

No conclusions regarding *Arachis kretschmeri's* shade tolerance or adaptation could be reached from the results obtained. The cuttings that were planted into pots failed to survive beneath 76 and 84% shade, and while those under 63% and the control treatment did, there was very little growth by the cuttings under either treatment. As a result of this the relative yield beneath 63% shade appears to be very high while the actual yields were the lowest of any species under those shade treatments. It was not possible to obtain light response curves from plants grown later under 84% shade due to their failure to grow and produce new leaves or to even survive for any period of time. It is suspected that the establishment of the species from cuttings may not be suitable for testing of the species in this regard, as the plant from which the cuttings were made was large, healthy, and growing well under full light in the field. However the cuttings placed under the control treatment and 63% shade failed to produce any significant amounts of biomass suggesting that, despite the production of fine roots by the cuttings at the time of planting, the plants need to be established from seed in order to properly assess their performance under shaded conditions. Little information is available regarding properties of *A. kretschmeri*, let alone its performance under shade.

2.4.2 Species adapted to wet/dry tropical areas

The most promising species examined adapted to wet/dry tropical areas was Clitoria ternatea, which gave the best yield of any species under all shade levels. It was easily the most productive species under 63 and 76% shade, although the margin was much narrower under 84% shade. Its relative production was not as high as that of some other species under 76 and 84% shade. Despite not having the greatest relative yields under the heavier shade treatments, C. ternatea appears to have potential for shaded situations due to its high actual production. Several other of the plant's properties will have to be borne in mind when considering it for use beneath plantations. The susceptibility of the plant to frequent low cutting and continuous heavy grazing is due to the location of the growing points on the ends of the main branches (Staples 1992a), and its high palatability to cattle can result in selective grazing, which may result in its failure to persist (Skerman et al. 1988). Clitoria ternatea does not appear to have been widely tested for its performance under shade. Sanchez & Ibrahim (1991) found it to be more shade-tolerant than the legume species S. guianensis and C. pubescens when grown in pots under an 8-year-old rubber plantation with 100, 27, 8, 6 and 3% PAR. Beneath artificial shading giving 50 and 20% light, Stur (1991) found C. ternatea to be among the top 30 yielding species from a total of 84 species. The results obtained were somewhat similar to those found in this work, with its actual yield ranking substantially higher than its relative yield ranking. Beneath 50 and 20% light, the ranking of C. ternatea by actual yield was 25th and 18th, however it's ranking in terms of relative yield was much lower, 60^{th} and 53^{td} respectively. Staples (1992a) does not mention C. ternateas' performance under shade but indicates that it grows best in full sun.

Arachis stenosperma was another species, which performed well under the heavily shaded treatments. Beneath full light and 84% shade it was second only to *C. ternatea* as the most productive species, but also, like *C. ternatea*, its relative yield was not particularly high under shade. Results obtained in this trial indicate that further research examining *A. stenosperma* should be undertaken. No previous work could be found relating to the performance of *A. stenosperma* under shaded conditions, and information relating to the species itself was difficult to find. Kretschmer *et al.* (1999) found that the spread of *A. stenosperma* and other species of *Arachis*, except *A. kretschmeri*, was good to excellent and that the harvest of seed of *A. stenosperma*, from a small area in a young, producing, citrus grove, was the greatest of the species tested along with an unnamed species of *Arachis*.

Both Macroptilium atropurpureum and M. lathyroides retained good relative yields beneath shade, and beneath 84% shade they had the greatest and third greatest relative yields of the species tested, respectively. The actual yields of M. atropurpureum were not particularly high under low light but improved with respect to other species, as shade increased. M. lathyroides gave a better yield of dry matter than M. atropurpureum under all treatments. Both species appear to have potential for use under shaded conditions, however, the yield of M. atropurpureum under the control treatment was lower than expected. Skerman et al. (1988) found it grew reasonably well in shade, but preferred abundant sunlight. More specific information is given by Eriksen & Whitney (1982), who found it to grow reasonably well in moderate shade but to yield poorly under heavy shade. Under moderate shade beneath coconuts in Vanuatu, M. atropurpureum was found to be useful in smothering Cassia tora (Reynolds 1995). Wong (1991), however, indicated M. atropurpureum's shade tolerance as being low, while Stur (1991) found that under 50% light it gave the 20th greatest yield out of 84 species of legume tested, and under 20% light its ranking increased to the 5th highest yielding species. Little information regarding the performance of M. lathyroides is available. Skerman et al. (1988) indicated that the lower parts of the plant can become woody in response to shade, and that it is not unduly suppressed by low light levels, except in the seedling stage.

Both of the species of *Stylosanthes* performed very poorly under the shaded treatments. *Stylosanthes hamata* failed to survive beneath 76 and 84% shade, and while *S. scabra* survived under all shade treatments the yield of dry matter by plants was very low. The relative yields of both species were also very low under all shade treatments. These results and those physiological measurements

obtained in Chapter 3, clearly indicate that neither *S. hamata* nor *S. scabra* are suited for growth, or even survival, under moderate to heavily shaded conditions. Results obtained here concur with the findings of Evans *et al.* (1992) who found both *S. hamata* and *S. scabra* to have poor shade tolerance. *Stylosanthes hamata* gave above average yields when grown under 50% light (21st out of 84 species), however its yield and relative ranking were greatly decreased when grown under 20% light, with the species no longer listed in the 30 greatest yielding species (Stur 1991).

The yields of dry matter produced by *C. brasilianum* were not high compared to other species, however its relative yields were among the highest of all species under the shaded treatments. The high relative yields given by *C. brasilianum* suggest a degree of shade tolerance and hence potential use under shaded conditions, although the production of dry matter in less shaded situations may be inferior to that of other species. The only reference found of past work examining the performance of *C. brasilianum* under shade was by Amar (1996), who found in a pot trial that the yield of *C. brasilianum* increased from 31.7 g per pot under full light to 54.4 g per pot beneath 78% shade. However, in a second pot trial conducted by the same author under full sun and 68% shade, no significant difference between yields was detected.

Rhynchosia minima did not yield large amounts of dry matter, particularly beneath the 76 and 84% shade treatments. As a result of a low yield beneath the control treatment, relative yields were high despite the poor production of dry matter. Results obtained in this project do not indicate that *R. minima* is a potentially useful species for the production of forage under shaded conditions. In an earlier study, *R. minima* had a relative yield of more than 80% under 50% light, and was ranked as the 13th most productive of 84 species, although under 20% light the relative yield was not given and the species was no longer ranked among the 32 best yielding species (Stur 1991).

Yields of *Chamaecrista rotundifolia* were high under the control treatment and it maintained levels of production beneath 63 and 76% shade that were above average. However the performance of the species beneath 84% shade was very poor with little dry matter produced. Relative yields of the species were approximately average under 63 and 76% shade, but fell to the lowest of any surviving species in this trial. The results obtained here suggest that *C. rotundifolia* has a possible use beneath moderate to heavy shade, however performance beneath very heavy shade appears to be poor. After an initial poor yield due to a fungal disease, *C. rotundifolia* was found to yield well in later harvests in a coconut plantation, with an estimated 73% PAR (Kaligis & Sumolang 1991). However under lower light levels of 58% PAR, also beneath coconuts, Rika *et al.* (1991) found the performance of *C. rotundifolia* initially to be below average and to deteriorate in subsequent harvests.

The performance of *Macroptilium martii* was poor under all treatments with low yields of dry matter, and despite a low yield under the control treatment, low relative yields as well, especially beneath 84% shade. It must be noted that, by the time of harvest, plants of *M. martii* were beginning to senesce beneath the control treatment, due to the annual nature of the species, while plants beneath the shaded treatments were not, suggesting that shading may have prolonged the vegetative growth of the plants. However the results indicate that *M.* martii is shade-intolerant with little potential for use in shaded situations. The only information available on the effects of shading on *M. martii* was found in Amar (1996), who found the production of dry matter to increase beneath 78% shade in comparison to full sun, but no reasons for the result were suggested. When examined in a second trial by the same author, under full sun and 68% shade in a Red Kandosol taken from beneath a tree canopy and in the open, the greatest yield of dry matter was again found under the shaded treatment. It is possible that in this trial light may not have been the limiting factor to growth as the Red Kandosol soil used was a very infertile soil, with particularly low levels of available phosphorus, as the yields produced by the plants were very low - 1.4 and 1.7 g per pot under full light and 68% shade respectively.

Production by *Desmodium scorpiurus* was the third greatest of the species tested beneath full light, but when grown beneath any of the shaded treatments the level of production fell to much lower levels. Also the relative production by the species was very low beneath 63 and 84% shade, however

there was an increase in yield when shading was increased from 63 to 76%, which resulted in a larger relative yield under that shade treatment, but it was still not high when compared to some other species. The data here suggests *D. scorpiurus* to be a shade-intolerant species, and hence of little use beneath tree plantations with moderate to heavy shade. The work of Stur (1991) found *D. scorpiurus* to rank 22nd and 23rd out of 84 species of legume when grown beneath 50 and 20% light respectively. It was also found to give middling yields when grown beneath 73% PAR by Kaligis & Sumolang (1991), while Rika *et al.* (1991) found it to give below average yields at every harvest under 58% PAR.

Centrosema pascuorum was another species, which had an approximately average yield beneath the control treatment, but its yields were severely depressed under the shaded treatments. As a result the relative yields were also low. The results indicate C. pascuorum is a species which may not be suited for growth under shaded conditions. Stur (1991) found C. pascuorums' yield ranking to improve by 20 ranks or more, to $22^{\rm nd}$, when light was decreased from 50 to 20% PAR. Mantiquilla et al. (2000) found C. pascuorum to grow well during the first wet season beneath coconuts with a light transmission between 60 - 70%, however it did not regenerate in the following wet season.

Arachis stenosperma performed well under all shade treatments producing the second greatest yield under the control and 84% shade treatments. Its relative yields were not as great as some species and tended to be around the average value. The species displays promise for use under shaded conditions due to its good production under the heavier shade treatments and also due to its low stoloniferous habit that would be expected to make it tolerant to defoliation or grazing. Information regarding the species is sparse, with some work conducted in Florida by Kretschmer et al. (1999), examining A. stenosperma as a ground cover for use in citrus groves. Initial results found A. stenosperma to have good to excellent plant spread and pod production, and also excellent drought tolerance. Li et al. (2001) suggest that A. stenosperma is not suitable as a summer cover crop for vegetable production, due to the long time taken to establish and provide ground cover, although it was suggested that it could be evaluated as a cover crop for tropical fruit groves.

Due to the mixture of species (*Desmanthus virgatus*, *D. pubescens* and *D. leptophyllus*) used in the cultivar marketed as *D. virgatus* cv. Jaribu, no definite conclusions could be reached regarding its suitability for use under shaded conditions. The performance of plants in the pot trials was poor, producing the lowest yields of any of the species tested beneath the control, with yields remaining low beneath the shaded treatments. Due to the low control yield, relative yields were above average. The high relative production would suggest shade tolerance, however the actual amounts of dry matter produced under the shade treatments are low and may not be enough to be useful in a grazing system. It is also suspected that the growth of control plants was less than should have been and that growth was suppressed due to some unidentified factor. Amar (1996) examined the growth of two lines of *D. virgatus* (CPI 92803 and 79653) beneath full sun and 78% shade with no significant differences detected between shade treatments. Yields of plants were much greater than in this trial (between 21 and 38 g per pot). Ultimately no conclusions regarding *D. virgatus* cv. Jaribus' potential for use can be made owing to the mixture of species in the cultivar, and secondly the suspected suppression of yield in control plants.

Table 2.10 Production of above-ground dry matter by 35 species of legume, under four shade levels expressed as a percentage of that produced under full sun (control).

a) Wet tropical species

Accession	Control	63% shade	76% shade	84% shade
Centrosema macrocarpum	100	68.8	65.1	34.2
Calopogonium mucunoides	100	79.3	35.1	33.0
Desmodium uncinatum	100	62.3	35.2	23.5
Arachis pintoi	100	32.5	20.9	23.3
Desmodium heterophyllum	100	42.3	31.7	19.2
Centrosema pubescens	100	43.8	31.8	19.0
Desmodium canum	100	23.1	20.7	16.5
Pueraria phaseoloides	100	44.1	32.3	16.2
Desmodium intortum	100	46.9	18.7	14.1
Desmodium ovalifolium	100	21.4	13.3	13.5
Vigna luteola	100	53.5	12.9	12.6
Centrosema acutifolium	100	34.4	23.8	11.8
Flemingia congesta	100	19.9	10.3	8.2
Aeschynomene americana	100	21.8	9.3	6.3
Neonotonia wightii	100	15.0	26.9	6.2
Desmodium triflorum	100	33.0	7.4	5.7
Macrotyloma axillare	100	53.0	2.1	1.5
Stylosanthes guianensis	100	4.0	1.8	0.9
Aeschynomene villosa cv. Kretschmer	100	8.9	3.3	-
Aeschynomene villosa	100	7.7	2.2	-
Arachis kretschmeri	100	91.2	0.0	-

b) Wet/dry tropical species

Accession	Control	63% shade	76% shade	84% shade
Macroptilium atropurpureum	100	55.9	65.6	38.5
Centrosema brasilianum	100	61.1	68.9	29.8
Macroptilium lathyroides	100	70.2	72.8	25.7
Rhynchosia minima	100	75.6	20.5	16.1
Arachis stenosperma	100	37.6	24.2	15.5
Desmanthus virgatus	100	86.8	68.1	15.1
Clitoria ternatea	100	63.4	43.6	14.4
Arachis paraguariensis	100	19.9	19.4	13.0
Stylosanthes scabra	100	14.4	6.3	7.2
Centrosema pascuorum	100	9.8	9.5	6.4
Desmodium scorpiurus	100	4.3	18.1	4.5
Macroptilium martii	100	11.0	27.4	2.3
Chamaecrista rotundifolia	100	37.8	28.6	2.2
Stylosanthes hamata	100	6.1	0.0	-

Physiological performance of forage legumes grown under shade

3.1 Introduction

Many plants have a great plasticity in their response to changes in light level within a particular habitat, with this potential for acclimation enabling them to exploit more variable environments than plants with a lower level of adaptability (Atwell *et al.* 1999). Plants may be divided into two broad categories based upon their photosynthetic characteristics; C₃ species, which include temperate grasses and legumes, most broad leaf plants and tropical legumes, with, plants in this group using the Calvin pathway of CO₂ fixation; and C₄ species which include all improved and most native grasses of tropical and subtropical areas, with these plants utilizing the C₄ pathway of CO₂ fixation (Ludlow 1978).

Low light intensities limit photosynthesis and therefore impose stresses upon plants through lower net carbon gain and plant growth (Lambers *et al.* 1998). It is estimated that only about 1% of visible light striking the leaf is utilized for photosynthesis, with the energy of photons hitting various pigments in the chloroplasts collected by chlorophyll molecules, in light-harvesting protein complexes, transferred by the Hill reaction to electrons (Nilsen & Orcutt 1996). Plant responses to low light intensities can be at the structural or the biochemical level (Lambers *et al.* 1998). Lambers *et al.* (1998) indicate that all plants have the capability to acclimate to a low light environment to a greater or lesser degree. There are a number of plant responses to shade which include a reduced respiration rate, an increased shoot:root ratio and an increase in the specific leaf area (Humphreys 1994). Species, or even genotypes within a species, having characteristics that are adaptive under low light conditions are termed "shade-adapted plants". The term "shade plant" includes genotypes which are adapted, or, phenotypes that are acclimated to low light environments, while the term "sun plant" refers to a plant grown in high light conditions or shade-avoiding species.

The photosynthetic light response curves have general properties that are uniform among species. Figure 3.1 displays a generalized light response curve with critical points marked. With increasing light absorption, photosynthesis will increase in a linear manner. The initial part of the light response curve is linear due to light being the limiting factor (Nilsen & Orcutt 1996). However, as light intensity increases, the curve will eventually lose its linearity and photosynthesis no longer increases with light intensity as light no longer remains the limiting factor to photosynthesis. The light intensity corresponding to the point where photosynthesis no longer increases with increasing light is known as the light saturation point. The light saturated rate of photosynthesis is dependent upon the capacity of the electron transport chain to produce ATP and NADPH, the capacity of the Calvin cycle, rubisco activity level, nitrogen concentration and the rate at which triose phosphates are used by the cell (Nilsen & Orcutt 1996). The light intensity where CO₂ assimilation is balanced by CO₂ loss due to respiration is known as the compensation point, below which there is insufficient light to compensate for respiratory CO₂ loss in photorespiration and dark respiration (Lambers et al. 1998). The slope of the initial linear part of the light response curve is termed the apparent quantum yield, when based upon incident light and the quantum yield when based upon absorbed light (Lambers et al. 1998), and represents the increase in carbon gain for any increase in energy absorbed (Nilsen & Orcutt 1996). Typically sun plants have greater light saturation points and light saturation rates than shade plants, while shade plants will tend to have lower light compensation points and a greater quantum yield (Boardman 1977; Lambers et al. 1998; Ludlow 1978; Nilsen & Orcutt 1996). The photosynthesis of sun plants will decrease substantially beneath shade in comparison to full light, as shown by Ward & Woolhouse (1986). The lower rate of photosynthesis of sun plants under shade may still be comparable to that given by shade plants, however shade-adapted plants are unable to adapt to high light with an increase in photosynthesis (Wilson & Ludlow 1991). Excess energy, which the plant is unable to dissipate safely through photosynthesis or other mechanisms, may result in damage to the photosystem and leaf necrosis, and is termed photoinhibition (Bjorkman 1981).

Most studies examining shade-tolerance or adaptation of pasture plants have tended to focus upon production and persistence figures from the field in order to determine suitability for use beneath plantations, with few utilizing physiological measurements such as light response curves to support results. The aim of this study was to quantify the light response curves of the legumes from the pot trials, to better understand their ecophysiological response to shade.

Figure 3.1 Example of a light response curve and critical points.

3.2 Materials and methods

3.2.1 Plant production and growing conditions

500

Plants upon which measurements were made were taken from the pot trials described in Chapter 2. For species that failed to survive beneath shaded treatments (*Aeschynomene villosa* cv. Kretschmer, *Arachis kretschmeri* and *S. hamata*), plants were later grown beneath the control and 84% shade treatments in order for measurements to be made. Despite repeated attempts, no seedling of *A. villosa* survived under the 84% shade treatment long enough to reach a suitable size for measurements to be made.

1000

Irradiance (µmol m⁻² s⁻¹)

1500

2000

3.2.2 Gas exchange measurements

Light response curves were measured three months after planting, using a Li- 6400 gas exchange analyser (Li-Cor, Nebraska). Measurements were made on three plants, from both the unshaded control and the 84% shade treatment, on the first fully expanded new leaf of each plant at 28°C, with a gas flow rate of 500 μmol/s. Irradiance levels at which photosynthetic CO₂ uptake was measured

were 0, 5, 10, 20, 40, 60, 100, 500, 800, 1000 and 1500 μ mol/m²/s. Leaves were left in the leaf chamber for five minutes to adjust to each new irradiance level with measurements taken within the following five minutes once photosynthesis had reached a steady state. A light response curve was then constructed using the computer program Photosyn Assistant 1.1 (Dundee Scientific, 1998, U.K.). Estimation of apparent quantum yields, efficiency and compensation points were calculated from the equation of line of best fit on the initial linear part of the curve.

3.3 Results

Light response curves for each species are displayed below (Figures 3.2 a - s, and 3.3 a-n), and summary statistics in Tables 3.1 and 3.2. The closeness of curves from the control and 84% shade, suggests shade adaptation, while large differences between curves indicates sun-adapted species.

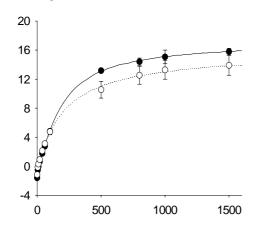
When the light curves are viewed in conjunction with the dry-matter results obtained in Chapter 2 it can be seen that many of the species performing well under the shaded treatments had light response curves which suggested that they were not shade tolerant (a large difference between the control and 84% shade light response curves). Species could be basically grouped into three categories;

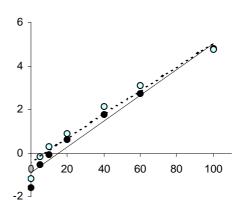
- a) Species that had substantial differences between light response curves from the control and 84% shade treatment, yet yielded well under the shaded treatments (*D. heterophyllum, C. acutifolium, C. macrocarpum, P. phaseoloides, M. atropurpureum* and *M. lathyroides*);
- b) Species that yielded well under shaded treatments with similar light response curves under the control and 84% shade treatment (A. pintoi, A. stenosperma, C. mucunoides, C. brasilianum, C. pascuorum, C. ternatea, D. canum, D. virgatus, D. intortum, D. triflorum, R. minima and D. uncinatum);
- c) Species in which there were substantial differences between the light response curves of the 84% shade and the control treatment, and which also had poor yields beneath the shaded treatments (A. americana, A. villosa cv. Kretschmer, D. scorpiurus, F. congesta, M. axillare, M. martii, S. guianensis, V. luteola, C. rotundifolia and S. scabra);
- d) Remaining species that did not fit any of these categories (D. ovalifolium, C. pubescens, A. paraguariensis, S. hamata).

For more detailed analysis of these results, see Addison (2003).

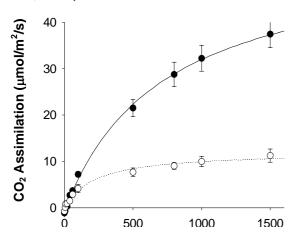
Figure 3.2 Light response curves (CO₂ assimilation vs. light intensity) and line of best fit of the initial linear section of the curve of 19 species of tropical forage legume, adapted to the wet tropics, grown beneath control ($\stackrel{-}{-}$) and 84% ($\stackrel{\equiv}{-}$) shade treatments. Error bars indicate the standard error (n=3).

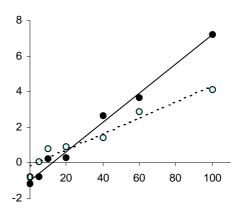
a) *Arachis pintoi*



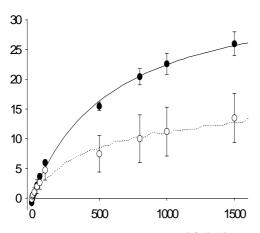


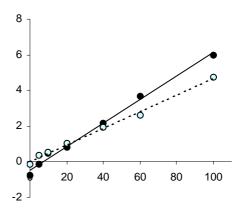
b) Aeschynomene americana





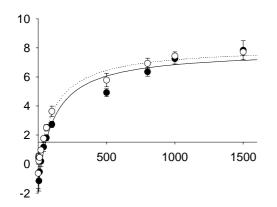
c) Aeschynomene villosa cv. Kretschmer

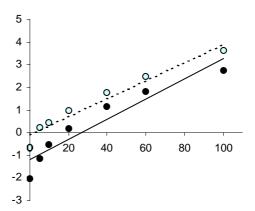




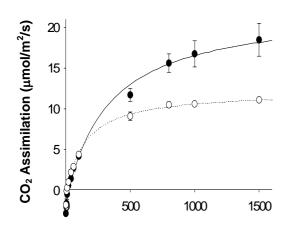
Light Intensity (μmol/m²/s)

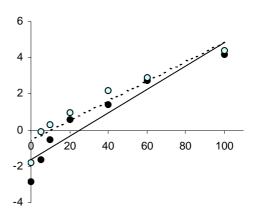
d) Calopogonium mucunoides



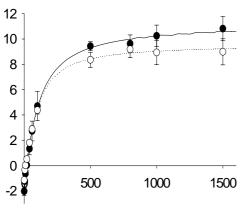


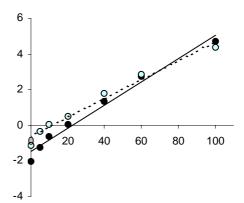
e) Desmodium canum





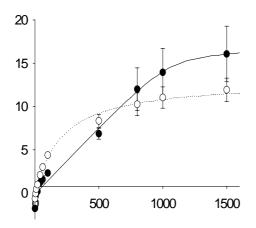
f) Desmodium intortum

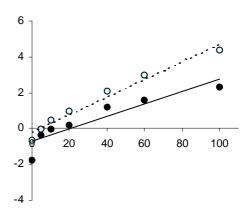




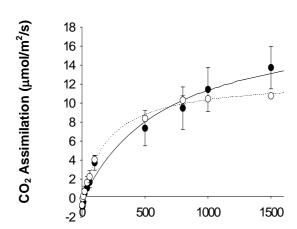
Light Intensity (µmol/m²/s)

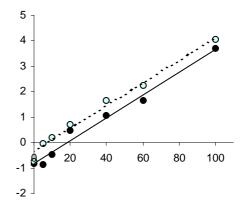
g) Desmodium ovalifolium



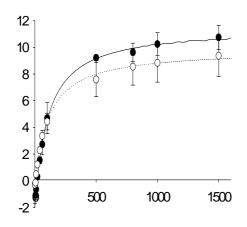


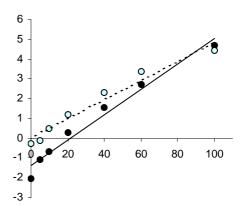
h) Desmodium triflorum





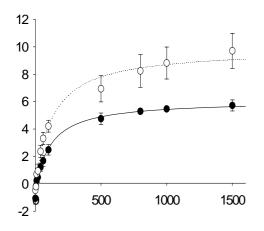
i) Desmodium uncinatum

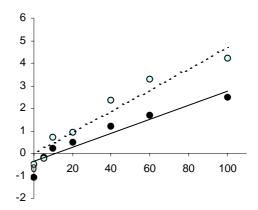




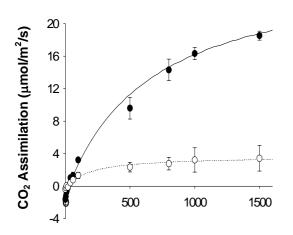
Light Intensity (µmol/m²/s)

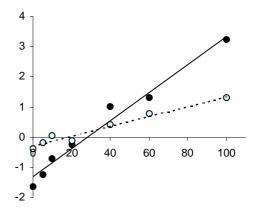
j) Desmodium heterophyllum



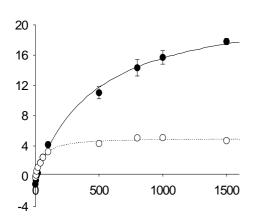


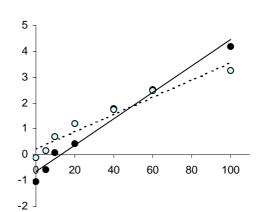
k) Desmodium scorpiurus





l) Centrosema acutifolium

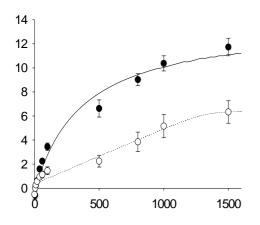


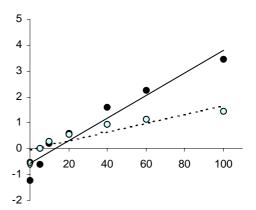


Light Intensity (µmol/m²/s)

Figure 3.2 cont.

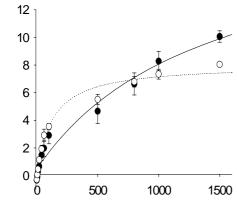
m) Centrosema macrocarpum

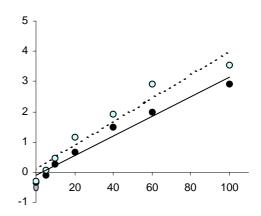




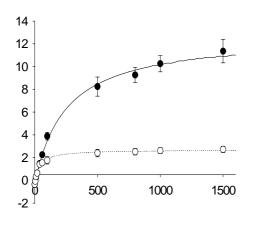
n) Centrosema pubescens

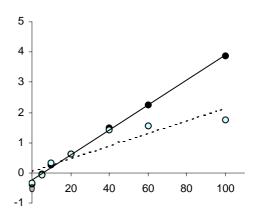






o) Flemingia congesta

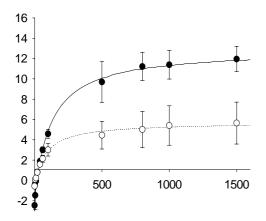


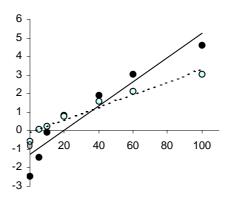


Light Intensity (µmol/m²/s)

Figure 3.2 cont.

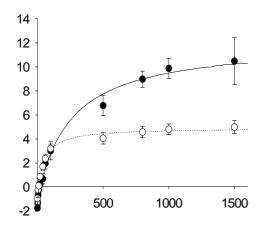
p) Macrotyloma axillare

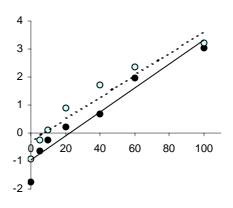




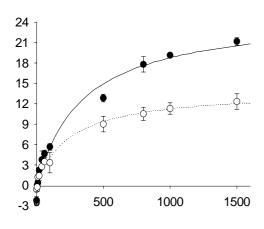
q) Pueraria phaseoloides

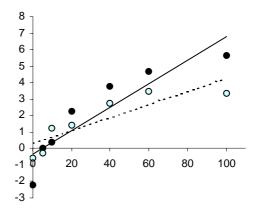
CO₂ Assimilation (µmol/m²/s)





r) Stylosanthes guianensis





Light Intensity (μmol/m²/s)

s) Vigna luteola

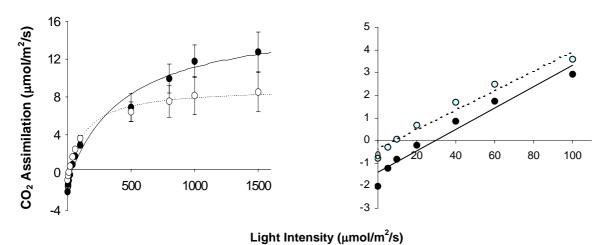
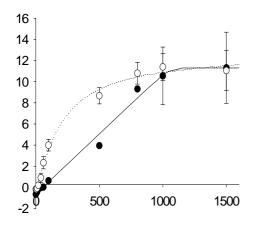
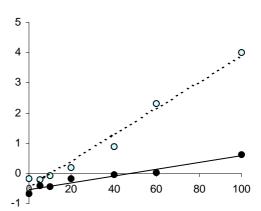


Figure 3.3 Light response curves (CO₂ assimilation vs. light intensity) and line of best fit of the initial linear section of the curve of 13 species of tropical forage legume, adapted to the wet/dry tropics, grown beneath control ($\overline{}$) and 84% ($\overline{}$) shade treatments. Error bars indicate the standard error (n=3).

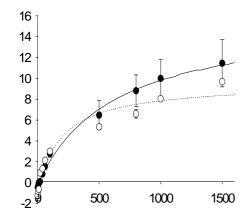
a) Arachis paraguariensis

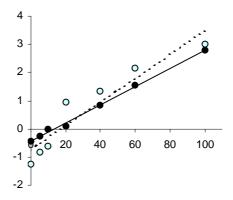




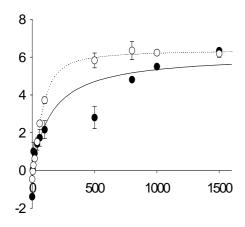
b) Arachis stenosperma

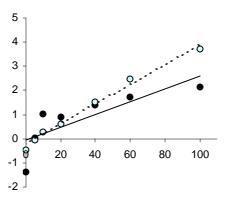






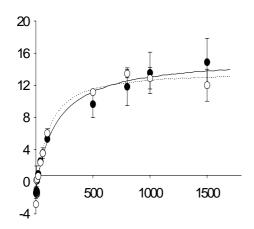
c) Centrosema brasilianum

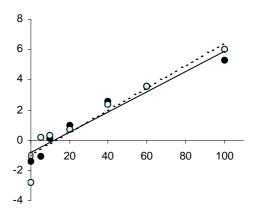




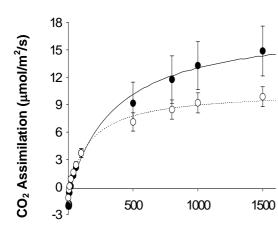
Light Intensity (µmol/m²/s)

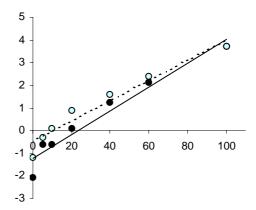
d) Centrosema pascuorum



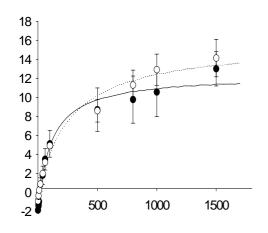


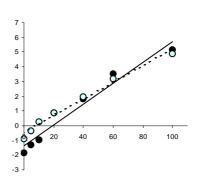
e) Chamaecrista rotundifolia





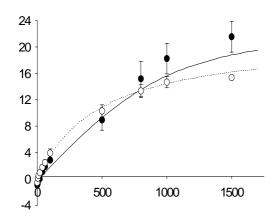
f) Clitoria ternatea

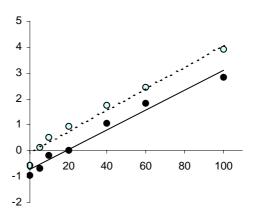




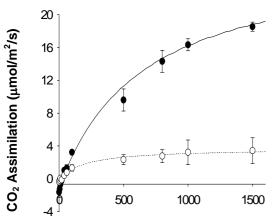
Light Intensity (μmol/m²/s)

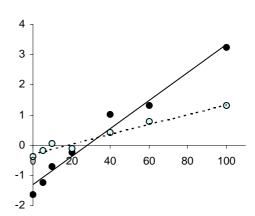
g) Desmanthus virgatus



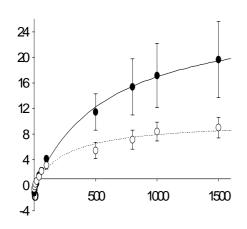


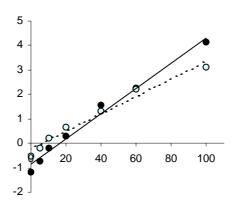
h) Desmodium scorpiurus





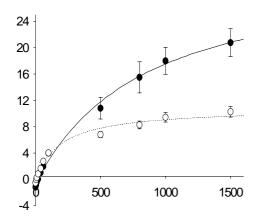
i) Macroptilium atropurpureum

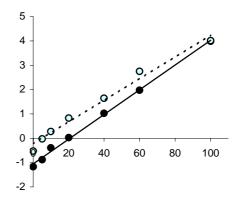




Light Intensity (µmol/m²/s)

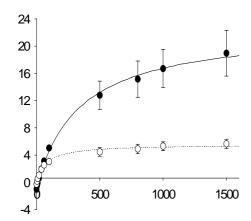
j) Macroptilium lathyroides

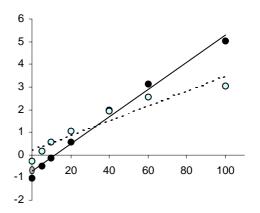




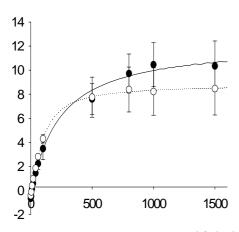
k) Macroptilium martii

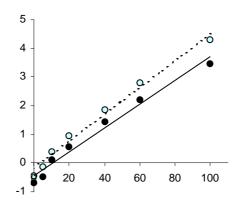






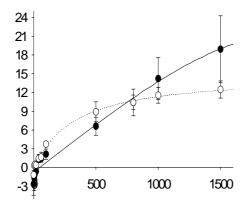
1) Rhynchosia minima

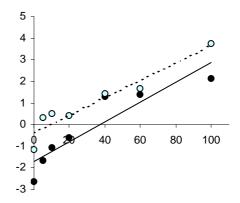




Light Intensity (µmol/m²/s)

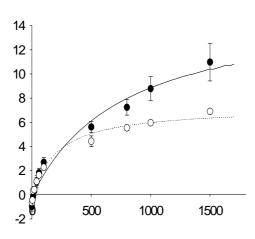
m) Stylosanthes hamata

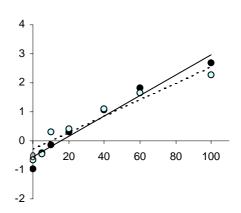




n) Stylosanthes scabra

CO₂ Assimilation (µmol/m²/s)





Light Intensity (µmol/m²/s)

Table 3.1: Summary statistics for light response curves (CO₂ assimilation vs. light intensity) of 19 species of tropical forage legume, adapted to the wet tropics, grown beneath control and 84% shade treatments.

-	Equation of th	e line of best fit		\mathbb{R}^2
Wet tropical	Control	84% shade	Control	84% shade
species				
A. pintoi	y = 0.0594x - 0.8865	y = 0.0555x - 0.4526	0.9718	0.9644
A. americana	y = 0.082x - 1.0165	y = 0.045x - 0.1667	0.9892	0.9480
A. villosa cv.	y = 0.0659x - 0.4657	y = 0.0464x + 0.0241	0.9937	0.9947
Kretschmer				
D. canum	y = 0.0645x - 1.6035	y = 0.0543x - 0.5525	0.9018	0.9023
D. intortum	y = 0.0653x - 1.4974	y = 0.0535x - 0.6434	0.9817	0.9752
D. ovalifolium	y = 0.0348x - 0.724	y = 0.0489x - 0.1824	0.8372	0.9721
D. triflorum	y = 0.0451x - 0.8322	y = 0.0447x - 0.3494	0.9837	0.9843
D. uncinatum	y = 0.0644x - 1.3744	y = 0.049x - 0.0213	0.9733	0.9600
D. heterophyllum	y = 0.0314x - 0.3645	y = 0.0478x - 0.0561	0.9045	0.9388
D. scorpiurus	y = 0.0467x - 1.3184	y = 0.0164x - 0.277	0.975	0.9671
C. mucunoides	y = 0.0444x - 1.1788	y = 0.0396x - 0.0626	0.899	0.9558
C. acutifolium	y = 0.0509x - 0.65	y = 0.0331x + 0.2393	0.9774	0.9467
C. macrocarpum	y = 0.0437x - 0.5704	y = 0.0172x - 0.0341	0.9359	0.831
C. pubescens	y = 0.0324x - 0.1058	y = 0.0392x + 0.0788	0.9710	0.9395
F. congesta	y = 0.0415x - 0.2342	y = 0.021x + 0.0443	0.9980	0.8271
M. axillare	y = 0.0652x - 1.2866	y = 0.034x - 0.0953	0.9064	0.9492
P. phaseoloides	y = 0.043x - 0.9808	y = 0.0396x - 0.3142	0.9341	0.9223
S. guianensis	y = 0.0711x - 0.3154	y = 0.0395x + 0.2949	0.8288	0.7539
V. luteola	y = 0.0473x - 1.4211	y = 0.0434x - 0.4085	0.9541	0.9674

Table 3.2: Summary statistics for light response curves (CO₂ assimilation vs. light intensity) of 13 species of tropical forage legume, adapted to the wet/dry tropics, grown beneath control and 84% shade treatments.

	Equation of the	e line of best fit		\mathbb{R}^2
Wet/dry species	Control	84% shade	Control	84% shade
A. stenosperma	y = 0.0321x - 0.4300	y = 0.0424x - 0.7537	0.9969	0.8965
A. paraguariensis	y = 0.0113x - 0.5299	y = 0.0437x - 0.4712	0.9417	0.9791
C. brasilianum	y = 0.0265x - 0.0522	y = 0.0414x - 0.2296	0.6473	0.9880
C. pascuorum	y = 0.0671x - 0.8219	y = 0.0742x - 1.0127	0.9484	0.9037
C. rotundifolia	y = 0.0526x - 1.2129	y = 0.0453x - 0.4920	0.9483	0.9469
C. ternatea	y = 0.0708x - 1.3441	y = 0.0567x - 0.4677	0.9543	0.9828
D. virgatus	y = 0.0384x - 0.7318	y = 0.0417x - 0.0948	0.9743	0.9753
D. scorpiurus	y = 0.0467x - 1.3184	y = 0.0164x - 0.277	0.9750	0.9671
M. atropurpureum	y = 0.0518x - 0.8582	y = 0.0362x - 0.2367	0.9853	0.9707
M. lathyroides	y = 0.0507x - 1.0497	y = 0.0447x - 0.2215	0.9976	0.9830
M. martii	y = 0.0604x - 0.7318	y = 0.033x + 0.1887	0.9895	0.9138
R. minima	y = 0.0414x - 0.4385	y = 0.0469x - 0.1821	0.9781	0.9851
S. hamata	y = 0.0456x - 1.6893	y = 0.0401x - 0.3572	0.8446	0.9057
S. scabra	y = 0.0353x - 0.5556	y = 0.0286x - 0.2930	0.9607	0.9208

3.4 Discussion

The similarity of light curves obtained for the species A. pintoi, A. stenosperma, C. mucunoides, C. brasilianum, C. pascuorum, C. ternatea, D. canum, D. virgatus, D. intortum, D. triflorum, R. minima and D. uncinatum all suggest a degree of shade adaptation as plants under the control treatment were not able to increase their photosynthetic capacity compared to plants under 84% shade. According to Wilson & Ludlow (1991), shade-adapted plants are unable to adapt to high light with an increase in photosynthesis. However when viewed in conjunction with dry matter production (Chapter 2), not all species appear to have the same potential for forage production under shaded conditions. Several species were still able to produce useful quantities of dry-matter under the control treatment (A. stenosperma, D. uncinatum, D. intortum, C. ternatea, C. mucunoides). The other species did not produce significant levels of plant material.

In some species there were large differences between the light response curves of the control and 84% shade treatments (*D. heterophyllum*, *C. acutifolium*, *C. macrocarpum*, *P. phaseoloides*, *M. atropurpureum* and *M. lathyroides*), despite the production of substantial amounts of dry matter under the more heavily shaded treatments, suggesting that these species have the capacity to become shade-acclimated rather than being shade-tolerant. Typically sun plants have their capacity for photosynthesis greatly reduced under shaded conditions (Ward & Woolhouse 1986), however the rate of photosynthesis may still be greater than that of shade-tolerant species (Wilson & Ludlow 1991).

Species in which there was a large difference between light response curves accompanied by a large decrease in dry-matter production under shade, with low plant yields compared to other species, can be classified as sun plants with little ability to acclimate to low light conditions. *Aeschynomene americana*, *A. villosa* cv. Kretschmer, *D. scorpiurus*, *F. congesta*, *M. axillare*, *M. martii*, *S. guianensis*, *V. luteola*, *C. rotundifolia* and *S. scabra* all displayed these traits, and hence are poorly suited for use under shaded conditions.

A more in-depth discussion of these results can be found in Addison (2003).

Performance of selected species beneath tree plantations

4.1 Introduction

The current cabinet timber industry in the wet tropics of north Queensland is characterized by having only small quantities of material available for harvesting from freehold land, with the consequent economic problems preventing the reopening of saw mills that closed following the World Heritage Area listing of the tropical rainforests in 1988 (Turvey & Larsen 2001). To many landowners one deterrent to establishing forestry plantings is the large time-lag before any substantial returns can be obtained from the land. By incorporating animals into timber plantations in a silvo-pastoral system, it is possible to obtain earlier income from the land while potentially providing a range of other benefits. Some potential advantages of such a system include increased and diversified income, better use of scarce resources, soil stabilization, the potential for higher yields through increased weed control, nutrient cycling and nitrogen accretion (Chen 1993), maintaining soil organic matter levels (Garrity 1994), and reduced nutrient leaching (Seyfried & Rao 1991).

In many developing countries landowners have traditionally grazed livestock beneath tree plantations, particularly oil palm, coconut and rubber (Ismail & Thai 1994; Kaligis *et al.* 1994a; Stur *et al.* 1994). However the acceptance of such agroforestry systems in Australia has been hindered by the belief that productive pastures cannot be maintained beneath tree plantations once canopy closure has occurred.

As trees grow the quantity and the quality of the light passing through the canopy to the ground level changes. Shelton (1993) indicates that, in many tree crops, canopy closure occurs relatively quickly, from 5-8 years of age, with an accompanying fall in light transmission to less than 30% and changes in the red/far red ratio. As a result of this, the production of forage is greatly reduced due to changes in the botanical composition of the herbaceous layer that sees an increase in shade-tolerant grasses and other unpalatable, shade-tolerant, weedy species. Consequently the carrying capacity of the land falls, along with a decrease in the live weight gain of animals (Shelton 1993).

In order to increase the productivity of such silvo-pastoral systems, there is a need to identify shade-tolerant legume and grass species for use beneath tree canopies. Ideally such species would be productive and persistent, palatable to stock, tolerant of defoliation, competitive with weeds, easy to establish and have a high rate of nitrogen fixation in legumes (Humphreys 1994).

Three field trials were established to examine growth and persistence of tropical forage legume species under established tree plantations. The first of these examined the performance of six accessions of legumes, suited for the wet tropics, under a mixed species plantation near Babinda. The second examined the performance of seven legume species, suited for the seasonal wet/dry tropics, under a 12-year-old African Mahogany (*Khaya senegalensis*) plantation near Clare. The third field trial examined the performance of 6 species of legumes, suited for the seasonal wet/dry tropics (including 4 accessions of *Arachis*), under young African Mahoganies planted at 2 different densities on the James Cook University campus, in Townsville.

4.2 Materials and methods

4.2.1 Performance of six forage legume accessions beneath a 5-year-old *Eucalyptus pellita* and mixed rainforest species plantation

Experimental site

The trial was conducted upon a Bingil series krasnozem at Babinda (17° 21' S, 145° 55' E). Top soil was a reddish brown (5YR4/4) clay loam over a red (2.5YR4/8) light clay subsoil. The soil was derived from amphibolite, a metamorphosed basic volcanic rock interbedded in metasediments (Murtha *et al.* 1996). Soil organic matter, nitrogen and phosphorus levels are shown in Table 4.1. Trees were planted on the site in January 1995 as rows of *Eucalyptus pellita* alternating with rows of mixed rainforest species that included *Elaeocarpus grandis*, *Cedrela odorata*, *Flindersia brayleyana* and *Castanospermum australe* at a spacing of 3 m x 4.5 m.

Table 4.1 Soil organic carbon, nitrogen, phosphorus, potassium and pH in a Bingil series krasnozem at the time of trial establishment (means, n = 5).

Depth	Organic C	Total N	Available P	Exchangeable K	pН
(cm)	(%)	(%)	(mg kg ⁻¹)	(me 100g ⁻¹)	$(1:5 H_2O)$
0-10	0.16	0.21	59.7	0.081	5.7
10-20	0.16	0.18	45.9	0.118	5.3
20-30	0.11	0.20	26.1	0.117	5.4
30-40	0.13	0.25	19.5	0.226	5.3
40-50	0.09	0.21	6.4	0.074	5.1

Trial establishment

Seed was planted on the 19th of September 2000, between adjacent *E. pellita* trees, from where any other living plant material was removed. Four furrows were dug in the soil, from tree base to tree base, spaced 50 cm apart, and a seed was planted every 10 cm along each furrow, and covered with soil. The species planted were *Aeschynomene americana* cv. Lee, *Aeschynomene villosa* 37235, *Aeschynomene villosa* cv. Kretschmer, *Aeschynomene villosa* cv. Reid, *Arachis pintoi* cv. Amarillo and *Stylosanthes guianensis* cv. Cook. Four replicates were established, with the location of the replicates kept at least three tree rows away from the boundaries of the plantation in order to avoid edge effects. Due to the nature of the location it was not possible to establish an unshaded control treatment for comparison.

Trial sampling and data collection

The trial was sampled in December 2000, April 2001, December 2001 and July 2002. Ground cover was estimated by a point sampling method using a frame of pins as outlined in Barbour *et al.* (1999). The number of plants was then recorded and plant material was harvested to 5 cm above ground level, or in the case of *Arachis pintoi* to within 5 cm of the centre of the plant. After harvesting the plots were weeded by hand and the harvested material dried at 70°C for several days in a forced-draft oven to a constant weight and then weighed. No dry matter was harvested from plants during the December 2000 sampling, as most plants were found to be too small for harvest and it was decided that any defoliation of the plants would reduce their chances of survival. From the data obtained the production of plant material was calculated on both a per plant and per hectare basis. The number of surviving plants was expressed as plants per metre due to the variation in plot lengths between trees resulting in differing amounts of seed being sown. Data were analyzed by analysis of variance and any significant differences compared by the least significant difference (LSD) method.

4.2.2 Performance of seven species of tropical forage legumes beneath a 12-year-old African mahogany (*Khaya senegalensis*) plantation.

Experimental site

This trial was established beneath an approximately 12-year-old African mahogany plantation planted at an 8.5 x 8.5 metre spacing at the Burdekin Agricultural College near Clare, located approximately 65 km south of Townsville (19° 47' S, 147° 13' E). The soil texture was a sandy loam overlying a light clay. Soils of this site have been described as mottled yellow podzolic soils with 30-60 cm of sandy loam horizon and bleached A2 horizon formed from alluvial deposits associated with abandoned or seldom active stream courses (Thompson *et al.* 1987).

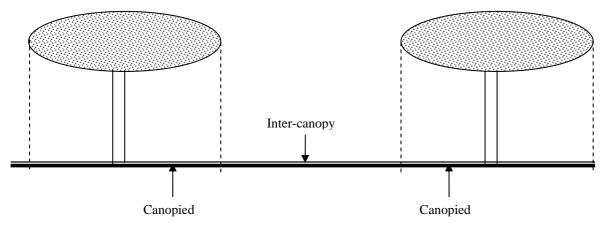
Trial establishment

The trial was established on the 16th of March 2000 after cultivation of the ground between trees with a powered hoe. Four furrows were made in the soil between adjacent trees, each approximately 0.5 – 1 cm deep. Furrows began and finished 0.5 m from the base of each tree and were spaced 50 cm apart. Between each pair of trees one species of legume was sown along each furrow, with one seed planted every 10 cm and covered with soil. Individual plots were established on the second or deeper tree rows in order to avoid edge effects. A total of seven species of legume were used in the trial (listed in Table 4.8), each replicated four times. A control plot was established on nearby open ground in the same manner as already described, with the exception of each plot being 4 m long. Only the species *Desmanthus virgatus* was inoculated, as the remaining species had been found to effectively nodulate with native *Rhizobia* present in the soil (Cameron & Lemke 1997; Clements 1992; Edye & Topark-Ngarm 1992; Jones 1992; Skerman *et al.* 1988; Staples 1992a).

Trial sampling and data collection

As the plantation had not reached canopy closure, three areas were identified where tree canopy and shading were thought to be substantially different from one another. The first location was the control treatment, which had no shading or canopy cover, as it was located away from any trees. The second and third areas were located within each trial plot. Each individual plot was divided into canopied and inter-canopied areas. Canopied areas were considered to be the sections of the four furrows sown with legume seed that were located from the edge of the canopy to the trunk of the tree. Inter-canopy areas were defined as the areas of the furrows, which were located between the edges of the adjacent tree canopies (see Figure 4.1)

Figure 4.1 Diagram showing delineation of canopied and inter-canopy areas.



Initial differences in seed germination were examined on the 8th of June 2000 (11 weeks after establishment), by measuring the length of each individual canopied and inter-canopy area, followed

by recording the number of plants present. From this the number of seeds sown could be calculated and hence the germination and initial survival of plants.

Ground cover was estimated by placing a frame of pins, as described in Barbour *et al.* (1999), and recording what vegetation, if any, each pin contacted first. The frame was placed in the centre of each location (halfway between tree canopies and under the mid point of a tree canopy).

Dry matter was harvested on the 24th of October 2000 (30 weeks after planting) by placing a 0.5 x 0.5 m quadrat in the centre of each location (control, canopied and inter-canopied), and harvesting plant material from 10 cm above ground level in the case of more erect species such as *D. virgatus*, and to within 10 cm of the plant base for prostrate species such as *Chamaecrista rotundifolia*. Plant material was then dried in a forced draught oven at 70°C for three days and then weighed.

No further collection of data was possible after this date as during the period of time between the 24th of October and the next sampling date the trial area was inadvertently slashed to ground level and sprayed with herbicide.

Shade levels were estimated using a hand held Li-Cor Quantum/Radiometer/Photometer (model LI-180) at midday on a clear day. Shade levels were determined to be as follows; June 2000, intercanopy areas 37.5%, canopied areas 24.6% with little change by October 2000, inter-canopied areas 38.7% and canopied areas 23.6% that of the unshaded control plots.

Data were analyzed by analysis of variance and any significant differences were further examined by the method of least significant difference (LSD).

4.2.3 Production and persistence of *Clitoria ternatea*, *Chamaecrista rotundifolia* and four accessions of *Arachis* under open conditions and beneath two densities of *Khaya senegalensis*.

Experimental site

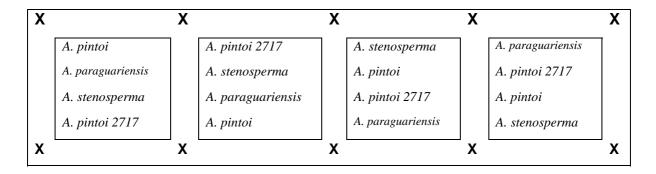
The trial was conducted on land located on the Townsville campus of James Cook University. African mahogany (*Khaya senegalensis*) seedlings were planted on the 16^{th} of August 1999. Trees were planted in two separate blocks at spacings of 1 x 1 m and 1.5 x 1.5 m. Tree density and establishment date were chosen in order to ensure that a suitable level of shade was present beneath tree canopies. When trees were aged 15 months (7^{th} November 2000), the trial was established by marking four lines between trees. Lines began 20 and 45 cm from the base of the trees under the 1 x 1 m and the 1.5 x 1.5 m spacings respectively. Species examined in the trial were:

Arachis pintoi cv. Amarillo A. pintoi ATF 2717 A. stenosperma ATF 377 A. paraguariensis ssp. paraguariensis Chamaecrista rotundifolia cv. Wynn Clitoria ternatea cv. Milgarra

Arachis paraguariensis ssp. paraguariensis was established from cuttings that had been treated with rooting hormone and placed in vermiculite. The remaining species were all established from seed. Arachis pintoi cv. Amarillo, A. pintoi ATF 2717, A. stenosperma ATF 377, A. paraguariensis ssp. paraguariensis and D. virgatus were all inoculated at the time of planting. As C. ternatea and C. rotundifolia have been found in the past to inoculate with naturally occurring Rhizobia (Jones 1992; Staples 1992a), no inoculation was deemed necessary. After planting, the seeds/cuttings were all hand-watered for the first week to aid establishment. After this period the only water plants received was from natural rainfall.

Beneath the trees, species of *Arachis* were sown both on the edge of the tree plot, to give an intermediate shade level where edge effects were expected to be present, and in the centre, with each species replicated four times at each location and tree density. Owing to space limitations, *C. ternatea* and *C. rotundifolia* were only located on the edges of the plots. A control plot was established under open conditions for comparison. Lines were 60 cm in length with 20 cm between lines. Seed/cuttings of the six species tested were planted every 10 cm along each line with one species planted per line. The location of each line of species was randomly determined, however it was ensured that each species occupied each of the four positions once (Figure 4.2).

Figure 4.2 Location of species relative to one another (**X** represents individual trees).



The soil upon which the trial was conducted belongs to the Black series (Murtha 1982), and consisted of a dark grey-brown sandy loam A horizon overlying a brown sandy clay loam to sandy clay B horizon that graded to coarse water-worn gravels from 1-1.5 m. Selected soil properties are shown in Table 4.2

Table 4.2 Soil properties for the African mahogany research plantation site on the JCU Townsville campus. * = data from Murtha (1982).

Horizon	Depth	pН	N	Available P	K*	Na*	Ca*	Sat.*
	(cm)	(H_20)	(%)	(mg/kg)	((m.e./100g)	(%)
A1	0-10	6.3	1.47	29	0.83	3.73	12.9	81
В	10-50	5.8	0.54	24	0.16	0.24	6.1	94

Sampling and data collection

Data were recorded for the trial on three dates: the 22nd of March 2001, 13th November 2001 and the 12th April 2002 (approximately 16, 50 and 71 weeks after planting). Ground cover was recorded utilizing a frame of pins as described in Barbour *et al.* (1999). The number of plants was recorded and plant material harvested to within 10 cm of the base of the plant for prostrate species, or to 10 cm above ground level for more upright species. Plant dry matter was dried in a forced-draught oven at 70°C for 3 days, to a constant mass and then weighed.

Shade levels were estimated beneath the tree canopies and in the open using a Li-Cor 1000 data logger. Readings were taken every 10 minutes beginning at 5 am and continuing until dark. Quantum sensors were placed in the open, in the central and edge parts of both tree densities, approximately 15 cm above ground level and above any understorey vegetation. Results were summed and expressed as a percentage of the open area (Table 4.3).

Table 4.3 Shade levels in the open and at 2 different locations in two densities of *Khaya senegalensis* expressed as a % of the control.

Location	March 2001	November 2001	April 2002
1 x 1m edge rows	81.7	39.2	44.5
1 x 1 m inner rows	87.1	42.1	53.2
1.5 x 1.5 m edge rows	65.9	34.5	42.5
1.5 x 1.5 m inner rows	71.2	33.6	40.8
Control	100.0	100.0	100.0

4.3 Results

4.3.1 Production, performance, ground cover and persistence of six forage legume accessions beneath a 5-year-old *Eucalyptus pellita* and mixed rainforest species plantation

Statistical summary of results

Significant to highly significant effects were found across all dates and in all attributes with the exception of individual plant size at the first sampling after establishment (December 2000)(Table 4.4).

Table 4.4 Summary of statistical results for growth of six forage legume accessions beneath a 5-year-old *Eucalyptus pellita* and mixed rainforest species plantation at Babinda.

Attribute	Dec 2000	April 2001	Dec 2001	July 2002
Yield (t/ha)	n.r.	**	***	***
Plant size (g/plant)	n.s.	*	***	***
Ground cover (%)	***	***	***	***
Density (plants/m)	**	**	***	***

n.r. = no result; n.s. = no significant effect; * = 0.05>P>0.01; ** = 0.01>P>0.001; *** = P>0.001.

Ground cover

The greatest ground cover was produced by *A. pintoi* and *S. guianensis* across all sampling dates. With the exception of *A. villosa* cv. Reid at the first sampling, *A. pintoi* and *S. guianensis* covered a much greater area than any of the remaining species (Table 4.5). At the first sampling date, December 2000, neither *A. pintoi* nor *S. guianensis* were found to be statistically different from *A. villosa* cv. Reid or each other. The area of ground covered by *A. pintoi* and *S. guianensis* increased over time. However the accessions *A. villosa* cv. Reid, *A. villosa* and *A. americana* also experienced an increase in ground cover by the second sampling date (April 2001), but the size of these increases in the first two accessions were much smaller than those of *A. pintoi*, *S. guianensis* and *A. americana*. *Aeschynomene villosa* cv. Kretschmer was the only species to suffer a decrease in this time. By December 2001 the percentage of ground covered by *A. pintoi* and *S. guianensis* had increased further, however a statistical difference between the two species was detected. All remaining species were covering a much smaller proportion of ground than in April 2001. By July 2002 *A. villosa*, *A. villosa* cv. Reid and *A. villosa* cv. Kretschmer had decreased to the extent of providing no measurable ground cover at all. *Aeschynomene americana* also decreased to very low levels of cover and, what plants were present, were small and unhealthy in appearance. *Arachis pintoi* clearly provided the

most ground cover, with over twice as much cover as *S. guianensis*, the only other species with any substantial ground cover. In comparison to the previous harvest in December 2001, *S. guianensis* had suffered a large decrease in the amount of ground it covered. *Arachis pintoi* however maintained approximately the same level of cover.

Yield per hectare

Arachis pintoi was consistently the greatest producer of dry matter with a substantial margin between it and other species (Table 4.6). Statistically it was not significantly different from other species in the April 2001 and July 2002 samplings, being grouped with A. americana and S. guianensis, respectively. Aeschynomene americana performed well during the first two samplings, but by July 2002 very little plant material was produced. Initially S. guianensis produced appreciable levels of dry matter, however in the December 2001 sampling, the yield had fallen to very low levels. The production of dry matter had increased considerably by July 2002 with S. guianensis producing similar amounts of dry matter to A. pintoi. Aeschynomene villosa cv. Reid initially had a yield comparable to S. guianensis, however at subsequent harvests it produced very little dry matter and was entirely absent by July 2002. Aeschynomene villosa, and A. villosa cv. Kretschmer yielded very little dry matter at all harvests, with no plants of either species surviving at the final sampling.

Yield per plant

In general A. pintoi and S. guianensis were the only species in which the mean plant weight increased after April 2001. The remaining accessions, Aeschynomene americana, A. villosa, A. villosa cv. Reid and A. villosa cv. Kretschmer, all underwent decreases in the mean plant weight after April 2002. Arachis pintoi, at all sampling dates, produced the largest plants. On April 2001 the difference between A. pintoi and A. americana, which produced the second largest plants at that sampling, was only small (0.21 g, see Table 4.7), with no statistical difference between the two species found. By December 2001, the average yield of A. pintoi plants was almost twice that of S. guianensis, the species with the second highest yield. At the final sampling, these were still the highest yielding accessions, although the difference between them was less (1.96 g per plant). Initially (April 2001), plants of A. americana were second in weight only to A. pintoi, however at the subsequent samplings the mean weight of plants fell considerably to very low levels. A similar pattern was observed in the accessions A. villosa, A. villosa cv. Reid and A. villosa cv. Kretschmer, however the initial average plant weight for these species was much lower than that of A. americana.

Number of plants per metre

All species of legume examined in the 3 – 7 month period after trial establishment, had relatively stable numbers of plants per metre. However, after this period, there was a marked decline in the number of plants of all species except *A. pintoi*. *Stylosanthes guianensis* consistently had the greatest average number of plants per metre of ground sown, although by the final sampling it was only 59% that found after 3 months (Table 4.8). The cultivars *A. villosa* cv. Reid and *A. villosa* cv. Kretschmer, initially had high survivorship, with *A. villosa* cv. Reid not found to be statistically separate from *S. guianensis*, which was the species with the highest average. After 22 months only *S. guianensis*, *A. pintoi* and *A. americana* had any plants left alive, with only a few small individuals of *A. americana* found.

Table 4.5 Mean, standard error and LSD groupings of percent ground cover of six tropical forage legumes planted beneath a 5-year-old (at trial establishment) *E. pellita* and mixed rainforest species timber plantation, at 3, 7, 15 and 22 months after trial establishment. Means in a column followed by the same letter do not differ significantly.

	Average % ground cover					
Species	Dec 2000	April 2001	Dec 2001	July 2002		
A. pintoi	$18.1 \pm 2.5 \text{ a}$	$30.0 \pm 5.4 \text{ a}$	$38.1 \pm 2.3 \text{ b}$	$35.6 \pm 9.2 \text{ a}$		
A. villosa cv. Reid	15.6 ± 2.3 a	$16.9 \pm 2.1 \text{ b}$	$3.1 \pm 0.6 c$	$0.0 \pm 0.0 \; c$		
S. guianensis	$13.1 \pm 2.1 \text{ ab}$	$32.2 \pm 1.5 \text{ a}$	$46.2 \pm 4.6 a$	$16.9 \pm 3.8 \text{ b}$		
A. villosa cv. Kretschmer	$7.5 \pm 1.0 \text{ bc}$	$6.8 \pm 0.6 \text{ cd}$	$0.6 \pm 0.6 c$	$0.0 \pm 0.0 \; c$		
A. americana	$3.7 \pm 2.9 \text{ c}$	$15.0 \pm 5.3 \text{ bc}$	$1.8 \pm 1.2 c$	$0.6 \pm 0.6 c$		
A. villosa	$2.5 \pm 1.4 \text{ c}$	$3.7 \pm 1.6 d$	$0.6 \pm 0.6 c$	$0.0 \pm 0.0 \; c$		
P value	0.0002	< 0.0001	< 0.0001	< 0.0001		

Table 4.6 Mean, standard error and LSD groupings of dry matter production (t/ha) of six tropical forage legumes planted beneath a 5-year-old (at trial establishment) *E. pellita* and mixed rainforest species timber plantation, at 7, 15 and 22 months after trial establishment. Means in a column followed by the same letter do not differ significantly.

	Average yield (t/ha)				
Species	April 2001	Dec 2001	July 2002		
A. pintoi	0.199 ± 0.051 a	0.304 ± 0.038 a	$0.360 \pm 0.061a$		
A. americana	0.106 ± 0.040 ab	0.194 ± 0.032 b	$0.0005 \pm 0.005 \text{ b}$		
S. guianensis	0.096 ± 0.012 bc	0.0004 ± 0.0002 c	0.290 ± 0.072 a		
A. villosa cv. Reid	0.078 ± 0.037 bc	0.0001 ± 0.0001 c	0 ± 0 b		
A. villosa	$0.018 \pm 0.014 \text{ bc}$	0.001 ± 0.001 c	0 ± 0 b		
A. villosa cv. Kretschmer	0.009 ± 0.002 c	0 ± 0 c	0 ± 0 b		
P value	0.0062	0.0001	< 0.0001		

Table 4.7 Mean, standard error and LSD groupings of mean plant weight (g) of six tropical forage legumes planted beneath a 5-year-old (at trial establishment) *E. pellita* and mixed rainforest species timber plantation, at 3, 7, 15 and 22 months after trial.

	Mean plant weight (g)				
Species	April 2001	Dec 2001	July 2002		
A. pintoi	$4.48 \pm 1.40 \text{ a}$	$8.17 \pm 1.50 \text{ a}$	$7.80 \pm 1.55 \text{ a}$		
A. americana	4.27 ± 1.60 a	$0.40 \pm 0.40 \text{ b}$	$0.11 \pm 0.10 \text{ b}$		
A. villosa	$1.34 \pm 1.02 \text{ b}$	0 ± 0 c	0 ± 0 b		
A. villosa cv. Reid	$1.20 \pm 0.19 \text{ b}$	0.06 ± 0.03 c	0 ± 0 b		
S. guianensis	$1.18 \pm 0.20 \text{ b}$	$4.10 \pm 1.04 \text{ b}$	$5.84 \pm 1.01 \text{ a}$		
A. villosa cv. Kretschmer	$0.24 \pm 0.05 \text{ b}$	0.03 ± 0.03 c	0 ± 0 b		
P value	0.0110	< 0.0001	< 0.0001		

Table 4.8 Mean, standard error and LSD groupings of the number of plants per metre for six tropical forage legumes planted beneath a 5-year-old (at trial establishment) *E. pellita* and mixed rainforest species timber plantation, at 3, 7, 15 and 22 months after trial establishment. Means in a column followed by the same letter do not differ significantly.

	Average number of plants per metre				
Species	Dec 2000	April 2001	Dec 2001	July 2002	
S. guianensis	3.27 ± 0.85 a	3.37 ± 0.67 a	2.42 ± 0.60 a	1.95 ± 0.41 a	
A. villosa cv. Reid	2.15 ± 0.53 ab	$2.12 \pm 0.62 \text{ ab}$	$0.17 \pm 0.04 \text{ c}$	$0.00 \pm 0.00 \text{ b}$	
A. pintoi	$1.57 \pm 0.29 \text{ bc}$	$1.80 \pm 0.05 \ bc$	$1.45 \pm 0.11 \text{ b}$	1.75 ± 0.04 a	
A. villosa cv. Kretschmer	$1.47 \pm 0.21 \text{ bc}$	$1.42 \pm 0.04 \text{ bc}$	0.05 ± 0.05 c	$0.00 \pm 0.00 \text{ b}$	
A. villosa	0.67 ± 0.19 c	0.40 ± 0.17 c	$0.07 \pm 0.05 \text{ c}$	$0.00 \pm 0.00 \text{ b}$	
A. americana	0.62 ± 0.17 c	$0.83 \pm 0.24 \text{ bc}$	0.02 ± 0.02 c	$0.09 \pm 0.05 \text{ b}$	
P value	0.0053	0.0046	< 0.0001	< 0.0001	

4.3.2 Performance of seven species of tropical forage legume beneath a 12-year-old African mahogany (*Khaya senegalensis*) plantation

Statistical summary of results

Highly significant interactions and differences due to species and location in ground cover and the number of plants per metre were found after 11 weeks (Table 4.9). However 30 weeks after planting, location and interaction effects were no longer significant for ground cover and the number of plants per metre. There were still highly significant differences between species, while the yield of dry matter was found to show highly significant differences between species, location and an interaction effect.

Table 4.9 Summary of statistical results for growth of 7 species of tropical forage legume beneath a 12-year-old African mahogany (*Khaya senegalensis*) plantation at Clare.

	June 2000 (11 weeks)			October 2000 (30 weeks)		
	Yield	Ground	No. of	Yield	Ground	No. of
Effect	(t/ha)	cover	plants/m	(t/ha)	cover	plants/m
Species	n.r.	***	***	***	***	***
Location	n.r.	***	***	***	n.s.	n.s
Interaction	n.r.	***	***	***	n.s.	n.s

n.r. = no result, n.s. = no significant effect; * = 0.05 > P > 0.01; ** = 0.01 > P > 0.001; *** = P > 0.001

Ground cover

a) Effect of location

Initially (June 2000) the overall ground cover was found to be greatest in the inter-canopy areas, followed by canopied areas, with the control treatment containing the lowest amount of ground covered by sown legumes. Inter-canopied and canopied areas were not statistically different from one another (Table 4.10). Ground covered by legumes was substantially less at all locations at the second sampling date, with the greatest coverage found in the control plots. Inter-canopied and canopied areas had similar amounts of ground cover, only 2.0 and 1.7% less than the control, respectively. No significant differences were detected between the locations.

Table 4.10 Means, standard errors and LSD groupings of percent ground cover under canopied, inter-canopied and clear (control) areas sampled on two different dates. Means in a column followed by the same letter do not differ significantly.

Location	June 2000	October 2000
Control	11.6 ± 1.9 b	10.0 ± 3.0
Inter-canopy area	$24.0 \pm 3.9 \text{ a}$	8.0 ± 1.4
Canopied area	$18.6 \pm 2.5 \text{ a}$	8.3 ± 1.5
Probability	0.0095	0.7770

b) Effect of legume species

At the June 2000 sampling *C. ternatea* covered the greatest area (Table 4.11), 18.4% more than *C. brasilianum*, the species with the second greatest ground cover. *Centrosema brasilianum* and *C. pascuorum* also provided relatively high levels of ground cover but were approximately half that of *C. ternatea*. By October 2000 there had been large decreases in the ground cover of *C. ternatea* and, in particular *C. pascuorum*. Despite the decrease, *C. ternatea* remained one of the species providing the greatest ground cover, second only to *C. brasilianum*. However *C. pascuorum* underwent a decrease of 22.5% and, as a result, was the species with the lowest level of ground cover.

Table 4.11 Mean, standard error and LSD groupings of ground covered by seven species of tropical forage legume grown beneath a 12-year-old *Khaya senegalensis* plantation. Means in a column followed by the same letter do not differ significantly.

Species	June 2000	October 2000
Clitoria ternatea	42.2 ± 3.9 a	16.7 ± 3.0 a
Centrosema brasilianum	$23.8 \pm 1.8 \text{ b}$	$20.5 \pm 1.8 \text{ a}$
Centrosema pascuorum	$22.7 \pm 5.2 \text{ b}$	0.2 ± 0.2 d
Chamaecrista rotundifolia	10.0 ± 1.8 c	9.2 ± 1.6 b
Stylosanthes scabra	6.2 ± 1.1 c	5.0 ± 1.1 bc
Stylosanthes hamata	6.1 ± 1.5 c	7.2 ± 0.8 b
Desmanthus virgatus	3.7 ± 0.9 c	0.7 ± 0.4 cd
Probability	<0.0001	<0.0001

c) Interaction effects

A highly significant interaction effect on ground cover was detected in the June sampling with no such interaction found during October. Within each location *C. brasilianum* and *C. ternatea* provided the greatest levels of ground cover, with *C. brasilianum* providing more ground cover at the intercanopied and canopied locations and *C. ternatea* the most in the control treatment (Table 4.12). No significant differences were found between the two species at any location. Similarly no statistical differences were found between the three species with the lowest ground cover across all locations; *S. scabra, D. virgatus* and *C. pascuorum*. No ground cover was provided at all by *C. pascuorum* at the canopied and inter-canopy locations and by *D. virgatus* in the control.

Table 4.12 Means, standard errors and LSD groupings of percent ground cover of seven species of tropical forage legume under canopied, inter-canopied and clear (control) areas sampled on two different dates. Means in a column followed by the same letter do not differ significantly.

Species	Control		Inter-canopy		Canopied		Probability	
	June 2000	Oct. 2000	June 2000	Oct. 2000	June 2000	Oct. 2000	June 2000	Oct. 2000
Clitoria ternatea	$27.5 \pm 4.5 \text{ aB}$	$27.5 \pm 5.0 \text{ a}$	58.7 ± 6.4 aA	$13.1 \pm 4.3 \text{ ab}$	$48.7 \pm 4.6 \text{ aA}$	$15.0 \pm 4.6 \text{ ab}$	0.0018	0.2177
Centrosema brasilianum	$22.5 \pm 3.1 \text{ a}$	$22.5 \pm 5.0 \text{ ab}$	$31.8 \pm 4.8 \text{ b}$	$19.3 \pm 2.5 \text{ a}$	$21.2 \pm 2.1 \text{ c}$	$20.6 \pm 3.7 \text{ a}$	0.1084	0.8595
Chamaecrista rotundifolia	$11.2 \pm 3.9 \text{ b}$	$11.2 \pm 8.7 \text{ bc}$	$12.5 \pm 3.9 \text{ c}$	$8.1 \pm 2.1 \text{ bc}$	$7.5 \pm 1.5 \text{ d}$	$9.3 \pm 1.5 \text{ bc}$	0.5531	0.8284
Stylosanthes hamata	$3.7 \pm 2.6 \text{ bc}$	$5.0\pm0.1~\mathrm{c}$	$8.7 \pm 4.6 \text{ c}$	$8.1 \pm 1.2 \text{ bc}$	$7.5 \pm 1.5 d$	$7.5 \pm 1.7 \text{ cd}$	0.4173	0.4635
Centrosema pascuorum	$2.5 \pm 1.6~\mathrm{cB}$	$1.2\pm1.2~\mathrm{c}$	$41.2 \pm 6.3 \text{ bA}$	$0.0\pm0.0~\mathrm{d}$	$37.5 \pm 7.7 \text{ bA}$	0.0 ± 0.0 e	< 0.0001	0.1278
Stylosanthes scabra	$2.5 \pm 1.6~\mathrm{cB}$	2.5 ± 2.5 c	$10.6 \pm 2.3 \text{ cA}$	$6.2 \pm 2.6 \text{ bcd}$	$7.8 \pm 0.7 \text{ dA}$	5.0 ± 1.0 cde	0.4173	0.4635
Desmanthus virgatus	$1.2 \pm 1.2 c$	$0.0\pm0.0~\mathrm{c}$	$4.3 \pm 1.8 \text{ c}$	$1.2 \pm 0.0 \text{ cd}$	$3.4 \pm 1.0 \ d$	$0.6 \pm 0.6 de$	0.2652	0.5283
Probability	< 0.0001	0.0146	< 0.0001	0.0001	< 0.0001	0.0001		

In June, the greatest ground cover within species was in the inter-canopy areas (Table 4.12), followed by the canopied areas in all species except *C. brasilianum* and *C. rotundifolia*, which had their second greatest ground cover under the control treatment. Of the seven species tested, only *C. pascuorum*, *C. ternatea* and *S. scabra* were found to show any significant differences.

The October harvest was found to contain no significant differences between any of the locations for any of the species (Table 4.12). *Centrosema brasilianum, C. pascuorum, C. ternatea* and *C. rotundifolia* covered the greatest ground area under the control treatment. However, the second greatest ground coverage for these species was under the canopied locations. In the remaining species, *D. virgatus, S. hamata* and *S. scabra*, the opposite effect was found to be present with the lowest levels of ground cover found beneath in the control treatment and the greatest in the intercanopied areas.

Yield per hectare

a) Effect of location

Dry matter was harvested only during the October sampling, and at that point the control treatment produced considerably more dry matter than either the canopied or inter-canopied areas (Table 4.13). Statistically the control treatment was significantly different from both the inter-canopy and canopied areas, however the inter-canopy and canopied areas displayed no such difference between each other.

Table 4.13 Means, standard errors and LSD groupings of dry matter production (kg per ha) of seven species of tropical forage legume under canopied, inter-canopied and clear (control) areas sampled on the 24th of October 2000. Means in a column followed by the same letter do not differ significantly.

488.8 ± 201.7 a
$122.9 \pm 38.8 \text{ b}$
$82.6 \pm 22.7 \text{ b}$
0.0030

b) Effect of legume species

Centrosema brasilianum produced the most dry matter, with an overall mean of nearly twice that of *C. ternatea*, the second highest yielding. *C. brasilianum* was also statistically different from all other species (Table 4.14). The lowest overall yield was given by *D. virgatus* which failed to produce any dry matter at any of the locations. However, it was not found to be statistically different from the other four lowest yielding species.

Table 4.14 Means, standard errors and LSD groupings for dry matter production (kg per ha) of seven species of tropical forage legume under canopied, inter-canopied and clear (control) areas sampled on the 24th of October 2000. Means in a column followed by the same letter do not differ significantly.

Species	Yield (kg/ha)
C. brasilianum	667.6 ± 256.5 a
C. ternatea	$359.1 \pm 92.9 \text{ b}$
C. rotundifolia	$118.8 \pm 46.8 \text{ bc}$
S. hamata	62.7 ± 16.9 bc
S. scabra	$40.7 \pm 12.4 \text{ c}$
C. pascuorum	$10.8 \pm 10.8 c$
D. virgatus	0.0 ± 0.0 c
Probability	<0.0001

c) Interaction effects

Within locations

Under control and intercanopy locations, *C. brasilianum* was the most productive of the species, followed in both cases by *C. ternatea* and *C. rotundifolia* (Table 4.15). In the canopied areas *C. ternatea* was found to be the most productive, but only by a small margin. *Centrosema brasilianum* yielded only 3.5 kg/ha less than *C. ternatea*, and the two species were not found to be significantly different from one another. At all locations *C. ternatea* and *C. brasilianum* were clearly the best producers, with the remaining species only yielding 50% or less of their above-ground biomass. Typically these lower yielding species were all contained in the lowest averaging statistical grouping at all locations.

Within species

With the exception of *S. scabra*, the greatest yields within each species was in the control treatment (Table 4.15). In each case where significant differences were present (*C. brasilianum*, *C. ternatea* and *S. hamata*), the control was statistically different from the canopied and inter-canopy areas. The species *C. pascuorum* and, in particular, *D. virgatus* performed very poorly with dry matter produced only in the control treatment for *C. pascuorum* and not at all by *D. virgatus*. All species except *S. hamata* produced their lowest yields of dry matter under the canopied treatment.

Table 4.15 Means, standard errors and LSD groupings of dry matter production (kg per ha) of seven species of tropical forage legume under canopied, intercanopied and clear (control) areas, sampled on the 24th of October 2000. Means in a column followed by the same lowercase letter and means in a row followed by the same uppercase letter do not differ significantly.

Species		Dry matter (kg/ha)				
	Control	Inter-canopy	Canopied	Probability		
Centrosema brasilianum	2145.6 ± 113.6 aA	370.9 ± 167.6 aB	225.4 ± 69.6 aB	< 0.0001		
Clitoria ternatea	$780.8 \pm 105.9 \text{ bA}$	$278.3 \pm 137.6 \text{ abB}$	$228.9 \pm 81.0 \text{ aB}$	0.0489		
Chamaecrista rotundifolia	$252.1 \pm 207.4 \text{ c}$	$119.0 \pm 67.0 \text{ abc}$	$52.0 \pm 19.1 \text{ b}$	0.3326		
Stylosanthes hamata	$156.6 \pm 7.9 \text{ cA}$	$36.3 \pm 11.3 \text{ bcB}$	$42.2 \pm 12.9 \text{ bB}$	0.0011		
Centrosema pascuorum	$54.2 \pm 54.2 \text{ c}$	0.0 ± 0.0 c	0.0 ± 0.0 b	0.1278		
Stylosanthes scabra	32.1 ± 24.5 c	56.1 ± 24.5 bc	$29.6 \pm 15.6 \text{ b}$	0.6504		
Desmanthus virgatus	0.0 ± 0.0 c	0.0 ± 0.0 c	0.0 ± 0.0 b	n.r.		
Probability	<0.0001	<0.0342	<0.0011			

Number of plants per metre

a) Effect of location

At the initial June sampling the greatest number of plants per metre was present in the control plots, followed by the inter-canopy area and finally the canopied areas (Table 4.16). By October the control treatment was found to contain the lowest number of plants per metre while the greatest were found in the inter-canopied areas, although these differences were not statistically significant. The overall numbers of plants per metre decreased substantially between June and October, with the average number decreasing at each location.

Table 4.16 Means, standard errors and LSD groupings of the mean number of plants per metre of seven species of tropical forage legume under canopied, inter-canopied and clear (control) areas sampled on the 24th of October 2000. Means in a column followed by the same letter do not differ significantly.

Location	Number of plants per metre			
	June 2000	Oct. 2000		
Control	1.76 ± 0.33 a	0.21 ± 0.06		
Inter-canopy area	1.31 ± 0.09 ab	0.36 ± 0.07		
Canopied area	$1.11 \pm 0.08 b$	0.23 ± 0.04		
Probability	0.0169	0.1439		

b) Effect of species

Table 4.17 displays the overall means and statistical groupings of plants per metre for each species. At the initial June sampling *C. ternatea* had the greatest mean number of plants and was statistically different from the other species. *Centrosema pascuorum* and *C. brasilianum* had the second and third greatest mean numbers of plants and were also both significantly different from one another and all other species. The remaining species clearly had smaller means than these species and were all contained in a fourth statistical grouping. By October 2000, *C. ternatea* remained the species with the greatest mean and was still statistically separate from the other species. However *C. pascuorum* underwent a large decline in the number of plants, becoming the species with the fewest plants per metre of ground sown. *Centrosema brasilianum* remained as one of the most abundant species, followed by *S. hamata>C. rotundifolia>S. scabra>D. virgatus>C. pascuorum*.

Table 4.17 Mean, standard error and LSD groupings of the mean number of plants per metre of ground sown with 7 tropical forage legumes beneath a 12-year-old *Khaya senegalensis* plantation. Means in a column followed by the same letter do not differ significantly.

	Number of plants per metre			
Species	June 2000	October 2000		
Clitoria ternatea	2.77 ± 0.21 a	0.71 ± 0.08 a		
Centrosema pascuorum	$2.09 \pm 0.16 \mathrm{b}$	$0.006 \pm 0.006 d$		
Centrosema brasilianum	$1.46 \pm 0.11 \text{ c}$	$0.45 \pm 0.07 \text{ b}$		
Stylosanthes hamata	$0.77 \pm 0.11 d$	$0.30 \pm 0.07 \text{ bc}$		
Stylosanthes scabra	$0.68 \pm 0.07 \text{ d}$	$0.16 \pm 0.04 \text{ cd}$		
Chamaecrista rotundifolia	$0.45 \pm 0.04 d$	0.25 ± 0.05 c		
Desmanthus virgatus	$0.44 \pm 0.005 d$	$0.07 \pm 0.04 d$		
Probability	0.0006	< 0.0001		

c) Interaction effects

A highly significant interaction effect between species and location was only found in the June 2000 sampling while no significant interaction was found for October 2000.

Effect of location

In June 2000, under the control treatment, Clitoria ternatea had the highest abundance, (also for the entire trial), with nearly double the number of plants per metre of the next species, C. pascuorum, and was statistically different from all other species (Table 4.18). Centrosema pascuorum and C. brasilianum had the second and third greatest numbers of plants per metre respectively, and together formed the second statistical grouping. Remaining species were all contained in the third grouping and had much lower numbers than the first two groupings. The lowest of these were S. scabra and C. rotundifolia. The numbers of plants per metre in the inter-canopy areas were slightly lower than those found in the control plot. Clitoria ternatea remained the species with the greatest abundance (or survivorship), and was again statistically separate from all other species. Centrosema pascuorum and C. brasilianum also remained as the intermediate species contained in the second LSD grouping. The other species all had less than 0.7 plants per metre, with D. virgatus and S. scabra as the species with the lowest abundance (or survivorship). Numbers of plants in the canopied area were only slightly less than those found in the inter-canopy area for the species C. ternatea, C. pascuorum and C. brasilianum, while the numbers for the species D. virgatus, S. hamata, S. scabra and C. rotundifolia changed little. Clitoria ternatea remained the species with the greatest survivorship, although it was not significantly different from C. pascuorum. Centrosema brasilianum was contained in the same statistical grouping as S. hamata, which showed an increase under canopied conditions. Chamaecrista rotundifolia had the lowest mean abundance, but this was only slightly less than D. virgatus and S. scabra.

Within species *C. ternatea*, *C. brasilianum*, *C. rotundifolia* and *S. scabra* displayed significant differences between locations. For three of the species, *C. brasilianum*, *C. rotundifolia* and *S. scabra*, the inter-canopied and control treatments were not statistically different, with the greatest number of plants per metre found in the inter-canopied areas for *C. rotundifolia* and *S. scabra*, and under the control for *C. brasilianum* and *C. ternatea*. *Clitoria ternatea* was the species with the greatest abundance (or survivorship) under all treatments with the control significantly different from the other two treatments.

Legume abundance was much lower during October 2000, with no species having an average of greater than 1 plant per metre (Table 4.18). In the control plot, *C. ternatea* had the greatest number with over twice as many as the next closest species, *C. brasilianum* and *S. hamata. Clitoria ternatea* was the only species in the first statistical grouping and all the other species were not statistically different from each other. No plants of *D. virgatus* survived. Legume abundance was lower in the inter-canopy areas, with *C. ternatea* again most abundant. No significant difference was found between *C. ternatea* and *C. brasilianum*, the species with the second highest mean abundance. No plants of *C. pascuorum* were found, while at this location some plants of *D. virgatus* had survived although only in very low numbers. Legume survivorship was lowest beneath the tree canopies on both sampling dates. Similar to the inter-canopy area, no surviving plants of *C. pascuorum* were found and only a few individuals of *D. virgatus*. *C. ternatea* was most abundant, although it was not significantly different from *C. brasilianum*. A total of four statistical groupings were found, with the group with the lowest means containing the species *S. scabra>C. rotundifolia>D. virgatus>C. pascuorum*.

Only one significant difference was found within species at this sampling date. *Centrosema brasilianum* had the greatest numbers of plants per metre at inter-canopy locations, with a significant difference found between the inter-canopy locations and the canopied and control locations. Several other species survived best at the inter-canopy locations (*C. ternatea*, *S. hamata* and *C. rotundifolia*). *Stylosanthes scabra* was unusual in that the greatest numbers were found beneath the canopied areas, although the difference between there and the other two locations was small (0.03 plants/m).

Species	Plants per metre							
	Control		Inter-canopy		Canopied		Probability	
	June 2000	Oct. 2000	June 2000	Oct. 2000	June 2000	Oct. 2000	June 2000	Oct. 2000
Clitoria ternatea	$5.25 \pm 0.22 \text{ aA}$	0.65 ± 0.03 a	$2.85 \pm 0.21 \text{ aB}$	0.91 ± 0.10 a	2.33 ± aB	0.54 ± 0.11 a	0.0005	0.0869
Centrosema pascuorum	$2.75 \pm 0.17 \text{ b}$	$0.03 \pm 0.03 \text{ b}$	$1.97 \pm 0.25 \text{ b}$	0 ± 0 e	$1.89 \pm a$	$0 \pm 0 d$	0.2651	0.1278
Centrosema brasilianum	$2.31 \pm 0.37 \text{ bA}$	$0.25 \pm 0.12 \text{ bB}$	$1.61 \pm 0.12 \text{ bAB}$	$0.65 \pm 0.07 \text{ abA}$	$1.29 \pm bB$	$0.36 \pm 0.09 \text{ abB}$	0.0448	0.0424
Desmanthus virgatus	0.75 ± 0.14 c	0 ± 0 b	$0.46 \pm 0.05 d$	$0.08 \pm 0.08 \ de$	$0.38 \pm d$	$0.09 \pm 0.06 \text{ cd}$	0.1661	0.7269
Stylosanthes hamata	0.56 ± 0.15 c	$0.25 \pm 0.06 \text{ b}$	$0.62 \pm 0.08 \text{ cd}$	$0.39 \pm 0.18 \text{ bc}$	$0.88 \pm bc$	$0.24 \pm 0.01 \text{ bc}$	0.4880	0.6948
Chamaecrista rotundifolia	$0.37 \pm 0.07 \text{ cAB}$	$0.18 \pm 0.12 \text{ b}$	$0.61 \pm 0.11 \text{ cdA}$	$0.35 \pm 0.09 \text{ cd}$	$0.36 \pm dB$	$0.17 \pm 0.09 \text{ bcd}$	0.0481	0.3835
Stylosanthes scabra	$0.37 \pm 0.16 \text{ cA}$	$0.15 \pm 0.15 \text{ b}$	$0.46 \pm 0.13 \text{ dA}$	$0.15 \pm 0.05 \text{ cde}$	$0.59 \pm cdB$	$0.18 \pm 0.06 \text{ bcd}$	0.0450	0.9516
Probability	<0.0001	0.0225	<0.0001	<0.0001	<0.0001	0.0009		

4.3.3 Production and persistence of *Clitoria ternatea, Chamaecrista rotundifolia* and four accessions of *Arachis* under open conditions and beneath two densities of *Khaya senegalensis*.

Statistical summary of results

Highly significant differences were present between legume species, in all attributes across all sampling dates (Table 4.19). No significant difference was present during the March 2001 sampling between tree densities, nor was there an interaction between tree density and legume species with relation to the number of surviving plants. Also ground cover was not significantly affected by tree density at the April 2002 sampling.

Dry matter production

Clitoria ternatea and Arachis paraguariensis were the two greatest yielding species across all tree densities and sampling dates (Table 4.20), with one or both of these species contained within the highest yielding statistical grouping. Arachis stenosperma was generally the third greatest yielding species, however its yields were considerably less than for C. ternatea and A. paraguariensis. The remaining species, A. pintoi cv. Amarillo, A. pintoi ATF 2717 and C. rotundifolia, yielded poorly compared to the former species at each sampling date. These species were always contained within either the lowest or middle statistical groupings. By April 2002 C. ternatea and A. paraguariensis were the only species surviving in the control treatment. Chamaecrista rotundifolia was frequently the poorest performing species.

The species, *A. pintoi* cv. Amarillo, *A. pintoi* ATF 2717, *A. stenosperma* and *C. rotundifolia* tended to have the greatest yields at the initial sampling and declined in subsequent harvests, most notably in the control treatment where no yield was recorded by April 2002. Other than for these species, November 2001 was the sampling date with the lowest yields for all other species under all tree densities.

Within legume species

Within species, *A. paraguariensis* yielded the greatest quantities of dry matter in the control plots at each harvest date, with the control treatment statistically different from the 1 x 1 and 1.5 x 1.5 m tree spacings. However the other high yielding species, *C. ternatea*, yielded best in the control plots in the first two samplings. In the April 2002 harvest the greatest yield was produced under the 1.5 x 1.5 m tree spacing (Table 4.21), although it was not significantly different from the control. Significant differences were not found between tree densities within the species *A. stenosperma*, *C. rotundifolia* and *A. pintoi* cv. Amarillo at all sampling dates, and *A. pintoi* ATF 2717 at the November 2001 and April 2002 samplings. Despite the absence of statistical differences between tree densities in these species, the yield of dry matter was substantially greater under the control treatment than under either tree density in the first two samplings. By April 2002 none of the species, except *C. ternatea* and *A. paraguariensis*, had survived under the open conditions of the control, but persisted under the 1.5 x 1.5 and 1 x 1 m tree densities and yielded small quantities of dry matter. *Chamaecrista rotundifolia* was the exception to this, as by April 2002 no plants remained under any treatment.

Ground cover

At the initial March 2001 sampling beneath the 1 x 1 m spacing, no statistical differences were detected between species. At all remaining tree densities and sampling dates significant differences were found between legume species (Table 4.22). Beneath all tree densities and on all sampling dates *C. ternatea* covered the largest fraction of ground, except in November 2001 and April 2002 under the 1 x 1 m spacing. Generally *A. paraguariensis* was the species covering the most ground after *C. ternatea*, however during the March 2001 sampling remaining species had lower but similar levels of ground cover. *C. ternatea* and *A. paraguariensis* were always grouped in one of the two highest statistical groupings. *Chamaecrista rotundifolia* was consistently the species with the lowest level of ground cover. By April 2002 *C. rotundifolia* was absent from all tree densities along with three other species beneath the control treatment.

 Table 4.19 Statistical summary of results

	March 2001				Novembe	r 2001	April 2002			
	Yield	Ground	No. of plants	Yield	Ground	No. of plants	Yield	Ground	No. of plants	
Effect	(g)	cover		(g)	cover		(g)	cover		
Species	***	***	***	***	***	***	***	***	***	
Tree	***	***	n.s.	***	***	***	***	n.s.	***	
Density										
Interaction	***	***	n.s.	**	**	*	***	***	***	

 $n.r. = no \text{ result}; \ n.s. = no \text{ significant effect}; \ ^* = 0.05 > P > 0.01; \ ^{**} = 0.01 > P > 0.001; \ ^{***} = P > 0.001.$

Table 4.20 Dry matter production (g) by six accessions of legume under open conditions (control) and beneath two densities of *Khaya senegalensis*, on three sampling dates. Means in a column followed by the same lowercase letter are not significantly different.

		1 x 1 m			1.5 x 1.5 m			Control	
Species	March 2001	Nov 2001	April 2002	March	Nov. 2001	April 2002	March 2001	Nov 2001	April 2002
				2001					
C. ternatea	27.4 ± 17.0 a	$5.3 \pm 2.4 \text{ b}$	55.9 ± 25.9 a	91.8 ± 25.3 a	$16.0 \pm 1.9 \text{ a}$	194.7 ± 24.9 a	231.7 ± 46.9 b	28.7 ± 3.3 a	169.3 ± 33.6 a
A. paraguariensis	$20.3 \pm 4.2 \text{ ab}$	$10.7 \pm 1.1 \text{ a}$	$55.3 \pm 9.4 \text{ a}$	$39.3 \pm 4.7 \text{ b}$	$15.3 \pm 1.3 \text{ a}$	$50.2 \pm 6.8 \text{ b}$	367.7 ± 77.0 a	$22.7 \pm 3.6 \text{ a}$	147.4 ± 39.4 a
A. stenosperma	$8.1 \pm 1.9 \text{ bc}$	$1.4 \pm 0.9 \text{ b}$	$7.2 \pm 1.7 \text{ b}$	$40.4 \pm 5.1 \text{ b}$	$2.3 \pm 0.9 \text{ b}$	$6.2 \pm 1.5 \text{ c}$	144.5 ± 21.3 bc	$8.5 \pm 0.2 \text{ b}$	0 ± 0 b
A. pintoi ATF 2717	$7.5 \pm 2.1 \text{ c}$	$3.1 \pm 1.1 \text{ b}$	$8.6 \pm 3.5 \text{ b}$	$17.7 \pm 2.5 \text{ c}$	$3.8 \pm 1.0 \text{ b}$	$2.2 \pm 1.2 c$	$81.5 \pm 23.8 \text{ cd}$	$11.7 \pm 2.7 \text{ b}$	0 ± 0 b
A. pintoi cv. Amarillo	$4.1 \pm 1.2 \text{ c}$	$4.1 \pm 1.6 \text{ b}$	$4.3 \pm 1.8 \text{ b}$	$10.8 \pm 2.4 \text{ c}$	$4.5 \pm 1.5 \text{ b}$	$1.9 \pm 0.7 \text{ c}$	$18.4 \pm 11.2 d$	$5.3 \pm 2.6 \text{ b}$	0 ± 0 b
C. rotundifolia	$0.5 \pm 0.4 \text{ c}$	$0.9 \pm 0.9 \text{ b}$	0.0 ± 0.0 c	$5.4 \pm 3.2 \text{ c}$	$2.7 \pm 2.7 \text{ b}$	0 ± 0 c	$13.0 \pm 13.0 \text{ d}$	$8.5 \pm 3.9 \text{ b}$	0 ± 0 b
P	0.0124	< 0.0001	< 0.0001	<0.0001	< 0.0001	< 0.0001	<0.0001	< 0.0001	<0.0001

Table 4.21 Dry matter production (g) by six accessions of legume under open conditions (control) and beneath two densities of *Khaya senegalensis*, on three sampling dates, showing within species differences. Means in a column followed by the same lowercase letter are not significantly different.

		C. ternatea			A. paraguariensis		A. stenosperma			
Tree spacing	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	
Control	231.7 ± 46.9 a	28.7 ± 3.3 a	169.3 ± 33.6 a	367.7 ± 77.0 a	22.7 ± 3.6 a	147 ± 39.4 a	144.5 ± 21.3 a	8.5 ± 0.2 a	0.0 ± 0.0 b	
1.5 x 1.5 m	$91.8 \pm 25.3 \text{ b}$	$16.0 \pm 1.9 \text{ b}$	194.7 ± 24.9 a	$39.3 \pm 4.7 \text{ b}$	$15.3 \pm 1.3 \text{ b}$	$50.2 \pm 6.8 \text{ b}$	$40.4 \pm 5.1 \text{ b}$	$2.3 \pm 0.9 \text{ b}$	$6.2 \pm 1.5 \text{ a}$	
1 x 1 m	27.4 ± 17.0 b	$5.3 \pm 2.4 \text{ c}$	55.9 ± 25.9 b	$20.3 \pm 4.2 \text{ b}$	$10.7 \pm 1.1 \text{ b}$	$55.3 \pm 9.4 \text{ b}$	$8.1 \pm 1.9 \text{ c}$	$1.4 \pm 0.9 \text{ b}$	$7.2 \pm 1.7 \text{ a}$	
P	0.0045	0.0005	0.0201	< 0.0001	0.0019	0.0013	< 0.0001	0.0005	0.0355	

	A. pintoi cv. Amarillo				A. pintoi ATF 2717		C. rotundifolia			
Tree spacing	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	
Control	18.4 ± 11.2	5.3 ± 2.6	0.0 ± 0.0	81.5 ± 23.8 a	11.7 ± 2.7 a	0.0 ± 0.0	13.0 ± 13.0	8.5 ± 3.9	0.0 ± 0.0	
1.5 x 1.5 m	10.8 ± 2.4	4.5 ± 1.5	1.9 ± 0.7	$17.7 \pm 2.5 \text{ b}$	$3.8 \pm 1.0 \text{ b}$	2.2 ± 1.2	5.4 ± 3.2	2.7 ± 2.7	0.0 ± 0.0	
1 x 1 m	4.1 ± 1.2	4.1 ± 1.6	4.3 ± 1.8	$7.5 \pm 2.1 \text{ b}$	$3.1 \pm 1.1 \text{ b}$	8.6 ± 3.5	0.5 ± 0.4	0.9 ± 0.9	0.0 ± 0.0	
P	0.1091	0.9103	0.1612	< 0.0001	0.0023	0.0854	0.5143	0.1873	-	

Table 4.22 Ground cover (%) of six accessions of legume under open conditions (control) and beneath two densities of *Khaya senegalensis*, on three sampling dates. Means in a column followed by the same lowercase letter are not significantly different.

		1 x 1 m			1.5 x 1.5 m			Control	
Species	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002
C. ternatea	62.5 ± 10.3	15.0 ± 5.0 b	57.5 ± 21.7 ab	90.0 ± 7.0 a	45.0 ± 2.8 a	81.2 ± 6.2 a	100.0 ± 0.0 a	67.5 ± 7.5 a	100.0 ± 0.0 a
A. pintoi cv. Amarillo	58.7 ± 12.8	$11.2 \pm 4.4 \text{ b}$	$25.0 \pm 8.8 \text{ abc}$	$81.2 \pm 7.6 \text{ ab}$	$12.5 \pm 4.1 \text{ b}$	$10.0 \pm 3.4 \text{ cd}$	$95.0 \pm 5.0 \text{ a}$	$12.5 \pm 6.3 \text{ b}$	$0.0\pm0.0~\mathrm{c}$
A. paraguariensis	55.0 ± 6.8	$30.0 \pm 2.6 \text{ a}$	$57.5 \pm 6.5 \text{ a}$	$70.0 \pm 5.0 \text{ ab}$	$42.5 \pm 3.6 \text{ a}$	$41.8 \pm 5.2 \text{ b}$	$92.5 \pm 2.5 \text{ a}$	$52.5 \pm 8.5 \text{ a}$	$90.0 \pm 7.0 \text{ b}$
A. pintoi ATF 2717	50.0 ± 7.0	$8.7 \pm 2.9 \text{ b}$	$33.7 \pm 9.2 \text{ cd}$	$66.2 \pm 3.2 \text{ b}$	$10.0 \pm 2.7 \text{ b}$	$7.5 \pm 1.3 \text{ d}$	$95.0 \pm 2.8 \text{ a}$	$27.5 \pm 6.3 \text{ b}$	$0.0\pm0.0~\mathrm{c}$
A. stenosperma	50.0 ± 5.9	$3.7 \pm 2.6 \text{ b}$	$28.7 \pm 7.4 \text{ bcd}$	$72.5 \pm 6.5 \text{ ab}$	$6.2 \pm 2.6 \text{ b}$	$20.0 \pm 5.1 \text{ c}$	$87.5 \pm 6.3 \text{ a}$	$20.0 \pm 0.0 \text{ b}$	$0.0\pm0.0~\mathrm{c}$
C. rotundifolia	15.0 ± 8.6	$2.5 \pm 2.5 \text{ b}$	$0.0\pm0.0~\mathrm{d}$	$25.0 \pm 15.0 \text{ c}$	$7.5 \pm 7.5 \text{ b}$	$0.0\pm0.0~\mathrm{d}$	$35.0 \pm 20.2 \text{ b}$	$20.0 \pm 7.5 \text{ b}$	$0.0\pm0.0~\mathrm{c}$
P	0.0684	>0.0001	0.0054	0.0002	< 0.0001	< 0.0001	0.0007	0.0001	< 0.0001

Within species

No significant differences were detected between tree densities for the species *A. pintoi* cv. Amarillo and *C. rotundifolia* at any of the three sampling dates (Table 4.23). Despite the absence of a statistical difference between tree densities the fraction of ground covered by *A. pintoi* cv. Amarillo was greater at the lower tree density and reached its maximum under the control treatment. However by April 2002 the opposite trend was apparent with no ground cover in the control treatment, increasing under 1.5 x 1.5 m spacing to a maximum under the 1 x 1 m tree spacing. *C. rotundifolia*, initially displayed a similar trend of increasing ground cover as tree spacing increased, however by April 2002 the species provided no ground cover under any tree spacing. Within the species *C. ternatea* and *A. paraguariensis* the greatest levels of ground cover were present in the control treatment, although the control treatment and the 1.5 x 1.5 m spacing were often not significantly different from one another. *Arachis stenosperma* and *A. pintoi* ATF 2717 had the greatest percentages of ground cover in the control treatments, followed by the 1.5 x 1.5 m and then the 1 x 1 m tree spacing in the March 2001 and November 2001 samplings. However in the April 2002 sampling no ground cover was present under the control treatment, increasing to a maximum beneath the 1 x 1 m spacings.

Number of plants

Clitoria ternatea frequently had the greatest number of surviving plants, while *C. rotundifolia* had the lowest. Statistical differences were present at all dates under all tree spacings (Table 4.24). *Arachis paraguariensis* frequently had the second greatest number of surviving plants after *C. ternatea* and was not significantly different from it in all cases save one (Control in March 2001). By April 2002 *C. ternatea* and *A. paraguariensis* were the only species surviving in the control treatment, while *C. rotundifolia* had failed to persist under any treatment by this date.

Within species

Tree density was found to significantly affect the number of surviving plants in only four cases; *A. stenosperma* November 2001 and April 2002, *A. pintoi* ATF April 2002 and *A. pintoi* cv. Amarillo April 2002 (Table 4.25). The three significant differences detected at the April 2002 sampling all contained the 1.5 x 1.5 and the 1 x 1 m tree spacings in the statistical grouping with the highest mean followed by the control treatment in the second grouping with a mean of 0. *Arachis stenosperma* had distinctly more surviving plants under the control treatment in November 2001 than under either of the tree spacings. In remaining species the control treatment tended to have higher numbers of surviving plants than the 1 x 1 or 1.5 x 1.5 m tree spacings, however there were several exceptions (*A. paraguariensis* March 2001, *A. stenosperma* March 2001, *A. pintoi* cv. Amarillo November 2001 and *C. rotundifolia* March 2001).

Table 4.23 Ground cover (%) of six accessions of legume under open conditions (control) and beneath two densities of *Khaya senegalensis*, on three sampling dates. Means in a column followed by the same lowercase letter are not significantly different.

	C. ternatea			_	A. paraguariensis	7	A. stenosperma			
Tree spacing	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	
Control	100.0 ± 0.0 a	$67.5 \pm 7.5 \text{ a}$	100.0 ± 0.0	92.5 ± 2.5 a	52.5 ± 8.5 a	90.0 ± 7.0 a	87.5 ± 6.3 a	20.0 ± 0.0 a	$0.0 \pm 0.0 \text{ b}$	
1.5 x 1.5 m	$90.0 \pm 7.0 \text{ a}$	$45.0 \pm 2.8 \text{ b}$	81.2 ± 6.2	$70.0 \pm 5.0 \text{ b}$	$42.5 \pm 3.6 \text{ a}$	$41.8 \pm 5.2 \text{ b}$	$72.5 \pm 6.5 \text{ a}$	$6.2 \pm 2.6 \text{ b}$	$20.0 \pm 5.1 \text{ ab}$	
1 x 1 m	$62.5 \pm 10.3 \text{ b}$	$15.0 \pm 5.0 \text{ c}$	57.5 ± 21.7	$55.0 \pm 6.8 \text{ b}$	$30.0 \pm 2.6 \text{ b}$	$57.5 \pm 6.5 \text{ b}$	$50.0 \pm 5.9 \text{ b}$	$3.7 \pm 2.6 \text{ b}$	$28.7 \pm 7.4 \text{ a}$	
P	0.0134	0.0003	0.1238	0.0038	0.0097	0.0006	0.0047	0.0033	0.0365	

	A. pintoi cv. Amarillo			A. pintoi ATF 2717			C. rotundifolia		
Tree spacing	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002
Control	95.0 ± 5.0	12.5 ± 6.3	0.0 ± 0.0	95.0 ± 2.8 a	27.5 ± 6.3 a	$0.0 \pm 0.0 \text{ b}$	35.0 ± 20.2	20.0 ± 7.5	0.0 ± 0.0
1.5 x 1.5 m	81.2 ± 7.6	12.5 ± 4.1	10.0 ± 3.4	$66.2 \pm 3.2 \text{ b}$	$10.0 \pm 2.7 \text{ b}$	$7.5 \pm 1.3 \text{ b}$	25.0 ± 15.0	7.5 ± 7.5	0.0 ± 0.0
1 x 1 m	58.7 ± 12.8	11.2 ± 4.4	25.0 ± 8.8	$50.0 \pm 5.9 \text{ c}$	$8.7 \pm 2.9 \text{ b}$	$33.7 \pm 9.2 \text{ a}$	15.0 ± 8.6	2.5 ± 2.5	0.0 ± 0.0
P	0.0990	0.9750	0.0679	0.0003	0.0076	0.0055	0.6671	0.2414	-

Table 4.24 Number of plants of six accessions of legume under open conditions (control) and beneath two densities of *Khaya senegalensis*, on three sampling dates. Means in a column followed by the same lowercase letter are not significantly different.

		1 x 1 m			1.5 x 1.5 m			Control	
Species	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002
C. ternatea	3.3 ± 0.5 a	$2.2 \pm 0.8 \text{ ab}$	$2.5 \pm 0.9 \text{ a}$	$3.0 \pm 0.6 \text{ ab}$	$2.7 \pm 0.8 \text{ ab}$	2.7 ± 0.5 a	$3.2 \pm 0.5 \text{ a}$	$3.5 \pm 0.5 \text{ a}$	$3.3 \pm 0.2 \text{ a}$
A. stenosperma	$2.9 \pm 0.2 \text{ a}$	0.5 ± 0.4 c	$1.7 \pm 0.3 \text{ a}$	$3.0 \pm 0.4 \text{ a}$	$0.8 \pm 0.3 \; d$	2.1 ± 0.2 ab	$2.7 \pm 0.2 \text{ ab}$	3.0 ± 0.0 a	0.0 ± 0.0 b
A. paraguariensis	2.2 ± 0.3 ab	$2.6 \pm 0.2 \text{ a}$	$2.2 \pm 0.2 \text{ a}$	2.4 ± 0.2 abc	$2.8 \pm 0.1 \text{ a}$	$2.2 \pm 0.3 \text{ ab}$	$1.7 \pm 0.2 \text{ bc}$	3.0 ± 0.0 a	$3.0 \pm 0.0 \text{ a}$
A. pintoi ATF 2717	$2.1 \pm 0.3 \text{ ab}$	$1.6 \pm 0.4 \text{ ab}$	$2.0 \pm 0.4 \; a$	2.0 ± 0.3 bc	$1.2 \pm 0.3 \text{ cd}$	$1.1 \pm 0.2 \text{ c}$	$2.7 \pm 0.2 \text{ ab}$	$3.0 \pm 0.7 \ a$	0.0 ± 0.0 b
A. pintoi ev. Amarillo	$1.8 \pm 0.5 \text{ b}$	$1.1 \pm 0.3 \text{ bc}$	$1.4 \pm 0.2 \text{ a}$	$1.9 \pm 0.2 \text{ c}$	$1.8 \pm 0.2 \text{ bc}$	$1.6 \pm 0.3 \text{ bc}$	$2.2 \pm 0.2 \text{ ab}$	1.0 ± 0.4 b	0.0 ± 0.0 b
C. rotundifolia	$1.3 \pm 0.6 \text{ b}$	0.2 ± 0.2 c	0.0 ± 0.0 b	$0.8 \pm 0.5 d$	$0.2 \pm 0.2 d$	0.0 ± 0.0 d	$1.0\pm0.6~\mathrm{c}$	1.0 ± 0.4 b	0.0 ± 0.0 b
P	0.0246	0.0008	0.0033	0.0024	<0.0001	<0.0001	0.0054	0.0013	<0.0001

Table 4.25 Number of plants of six accessions of legume under open conditions (control) and beneath two densities of *Khaya senegalensis*, on three sampling dates. Means in a column followed by the same lowercase letter are not significantly different.

	C. ternatea				A. paraguariensis	S	A. stenosperma			
Tree spacing	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	
Control	3.2 ± 0.5	3.5 ± 0.5	3.3 ± 0.2	1.7 ± 0.2	3.0 ± 0.0	3.0 ± 0.0	2.7 ± 0.2	$3.0 \pm 0.0 \text{ a}$	$0.0 \pm 0.0 \text{ b}$	
$1.5 \times 1.5 m$	3.0 ± 0.6	2.7 ± 0.8	2.7 ± 0.5	2.4 ± 0.2	2.8 ± 0.1	2.2 ± 0.3	3.0 ± 0.4	$0.8 \pm 0.3 \text{ b}$	$2.1 \pm 0.2 \text{ a}$	
1 x 1 m	3.3 ± 0.5	2.2 ± 0.8	2.5 ± 0.9	2.2 ± 0.3	2.6 ± 0.2	2.2 ± 0.2	2.9 ± 0.2	0.5 ± 0.4 b	$1.7 \pm 0.3 \text{ a}$	
P	0.9247	0.6545	0.7059	0.2530	0.2758	0.0733	0.8870	0.0013	< 0.0001	

	A. pintoi cv. Amarillo			A	. pintoi ATF 271	17	C. rotundifolia			
Tree spacing	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	March 2001	Nov 2001	April 2002	
Control	2.2 ± 0.2	1.0 ± 0.4	$0.0 \pm 0.0 \text{ b}$	2.7 ± 0.2	3.0 ± 0.7	$0.0 \pm 0.0 \text{ b}$	1.0 ± 0.6	1.0 ± 0.4	0.0 ± 0.0	
1.5 x 1.5 m	1.9 ± 0.2	1.9 ± 0.2	$1.6 \pm 0.3 \text{ a}$	2.0 ± 0.3	1.2 ± 0.3	$1.1 \pm 0.2 \text{ a}$	0.8 ± 0.5	0.2 ± 0.2	0.0 ± 0.0	
1 x 1 m	1.8 ± 0.5	1.1 ± 0.3	$1.4 \pm 0.2 \text{ a}$	2.1 ± 0.3	1.6 ± 0.4	$2.0 \pm 0.4 \text{ a}$	1.3 ± 0.6	0.2 ± 0.2	0.0 ± 0.0	
P	0.6900	0.0989	0.0033	0.3396	0.0602	0.0060	0.8257	0.2009	-	

4.4 Discussion

Arachis pintoi appears to be a species well suited for use beneath plantations in the wet tropics, showing excellent growth and spreading beyond its original plots in the field trial at Babinda. The low growing habit of the plant is a further advantage when used in conjunction with trees and it does not have the ability to smother young or small trees. Stylosanthes guianensis performed unexpectedly well after a poor beginning, although previous work had indicated that it would not be suited to use under tree plantations. It is likely that the light levels present in the plantation were sufficient for growth of the species, however, as the plantation ages and light levels fall it would fail to persist, as is suggested in previous results and by other workers. Aeschynomene americana cv. Lee, A. villosa cv. Reid, A. villosa 37235 and A. villosa cv. Kretschmer are not recommended for use in shaded conditions.

The yield of dry matter was clearly decreased by the presence of 12-year-old African mahogany trees in the Clare field trial, whether in the gap between canopies (inter-canopied areas) or directly beneath them (canopied areas). The differences between these areas within the plantation highlight the potential variability of pasture growth due to environmental variation within a plantation. Light was concluded to be the limiting factor to growth beneath the trees, having quite pronounced effects upon the production of dry matter. *Centrosema brasilianum* and *C. ternatea* were the most promising species, giving good yields of dry matter in the inter-canopied and canopied areas while giving even higher yields in control plots, indicating shade tolerance rather than shade adaptation. The climbing habit of both species may be a cause for concern, however no instance of either legume climbing trees was encountered. The premature termination of the trial did not allow for the continued monitoring of species to observe their responses to defoliation and their persistence, both of which need to be examined to gain a clearer picture of the species potential for use beneath tree plantations.

Clitoria ternatea and A. paraguariensis appear to be the most suitable of the species examined in the Townsville field trial, for use in agroforestry systems of the seasonal tropics. They produced useful quantities of dry matter under both tree densities and in control plots, displaying a versatility of use for both older, more heavily shaded, plantations and younger, lighter plantations. Also these two species displayed what appeared to be a tolerance of dry conditions, a highly desirable attribute in the seasonally dry tropics. Conclusions regarding other species were more difficult to draw due to the dry conditions limiting growth of the plants, not light, but in general the remaining species performed poorly in comparison.

Further research is needed to further confirm the potential of *C. ternatea*, and in particular *A. paraguariensis*, for use in silvo-pastoral systems as little information is available regarding the shade tolerance or adaptation of *C. ternatea* and virtually no information is available regarding *A. paraguariensis*.

The following general conclusions were drawn from the field trials

- 1) Shading reduced production of dry matter in most situations, however water may become the limiting factor to production at certain times in the seasonally dry tropics rather than light.
- 2) Shading generally decreased the level of ground cover provided by legumes as a result of decreasing growth.
- 3) Shading by trees did not consistently appear to affect the number of surviving plants while shade was limiting to growth. However when water appeared to become the limiting factor to growth, increased numbers of certain species of plants, mainly those that were more drought sensitive, were able to survive beneath trees than in the open.
- 4) The following species are recommended for use under shaded conditions within their environmental range; *Arachis pintoi, Arachis paraguariensis, Clitoria ternatea* and *Centrosema brasilianum*.
- 5) The species *Stylosanthes guianensis* cv. Cook appears to be suitable for use under light to moderate levels of shade, however under heavier shade it is unlikely to be productive.

Further research is required particularly in relation to long term trials and the effects of different defoliation regimes upon the production and persistence of the previously mentioned legume species in addition to work detailing their potential compatibility with shade tolerant grasses. In particular more work is required, not only upon the shade tolerance of *A. paraguariensis*, but also its other attributes as it is a species about which very little is known.

Pasture production and legume performance beneath an African Mahogany (*Khaya senegalensis*) Nelder Wheel sown with four commercially available pasture legumes

5.1 Introduction

Increased interest in agroforestry has occurred in recent years owing to the cessation of logging in the wet tropic rainforests of Queensland, following World Heritage listing in 1988. As a consequence interest in establishing timber plantations upon private land has increased, however one of the major obstacles to the establishment of such plantations is the long time-lag before returns can be made from the plantation. The establishment of agroforestry systems where forage is produced beneath tree plantations and grazed by livestock (a silvo-pastoral system) has been suggested as a means of obtaining earlier returns from the land while the timber component matures.

Additional benefits of establishing pasture in young plantations include maintaining soil organic matter levels, increasing nutrient levels (Garrity 1994), especially addition of nitrogen through N fixation by pasture legumes, diversification of income and increased sustainability through reduced erosion and nutrient leaching (Seyfried & Rao 1991). However a range of negative effects may also result, which can include a reduction of yield in one or both components of the system due to increased competition for available resources, both above and below ground.

It has been indicated by Wong (1991) that the major constraint to the growth of forage beneath tree plantations in the wet tropics is the availability of light, although it is likely that at high densities tree and pasture roots will compete strongly for nutrients and water (Eastham & Rose 1990). This suggests the possibility of water becoming the limiting resource in the seasonally dry tropics during the dry season, rather than light.

Most of the past research which has examined the suitability, particularly shade tolerance, of forage species for use beneath tree plantations has focused upon species adapted to the wet tropics, with relatively little attention given to species suited to the seasonally dry tropics. In recent years increasing areas of plantations of *Khaya senegalensis* (African mahogany) have been established around Townsville and Charters Towers (Collins and Sexton, *pers. comm.*), but there is little information available regarding suitable forage species for growth beneath plantations in these seasonally dry areas. In order to address this, a trial was established to examine four species of commercially available legume species under a range of densities of *Khaya senegalensis*, in combination with volunteer Guinea grass (*Panicum maximum*) and broadleaf weeds.

5.2 Materials and methods

5.2.1 Trial site

The trial was established upon a cleared plot of land on the Townsville campus of James Cook University. Prior to clearing, vegetation on the site was an Ironbark (*Eucalyptus drepanophylla*) woodland with an understorey dominated by the exotics Chinee Apple (*Ziziphus mauritiana*) and Guinea Grass (*Panicum maximum*). Soil on the site was an alluvial, dark grey-brown, massive sandy

loam grading to a massive brown sandy clay loam, grading to water-worn gravel at approximately 1 - 1.5 m and friable throughout (Murtha 1982). Soil properties are shown in Table 4.2.

5.2.2 Trial establishment

African mahogany seedlings were planted on the 16th of August 1999 in a Nelder wheel arrangement (Nelder 1962), and fertilized with 100 g per tree of Nitrophoska Blue at the ages of 11 days and 18 months. The wheel was composed of 16 equally spaced radii. Along each radius trees were planted at the following distances from the central tree: 1, 2.5, 4.5, 7.0, 10.0, 13.5, 17.5, 22 and 27 m. This spacing resulted in nine concentric rings in which tree densities were equivalent to 20541, 10270, 2282, 1467, 855, 543, 366 and 259 stems/ha, with the outermost ring acting as a buffer. Tree densities were extremely high in the centre of the wheel in order to obtain a high level of shading and effects upon pasture growth within the time frame of the project. Trees received irrigation up until 3 months prior to the first sampling date. Irrigation was ceased at this point in order to avoid the confounding effects of soil moisture content. The sixteen sectors of the Nelder wheel (the area between two rows of trees) were divided into four replicates of four sectors. One of four species of legume, Clitoria ternatea cv. Milgarra, Chamaecrista rotundifolia cv. Wynn, Centrosema brasilianum cv. Ooloo and Stylosanthes hamata cv. Verano, were sown in each sector of each replicate. Seed was broadcast following spraying with Roundup (glyphosate) and cultivation of the soil with a powered hoe. Seed was mixed with dry sand and applied using a hand spreader to obtain an even spread at the following rates: Clitoria ternatea 8 kg/ha, Centrosema brasilianum 5 kg/ha, Chamaecrista rotundifolia 4 kg/ha and Stylosanthes hamata 3 kg/ha. Legume seed was sown on the 14th of March 2000, when trees were seven months old. Growth beneath the trees was slashed periodically, to approximately 10 cm, in order to control growth of weeds. It is recognised that the replication within the trial is actually pseudo-replication; proper replication could be obtained through the establishment of additional Nelder wheels, however land and resources did not permit this.

5.2.3 Measurement of the light levels and soil moisture content

Light levels were measured using a Li-Cor 1000 data logger and quantum sensors located on stakes just above the level of the pasture at each tree density. Light intensity was recorded every 5 minutes beginning at 5am and ceasing at 7pm. Sensors were located at the mid-point between trees where tree shading would be expected to be the least. Results were summed and expressed as a percentage of a control that was placed in an unshaded area of the same field. Soil moisture content was determined by taking soil samples at depths of 0-10 cm, 20 - 30 cm and 40 - 50 cm using a hand auger on the day immediately preceding the commencement of pasture sampling. Samples were taken from the mid-point between adjacent trees at each tree density, within three sectors sown with the species C. ternatea. Soil was placed in sealed plastic bags and the moisture content determined according to the method of Rayment & Higginson (1992).

5.2.4 Pasture Sampling

Pasture sampling was conducted using a modified Botanal method (Tothill *et al.* 1992), where five reference quadrats $(0.5 \times 0.5 \text{ m})$ were established in areas which covered the range of pasture growth present. Dry matter yield in the quadrats was then scored from 0 to 100 (no dry matter to the maximum present at that time) by visual estimation. Quadrats were left in place over the course of pasture sampling for reference. Twenty calibration quadrats were placed throughout the course of the day, scored from 0-100, dry-matter harvested to ground level, dried for three days in a forced draught oven and weighed. Actual yield was plotted against the visual score and a calibration curve constructed by utilizing the line of best fit from which yields could be calculated from the score determined visually in the field. Calibration curves were found to fit data well (R^2 >0.83). The botanical composition of each quadrat was visually estimated at the same time as yield, with the components of the pasture broken into three: a) the legume species sown, b) grasses, which were

largely dominated by Guinea grass (*Panicum maximum*) but also included a small amount of Sabi grass (*Urochloa mosambicensis*), and c) broadleaf weeds which included any broadleaf species other than the sown legume species (largely Snake Weed, *Stachytarpheta jamaicensis*). The yield of each component was estimated by multiplying the total yield for the quadrat by the fraction of each component present in the quadrat. Ten randomly placed quadrats were taken for each species beneath each tree density, in each replicate, for a total of 1280 quadrats (10 quadrats x 4 species x 8 densities x 4 replications). Pasture performance was recorded in August 2001, November 2001 and February 2002. Sampling prior to these dates was not undertaken as trees were not deemed to be large enough to exert a significant effect upon the production of forage. Trees were approximately 2-years-old when pasture sampling began.

5.3 Results

5.3.1 Shade levels

Shade levels beneath the eight different densities varied from low levels under the lowest tree densities through to very heavy shade in the centre of the wheel, under the greatest tree density (Table 5.1). At all sampling dates shade levels fell quickly as tree density decreased, but tended to vary little under lower densities (855, 543, 366 and 259 trees/ha).

Table 5.1 Shade levels at the mid point between trees of eight densities of *Khaya senegalensis*, grown in Townsville in a Nelder wheel arrangement at ages of 24, 27 and 30 months.

Tree density		Shade (%)	
(stems/ha)	August 2001	November 2001	February 2002
20541	95.4	82.4	87.4
10270	88.0	60.1	64.8
2282	46.6	32.9	38.4
1467	39.8	33.2	31.0
855	17.9	18.7	27.8
543	11.9	25.2	28.0
366	15.4	21.6	29.5
259	13.7	22.8	24.2

5.3.2 Soil moisture content

Soil moisture was found to increase with decreasing tree density at all depths at the August 2001 sampling, however, by November 2001 the opposite was found with higher soil moisture levels found under higher tree densities at 0-10 and 20-30 cm, while there appeared to be no clear pattern at 40-50 cm depth. Soil moisture levels were very high in February due to rainfall prior to sampling, with no trends apparent (Table 5.2).

Table 5.3 Moisture content (mean \pm SE) of soil from 0-10, 20-30 and 40-50 cm beneath eight densities of *Khaya senegalensis*, taken at three different dates (n = 3).

Tree density	August 2001			N	November 200	1	February 2002			
(stems/ha)	0-10 cm	20-30 cm	40-50 cm	0-10 cm	20-30 cm	40-50 cm	0-10 cm	20-30 cm	40-50 cm	
20541	5.6 ± 0.3	5.3 ± 0.1	5.0 ± 0.1	5.3 ± 0.4	4.9 ± 0.2	5.0 ± 0.2	20.0 ± 0.3	17.3 ± 0.1	17.3 ± 0.1	
10270	5.7 ± 0.2	5.6 ± 0.2	5.2 ± 0.2	5.5 ± 0.1	4.8 ± 0.1	4.7 ± 0.2	21.3 ± 0.2	16.8 ± 0.2	16.7 ± 0.2	
2282	6.3 ± 0.8	5.7 ± 0.2	5.7 ± 0.2	5.8 ± 0.2	4.7 ± 0.2	4.6 ± 0.2	22.3 ± 0.8	16.9 ± 0.2	17.3 ± 0.2	
1467	6.5 ± 0.6	6.9 ± 0.4	6.7 ± 0.3	4.4 ± 0.2	4.7 ± 0.9	4.4 ± 0.4	22.6 ± 0.6	18.6 ± 0.4	16.1 ± 0.3	
855	6.5 ± 0.4	6.7 ± 0.3	7.0 ± 0.5	3.9 ± 0.5	4.0 ± 0.7	5.1 ± 0.6	23.1 ± 0.4	18.4 ± 0.6	17.5 ± 0.5	
543	6.4 ± 1.1	6.7 ± 0.4	6.9 ± 0.4	4.2 ± 1.1	4.3 ± 0.3	4.9 ± 0.6	21.8 ± 1.1	17.9 ± 0.4	16.8 ± 0.4	
366	6.6 ± 0.9	6.8 ± 0.6	6.8 ± 0.6	4.5 ± 0.8	5.0 ± 0.2	4.2 ± 0.1	20.4 ± 0.9	19.4 ± 0.6	16.9 ± 0.6	
259	7.3 ± 1.2	7.0 ± 0.3	7.4 ± 0.7	3.6 ± 0.8	4.5 ± 0.6	4.6 ± 0.5	21.4 ± 1.2	18.9 ± 0.3	18.3 ± 0.7	

5.3.3 Pasture production and composition

August 2002

Total dry matter production

Dry matter production was strongly depressed by the higher densities of trees present in the centre of the wheel (Figure 5.1a), to the extent that no pasture growth was present under the highest tree density. Beneath 855, 1467, 2282 and 20541 trees/ha, sectors sown with *C. ternatea* and *C. brasilianum* tended to produce slightly greater levels of pasture growth than in sectors sown with *S. hamata* and *C. rotundifolia*. Under two of the three remaining lower tree densities (259 and 543 trees/ha), sectors sown with *C. rotundifolia* produced the greatest dry-matter yield, while under densities of greater than 855 trees/ha *C. rotundifolia* sectors were the lowest yielding.

Legume yield

The yield of each of the four legume species decreased very significantly as tree density increased, with the greatest yield given by *C. rotundifolia* under 259 trees/ha (388 kg/ha) and the lowest by all four species which failed to produce any dry matter under 20541 trees/ha (Figure 5.1b). Under the more open treatments (259, 366 and 543 trees/ha), *C. brasilianum* and *C. rotundifolia* produced the greatest amounts of dry matter, with *C. brasilianum* the best performing legume under 855, 1467 and 2282 trees/ha. *Clitoria ternatea* performed poorly compared to the other three species under 259, 366, 543, 855 and 1467 trees/ha, but had the greatest yield of any legume species beneath 10270 trees/ha. *Centrosema brasilianum* consistently produced the greatest or second greatest yields under all tree densities except 10270 trees/ha. Relative to other species, yields of *C. rotundifolia* decreased when grown beneath densities of 855 trees/ha or greater, but yielded well at lower tree densities.

Grass yield

The growth of grasses was also severely depressed by higher tree densities (Figure 5.1c), with the greatest quantities of grass found in sectors sown with *C. rotundifolia* and *S. hamata* at tree stocking rates of 259, 366, 543 and 855 stems per hectare. At lower tree stocking rates, the *S. hamata* treatment continued to have relatively high yields of grass but sectors sown with *C. ternatea* and *C. brasilianum* had higher relative grass yields. No grass growth was present under 20541 trees/ha. The production of dry matter by grasses was much greater than that of either legumes or broadleaf weeds.

Broadleaf weeds

The production of dry matter by broadleaf weeds followed the same general pattern as that of legumes and grasses, falling substantially with increasing tree density (Figure 5.1d), and failing to grow beneath 20541 trees/ha. The species of legume sown did not appear to have any effect upon the level of broadleaf weed growth, with no clear trends apparent. Sectors sown with *Clitoria ternatea* contained the greatest abundance of broadleaf weeds under tree densities of 543, 855 and 1467 trees/ha, with *S. hamata* having the greatest under 259, 366 and 855 trees/ha.

November 2002

Total dry matter production

Levels of dry matter production at the November 2001 sampling were slightly higher than found in August 2001. Beneath the lower tree densities (259, 366, 543 and 855 trees/ha), little difference was present between sectors sown with different legume species (Figure 5.2a). Greater amounts of dry matter were produced in sectors sown with *S. hamata* beneath 1467 and 2282 trees/ha, while substantially more dry matter was produced in *C. brasilianum* sectors under 10270 stems/ha. No plant growth was present under 20541 trees/ha.

Legume vield

Centrosema brasilianum was conspicuous in its production of approximately twice the dry matter of other species beneath 259 and 366 trees/ha (Figure 5.2b). It continued to produce the greatest amount of dry matter under 543, 855 and 1467 trees/ha, although the margin between it and remaining species was not as large. At all tree densities, except 366 and 10270 trees/ha, *S. hamata* was the

legume with the lowest yields. *Clitoria ternatea* had an unusually high yield beneath 2282 trees/ha, but aside from this was not greatly different from *C. rotundifolia* at most tree densities.

Grass yield

Grasses significantly comprised the greatest component of pasture yield across all legume treatments. A substantial drop in grass yield was present beneath 1467 trees/ha in all treatments. Yields remained low as tree density increased and very little or no grass was present under the highest tree densities. Grass production was not consistently higher in conjunction with any particular legume species across all tree densities.

Weed yield

The growth of broadleaf weeds was quite varied between sectors sown with different legume species, under the same tree densities. No species of sown legume consistently had higher quantities of broadleaf weeds than any other, however *C. brasilianum* contained substantially lower amounts of broadleaf weeds than other species under densities of 366, 543 and 855 trees/ha. Beneath the two highest tree densities, 10270 and 20541 trees/ha, production of dry matter by weeds was very low or entirely absent.

February 2002

Total dry matter production

Levels of dry matter production were much greater at the February 2002 sampling than at either of the two previous sampling dates, approaching twice that of previous yields in some cases (Figure 5.3a). Beneath tree densities up to and including 1467 trees/ha, the lowest yields of dry matter were found in sectors sown with *S. hamata*. No species of sown legume consistently produced a greater total dry matter yield than others. In contrast to previous samplings, a small amount of dry matter was produced beneath 20541 trees/ha in sectors sown with *C. ternatea* and *S. hamata*.

Legume yield

Yields of leguminous dry matter (Figure 5.3b) were also higher in February 2002 than at the two previous sampling dates. *Clitoria ternatea* produced the greatest yields of dry matter under all densities except 366 trees/ha. In some cases the margin between *C. ternatea* and the species with the second greatest yield was substantial (259, 543 and 855 trees/ha), however beneath higher tree densities differences were much smaller. *Stylosanthes hamata* tended to have slightly lower yields than other species over a range of tree densities although the differences were not striking. *Clitoria ternatea* and *S. hamata* actually produced a small amount of dry matter (15 and 5 kg/ha respectively) beneath 20541 trees/ha where previously no growth had occurred.

Grass yield

Grasses clearly produced the majority of pasture dry matter in all treatments (Figure 5.3c). Sectors containing *S. hamata* tended to have less grass growth than sectors sown with other species, while the highest yields of grass were not consistently found in any particular legume treatment. In contrast to previous sampling dates, there was a small yield (5 kg/ha) of grass under 20541 trees/ha in the *C. ternatea* treatment, where previously no grass growth had occurred.

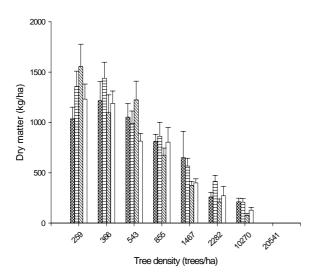
Weed yield

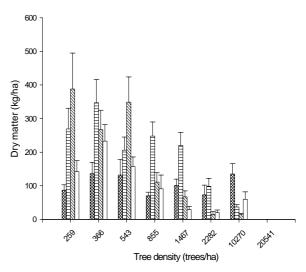
The greatest growth of the weed component was present in sectors sown with *C. ternatea* under 3 of the eight tree densities (259, 366 and 2282 trees/ha). Under higher tree densities (2282 and 10270 trees/ha) sectors sown with *C. rotundifolia* contained approximately twice the amount of broadleaf weeds present in other sectors.

Figure 5.1 Total yield and yields of legume, grass and broadleaf weed components of forage growth sampled in August 2001 beneath eight densities of *Khaya senegalensis*. Error bars represent the standard error of the mean.

a) Total yield

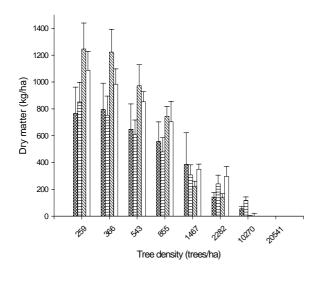
b) Legume component yield

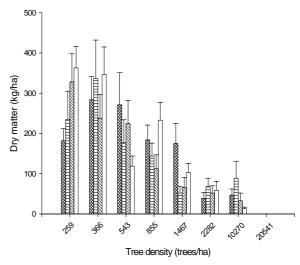




c) Grass component yield

d) Weed component yield

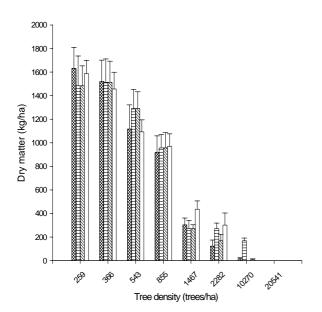




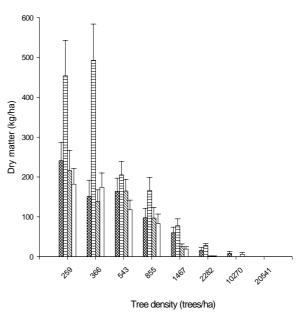
C. ternatea
C. brasilianum
C. rotundifolia
S. hamata

Figure 5.2 Total yield and yields of legume, grass and broadleaf weed components of forage growth sampled in November 2001 beneath eight densities of *Khaya senegalensis*. Error bars represent the standard error of the mean.



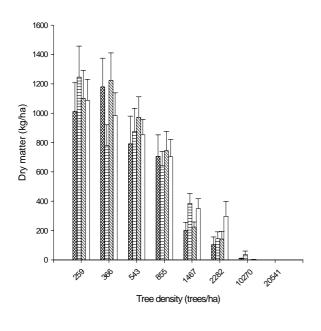


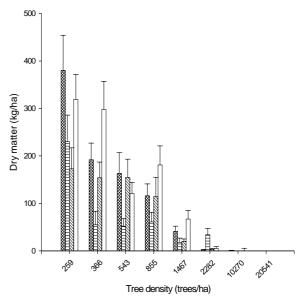
b) Legume component yield



c) Grass component yield

d) Weed component yield





XXXX C. ternatea

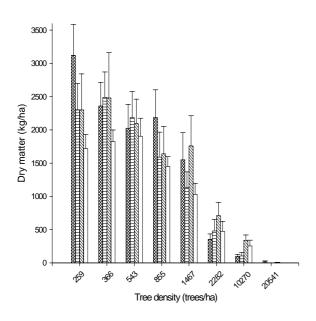
C. brasilianum

C. rotundifolia

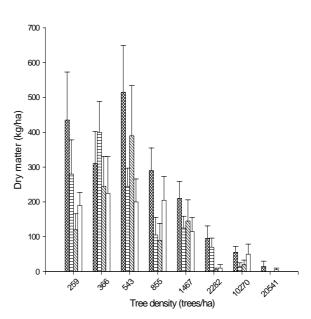
S. hamata

Figure 5.3 Total yield and yields of legume, grass and broadleaf weed components of forage growth sampled in February 2002 beneath eight densities of *Khaya senegalensis*. Error bars represent the standard error of the mean.

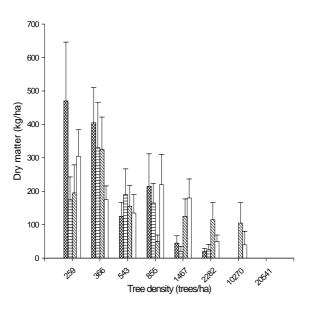
a) Total yield



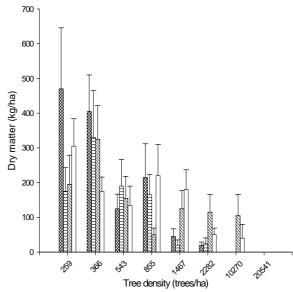
b) Legume component yield



c) Grass component yield



d) Weed component yield



- C. ternatea
- C. brasilianum
- C. rotundifolia
 - ☐ S. hamata

5.4 Discussion

5.4.1 Shade levels

Shade levels were very heavy beneath the higher tree densities (20541 and 10270 trees/ha) in August 2001, however in the subsequent November and February recordings the levels of shade were found to have decreased. These results initially appear to contrast with what would be expected, as it is well known that light levels decrease as a plantation ages, influenced by tree species, age density and planting arrangement. Shade levels tend to be highest in closely spaced plantations and lowest in young or old, widely spaced plantations (Chen 1989; Payne 1985; Santhirasegaram 1966). The increase in the height of the trees in the time between the first and subsequent measurements may have allowed an increase in the amount of diffuse light reaching the understorey layer. Such decreases in shade have been recorded in the past under ageing tree plantations, particularly oil palm and coconut plantations (Nelliat et al. 1974; Reynolds 1995; Wilson & Ludlow 1991), as older taller plantations allow greater levels of diffuse light to penetrate. Diffuse light has a greater ability to penetrate than direct light as it emanates from the whole sky, rather than the point source of the sun (Wilson & Ludlow 1991). Shade levels beneath the densities of 855, 543, 366 and 259 trees/ha increased over the three sampling dates with the increase attributed to tree and canopy growth, but despite the increases in shading the shade level beneath these tree densities would still only be described as "light".

5.4.2 Soil moisture content

The soil moisture contents recorded in August 2001 were found to increase as tree density declined. However the amount of soil moisture present in the soil did not change as depth increased. Moisture levels were generally lower in November, while in February 2002 very high levels of soil moisture were found due to very heavy rainfall several days prior to sampling (in excess of 500 mm).

The lower levels of soil moisture found under the higher tree densities during August 2001 can be attributed to the density of trees increasing water use from the soil. The understorey pasture was clearly not causing the decrease in soil moisture at higher tree densities as the amount of pasture was greatly reduced and entirely absent under 20541 trees/ha, where soil moisture was lowest at all three depths. If pasture was having a greater effect upon soil moisture than tree density then lower soil moisture contents would have been expected under low tree densities where pasture growth was greatest. However, by November 2001 the opposite was found to have occurred within the top 10 cm of the soil, where higher levels of soil moisture were present under the higher tree densities. No clear trend was apparent at depths of 20-30 cm or 40-50 cm. The results suggest that, although trees and pasture had continued using water from the soil, as indicated by the lower soil moisture contents at depths of 20-30 cm and 40-50 cm compared to August, light rainfall received prior to sampling may have been sufficient to increase the moisture content of the top 10 cm of soil.

It is likely that the differences between soils at different tree densities are due to the shade provided by more closely spaced trees reducing the evaporation of moisture, compared to the more open, lower tree densities that would have received a greater amount of direct sunlight. The rainfall received was not heavy enough to have penetrated to 20-30 cm or more, as indicated by lower soil moisture contents at these depths in comparison to those of the August sampling. The only information available from the February 2002 sampling was that the water received in rainfall several days prior to samples being taken had penetrated to a depth of at least 50 cm as indicated by the very high soil moisture content, but in the process it also erased any differences between tree densities.

The importance of competition for soil moisture between trees and pasture has been raised in the past, particularly in areas with prolonged dry seasons. Dijkman (1951) demonstrated the difference between dry season soil moisture contents under clean weeded rubber plantations and rubber with a cover crop. It was also found, in Sri Lanka, that a cover crop of *Centrosema pubescens* under mature

coconuts caused a sharp decline in yield, which was alleviated by ploughing the cover crop into the soil during the dry season (Salgado 1937). In a study of tree rooting systems in a similar Nelder wheel experiment, Eastham & Rose (1990) concluded that the presence of trees reduced pasture root length densities, possibly decreasing their ability to compete with trees for resources. It was also found that competition between trees at higher densities caused tree roots to be denser and to grow to greater depths than those of trees at lower densities.

5.4.3 Total dry matter yield

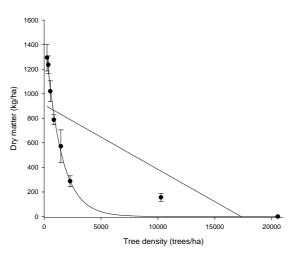
The decrease in overall dry matter production was readily apparent, as tree density increased. The primary cause of this is likely to have been the increasing levels of shading under the higher tree densities. Decreased soil moisture may also have had an impact upon the growth of understorey vegetation, recorded in the August sampling, due to increased competition for soil moisture under higher tree densities. What is not evident in Figures 5.1 –5.3 is the nature of this relationship between tree density and pasture growth. When a linear line of best fit is used to describe dry matter production (Figure 5.4 a-c), it can be seen that it does not provide a good fit (low R² values, see Table 5.3). However when an exponential line of best fit is used then R² values were increased substantially. Hence the production of dry matter decreased exponentially as tree density increased. Similar relationships between tree density and understory production have been found in the past. Gaines et al. (1954) found a curvi-linear relationship between herbage production and basal area of the tree stand, while Beal (1973) found that herbage yield was inversely related to tree density. Cameron et al. (1989) found that a pasture dominated by Setaria sphacelata, under a Nelder wheel of Eucalyptus grandis, did not have its growth significantly decreased under tree densities of less than 158 trees/ha, while under the higher tree densities pasture growth declined to almost nothing and availability of soil water was identified as a major constraint to growth.

Table 5.3 R-squared values of linear and exponential lines of best fit, applied to total dry matter production (kg/ha) under eight densities of *Khaya senegalensis* on three dates.

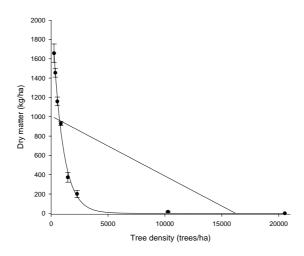
Sampling date	Correlation coefficient (R ²)	
	Linear	Exponential
August 2001	0.5934	0.9822
November 2001	0.4656	0.9958
February 2002	0.6471	0.9828

Figure 5.4 Average total dry matter production of forage beneath eight densities of *Khaya senegalensis* on three dates. Error bars depict the standard error of the mean.

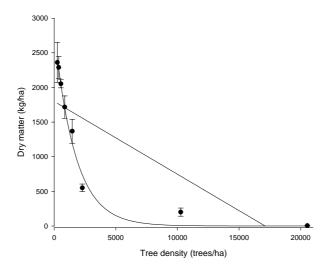
a) August 2001



b) November 2001



c) February 2002



5.4.4 Legume yield

The yield of the legume component of the pasture decreased substantially with increasing tree density. In August 2001 *Clitoria ternatea* generally gave the lowest yields of dry matter of the four legume species. This is suspected to be due to the slashing of the site three months prior to the sampling date. *C. ternatea* is susceptible to frequent low cutting, due to the location of its growing points at the ends of main branches, and its growth is limited by lack of moisture in the seasonally dry tropics, and it will shed its leaves in response to these (Staples 1992a). Hence, it is thought that the low yields of *C. ternatea* are due to the combination of cutting at the beginning of the dry season and the shedding of leaves and cessation of growth that accompanies water stress in the species. However its yields did improve in relation to that of other species under tree densities greater than 2282 trees/ha. *Chamaecrista rotundifolia* and *Centrosema brasilianum* yielded particularly well under lower tree densities and the reason for this is thought to be the low-lying habit of both species. The prostrate growth habit of *C. rotundifolia* allowed much of the individual plants to avoid the slashing. *Centrosema brasilianum* has a climbing/twining habit, however much of the plant avoided slashing due to its growing along the ground as a result of low levels of strata for plants to climb.

Yields of *C. ternatea* were greater during November 2001 than in the previous harvest and were not as low as other species. An unusually high yield was found beneath 10270 trees/ha in August and 2282 trees/ha in November. This suggests favorable conditions for *C. ternatea* that may be moving "outwards" from the high tree densities to lower densities as time progressed. Such a phenomenon has been reported in pasture in relation to pasture height by (Cameron *et al.* 1989), who described it as a ripple effect which peaked at 3580 trees/ha after 1.0 years and at 305 trees/ha after 4.0 years, and a similar effect with mean tree biomass. By February 2002 *C. ternatea* was consistently the greatest yielding legume with yields peaking under 543 trees/ha and producing a small amount of dry matter under 20541 trees/ha where previously no growth had occurred. The good performance of *C. ternatea* under all tree densities, once substantial rainfall was received, suggests either shade tolerance or shade adaptation in the species, and hence a potential for use in silvo-pastoral systems.

Centrosema brasilianum performed well at the August sampling, with particularly high yields in relation to other legume species under 1467 and 855 trees/ha. It is likely that *C. brasilianum* performed better than the other climbing species, *C. ternatea*, at this date due to many of the plants scrambling along the ground and a patchy distribution of other vegetation to act as a substrate for climbing which allowed greater amounts of the species to avoid defoliation than *C. ternatea* in the previous slashing. By November 2001 *C. brasilianum* was easily the best performing species at 254 and 366 trees/ha, and at 543, 855 and 1467 trees/ha although the margin was not as great. By February 2002 *C. brasilianum* was giving mixed results in relation to other species and no clear picture of the species performance could be formed.

The performance of *Chamaecrista rotundifolia* was good under 259 and 366 trees/ha at the August sampling, but it did not perform noticeably better than any other species of legume under remaining tree densities. *C. rotundifolia* was likely to have an advantage over the other three species after defoliation due to its very prostrate growth habit allowing much of the plant to escape defoliation. At the November sampling it had an average performance in relation to other species, however at the February 2002 sampling it was often the poorest yielding legume species (259, 855 and 2282 trees/ha). Due to the rapid growth of forage during this period, *C. rotundifolia* may have been at a disadvantage due to its prostrate habit and been unable to compete with the Guinea grass and broadleaf weeds for light in the same manner as the more erect *S. hamata* or the two climbing species, *C. ternatea* and *C. brasilianum*.

Stylosanthes hamata was generally the poorest performing of the legume species examined. Under no tree density, at any date, did S. hamata out-perform all three other legume species and it was often the poorest yielding species (approximately one-third of the time), although no firm conclusions regarding its suitability could be drawn. At the August sampling it performed better than C. ternatea at tree densities equal to or less than 855 trees/ha, due to the reasons previously mentioned regarding

C. ternatea, and due to S. hamata's semi-erect growth habit and its ready tolerance of heavy grazing (Skerman et al. 1988). Performance of S. hamata in the following periods was varied in relation to other species and no firm conclusion regarding its performance could be formed, however it was found that several plants were growing beneath 20541 trees/ha, with C. ternatea the only other species to do this.

5.4.5 Grass yield

Grasses were clearly the dominant component of the pasture, with Guinea grass (*Panicum maximum*) composing the vast majority of grass biomass, with yields declining markedly with increasing tree density. At the August sampling the greatest yield of grass was found in the *C. rotundifolia* and *S. hamata* legume treatments at tree densities of 855 trees/ha or less. The fact that the higher yields were found within sectors treated with prostrate or semi-erect legume species (*S. hamata* and *C. rotundifolia*), and not in either of the climbing/twining species (*C. ternatea* and *C. brasilianum*), suggests the growth habit of accompanying legume species had an influence upon grass performance. The greater yields of grass present in February 2002 were a result of the rainfall received during the previous three months. It would be expected that the upright growth habit of the grass would have tended to overtop the lower growing legume species *S. hamata* and *C. rotundifolia* in particular, while the climbing species were able to use the grass as a substrate for growth. The production of useful quantities of dry matter by the grass component, under tree densities of up to 2882 trees/ha, suggests that Guinea grass is potentially useful in agroforestry situations where there is adequate moisture.

5.4.5 Weed yield

The yield of broadleaf weeds decreased with increasing tree density. Only at the November sampling could a clear effect of sown legume species be seen on the abundance of weeds. Sectors sown with *C. brasilianum* contained noticeably lower amounts of weed dry matter than other species of sown legume at densities of 366, 543 855 and 1467 trees/ha. This decrease in weed dry matter production may be due to increased growth of *C. brasilianum*, which was found to yield greater amounts of dry matter than other legume species at the same tree densities. This suggests that the decrease in weed growth was a result of increased growth and competition from *C. brasilianum*, however if this were the case it would be expected that grass yields would also have been depressed, which was not found.

Chapter 6 - Research Outcomes.

6.1 Conclusions from the shade-house trials

In general shading was found to influence many of the factors measured, although some of these were not affected consistently across all species.

- Increasing shade lead to a decrease in the production of above and below-ground plant matter although the extent of this decrease varied substantially between species. Several species still produced more than 60% of maximum yields under 76% shade.
- Root nodulation decreased with shading, and hence shade may decrease the amount of N₂ fixation by legumes. The decrease in nodulation may have been due to more than one factor, such as lower N demand by plants under shade and/or a better supply of soil N available to plants through higher soil moisture and lower soil temperatures under shaded treatments. However the addition of fertiliser to pots is likely to have influenced the results.
- Concentrations of leaf N were found to increase with shading, possibly due to the same reasons as given for decreased nodulation.
- Changes in concentrations of leaf P in response to shade were irregular between species, with both increases and decreases found in plants grown under shade.
- The length of time until the production of the first flower was generally longer in plants grown beneath shade, suggesting that shading prolongs vegetative growth.
- Production of seed was greatly diminished under shade, however the weights of seeds produced were not less than those under the control treatment.
- Amounts of readily germinable seed were greater in some species when seed was produced under the shade treatments compared to the control. Similarly, levels of hard seed were reduced in some species when grown under shade. Levels of non-viable seed were not affected by shading. Time to 50% germination was significantly faster in several species when seed was grown under the shade treatments. All these factors suggest that some species may have their ability to persist decreased by shading, through its effects upon lowering seed production, lower levels of hard seed and increasing the fraction of seed germinating after wetting.
- Shoot:root ratio increased under shade, with the shoot system fraction increasing at the expense of the root system. Such increases in the shoot:root ratio could potentially lead to problems with water stress, recovery after defoliation and uprooting by stock.

The species Arachis pintoi, Desmodium heterophyllum, D. intortum and D. uncinatum are recommended for use under shaded conditions in wet tropical regions due to their shade tolerance and good production of dry matter under both control and shaded conditions, and also due to their prostrate or trailing/scrambling habit. Species recommended for wet/dry tropical areas include Macroptilium lathyroides and A. stenosperma. Other species which have good shade-tolerance, but have other issues that may have implications upon their suitability, are Centrosema macrocarpum, C. pubescens, C. acutifolium, Calopogonium mucunoides, Pueraria phaseoloides, and Neonotonia wightii (wet tropics), M. atropurpureum, Clitoria ternatea and Centrosema brasilianum (wet/dry tropics). These species all have a climbing habit, some being particularly vigorous (C. mucunoides, N. wightii and P. phaseoloides). Such climbing species have the potential to smother young or small trees and should not be sown beneath a plantation unless the landowner is prepared to put extra management into controlling climbing species, such as through careful management of grazing regime. The second issue with climbing species is that of persistence, with climbing/twining species not being as tolerant of defoliation (C. ternatea in particular) as species with a prostrate habit. Appropriate grazing strategies would need to be implemented in order to avoid the decline or loss of the legume component of the pasture. The species of legume planted beneath a timber plantation should also take into account other factors such as soil pH and drainage.

Further research is required in order to continue assessing the potential of new species, particularly those suited to the wet/dry tropical regions. Long-term field trials are required in order to more

accurately assess the performance of species, particularly the effects of defoliation, performance of stock in agroforestry systems utilising these species, compatibility with shade tolerant grasses and long-term persistence.

6.2 Conclusions from the field trials

Arachis pintoi and Stylosanthes guianensis showed the greatest promise of 6 non-climbing legume accessions assessed in a field trial under a 5-year-old mixed species plantation at Babinda, in the wet tropics. They were the only species showing significant ground cover and biomass 22 months after establishment.

Field trials of species likely to be suited for the seasonally dry tropics were conducted under a 12-year-old African Mahogany (*Khaya senegalensis*) plantation near Clare, and under young plantings (<3 y) of *Khaya* in Townsville. *Clitoria ternatea* and *Centrosema brasilianum* performed best, however legume growth beneath trees was depressed compared to growth in more open conditions.

From the trial under the Nelder Wheel in Townsville, it was concluded that forage production decreased exponentially with increasing tree density, with no growth present under 20541 trees/ha, except for a very small amount at the February sampling. Shade levels were found to be very heavy beneath higher tree densities, but decreased slightly as densities declined, to stabilize around 855 trees/ha or less.

Soil moisture was also found to be less at higher tree densities during the August sampling as a result of competition between trees. Measurements at the November sampling indicated that the small amount of rainfall received in the period between samplings had not infiltrated beyond the top 10 cm, while soil moisture levels decreased further at greater depths. Increased levels of soil moisture in the top 10 cm at this point were likely due to shade provided by trees decreasing evaporation from the soil and transpiration rates of understorey plants. No conclusions could be formed regarding soil moisture at the February sampling due to any differences being erased due to heavy rainfall prior to sampling.

Clitoria ternatea was the best performing legume at the February sampling when conditions for growth where favorable, however, issues connected with response to grazing or mowing may reduce its potential usefulness. Centrosema brasilianum proved to be the best species for use during the early period of the growing season (November), but both C. ternatea and C. brasilianum have climbing habits and may pose problems to young or small trees. Chamaecrista rotundifolia was most suited to conditions where slashing was frequent and, as such, may prove useful in plantations that are frequently defoliated (slashing or grazing), or where understorey growth is kept low. Stylosanthes hamata appears to be the least suited of the species for use under tree plantations, while C. ternatea and C. brasilianum are the most promising.

Grass was the dominant component of the pasture and the production of dry matter under tree densities up to and including 10270 trees/ha indicates that the dominant grass species *Panicum maximum* has the potential for use beneath trees, with other grass species, such as *Urochloa mosambicensis*, contributing very small amounts of dry matter and only present under lower tree densities.

Weed growth was also decreased by higher tree densities, and dominance by weedy species was not found beneath the heavier shade levels suggesting that Snake Weed (*Stachytarpheta jamaicensis*) is unlikely to become a serious problem under shaded conditions.

The differences between yields and legume performance between sampling dates indicates the dynamic nature of pasture beneath trees in the seasonally dry tropics and the importance of sampling date to detect changes in pasture growth, particularly in the transitional periods of the seasonally dry tropics. As a result of continued changes in performance relative to legume treatment, tree density

and time of year, results obtained here indicate the need for long-term trials with more intensive monitoring of pasture performance in order to obtain a clearer picture of legume and pasture performance beneath trees over time.

6.3 Further research

This study has identified 16 species of pasture legume that show promise for use under trees in farm forestry situations. However many of the species identified as shade tolerant or being relatively productive under shaded conditions have a climbing/twining habit that can cause concern in tree plantations, particularly in respect to potential smothering of small trees. When the climbing species are removed the remaining species recommended for the wet tropics are *D. intortum*, *A. pintoi*, *D. ovalifolium*, *D. canum*, *D. heterophyllum* and *D. uncinatum*, while *A. stenosperma* shows potential for the seasonally dry tropics. However climbing species may still potentially be used beneath older plantations or where a higher level of pasture management is acceptable in order to help prevent smothering of trees through controlling the frequency and intensity of grazing.

Further research should examine the possibility of controlling climbing legumes in tree plantations through grazing management, in order to broaden the range of legume species available for use. Research is also required to examine the longer-term persistence and productivity of the species identified in this study as tree plantations age and shade levels increase. Compatibility with shade tolerant grasses is an important aspect of pasture production beneath tree plantations, which has seen relatively little research and will have an important effect upon the persistence and productivity of both the grass and legume components of the pasture.

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