Shade tolerance of tropical forage legumes for use in agroforestry systems

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Abstract

The benefits of raising livestock in conjunction with tree plantations include the better use of land resources, an increased and diversified income, soil stabilisation and the potential for higher plantation yields through better weed control, nutrient cycling and nitrogen accretion. However, the significant acceptance of tree-pasture (silvopastoral) systems has been impeded by the belief that productive pasture cannot be maintained under tree canopies.

The aims of this project were to identify forage legume species suitable for use in silvopastoral systems in order to improve pasture quality under differing rainfall regimes in the tropics. A total of 35 species and cultivars of tropical pasture legumes were tested for shade tolerance beneath four levels of shade under shadehouse conditions, with a range of agronomic and ecophysiological parameters measured, including biomass production, root:shoot ratio, root nodulation, foliar nutrient content, time to flowering, seed production and light response curves.

Production of both above and below-ground biomass was strongly depressed by shading, although the extent of this varied between species. Many of the most promising species yielded well under both the control and the shaded treatments, indicating that they may be suitable for use in both younger, less shaded plantations and older, heavily shaded plantations. Concentrations of leaf N were affected by shading with increased N found under shade treatments compared to the control. There were no similar effects on leaf P concentrations. Root nodulation was strongly affected by shading and was greatly reduced or entirely absent under shaded treatments, suggesting that fixation of atmospheric nitrogen may be lower under shade than in the open. Shading prolonged the vegetative growth in many species, delaying flowering and greatly reducing seed production, although the size of individual seeds was maintained at the expense of seed numbers. An increase in the fraction of readily germinable seed and a decrease in the fraction of hard seed were found in several species when the seed was produced under shade under shade. Light curves were not always correlated, with the production of dry matter with several species that appear shade-tolerant from dry matter production producing light response curves suggesting otherwise.

Field trials were conducted in both the wet and seasonally dry tropics to examine the growth of selected legume species under timber plantations that were already established for a number of years, and under a relatively young Nelder wheel plantation of African Mahogany (*Khaya senegalensis*). Field trials, particularly the Nelder wheel trial, demonstrated the dynamic nature of pasture growth, particularly in the seasonally dry tropics, and the need for continuous monitoring of such trials to form a more complete picture. *Arachis pintoi* was clearly the best performing species unde a five-year-old mixed rainforest species/*Eucalyptus pellita* plantation in the wet tropics. In the seasonally dry tropics *Clitoria ternatea* and *Centrosema brasilianum* proved to be the best performing cultivars beneath both a conventional, 12-year-old African Mahogany stand and the Nelder wheel, with pasture production depressed by increasing tree densities. Pasture production was found to decrease exponentially with increasing tree density in the Nelder wheel plantation. Both *Clitoria ternatea* and *Centrosema brasilianum* were observed to climb trees during the trial, indicating the potential of vigorous climbing species to smother young or small trees. Soil moisture content was also found to decrease as tree density increased, suggesting that in the seasonally dry tropics light may not always be the limiting factor for growth.

Sixteen species were identified which are potentially useful, shade tolerant or shade adapted, pasture species for use beneath tree plantations in both the wet and the seasonally dry tropics. The most promising species suited to the wet tropics were *Arachis pintoi, Centrosema acutifolium, C. macrocarpum, C. pubescens, Calopogonium mucunoides, Desmodium intortum, D. ovalifolium, D. canum, D. heterophyllum, D. uncinatum* and *Pueraria phaseoloides.* The most promising species suited to the seasonally dry tropics were *Arachis stenosperma, Centrosema brasilianum, Clitoria ternatea, Macroptilium atropurpureum* and *M. lathyroides.*

Many of the species identified as being shade tolerant, or relatively productive under shade have a climbing habit which can cause concern due to the potential smothering of young or small trees. When climbing species are removed the remaining species suited to the wet tropics are *A. pintoi, D. canum, D. heterophyllum, D. intortum* and *D. ovalifolium,* and those to the seasonally dry tropics are *A. stenosperma* and *M. lathyroides*. However climbing species may still be of use beneath older plantations or

where a higher level of pasture management is acceptable to prevent the smothering of trees through a greater control of the intensity and frequency of grazing or cutting.

Additional research is required to examine the long-term persistence and performance of the species identified in this study as plantations age and shade levels increase. The compatibility of suitable legume species with shade tolerant grasses is an important aspect, which will affect the production and persistence of the legume species, that has seen relatively little research in the past.

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STATEMENT OF SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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1 - Introduction

1.1 Pre-amble

Following the closure of rainforests to logging with the declaration of the Wet Tropics of Queensland World Heritage Area in 1988, an increased interest in establishing timber plantations upon private land has emerged. Russell *et al.* (1993) identified an urgent need to increase high quality timber production on a global scale, owing to the shrinking natural supply of these timbers. The greatest potential within Australia for increasing timber production was noted by Cameron *et al.* (1989a) as being in the private sector, using agroforestry systems on farms. The International Council for Research into Agroforestry in Nairobi, Kenya, defines agroforestry as: “a land use that involves the deliberate retention, introduction or mixture of trees or other woody perennials in crop/animal production fields to benefit from the resultant ecological and economic interactions”. One aspect deterring private landowners from establishing timber plantations is the large amount of time, approximately 20 years or more, before any substantial returns are realized from the land. In many developing countries landowners have traditionally grazed livestock beneath tree plantations, in order to derive a second, short-term, return from the land. Grazing in such countries has typically focused on cattle grazing beneath oil palm, coconut and rubber plantations (Ismail and Thai 1994; Kaligis *et al.* 1994a; Stur *et al.* 1994). Combining tree plantations and grazing in a silvo-pastoral system can present a sustainable method of land use, offering short-term returns in addition to a range of potential benefits to the landowner.

1.2 Potential advantages and disadvantages of silvo-pastoral systems

A range of potential benefits and drawbacks of grazing stock in tree plantations have been identified, with potential benefits including:

1. increased space utilization, both above and below ground;
2. improved soil chemical, physical and biological characteristics with a reduction in the use of chemical fertilizers and improved infiltration of rainfall;
3. higher total biomass production than in a monoculture;
4. a reduction in microclimate extremes;

5. reduced soil erosion due to the presence of trees and improved under-story ground cover;
6. an increased and diversified income;
7. labour requirements may be more evenly distributed throughout the year and there is some potential to increase machinery use;
8. a wider range of products can be harvested from one piece of land;
9. the use of legumes may lead to increased soil fertility and
10. provision of shelter for stock beneath trees (shade, wind shelter etc.).

However along with potential benefits a range of detrimental effects have also been noted to arise in agroforestry systems. Such effects may include:

1. an increased competition for water, light and/or nutrients between the tree and pasture/crop components of the system leading to decrease in yield of one or both components;
2. damage to trees from equipment and livestock;
3. allelopathic effects;
4. provision of habitat for pests, especially birds, in tree-crop systems;
5. a reduced flexibility of land use due to the presence of trees;
6. an additional labor requirement for tree management;
7. potential weed problems through the spread of tree seed into adjacent crops or pastures;
8. agroforestry systems which offer significant financial gains directly from the tree component will largely be restricted to the better watered coastal areas and
9. gains in semi-arid regions are most likely to be secondary to wood production through improving animal health, survival, production and the control of erosion or salinity control.

(Cameron *et al.* 1991; Cheva-Isarakul 1991; Humphreys 1994).

1.3 Effects of trees on the below canopy environment

Essential to the success of any silvo-pastoral system is an understanding of the various environmental interactions, involved most notably the effect of trees upon the below canopy environment. Factors influencing these interactions between the tree and crop components include tree spacing, orientation, shade levels, shade tolerance of forage species, nitrogen economy, nutritive value of pasture species and competition between trees and pasture for resources.

1.3.1 Light

As plantation trees do not intercept all incoming light, there exists the potential for growth of other vegetation beneath the canopy. The degree of light interception by tree canopies varies widely, influenced by a wide range of factors that include tree species, plantation age, planting pattern, orientation and time of year. In open *Eucalypt* woodland light transmission was found to be up to 78% (Begg and Cunningham 1974), while beneath rubber plantations transmission may fall below 10% (Wilson and Ludlow 1991).

Smith (1982) divides radiation beneath canopies into two components; unfiltered solar radiation, both direct and diffuse that has passed through the vegetation, and filtered radiation which has been attenuated by the processes of absorption, reflection and scattering.

Light quantity

The level of light found beneath plantations is the single most significant factor influencing the production of pasture beneath tree plantations (Shelton *et al.* 1987). There is extensive literature on the distribution of radiation in plant communities and the effect of trees on light interception and the light environment in plantations. The production of dry matter has been found to be closely linked with light interception and differences between systems have been correlated with differences in light interception (Ludlow 1978; Smith and Whiteman 1983; Palmer 1993). When the canopy of one species overtops that of another, the taller canopy is likely to intercept the greater share of the light (Reynolds 1988). The amount of light beneath a tree canopy is influenced by two factors; the amount of light falling on the canopy and the canopy’s absorption of that light. The absorption of light by dust, water vapor, ozone and CO_2 in the atmosphere will affect the amount of light falling upon the canopy (Durr 1997). In addition to absorbing light as it travels through the atmosphere, dust and water vapor also have an important effect through Mie scattering, transforming direct light into diffuse skylight (Durr 1997). This diffuse skylight can be of great importance in the equatorial tropics under overcast conditions when all light reaching the tree canopy is diffuse. Such light arises from the whole sky, not just the point source of the sun, and has better penetration than direct light (Wilson and Ludlow 1991).

Light falling upon leaves in the canopy may either be reflected from the leaf surface or pass through with a variable amount of its energy absorbed by photosynthetic pigments (Woolley, 1971 cited by Amar 1991). Penetration of radiation is extremely variable in time and space due to variation in tree species, size and density, the movement of foliage, clouds and sun (Begg and Cunningham 1974). Sunflecks are an important component of both direct and diffuse light that has passed through the canopy relatively unattenuated by foliage. Sunflecks composed of direct light have been noted to be of particular importance to the growth and survival of understorey plants in rainforests, while sunflecks composed of diffuse light are important as they can enter gaps from any direction of the sky (Fitter and Hay 1981). The level of light transmission by a canopy is not uniform through time and space, as the transmission of light varies diurnally and spatially within plantations. Spatial variation typically results in lower light levels at the tree base increasing with distance to a maximum at the mid point between trees. An example of this phenomenon is given by Wilson and Ludlow (1991) who measured light transmission under a 5.5 year-old oil palm plantation measured at midday with values ranging from 73% in the middle of the interrow to 2.5% at the base of the tree stem. When all values were integrated, a result of 47% of the light transmission was obtained. Diurnal variation arises as the sun traverses the sky changing the location of sunflecks and shadows cast by trees. An example of diurnal variation of light levels is shown in Figure 1.1 where measurements were taken from the mid point between tree rows (2282 stems/ha) and in the open every 5 minutes from 5 am until after dark.

Light quality

The spectral quality of light beneath canopies is altered, particularly the proportions of red (*c.* 660 nm) and far-red (*c.* 730 nm) light, with leaves preferentially absorbing light in the 400 – 700 nm wave band (Smith 1982). There is usually a small peak in the green, and a large peak in the far-red wavelengths as far-red light is reflected from foliar surfaces with greater efficiency than shorter wavelength radiation (Smith 1982). Typically the red:far-red ratio (R:FR) of full sunlight is approximately 1:1.2 while under old coconut plantations and mature rainforest it may fall to levels as low as 1:1.03 and 1:0.43 respectively (Wilson and Ludlow 1991). These changes are perceived by plants through the phytochrome system and may induce morphological changes (Wilson and Ludlow 1991). Such changes can include decreased tillering of grasses (Deregibus *et al.* 1985), increased stem elongation and possible reductions in germination of light sensitive seeds (Humphreys 1994). Smith (1982) indicates that shade-intolerant species may display greater stem elongation than shade-tolerant species in response to a reduced R:FR ratio.

Adaptation to high and low light levels

All plants have the capability to acclimate to shaded environments to a greater or lesser extent (Lambers *et al.* 1998). Plants have traditionally been divided into sun and shade species with respect to their adaptations to high and low levels of light. Plants occupying sunny habitats (sun plants) are generally capable of higher photosynthetic rates at higher quantum flux densities than plants restricted to shaded locations (shade plants) (Lange *et al.* 1981). Generally, early succession species and species from high light environments are sun plants, while late succession and sub-canopy species tend to be shade plants (Nilsen and Orcutt 1996). Plants may display a range of adaptations to their light environment and though the level of irradiance affects all aspects of plant structure, those of leaf structure and plant architecture are the most studied (Nilsen and Orcutt 1996). Plant species adapted to high light levels, generally, have thicker and smaller leaves, with thicker cuticles thanthose adapted to shady environments (Boardman 1977; Nilsen and Orcutt 1996; Lambers *et al.* 1998).

Physiological differences are also present between sun and shade plants with sun leaves having higher light-saturated rates of photosynthesis, compensation points, light saturation points, dark respiration rates, photorespiration rates and transpiration rates than shade leaves. Shade leaves in turn tend to have higher quantum yields and a greater likelihood of photoinhibition than sun leaves (Nilsen and Orcutt 1996). There are many other adaptations that plants may display according to light environment that will not be discussed, but are listed in Table 1.1.

Figure 1.1 Photosynthetic photon flux densities (PPFD) levels in the open and beneath 2282 stems/ha of *Khaya senegalensis*, recorded every 5 minutes from 5 am until after dark, February 2001 (Addison, unpublished data).

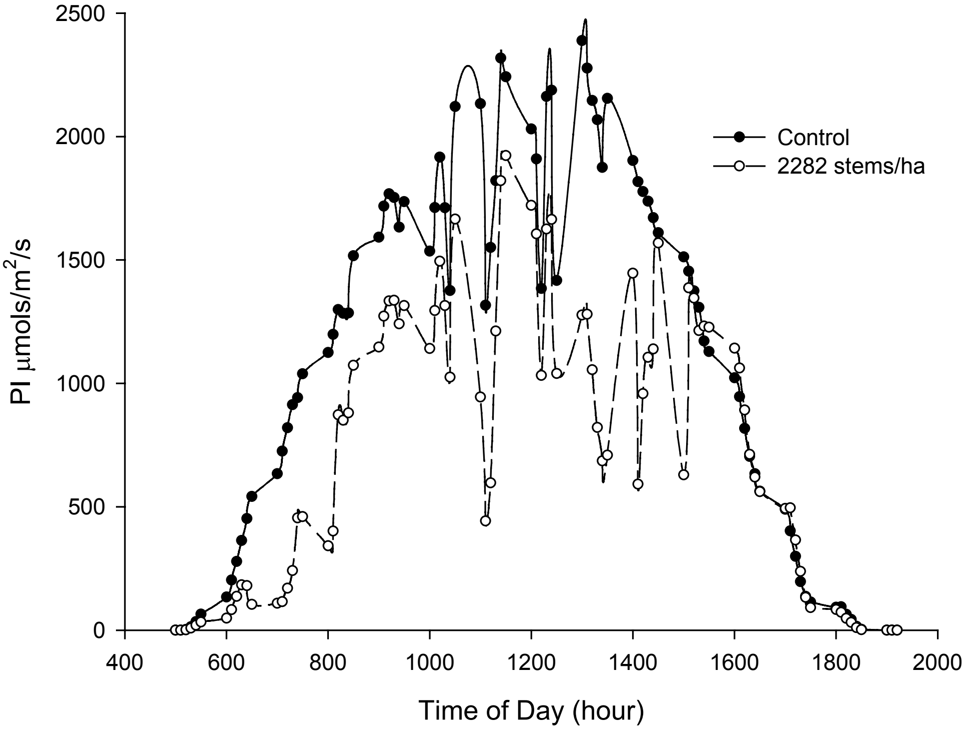

Table 1.1 General differences between leaves of plants adapted to high and low light intensities. Taken from Boardman (1977), Nilsen and Orcutt (1996) and Atwell (1999).

Characteristic	High light (Sun leaf)	Low light (Shade leaf)
Morphological features		
Leaf area	-	+
Leaf thickness	+	-
Cell abundance	+	-
Cuticle thickness	+	-
Leaf area ratio	-	+
Root/shoot ratio	+	-
Density of stomata	+	-
Specific leaf weight	+	-
Cell ultrastructure features		
Cell size	-	+
Cell wall thickness	+	-
Chloroplast frequency	+	-
Chloroplast orientation	Vertical	Horizontal
Proportion of stacked membrane	-	+
Starch grains in chloroplasts	+	-
Chemical features		
Caloric content	+	-
Water content of fresh tissue	-	+
Cell sap concentration	+	-
Lipids	+	-
Anthocyanins, flavenoids	+	-
Chlorophyll content	+	-
Chlorophyll / Rubisco ratio	-	+
Chlorophyll a/b ratio	-	+
Light harvesting complex (PSII)	-	+
Physiological functions		
Quantum yield	-	+ (or equal)
Light-saturated photosynthesis	+	-
Light compensation points	+	-
Light saturation point	+	-
Photoinhibition likelihood	-	+
Dark respiration	+	-
Photorespiration	+	-
Transpiration	+	-

1.3.2 Soil moisture

Decreased pasture/crop performance due to competition for water has been demonstrated in the past. Below-ground competition for soil moisture has been found to be a major factor causing yield reduction in tropical, semi-arid, alley-cropping systems (Singh *et al.* 1989; Ong *et al.* 1991). Associations between trees and pastures can become dominated by competition for water in sub-humid areas, particularly if the tree crop has roots in the upper soil layers (Humphreys 1981). Reynolds (1995) found that growth and yields of coconuts can be influenced by the presence of competitive inter-crops if soil moisture becomes critical during even part of the year. Differences in soil moisture levels were found by Williams and Joseph (1976) between clean weeded rubber and rubber sown with a cover crop during the dry season at depths of 0-5 cm, 15-20 cm and 25-30 cm, with greater levels of soil moisture present in the clean weeded treatment. In areas with a distinct dry season and tropical savannahs, the management of tree density is a key factor in determining soil moisture available for growth (Burrows and Frost 1993). It is noted, however, by Humphreys (1994) that effects of trees upon soil moisture will vary according to the seasonal distribution of rainfall. Effects of trees upon pasture growth can vary from strong competition to stimulation (Scanlan *et al.* 1992). Jose *et al.* (2000) concluded that severe competition for water, not light, was the cause of decreased grain yields of maize in an ally-cropping system in the mid-western United States. The cutting of tree roots resulted in higher soil moisture contents within maize alleys. The depletion of soil moisture resulted in smaller maize plants with significantly lower grain yields in plots where competition with trees was present. Decreased yields of copra due to competition for soil moisture between trees and sown pasture was reported by Krisha Marar (1953) (cited in Whiteman *et al.* (1974)), while Fremond (1966) noted that moisture competition was most severe with young palms while older palms were little affected by under-sowing with *Centrosema pubescens*. When deep soil layers supply a large proportion of moisture for tree growth, pasture production will not be as affected as upon shallow soils. In a study conducted by Scanlan and Mckeon (1993), pasture growth was found to be very low if tree basal area exceeded 15 m^2 ha^{-1}, at Gayndah in southeast Queensland. However this reduction in pasture productivity was also found to be highly sensitive to the shallowness of the soil.

Trees may also have beneficial effects upon the water relations of pasture. Decreased radiation loads under tree canopies may benefit shaded pasture as plants under shade have higher leaf water potentials than do those in full sun (Wong and Wilson 1980). Evaporative demands may be much lower and soil moisture availability for pasture maintained at higher levels under shade than in the open, largely through the effects of less evaporation from the soil surface and lower transpiration rates (Wilson and Wild 1991). Reynolds (1995) suggested that these effects may reduce periods when pasture growth is restricted by soil water during the dry season. Ultimately, if a below canopy crop or pasture is going to benefit or suffer in terms of soil moisture from a relationship with an associated tree crop, will depend upon the extent of the beneficial (reduced evaporative demand, higher leaf water potential, lower transpiration rates) versus detrimental effects (competition for water between trees and understory crops/pastures).

1.3.3 Nutrients

There are two major mechanisms by which trees can enhance soil fertility in agroforestry systems (Jose *et al.* 2000). One is the addition of organic matter to the soil through leaf and root decay, and the second through nitrogen fixation by leguminous trees. Trees with a vertical, deep root distribution, that is concentrated below the trunk, have been thought to offer less competition for nutrients to companion species than do surface rooting trees. By accessing nutrients deep in the soil profile and ultimately returning them to the surface through leaf litter, deep-rooted trees may act as nutrient pumps making nutrients available to companion crops that would otherwise have been inaccessible (Humphreys 1994).

If either the tree or inter-crop competes too strongly, then a reduction in yield can occur in one or both of the system components. A moderately high and well balanced nutrient cycle is ideal, giving rapid return of nutrients from herbage, possibly augmented by inputs of fertilizer, into soil organic matter (Reynolds 1995). Where livestock are present the rate of nutrient cycling will be improved as forage is eaten by livestock and recycled as excreta. Even though only about 40% of the forage is excreted, the faster turnover of nutrients can result in an improvement in the tree crop yield (Mohd. Najib 1991). The species comprising the understory crop or pasture will also exert an effect upon the performance of the tree crop species. Watson *et al.* (1964) reported on a comparative study of different vegetative ground covers, where creeping legumes increased the growth rate of immature *Hevea brasiliensis*, increased soil nitrate and rubber leaf N content. They were also found to increase the weight and nutrient content of *Hevea* leaf litter compared to grass ground covers (*Paspalum conjugatum* and *Axonopus compressus*), while woody bushes depressed early growth. Positive gains from the fixation of N by leguminous cover crops have been reported by a number of workers for rubber (Broughton 1977), oil palm (Agamuthu *et al.* 1981) and coconuts (Ochs *et al.* 1993). However reports of below canopy crops causing reductions in yields of tree crops have also been made. Reynolds (1995) indicated that monospecific grass swards may cause a reduction in coconut yields, especially where the fertilizer needs of the pasture are not met. Banana plants grown with a ground cover of *Arachis pintoi* were found to produce 9% fewer bunches than those grown on bare soil, with 4% fewer fingers per bunch and consequently the weight of marketable fruit was reduced by 31% (Johns 1994). The presence of *A. pintoi* reduced the total fruit production in the final year of the trial by 25% and marketable fruit production by 40%. However after 5.5 years, many of the soil chemical properties had changed in plots sown with *A. pintoi.* Organic carbon concentrations to 30 cm depth were 5.6% greater, as was total N was 8.5% greater exchangeable K (52%), calcium (26%), magnesium (43%), sodium (23%), electrical conductivity (24%) and pH (0.13 units). Differing interactions between tree species and forage species have been observed in the past. An example of this is given by Richards and Bevege (1967) who found that the growth of the native conifers *Arucaria cunninghamii* and *Agathis robusta* was better in the presence of the forage legumes *Lotononis bainesii, Desmodium uncinatum* and *Macroptilium atropurpureum*, while that of the exotic species *Pinus elliottii* var. *elloittii* and *Pinus caribaea* var. *hondurensis* was slightly reduced.

It has been observed in the past that some grasses have a higher nutrient concentration and grow better close to trees. These effects have been largely attributed to the transfer of nutrients to the drip ring through stock concentration, leaf fall and increased levels of organic matter (Humphreys 1994). There have been well documented cases of pasture grasses such as *Panicum maximum* var. *trichoglume,* exhibiting higher total biomass yields under moderate levels of shade than under full sun light (Wong and Wilson 1980; Wong *et al.* 1985b; Wilson *et al.* 1986; Humphreys 1991). Growth under shade was also associated with increased concentrations of tissue N and occurred where soil N availability was limiting to growth (Stritzke *et al.* 1976; Eriksen and Whitney 1981; Deinum 1984; Fleisher *et al.* 1984; Wilson *et al.* 1986). The effect was shown to reside in the soil as an experiment conducted by Wilson and Wild (1991) found no such effect in shaded plants grown in solution culture. The extra N does not appear to be from additional root N fixing (Eriksen and Whitney 1982; Smith *et al.* 1984; Wilson *et al.* 1986), or from redistribution of N from roots to shoot. Shelton *et al.* (1987) suggested that available soil N levels are increased by shading. Lower soil temperatures and higher levels of soil moisture under shade stimulate N mineralisation as soil microorganisms and fauna may be more active under such conditions than under full sun (Wilson and Wild 1991). However the effect is only apparent in soils where N is limiting to growth, as work conducted in the past has shown the effect not to occur when N fertilizer is applied (Eriksen and Whitney 1981; Samarakoon 1987; Samarakoon *et al.* 1990a).

1.3.4 Pasture production beneath tree plantations

Forage production is likely to be reduced under plantations as a result of shading and/or competition for nutrients and water. Negative linear, logarithmic, curvi-linear and exponential relationships between tree basal area and forage production have been reported (Pase 1958; Jameson 1967; McConnell and Smith 1970; Beal 1973; Whiteman 1980; Chen and Bong 1983; Cameron *et al.* 1989a). McPherson (1992) indicated that if either woody or herbaceous vegetation held a competitive advantage over the other, then the relationship would be expected to be non-linear. If no advantage were present then a linear relationship would be expected.

Tree basal area and density both exert a major influence upon the level of shading experienced by forage growing beneath trees, with the herbage yield of tropical grasses generally decreasing with increasing shade (Wong *et al.* 1985a). However under certain circumstances higher yields may be obtained due to increased N availability, as previously mentioned. Many studies have documented decreased yields of forage plants when grown under shade compared to full sun (Burton *et al.* 1959; Walker *et al.* 1972; Beal 1973; Wells 1974; Scanlan 1986; Anderson *et al.* 1988; Somarriba 1988; Cameron *et al.* 1989b; Scanlan and Burrows 1990; Scanlan 1991; Halim 1992b; Devkota *et al.* 2001; Varella *et al.* 2001a). The majority of studies agree with Halls (1970) that herbaceous production is inversely related to timber density.

1.3.5 Pasture quality

Shade has frequently been found to alter pasture quality, either through changes in the chemical and structural composition of plants or in species composition of the pasture. Effects of shading upon pasture quality may be summarized as:

- the lowering of plant soluble carbohydrate levels, usually with an accompanying increase in cell wall content;
- higher silica content and lignification;
- lower levels of cell wall digestibility;
- decreases in the proportion of readily digested mesophyll tissue relative to the less digestible epidermis;
- stem elongation and reduced tillering;
- an increase in the percentage of tissue moisture;
- a possible increase in crude protein;
- decreases in non-structural carbohydrate concentrations;
- possible effects upon intake.

(Wilson 1982; Humphreys 1994)

The phenomenon of increased forage N under shade is widespread and can have real benefits where N soil levels of around 1% occur (Wong and Wilson 1980; Wilson *et al.* 1986; Samarakoon *et al.* 1990b; Norton *et al.* 1991), however this effect in tropical grasses is likely to be a result of improved N availability under shaded conditions as previously mentioned.

Other aspects of the pastures' nutritive value show a diversity of responses to shade. Norton *et al.* (1991) examined five tropical grasses and found shading to have no significant effect upon dry matter digestibility, feed intake or cell wall composition and the effects upon cell wall content, acid detergent fibre, lignin and P content were small and inconsistent between species. Wilson and Wong (1982) however found a decrease in the digestibility of *Panicum maximum* var. *trichoglume* grown under shade. Samarakoon (1990b) suggested only shade intolerant species have their quality reduced by shade, due to greatly reduced total soluble carbohydrates, greater culm elongation and the possibility of greater susceptibility to fungal attack. Shading has been reported to increase lignin content and reduce the total non-structural carbohydrate content of plants, which may act to reduce digestibility of plant tissue (Wilson and Wong 1982; Samarakoon *et al.* 1990b). However other tissue modifications caused by shading such as increased crude protein content, reduced vascular development and lower crude fibre content may enhance digestibility (Wilson 1982; Wilson and Wong 1982; Wilson 1991).

1.3.6 Relative humidity

The relative humidity of air under tree canopies is likely to be greater than in the open (Wilson and Ludlow 1991), although there is little data. Wong and Wilson (1980) reported the mean minimum relative humidity increased by 1.2 – 2.2% under artificial shading compared with full sunlight. Lower vapor pressure deficits were reported by Parker and Miller (1982) under isolated *Quercus agrifolia* trees than in the open. Ludlow (1981) however, indicates that the saturation deficit (saturated vapor pressure at the temperature minus the actual vapor pressure) can be a more useful description of the dryness of the air than relative humidity, as evaporation and transpiration are determined by the soil-air and leaf-air vapor pressure gradients.

1.3.7 Temperature

Lower maximum and higher minimum air temperatures are found under tree canopies compared to those in the open. Chen (1989) reported air temperatures above pasture to be approximately 2 - 3°C lower at midday under mature rubber than in the open. Artificial shade appears to give similar small differences in maximum and minimum air temperatures (Wong and Wilson 1980). Jackson *et al.* (1990) indicated that air circulation between the under-canopy and the outside-canopy zones was great enough to partially override the cooling effect of canopy shade, resulting in small air temperature differences between under and outside canopy areas.

Soil temperatures have been found to be more influenced by shading than air temperatures. Generally, below tree crowns, soil temperatures are lower than in the open, with differences of up to 10°C or 12°C reported (Kelly and Walker 1976; Teidmann and Klemmedson 1977; Parker and Muller 1982; Belsky *et al.* 1993; Ko and

Reich 1993). Canopy effects on soil temperature vary as a function of light intensity and duration (Belsky and Canham 1994), and as a result the effects of tree cover on soil temperature may vary over the day and between seasons. Soil temperatures beneath *Quercus* tree canopies in Wisconsin were found by Ko and Reich (1993) to be 2.3°C – 5.2°C lower than those in open areas at 1600h, while at 0800h differences were only 0.7°C – 1.8°C. Teidmann and Klemmedson (1977) found that vegetative cover causes soil temperatures to decline in spring and summer, and to increase during winter, in comparison to bare ground. The effects of shading upon soil temperature are most pronounced on the soil surface and decrease with depth (Teidmann and Klemmedson 1977; Belsky *et al.* 1989; Wilson and Wild 1991).

1.4 Legume genotypes studied

The species detailed in the following section were used in trials and studies during the course of the project. Species were selected for one or more of the following reasons: absence of information relating to suitability for use in agroforestry situations, conflicting reports relating to suitability, a general absence of information relating to the species itself, and species of known performance under such situations used as yardsticks for the comparison of other species.

Arachis kretschmeri
Common names: Pantanal Peanut

A. kretschmeri is a prostrate or erect, many branched, slightly stoloniferous species, with a large tap root. It has heavy seed production with indeterminate flowering producing a single (frequently double) fruit per peg with the fruit buried 2.5 to 7.5 cm below the ground (Kretschmer and Wilson 1988). Collected in the lower Pantanal area of Mato Grosso, Brazil, *A. kretschmeri* belongs to the section *Procumbensae* (Kretschmer and Wilson 1988). Species of this section do not produce true rhizomes or stolons, but their prostrate basal branches may be partially covered by mud during floods with buds potentially sprouting from these branches giving the impression of rhizomatous growth (Valls and Simpson 1994). Most species of section *Procumbensae* produce horizontal pegs, which sometimes are very long, with seeds tending to develop near the surface (Valls and Simpson 1994). In trials conducted by Kretschmer and

Wilson (1988), the persistence under clipping was found to be good, however yields were less than those of *Macroptilium atropurpureum*. The root knot nematode *Meloidogyne* spp. was observed on roots, however no effects were visually apparent. *In vitro* organic matter digestibility was found to be substantially higher than for either *M. atropurpureum* or *Desmodium heterocarpon* (70%, 56% and 39% respectively). Persistence under grazing was not good in many of the trials' earlier plantings, however this was attributed to the use of vegetative material, rather than seeds, as vegetatively-propagated material was only able to develop fibrous root systems, whereas plants grown from seed were able to produce tap roots (Kretschmer and Wilson 1988).

Arachis pintoi Krap. & Greg., nom. nud.
Common name: Pinto Peanut

Arachis pintoi is a stoloniferous, perennial herb, rooting at the nodes with yellow flowers and tetrafolioate leaves originating in the valleys of the Jequitinhonha, Sao Francisco and Tocantins rivers in central Brazil (Cook 1992; Reynolds 1995). Seed is produced in a pod that develops a long tube, which bends down and buries the seed in the top 5 cm of soil (Evans and Macfarlane 1990). Stems are initially prostrate, becoming ascendant to 20 cm in dense swards (Cook 1992). *Arachis pintoi* is suited to wet/flooded soils that are acid to neutral and has proven adaptable to soils ranging from sandy to clay in texture, low to neutral pH and low to high fertility (Cook 1992; Reynolds 1995). Cameron *et al.* (1989b) noted it as a very persistent legume under heavy grazing, while Cook (1992) indicated it will not only tolerate, but increase, under heavy grazing. This is probably due to its prostrate growth habit, dense stolons, capacity to flower year round, to set seed under grazing and to root from stolons (Reynolds 1995). Due to shedding many of its leaves during drought periods, *A. pintoi* is not thought to be particularly drought tolerant (Fisher and Cruz 1994). It has been suggested by Schultze-Kraft (1986) that low dry season productivity could be a major limitation to the use of the species, although plants can survive more than three months of drought. The production of *A. pintoi* has been found to range from 5 t/ha when grown with *Brachiaria dictyoneura,* which produced 20 t/ha, through to 10 t/ha when grown with *B. ruziziensis* that, in turn, yielded 11 t/ha. In pure stands yields have ranged from 5 t/ha beneath 30% shade in Indonesia to 3 t/ha under full sun in Malaysia (Cook 1992). The in-vitro digestibility of *A. pintoi* ranges from 60 – 70%, with nitrogen concentrations from 2.5 – 3.0% (Reynolds 1995). Crude protein levels around 17% were found in a grazing trial conducted in Colombia (Lascano and Thomas 1988). Grazing animals may need a period of time to get used to grazing *A. pintoi,* however after this initial period it is well accepted by cattle (Carulla *et al.* 1991; Cook 1992). It is considered to have good potential for use under coconuts and other tree plantations as a pasture legume, and also as a ground cover in plantations where stock must be excluded (Cook 1992; Reynolds 1995).

Arachis paraguariensis Chodat & Hassler

Belonging to the section *Erectoides,* series *Tetrafolioatae, Arachis paraguariensis* is a perennial which has an erect growth habit with tuberous roots, long horizontal pegs, tetrafoliate leaves and yellow to light orange papilionate flowers supported by a calyx tube (Gregory *et al.* 1980; Valls and Simpson 1994). Seeds are produced in single seeded, under-ground pods (Still *et al.* 1987). Members of section *Erectiodes* are able to produce tall plants, sometimes in large clumps, but are mostly slow growers and not likely to resist grazing or trampling (Valls and Simpson 1994). Peanut stunt virus is the only disease to be recorded in the species. *Arachis paraguariensis* is known to have great regenerative capacity (Still *et al.* 1987).

Arachis stenosperma Greg. & Greg.

A member of the section *Arachis,* series *Perennes, Arachis stenosperma* is indicated by Valls and Simpson (1994) to be an informal Latin name or diagnosis. Very little information is available regarding *A. stenosperma.* Kretschmer *et al.* (1999) found that the spread of *A stenosperma* and other species of *Arachis*, save *A. kretschmeri*, was good to excellent, and that the harvest of seed of *A. stenosperma* from a small area in a young, producing, Florida, citrus grove, was the greatest of the species tested, along with an unnamed species of *Arachis.*

Aeschynomene americana L.
Synonyms: *Aeschynomene javanica*, *A. glandulosa*, *A. guayaquilensis*, *A. tricholoma*, *Hippocrepis mimosula*
Common names: American Jointvetch, Thornless Mimosa, Bastard Sensitive Plant

This legume is an annual or short-lived perennial, shrub-like legume, 1 – 2 m tall, leaves 2 – 7 cm long with 8 to 35 pairs of leaflets, inflorescence a loose, few flowered raceme, often branched with flowers papilionaceeous, 3 – 10 mm long, yellow, orange or mauve in colour, usually with red or purple stripes (Skerman *et al.* 1988; Bishop 1992). *Aeschynomene americana* originates from the Caribbean and adjacent areas, usually in moist or wet places up to 1400 m above sea level (Bishop 1992). Growing in poorly drained or waterlogged conditions, the best growth of *A. americana* occurs in hot, moist climates with an average rainfall of over 1000 mm (Bishop 1992). Cultivar Lee has orange flowers and a semi-erect growth habit, with profuse basal branching. It is predominantly perennial with plants in grazed plots at Proserpine and Mackay living longer than 4 years (Bishop *et al.* 1995). Cultivar Lee is well adapted to environments with more than 1000 mm annual rainfall, but will grow on fertile soils receiving less than 900 mm. Adventitious roots are produced from stems touching moist soil and it is very suited for use on low-lying, waterlogged soils (Bishop *et al.* 1995). *A. americana* can be susceptible to competition from vigorous grasses in the seedling regeneration phase at the beginning of each season, but once established mature plants are able to withstand competition (Skerman *et al.* 1988). Dry matter yields of between 10 – 15 t/ha have been reported in Queensland over a full season’s growth (Bishop 1992). On Cunnunurra clay a maximum dry matter yield of 13 325 kg/ha was obtained in 220 days, with applied nitrogen decreasing yields but increasing protein content from 9.4 to 13.4% (Parberry 1967a).

Aeschynomene villosa Poir.
Common name: Villosa Jointvetch

Occurring from southern Arizona, through Mexico, to north-western South America and the Caribbean at elevations up to 2250 m, *A. villosa* is a variable annual/perennial, prostrate/erect species growing best on sandy loams to light clays in environments receiving 1000 mm or more annual rainfall, but does not appear to tolerate prolonged waterlogging (Hacker 1990; Partridge 1998; Bishop and Cook 2001; Kretschmer and Pitman 2001) . Leaves are comprised of 10 – 25 pairs of leaflets, alternating on either side of the rachis that is between 15 – 60 mm long, with the leaflets up to 8 mm long, 1.5 mm wide getting progressively shorter towards the tip of the rachis and sensitive to touch (Hacker 1990). The inflorescence is axillary, leafy, 3 – 10 flowered, with flowers 3 – 9 mm long and hairy with a pair of hair fringed 2.5 mm bracteoles on either side (Hacker 1990). The cultivars Reid and Kretschmer are both perennial and well adapted to environments receiving more than 1000 mm annual rainfall, however where winter rainfall is received, and spring and early summer rainfall is more reliable, they can persist in areas with 900 mm annual rainfall (Bishop and Cook 2001). Both cultivars have been successfully grown on soils ranging from sandy loams to heavy cracking clays and tolerate waterlogging but not to the extent of *A. americana* (Bishop and Cook 2001). Leaf and stem material is readily accepted by cattle with evaluations conducted in Florida showing that the species can persist under a variety of grazing management systems (Bishop and Cook 2001; Kretschmer and Pitman 2001).

Calopogonium mucunoides Desv.
Synonyms: *Calopogonium orthocarpum*, *Stenolobium branchycarpum*
Common name: Calopo

Native to tropical South America, *C. mucunoides* is a vigorous creeping, twining or trailing annual or short-lived perennial, forming a tangled mass of foliage 30 – 40 cm deep (Skerman *et al.* 1988; Chen and Aminah 1992; Kretschmer and Pitman 2001). Stems are densely covered with long brown hairs, leaves trifoliate, petiole up to 16 cm long, leaflets elliptic, ovate or rhomboid-ovate, inflorescence a slender raceme up to 20 cm long with flowers in fasicles of 2 – 6, blue or purple in colour (Chen and Aminah 1992; Reynolds 1995). Pods are 2.5 to 4 cm long, compressed, linear, yellowish-brown and densely covered in long erect hairs with 4 – 8 seeds (Skerman *et al.* 1988). *C. mucunoides* requires at least 1125 mm rainfall per year and is suited to the hot, humid tropics with vigorous growth occurring on soils of all textures (Skerman *et al.* 1988; Chen and Aminah 1992). The main deficiencies of *C. mucunoides* are given by Skerman *et al.*(1988) as being intolerance of dry conditions, with plants dying out under dry conditions and regenerating in the wet season from seed; its short life span since it may only persist for 1 or 2 years; and its unpalatability, which is attributed to the hairiness of leaves and stems. Its vigorous early growth makes it useful as a pioneer species to protect the soil surface, smother weeds, fix nitrogen and improve soil fertility (Skerman *et al.* 1988; Chen and Aminah 1992; Reynolds 1995). Reynolds (1995) notes that it is a particularly useful species beneath coconut plantations due to its tendency to die back in dry periods and not compete with the coconut palms for moisture and nutrients, however Chen and Aminah (1992) indicate that, when grown with young oil palm and rubber trees, regular slashing is required to prevent the over-growing of trees.

Centrosema acutifolium Benth.

C. acutifolium is a perennial, trailing, twining herb originating in tropical America, restricted to 4 – 6°N in Colombia and Venezuela, and central-west and south-east Brazil, and is used as a forage for ruminants in grazed pastures or in cut-and-carry systems (Schultze-Kraft 1992a). *C. acutifolium* var. *orinocense* has trifoliate leaves with younger leaflets distinctly purplish, petioles and petiolules pubescent and reddish at the base, leaflets ovate to ovate-lanceolate, apically acuminate, central leaflet symmetrical 5 – 8.5 cm long and lateral leaflets asymmetrical, 4 – 7.5 cm in length. The inflorescence is an axillary raceme with up to 24 flowers; inserted by pairs along the rachis, light violet in colour. The dehiscent pods may be linear or slightly bent, up to 20 cm long and contain 10 – 15 seeds (Schultze-Kraft 1992a). Two morphologically and physiologically distinct forms of *C. acutifolium* are indicated by Schultze-Kraft (1992a), related to their geographical origin; var. *orinocense* has a small distributional niche in Colombia and Venezuela and var. *matogrossense* in central west Brazil. *C. acutifolium* is suited to sub-humid, tropical environments receiving 1000 – 2500 mm annual rainfall with a distinct dry season and is able to withstand dry seasons up to 5 months in length (Schultze-Kraft 1992a). It is similar to *C. pubescens* in appearance and nutritional quality but can tolerate high levels of Al and Mn in acid soils of pH’s down to approximately 4.3 with low nutrient requirements (Schultze-Kraft 1990; Schultze-Kraft *et al.* 1990; Kretschmer and Pitman 2001). The main differences which separate *C. acutifolium* from *C. pubescens*, are the purplish colour of young leaflets, the short bracteoles and calyx teeth, the scabrid pod indumentum and its’ cylindrical seeds

(Schultze-Kraft 1992a). *C. acutifolium* var. *orinocense* requires well-drained, light-textured soils, while var. *matogrossense* grows particularly well on heavier soils, including those with seasonal drainage problems (Schultze-Kraft 1992a). Production of dry matter by *C. acutifolium* has been found to vary depending upon site characteristics, Cirgarroa (1985) and Enriquez Quiroz (1986) (both cited by Argel *et al.* 1990) reported between 160 kg/ha and 3397 kg/ha produced every twelve weeks over a range of different conditions, while Schultze-Kraft (1992a) indicated that yields may be as high as 5 t/ha on sites of higher fertility.

Centrosema brasilianum (L.) Benth.
Synonyms: *Clitoria brasiliana*, *Centrosema angustifolia*

Centrosema brasilianum is an ascendant, twining perennial with slender stems. Trifoliate leaves contain linear to oblong, ovate to broad-lanceolate or lanceolate leaflets, 3 – 7 cm x 1 – 3 cm wide that are glaborous, obtuse and mucronate at the apex and rounded at the base (Skerman *et al.* 1988; Cameron and Lemke 1997). Flowers are produced upon a few-flowered raceme, with a 1 cm long peduncle. However Cameron and Lemke (1997) indicate that cultivar Oolloo has solitary flowers. Petals are purple, violet, violet-blue or white, pods are dehiscent, linear, 10 – 15 cm long, 5 mm wide with a 6 – 31 mm beak and contain 12 – 19, mostly cylindrical seeds (Skerman *et al.* 1988; Cameron and Lemke 1997).

C. brasilianum probably originated in the South American tropics, where it is widely distributed in both semi-arid and sub-humid regions between 16°S in Brazil to 10°N in Venezuela (Schultze-Kraft and Belalca'zar 1988; Cameron and Lemke 1997). Its' main attribute of interest is the drought resistance of the semi-arid ecotypes (Skerman *et al.* 1988), with several lines displaying the ability to remain green during the dry season, showing a potential to provide high quality feed at a time when little other good quality herbage is available (Clements *et al.* 1984). Characteristics such as high water-use efficiency, low transpiration rates and a tolerance of low leaf water potentials indicates a well developed drought avoidance mechanism in the species (Ludlow *et al.* 1983). Clements (1990) indicates that the moisture stress avoidance or tolerance mechanisms in *C. brasilianum* are poorly understood, but appear to differ from those of *C.*

pascuorum and *C. rotundifolium*. The ability of *C. brasilianum* to remain green, and even grow slowly, during droughts can be partially explained by its stronger stomatal control of water loss than other species of *Centrosema*. Ludlow *et al.* (1983) found its stomatal control of water loss to be less than that of Siratro (*Macroptilium atropurpureum*), and its tolerance of leaf water deficits to be less than that of *C. pascuorum* and no greater than *C. pubescens.* In light of this information it seems likely that *C. brasilianum* may have a deep root system, able to reach soil moisture unavailable to other species. Schultze-Kraft (1990) noted that the species appears to be adapted to acid, low fertility soils, while its presence in the Pantanal suggests some adaptation to less well drained conditions. *C. brasilianum* is thought to be one of the most productive and best-adapted genotypes in rainfall zones of 600 – 1500 mm in the Northern Territory (Cameron (1989), cited by Amar (1996)).

C. brasilianum is the species of *Centrosema* with the greatest susceptibility to a number of diseases, particularly *Rhizoctonia* (leaf blight). This disease has been the major obstacle to the release of commercial cultivars in South America (Clements *et al.* 1984; Lenne *et al.* 1985). It was noted by Cameron and Lemke (1997) that cultivar Oolloo can be affected by *Rhizoctonia* during wet periods, but the areas affected were usually small.

Yields of dry matter varied from 776 kg/ha to 1622 kg/ha at Carigmagua, Colombia, during the dry and wet seasons respectively. During the maximum rainfall period at Puerto Bermudez and Coca, yields were reported by Reyes *et al.* (1990) to range from 430 to 3109 kg/ha every six weeks respectively. At Katherine in the Northern Territory, in a pasture sown with a mixture of accessions, grazed at 3.3 steers/ha during the dry season for 7 years and allowed rest periods to allow the legume to recover from selective grazing, live weight gains by cattle were similar to those obtained on *C. pascuorum* pasture (Clements 1990). Cultivar Oolloo, grown in the Northern Territory, without inoculation yielded 3 – 4 t/ha under rain-fed conditions (Cameron (1996) cited by Amar (1996)).

Centrosema macrocarpum Benth.
Synonym: *Centrosema lisboae*

Centrosema macrocarpum is a tap-rooted, robust, perennial vine that has a variable tendency to root at the nodes. Leaves are trifoliate, petioles and petiolules pubescent, leaflets broadly to narrowly ovate, apically acute to acuminate, rounded or slightly wedge-shaped at the base, mostly 8-13 cm x 3-8 cm in size, with the central leaflet larger and longer petiolated than the laterals (Schultze-Kraft 1992c). The inflorescence may contain up to 30 flowers inserted in pairs along the rachis in an axillary raceme. The papilionaceous flowers are cream coloured with a purple centre, 3-6 cm in diameter, subtended by a pair of ovate-lanceolate-falcate bracteoles, 5 toothed, with the cardinal tooth considerably longer than the others. Pods are up to 30 cm long x 1 cm wide, linear, compressed and dehiscent, containing up to 25 seeds 5 mm x 3mm in size (Schultze-Kraft 1992c).

The distribution of *C. macrocarpum* ranges from 19°N to 19°S in tropical America on acid, low fertility soils in regions with an annual rainfall as low as 430 mm (Santa Marta, Colombia) to as high as 4000 mm (Sona, Panama), with most collections made in areas with annual rainfall between 1100 – 1800 mm, with 2 – 6 dry months (Schultze-Kraft *et al.* 1990).

Once established it is very drought tolerant and has the ability to remain green for as long as 3 – 4 months during the dry season and is best adapted to the humid and sub-humid tropics (Schultze-Kraft 1992c). *C. macrocarpum* has been described as a species with high potential by Schultze-Kraft (1990) as it has vigorous growth and excellent dry season performance, with dry matter yields of 813 kg/ha to 4789 kg/ha per 12 week period on an acid, moderately fertile soil in Mexico and Central America, while an average of 15 t/ha was obtained at a site with bimodal rainfall distribution and a highly Al saturated ultisol soil in Colombia (Argel *et al.* 1990). The dry matter produced by *C. macrocarpum* is both a palatable and high quality forage. Crude protein content in leaves varies from 9% to 30% (CIAT 1984: Flores 1984 cited by Grof *et al.* 1990), while in vitro dry matter digestibility ranges between 45-70% (Schultze-Kraft 1992c).

Centrosema macrocarpum is unable to withstand heavy grazing and, when used in grazed pastures its persistence will be improved if allowed to establish well prior to first grazing and if stocking rates are not excessive (Schultze-Kraft 1992c; Horne and Stur

1999). The species is also known for its high tolerance of acid soils, Al and Mn toxicity and low levels of available P (Schultze-Kraft 1990; Schultze-Kraft 1992c). The major limitations of the species are noted to be a lack of persistence under grazing, particularly when associated with aggressive grasses, such as *Andropogon gayanus*, and a restricted flowering and seed set in some locations (Thompson and Grof 1986, da Veiga and Serrao 1986, both cited by Argel *et al.* 1990; Schultze-Kraft 1990).

Centrosema pascuorum Martius ex. Benth.
Synonyms: *Centrosema virginianum*, *B. angustifolium*
Common name: Centurion

This is a prostrate annual with the ability to twine or scramble up associated species, and a weak ability to perenniate and produce roots on trailing stems under favourable conditions (Anon. 1985; Skerman *et al.* 1988; Clements 1992). Stems are up to 2 m long, cylindrical, glaborous to scarcely pilose, branched at the nodes and rooting at the nodes under moist conditions. Leaves are trifoliate, often held erect, leaflets linear-lanceolate 5 - 10 cm long and 5 – 10 mm wide. Inflorescences are racemose, 1 – 4 flowered, with 1 – 2 peduncles per leaf axil. It has resupinate flowers at the end of a 7 – 12 mm peduncle, pedicels 4 – 10 mm long , subtended by an ovate bract 2 – 4 mm in length, with the distal end having two conspicuously paired bractoles. The calyx tube is 3 – 4 mm bearing 5 linear teeth, the 2 upper teeth 3 – 5 mm long and the lowest 4 – 7 mm. There are minute hooked hairs on the external surfaces of leaflets and stems. The corolla is 1.5 – 2.5 cm long and wide, and is crimson in colour. The dehiscent pods are linear, 4 – 8 cm x 3 – 4 mm, laterally compressed with a dark longitudinal stripe near each suture and contain up to 15 ovoid to cylindrical, slightly laterally compressed seeds, approximately 4 mm long (Anon. 1985; Skerman *et al.* 1988; Clements 1992).

Centrosema pascuorum has a natural distribution restricted to arid tropical areas of north-eastern Brazil, Colombia, Ecuador, Guyana, Venezuela, Panama, Costa Rica, Honduras, Guatemala and southern Mexico (Anon. 1985; Skerman *et al.* 1988; Clements 1992). An unusual characteristic of *C. pascuorum* is its ability to tolerate both drought and prolonged waterlogging, but despite this it has proven to have a limited area of adaptation in Australia. It is well adapted to tropical regions with reliable wet seasons 4-6 months in length with 700 – 1500 mm of rainfall, while in areas of less reliable rainfall or lower temperatures it has rarely persisted for more than 2 or 3 years (Anon. 1985; Skerman *et al.* 1988; Clements 1992). It is adapted to soils of near-neutral pH with textures ranging from sand to heavy clay and is known to show poor adaptation to infertile, acidic soils (Thomas and Penteado 1990). It is an aggressive species that regenerates readily and can compete strongly with associated grasses (Anon. 1985).

Yields of dry matter by *C. pascuorum* in ungrazed, well-fertilised, legume dominant swards in the Northern Territory were between 4 – 6 t/ha/year, producing palatable, high quality forage, with N concentrations ranging from 2.5 – 4.5% (Anon. 1985). In small plots in Thailand, yields of up to 9 t/ha have been recorded (Clements 1992). *C. pascuorum* is both extremely drought tolerant and drought escaping. Under moisture stress new leaves become smaller, narrower and more hairy, with the tip of the leaf kept pointed towards the sun (Skerman *et al.* 1988). It is also able to tolerate remarkably high internal moisture deficits (Anon. 1985), with a water-stress tolerance of –12.1 ± 0.18 MPa and a leaf water potential at zero conductance of –8.0 MPa reported by Ludlow *et al.* (1983).

Although susceptible to the fungal pathogens leafspot (*Cercospora canescens* and *Pseudocercospora bradburyae*), anthracnose (*Colletotrichum truncatum*), foliar blight (*Rhizoctonia solani*) and *Neocosmospora vasinfecta*, they are not usually serious in areas where the species is well adapted. It is also susceptible to sucking insects and root-knot nematode during seed production (Clements 1992).

Centrosema pubescens Benth.
Synonym: *Centrosema molle* Martius ex. Benth.
Common names: Centro, Butterfly Pea

This vigorous, climbing perennial originated in south and central America and is now one of the most widely distributed of all legumes in the humid tropics (Teizel and Chen 1992). It has trifoliate, slightly hairy leaves, and stems that do not become woody for at least 18 months. Leaflets are elliptic or ovate-elliptic, obtuse or shortly obtusely acuminate and 1 – 7 cm by 0.5 – 4.5 cm in size. Runners have a tendency to root at the nodes if soil moisture is high. Flowers are pale mauve in colour with purple lines in the centre, borne in axillary racemes with 3 – 5 flowers per raceme. Pods are linear, 4 – 17 cm x 6 – 7 mm in size, flattened with prominent margins, straight or slightly twisted, acumate and dark brown when ripe, containing up to 20 seeds (Skerman *et al.* 1988; Teizel and Chen 1992; Reynolds 1995).

Although able to form compact, dense cover 35 – 45 cm deep in pure swards, it is slow to establish and requires good conditions during the establishment period (Skerman *et al.* 1988; Teizel and Chen 1992; Reynolds 1995). *C. pubescens* prefers rainfall of 1500 mm or more per year, but can grow in areas receiving between 750 – 1000 mm, however, where rainfall exceeds 2500 mm it may be attacked by leafspot (*Cercospora*) (Skerman *et al.* 1988; Teizel and Chen 1992; Reynolds 1995). Able to survive a 3 – 4 month dry-period, growth in the dry season can be improved with irrigation, however the cooler temperatures associated with the dry-season may inhibit growth (Sweeney and Hopkinson 1975; Lazier and Clatworthy 1990). It has the ability to grow on a wide range of soils, with an optimum pH range between 4.9 to 5.5 and textures ranging from sandy-loam to clays (Steel *et al.* 1980a). *C. pubescens* grows well on fertile soils and, on poor soils, responds to phosphorus, molybdenum and possibly magnesium fertilisation (Steel and Humphreys 1974; Eng *et al.* 1978; Skerman *et al.* 1988). Yields of up to 12 t/ha have been obtained in pure stands, while Payne *et al.* (1955) obtained an average yield of 4.9 t/ha/year over a three year period in Fiji.

Chamaecrista rotundifolia (Persoon) Greene
Synonym: *Cassia rotundifolia*
Common names: Roundleaf Cassia, Roundleaved Cassia

C. rotundifolia is a sub-woody, semi-erect, short-lived perennial of self-regenerating annual which is native to an area that extends from Mexico through Brazil and Uruguay, and also includes the Caribbean region. Stems are 30 – 110 cm long, radiating from the root-stock which has a woody-fibrous, blackish taproot up to 1 cm thick. Leaves are bifoliate, with petioles up to 1 cm long with sub-rounded to broadly ovate leaflets 12 – 38 mm x 5 – 25 mm, that face upward by day and fold face-to-face at night. 1 – 3 yellow flowers are produced in racemose, axillary clusters with pedicels up to 6 cm long. The pods are linear, 20 – 45 mm long by 2.5 – 5.0 mm wide, oblongoid, flat, dehiscent and blackish-brown in colour when ripe. Seeds are flattened and rectangular, 2 – 3 mm long (Anon. 1984; Skerman *et al.* 1988; Jones 1992).

C. rotundifolia is best suited to areas with 700 – 1400 mm rainfall in the seasonally dry tropics, it is not suited to heavily textured or poorly drained soils and is best adapted to free-draining, light soils. It will not tolerate waterlogging (Whiteman *et al.* 1984; Reid 1990; Jones 1992). It has proved to be persistent under a wide range of grazing pressures, however when grown in association with vigorous grasses or under light grazing pressure its production and persistence has been poor (Jones 1992). Dry matter yields of over 7 t/ha were reported at Beerwah and Gatton, with dry matter indicated by Reid (1990) to be palatable when not allowed to become rank, while Jones (1992) states that cattle will tend to selectively graze grass in a mixed *C. rotundifolia*/ grass sward at the beginning and middle of the growing season.

There have been no serious diseases or pest problems reported, with the main deficiency of the species being its restriction to lighter textured soils (Anon. 1984; Skerman *et al.* 1988; Jones 1992).

Clitoria ternatea L.
Synonyms: *Clitoria zanzibarensis*, *C. tanganicensis*, *C. mearnsii*
Common names: Butterfly Pea, Kordofan Pea, Blue Pea, Asian Pigeon-wings

This is a perennial herb with a climbing, scrambling or trailing habit and a strong woody rootstock. *C. ternatea* has pinnate leaves with 5 or 7 elliptical, oblong, oblong-lanceolate or nearly round leaflets, 1 – 7 cm x 0.3 – 4 cm in size, shortly pubescent underneath (Skerman *et al.* 1988; Hall 1992; Staples 1992a). Flowers are deep blue or occasionally pure white, 4 – 5 cm long, axillary, paired or solitary. The peduncle is 3 – 10 mm long, pedicel 6 – 9 mm and twisted 180° so that the standard is held lowermost. The pod is linear, beaked, 6 – 12.5 cm x 7 – 12 mm, slightly pubescent and dehiscent when dry. Seeds are oblong or oblong-reniform, somewhat flattened 4.5 – 7.5 mm x 3 – 4 mm, olive, pale black or shiny black and minutely pitted with 8 – 10 seeds per pod (Skerman *et al.* 1988; Hall 1992; Staples 1992a).

The origin of *C. ternatea* is obscured by extensive cultivation and naturalisation in Asia, Africa, the Americas and the Pacific Islands (Staples 1992a), although Skerman (1988) labels it as a native of tropical America.

Clitoria ternatea has a reputation for drought tolerance in the seasonally dry tropics receiving between 500 – 900 mm of rainfall per year, with annual rainfall requirements for survival as low as 400 mm (Staples 1992a), and best performance around 1500 mm (Skerman *et al.* 1988). Growth is limited by lack of moisture, with leaves shed in response to water stress (leaves may also be shed due to low temperatures in cooler regions). *C. ternatea* will not tolerate waterlogging or flooding (Farinas 1966 cited by Skerman *et al.* 1988).

C. ternatea is adapted to soil textures from loams to heavy clays and pHs of between 5.5 – 8.9, and prefers fertile, friable soils, as it performs poorly on infertile, sandy soils if not fertilised (Hall 1992; Staples 1992a). Yields of forage by *C. ternatea* can vary greatly due to differing environmental conditions and management. On infertile, grey clay dry matter yields were only 330 kg/ha in undisturbed native pasture during the establishment season, while upon a Cunnunurra clay in the Kimberleys, 3 lines of *C. ternatea* averaged 13 t/ha of dry matter under irrigation (Parberry 1967a; Hall 1992). N concentration of material produced varies depending on the season and stage of growth. Concentrations of N have ranged from 1.7 – 4.0% in whole plant tops, while those in leaf only and whole plant tops were reported to be 3.05 and 1.49% respectively (Hall 1992). A digestibility of 74% was reported in sheep by Bogdan (1977). In the Burdekin delta, north Queensland, cattle averaged a greater daily live-weight gain on a *C. ternatea*/*Brachiaria mutica* (Paragrass) pasture than on either Stylo or Centro mixtures (Barrau 1953). The material produced is very palatable to stock and a lack of persistence is often due to selective grazing. The main deficiency in the species is its intolerance of heavy grazing or frequent, low cutting, due to the location of the growing points at the ends of the main stem and axillary branches with ungrazed stems providing growing points for early summer growth with few new crown shoots developing (Hall 1992; Staples 1992a).

Desmanthus virgatus (L.) Willd.
Synonyms: *Mimosa virgata*, *Desmanthus depressus*
Common names: False Tamarind, Dwarf Koa, Desmanthus, Hedge Lucerne, Donkey Bean, Bundle Flower

A native of the Americas, including Florida, Texas, Arizona, Mexico, the West Indies, Galapagos Islands, Hawaii and Argentina, *D. virgatus* now has a world-wide distribution in the tropics and sub-tropics (Burt 1986). The species has a very variable growth habit which ranges from a prostrate, spreading or decumbent habit to an erect suffructescent form, up to 3 m tall (Pengelly and Topark-Ngarm 1992). A perennial or sometimes annual species with bipinnate leaves, 2 – 8 cm long, containing 2 – 7 pairs of pinnae 11 – 30 mm long with 10 – 25, nearly sessile, leaflets 2.4 – 7.0 mm long. The inflorescence is a small globose, 6 – 10 flowered head with a peduncle up to 7.5 cm long, white to cream in colour, located towards the tips of twigs. The flowers are all erect, sessile, bisexual although some lower flowers may be neuter. Pods are linear to falcate, 3 – 10 cm x 3 – 4 mm, dehiscent with two valves, containing 20 – 30 glossy brown, ovoid to ellipsoid seeds (Skerman *et al.* 1988; Pengelly and Topark-Ngarm 1992; Ossiya 1993).

Most commonly *D. virgatus* is associated with neutral-alkaline, clay to clay loam soils, but has a wide range of adaptation in the tropics and sub-tropics. It grows in environments with a rainfall varying from 260 – 2000 mm per year and on soils ranging from alkaline coral sands, to saline clays to acid sandy loams (Whyte and Nilsson-Leissner 1969). Preferring a pH of between 5.0 – 6.5, it grows best in hot weather and is quite drought tolerant. It is adapted to defoliation and produces highly palatable material. Crude protein contents of 10.55, 12.27 and 15.52% were reported for whole plant tops cut at 61, 91 and 122 day intervals by Skerman *et al.* (1988). Production of dry matter averaged just under 7.6 t/ha at Sigatoka, Fiji, of which 64% was produced in the wet season in an area receiving 2000 mm of rainfall per year (Payne *et al.* 1955). Whole plant dry matter yields of 35.08 t/ha/year were obtained by Parberry (1967b) without any added nitrogen at Kimberley Research Station in northern Australia on Cununurra clay, while the addition of 100 kg/ha of N reduced yields to 26.05 t/ha. When foliage above 45 cm only was harvested, 63.29 t/ha were obtained from unfertilised plots and 70.33 t/ha from N fertilised plots from four cuts per year.

Desmodium canum (Gmel.) Schinz and Thellung
Synonyms: *Desmodium incanum*, *D. sparsifolium, Hedysarum canum*, *Hedysarum racemosum*, *Aeschynomene spicata*
Common names: Creeping Beggar Weed, Kaimi Clover

A perennial herb of varying habit from ascending to erect, 0.6 – (rarely) 3 m tall, with woody trailing/creeping stems that root readily at the nodes and a deep well branched root system (Hacker 1992b). Leaves upon upright stems are lanceolate and usually have a white mark on the midrib, while those on trailing stems are normally oval and round with no marking. All leaves are trifoliate, stipulate, petiolate, with terminal leaflets 2 – 9 cm x 1.5 – 4.5 cm in size and lateral leaflets up to 6 x 3 cm (Hacker 1992b). The inflorescence is a terminal or axillary raceme, up to 20 cm long with lavender, blue or red flowers. Pods between 2.5 – 4 cm long and 0.3 cm wide, covered in hooked hairs, with a straight upper margin and a strongly indented lower margin and up to eight articles of 3.5 – 5 mm by 2 – 3.5 mm in size. Seeds are kidney shaped, light brown in colour and 1 x 0.5 mm in size (Skerman *et al.* 1988; Hacker 1992b).

D. canum is widespread in the wet tropics but is native to the area from the southern United States to Uruguay and Argentina. It grows best in areas of 1500 – 3075 mm annual rainfall, but can persist in regions receiving 1000 mm per year. Able to grow on a wide range of soil textures from sands to light clays with a pH range of 4.0 – 8.0, it performs best upon fertile, neutral to slightly alkaline soils (Skerman *et al.* 1988; Hacker 1992b). It is usually considered to be low-yielding, able to yield up to 6.5 t/ha of dry matter with low seedling vigour and some unpalatability due to a high tannin content (Skerman *et al.* 1988; MacFarlane *et al.* 1991). It is compatible with a number of sward forming grasses and is able to withstand heavy grazing due to its stoloniferous habit, and was found by Hacker (1992b) to be amongst the most persistent legume species under heavy grazing, lasting for 12 years at Topaz in north Queensland (Kelly 1964).

It is sensitive to the disease Peanut Mottle Virus and to Littleleaf and Desmodium Mosaic Virus, in addition to several fungal diseases having been reported but rarely causing serious problems (Skerman *et al.* 1988; Hacker 1992b). The main deficiencies in the species are given by Skerman (1988) as low yields of dry matter, low seedling vigour, not fixing large amounts of N and an inclination to become woody.

Desmodium heterophyllum (Wild.) DC.
Synonym: *Hedysarum heterophyllum* (Willd.)
Common names: Desmodium, Carpon Desmodium, Hetero, Spanish Clover

D. heterophyllum is a prostrate perennial creeper which can form swards up to 15 – 20 cm, which occurs naturally in Mauritius, India, Nepal, Sri Lanka, Burma, Thailand, Indo-China, Malaysia, China and Taiwan deep (Hacker and Teitzel 1992; Reynolds 1995). Stems are reddish-brown, hairy, freely branching, rooting at the nodes and up to 1.5 m in length. Leaves are trifoliate, but on lower parts often unifoliate, with the terminal leaflet larger and on a longer stalk than the laterals, obovate or elliptical in shape and usually 10 – 25 x 8 – 14 mm in size (Hacker and Teitzel 1992). The purple, white or reddish-pink flowers are approximately 5 mm long, borne on a few-flowered axillary or terminal racemes up to 6 cm long, and/or in leaf-opposed clusters of 1-3 flowers. Pods are 10 – 20 mm x 3 – 5 mm, finely pubescent with the isthmus between the articles approximately ¾ the width of the pod, which dehisces along the lower margins when ripe. Seeds are kidney shaped, 2.25 – 2.5 mm x 1.5 – 1.75 mm, turning yellowish brown to dark brown with age (Anon. 1990; Hacker and Teitzel 1992).

One of the main attributes of *D. heterophyllum* is its ability to form a productive and long-term association with sward forming grasses and its adaptability to a wide range of soils. Suited to the humid tropics with an annual rainfall exceeding 1500 mm and soil textures from sands to clays, *D. heterophyllum* is unusual in that, unlike most tropical legumes, it tolerates heavy grazing and has an excellent ability to spread naturally by its freely branching stolons and free seeding habit (Harding and Cameron 1972; Steel *et al.* 1980b; Cameron 1987). Heavy grazing is necessary in the wet summer period to prevent suppression by grasses and lower yields due to shading (Evans *et al.* 1992). Persistence on soils of low fertility has been poor, particularly those deficient in trace elements (Hacker and Teitzel 1992).

D. heterophyllum is commonly established from vegetative cuttings owing to the poor synchrony of seed production and the fragility of ripe pods, that are carried close to the upper levels of the herbage. Forage produced is slightly unpalatable during early growth which aids establishment, has N concentrations of around 2.8 – 3.0% and crude protein contents of 17 – 18% (Anon. 1973; Hacker and Teitzel 1992). It is sensitive to cercospora leaf spot (*Cercospora* sp.), foliar blight (*Rhizoctonia solani*) and legume little leaf virus but these do not cause significant damage to well grazed swards. Cattle live weight gains of greater than 785 kg/ha/year on pangola grass/*D. heterophyllum* and signal grass/*D. heterophyllum* mixtures stocked at 4.1 head/ha have been reported at South Johnstone Research Station (Annon. 1990; Hacker and Teitzel 1992).

Desmodium intortum (Miller) Urban.
Synonyms: *Hedysarum intortum*, *Desmodium aparines*
Common name: Greenleaf Desmodium

Native to the Americas from southern Mexico to southern Brazil *D. intortum* favours a well-distributed rainfall of over 875 mm and usually requires more than 1100 mm of rainfall per year. It will grow on a range of soils from sands to clay loams, provided they have a pH greater than 5.0 and are not saline (Skerman *et al.* 1988; Hacker 1992c).

It is a large trailing/scrambling, tap-rooted perennial that roots at the nodes if in contact with moist soil, and has long, freely branching stems, densely covered with short, hooked hairs, which are sticky to the touch. Leaves are trifoliate, with leaflets usually ovate, 3 – 12 cm x 1.5 – 7 cm, often with a reddish-brown to purple flecking on the upper surface (Skerman *et al.* 1988; Hacker 1992c). Flowers are deep lilac or pink in a terminal raceme that is up to 20 cm long (Evans and Macfarlane 1990). Containing 8 – 12 seeds, the pod is covered with short hooked hairs that can adhere to animals and clothing, is slightly indented along the upper margin and more strongly on the lower margin between articles that are 3 – 7 mm long, with the pod breaking up at maturity. Seeds are kidney-shaped and 2 x 1.3 mm in size (Anon. 1972a; Skerman *et al.* 1988; Hacker 1992c).

Desmodium intortum combines well with a number of grasses such as *Setaria* spp., *Paspalum commersonii, Panicum maximum, Pennisetum purpureum, Melinis miutiflora,* and *Pennisetum clandestinum* and *Digitaria eriantha* if adequately fertilised (Younge *et al.* 1964). It will suppress weeds when well established but does so poorly during the early stages of growth (Boultwood 1964). Cattle grazing *D. intortum* were observed by Bryan (1966) to normally remove the terminal part of the shoot and then browse the leaves which left large numbers of axillary buds that ensured rapid regrowth. However if grazing is intermittent and intense, a greater proportion of buds and stems may be removed with a much slower recovery from grazing as the result. Hacker (1992c) indicates that it is eliminated from pasture by frequent close cutting or heavy grazing, and even in a suitable environment may only persist for 5 – 10 years. Dry matter yields of 12.5 – 19 t/ha have been recorded in the past (Roe and Jones 1966; Whitney *et al.* 1967), with N concentrations ranging from 2 – 4.2 %, in-vitro digestibility of 52.5 – 60% with tannin levels in leaves of 3 – 9% and 1.5 – 3.7% in the stems, which may contribute to the slightly low in-vitro digestibility values (Anon. 1972a; Skerman *et al.* 1988; Hacker 1992c). It is susceptible to extended dry periods and carries little foliage during the dry season when it sheds most of its leaves (Horell 1958 cited by Skerman *et al.* 1988). The greatest deficiencies in the species are reported to be its low seedling vigour, poor drought and salinity tolerance, its relatively low digestibility and tendency to be grazed out unless fertilised. However despite its restricted range of adaptation, in areas where it is suited it is a productive legume capable of fixing substantial amounts of N, with Whitney (1970) reporting over 300 kg N/ha/year fixed by *D. intortum* in Hawaii.

Desmodium ovalifolium Wallich ex. Merill
Synonyms: *Desmodium polycarpon* var. *ovalifolium*, *D. heterocarpon* ssp. *heterocarpon* var. *ovalifolium*

Desmodium ovalifolium is a perennial sub-shrub or creeping stoloniferous herb, growing up to 1 – 2 m tall. Stems are many branched with a silky pubescence on young portions and old stems becoming woody at the base. Leaves may be 1 – 3 foliate but in young plants leaves are always unifoliate. Leaflets are round, oval or obovate with the terminal leaflet larger than the two laterals, all glaborous on the upper surface. The inflorescence is a densely flowered raceme with purple or deep pink flowers that turn bluish after anthesis. The pod is a lomentum, densely pubescent, dehiscent, composed of 2 – 8 almost quadrate articles 2.5 – 3.5 mm long (Bogdan 1977; Skerman *et al.* 1988; Schultze-Kraft 1992b).

Originating in tropical south-east Asia, *D. ovalifolium* is well adapted to the humid and sub-humid tropics with no more than 2 – 3 consecutive dry months and an annual rainfall of 2000 mm or more (Skerman *et al.* 1988; Schultze-Kraft 1992b). Growing well on a range of soils from those with light textures through to poorly drained, heavy textured soils, it is well adapted to acid, low fertility soils with high Al saturation and low levels of available P (Imrie *et al.* 1983; Schultze-Kraft 1992b). It combines well with sward forming grasses such as *Brachiaria humicicola* (Koronivia grass) and can withstand heavy grazing due to its stoloniferous habit (Reynolds 1995). Yields of between 2 – 3.5 t/ha per 12 weeks have been obtained on acidic, infertile soils with adequate moisture, while on sites of greater fertility yields of 6 t/ha per 12 weeks have been recorded (Schultze-Kraft 1992b). However one of the major failings of the species is the moderate – low palatability of forage that is caused by high concentrations of anti-nutritional compounds such as tannins (Schmidt and Schultze-Kraft 2000).

The diseases *Sclerotium salmonicolor* (Pink disease), *Meliodogyne javanica* (Root-knot nematode), *Pterotylenchus cedidogenus* (a stem-gall nematode) and *Synchytrium desmodii* (a false rust or wart disease) have been reported as problems in the past (Grof 1982; Schultze-Kraft 1992b; Reynolds 1995). It is also indicated to have a good drought tolerance by Skerman *et al.* (1988).

Desmodium scorpiurus (Sw.) Desv.
Synonym: *Hedysarum scorpiurus*

Widespread in the tropics, *D. scorpiurus* originated in tropical America and is a straggling, climbing or procumbent herb that is vigorous and widely adaptable. Racemes are up to 10 cm long with few small, blue flowers approximately 4 mm long forming 5 – 8 seeded pods that break into segments when dry and ripe. It forms a good mixture with short grasses such as *Axonopus* and *Paspalum* and spreads rapidly due to the ability of pods to adhere to animals (Skerman *et al.* 1988). It is a very palatable species with protein levels of 19.3% and a digestibility of 44.7% (Miller and Rains 1963 cited by Skerman *et al.* 1988) and is able to withstand treading by stock.

Desmodium triflorum (L.) DC.
Synonyms: *Meibomia triflora, Desmodium bullamense*, *Hedysarum triflorum*, *Desmodium parvifolium*
Common names: Tropical Clover, Three-flowered Beggar Weed, Small Leaf Desmodium

A creeping, prostrate, annual or perennial herb which can form dense mats, *D. triflorum* has a pan-tropical distribution. It has a woody rootstock with a long taproot with stems 8 – 50 cm long, that may root at the nodes. Leaves are trifoliate with obovate leaflets 4 – 12 mm in size, although leaves may be occasionally unifoliate. Flowers are blue, pink, or purple in colour, approximately 5 mm long and borne in groups of 1 – 3 in leaf axils. The pod is articulated, constricted between articles (2 – 3.5 mm long and wide), indehiscent with strong reticulation, containing seeds approximately 1.2 x 1.7 mm in size (Skerman *et al.* 1988; Pengelly 1992b; Reynolds 1995).

It is widespread in the wet tropics and often found growing in lawns and native pastures (Skerman *et al.* 1988). It appears to be well adapted to a wide range of soils and is drought tolerant although not able to withstand extended dry periods (Pengelly 1992b). *Desmodium triflorum* is very resistant to grazing or cutting and produces palatable dry matter of 2-3% N, with crude protein values of 13.5% and 18% (Otero 1952; Bermudez *et al.* 1968 both cited by Skerman *et a.* 1988). The major deficiency with *D. triflorum* is that it produces very little dry matter, which seriously detracts from its value as a species for forage production.

Desmodium uncinatum (Jacq.) DC.
Synonyms: *Meibomia incinata*, *Hedysarum uncinatum*
Common names: Silverleaf Desmodium, Silverleaf Spanish Clover

Indigenous to northern Argentina, Brazil and Venezuela, *D. uncinatum* is a large rambling perennial herb with trailing stems up to several metres long, densely covered in short hooked hairs, making stems sticky to the touch. Stems will form roots if in contact with soil and will scramble, but not climb, through surrounding vegetation. It may form a taproot of over 2 cm in thickness. The trifoliate leaves are alternate, ovate 3 – 6 cm x 1.5 – 3 cm wide, with a narrow, elliptical silvery shiny area about the midrib on the upper surface. Flowers are pink, 7 – 12 mm long and borne in a terminal or axillary raceme that is up to 50 cm long. Pods are sickle shaped, 10 – 50 x 3 – 4 mm, slightly indented on the upper margin with up to 12 articles that break easily at maturity and may adhere to animals and clothing due to hooked hairs (Anon. 1972b; Skerman *et al.* 1988; Hacker 1992a; Reynolds 1995).

A summer growing species which requires an annual rainfall greater than 1000 mm, well distributed throughout the growing season and adapted to a wide range of soils from sands to clays, it has been found to be productive on red basaltic loams and on gleyed podsolic soils (Mears *et al.* 1964). It will grow between pHs of 5.0 – 7.0, but does not tolerate salinity (Skerman *et al.* 1988). Establishment and growth in the first year is slow but after this period it can produce yields of up to 15 t/ha of dry matter (Risopoulos 1966), and is more persistent and productive on reasonably well drained and fertile soils (Anon. 1972b). Intensive stocking for short periods of time can cause considerable runner damage as cattle initially eat young terminal shoots followed by leaves and finally the stolons. Grazing or cutting to less than 10 cm will result in the disappearance of the legume from pasture. Stock may take some time to become used to grazing *D. uncinatum* as palatability is not high (Hacker 1992a). It combines well with a number of summer-growing sward forming grasses such as *Paspalum notatum, Setaria sphacelata* and *Paspalum plicatulum* (Andrews and Bryan 1958). It is subject to attack in Australia by weevil larvae of *Amnenus* and *Leptopius,* which can damage or possibly sever the taproot, resulting in an increased susceptibility to water stress which, under ordinary circumstances, is poor (Skerman *et al.* 1988; Hacker 1992a). It is also very susceptible to little leaf virus but it usually only affects isolated plants, which recover rapidly under favourable conditions (Hutton and Grylls 1965; Hacker 1992a).

A robust plant that spreads rapidly and can fix up to 160 kg/ha/year of N, *D. intortum*'s main deficiencies are its limited range of adaptation and inability to withstand heavy grazing, but under suitable conditions it is a productive legume (Skerman *et al.* 1988; Hacker 1992a).

Flemingia macrophylla (Willd.) Mar.
Synonyms: *Flemingia congesta*, *F. latifolia, Moghania macrophylla*

Flemingia macrophylla is a woody/erect shrub up to 4 m tall, with branches triangular when young and almost round when older. Leaves are digitally trifoliate with lanceolate leaflets 6 – 16 x 4 – 7 cm and veins covered in silky hairs. Flowers have a greenish standard with red blotches or stripes and are arranged in a dense axillary raceme. It produces two seeded pods, oblong and inflated, covered in fine glandular hairs, dark brown in colour and dehiscent. Seeds are shiny black, round and 2 – 3 mm in diameter (Skerman *et al.* 1988; Budelman and Siregar 1992).

With a natural habitat along watercourses, it is capable of surviving on very poorly drained soils subject to waterlogging. Originating in south-east Asia, Taiwan, southern China, India, Sri Lanka and Papua New Guinea, *F. macrophylla* occurs within a wide range of rainfall patterns, from 1100 – 2850 mm/year but cannot tolerate long dry spells (Budelman and Siregar 1992).

Plants require good weed control when young and are slow to establish, although once they have done so, require little attention. Leaf material has N concentrations of between 2.3 – 3.8%, although digestibility is reported to be much lower than that of *Leucaena leucocephala*. An average yield of 12 t/ha of leaf dry matter was obtained on the Ivory Coast, although it is reported that more typical yields are around 8 t/ha in south-east Asia . Leaf material decomposes slowly and as a result is useful as a mulch for the control of weeds and erosion (Budelman and Siregar 1992).

Macroptilium atropurpureum (DC.) Urban.
Synonym: *Phaseolus atropurpureus*
Common names: Siratro, Purple Bean, Atro

This is a deep rooted perennial herb with twining stems that may root anywhere along their length, especially on moist clays. A climber that mixes well with a number of grasses, it has trifoliate leaves, often 2 – 3 lobed, slightly hairy on the upper surface and silvery and very hairy on the lower surface. Lateral leaflets are obtuse, ovate or rhomboid, 2.5 – 8 cm x 2.5 – 5 cm and often asymmetrically lobed. The inflorescence is a raceme 10 – 30 cm long with 6 – 10 dark purple flowers approximately 2 cm long and crowded at the apex. The cylindrical pods are approximately 8 cm long, violently dehiscent, usually with 10 seeds that are 3 – 4 mm long and light brown to black in colour (Skerman *et al.* 1988; Jones and 't Mannetje 1992b; Reynolds 1995).

Growing best under 700 – 1500 mm annual rainfall, *M. atropurpureum* has been found in areas receiving as little as 250 mm per year. It grows on a wide range of soils, with the exception of poorly drained soils (Davies and Hutton 1970). *Macroptilium atropurpureum* has good drought tolerance and performs best in areas receiving more than750 mm of rainfall, however it is not suited to the wet tropics (>1750 mm rainfall) as productivity and survival are greatly reduced by *Rhizoctonia* leaf rot (Kretschmer 1966; Bogdan 1977; Steel *et al.* 1980b; Whiteman 1980; Skerman *et al.* 1988; Jones and 't Mannetje 1992b). It requires available soil P levels of at least 10 mg/kg or preferably 15 mg/kg (bicarbonate extraction), will grow on soils of pH 4.5 – 8.0, and is one of the best tropical legumes for use under moderately saline conditions (Skerman *et al.* 1988; Jones and 't Mannetje 1992b).

Dry matter yields of nearly 8 t/ha have been reported, with mixtures of *M. atropurpureum*/grass giving yields of up to 12 t/ha although *M. atropurpureum* seldom makes up more than 30% of the dry matter (Van Rensburg 1967; Jones and 't Mannetje 1992b). However it has a tendency to shed leaves and the death of stems in response to water stress during the dry season, with Jones (1967) reporting a 75% loss of dry matter and over 80% of nitrogen, in *M. atropurpureum* over 2 winter periods. Nitrogen concentrations in *M. atropurpureum* range from 2 – 4%, with dry matter digestibility of 50.4%, and 60 – 70% in young material and falling as low as 45% in older material with a lower leaf content (Skerman *et al.* 1988; Jones and 't Mannetje 1992b). Material produced by *M. atropurpureum* is palatable to stock although cattle have been observed to prefer *Panicum maximum* early in the growing season (Stobbs 1969).

A very useful legume with a fairly wide area of adaptation, good yields of palatable and nutritious dry matter, the major deficiencies in *M. atropurpureum* include a low cold tolerance, an inability to withstand heavy grazing and its decline under frequent cutting (Skerman *et al.* 1988; Jones and 't Mannetje 1992b).

Macroptilium lathyroides (L.) Urban.
Synonyms: *Phaseolus lathyroides, P. semi-erectus, P. crotalariodes*
Common names: Phasey Bean, Murray Phasey Bean, Wild Pea Bean

This is a herbaceous annual or short-lived perennial, 0.5 – 1.5 m tall, erectly branching with the base of the stem becoming slightly woody, sometimes becoming trailing or twining, especially under shade or when grown with tall grasses. The terete stems are covered in long, deciduous, reflexed hairs. The trifoliate leaves have ovate or lanceolate, unlobed leaflets 3.5 – 7.5 cm long. The inflorescence is a raceme that is either erect or semi-erect, up to 15 cm long, flowers red to purple in colour, approximately 1.5 cm long, forming sub-cylindrical pods, 7.5 – 10 cm long and 3 mm wide, containing 18 – 30 oblong to rhomboidal seeds, 3 mm long and light and dark brown in colour. The pod is violently dehiscent (Anon. 1972c; Skerman *et al.* 1988; Jones and 't Mannetje 1992a).

Macroptilium lathyroides originated in tropical America and is now widespread and naturalised in the tropics. It is adapted to rainfall from 475 – 3000 mm per annum, is fairly tolerant of waterlogging and also escapes drought through its free-seeding habit (Skerman *et al.* 1988; Jones and 't Mannetje 1992a). It is also adapted to a wide range of soils from sands, given reliable rainfall, through to heavy clays, which may be acid to alkaline in pH, and is fairly tolerant of salinity. *M. lathyroides* may be cut or grazed, however it will not tolerate heavy grazing or close cutting and seeding may be greatly reduced or eliminated as a result. It was found by Paltridge (1955) that, under continuous grazing, *M. lathyroides* did not persist and that it should be rested for 6 – 8 weeks during the summer growing period as it was selectively grazed during the early growth period. Although it seeds readily, recruitment is usually poor and as a result persistence is poor in permanent pastures after the second year (Jones and 't Mannetje 1992a). Dry matter yields of 13 t/ha have been reported 90 days after sowing, with up to 15 t/ha of green material reported by Crowder (1960) (cited by Skerman *et al.* 1988) when cut at a height of 1.25 – 1.5 m. Material produced by *M. lathyroides* has a high feeding value with crude protein levels of between 7.6 - 19.2%. N contents vary from 1%, after the loss of most leaves, to 4% in young vegetative material with a digestibility between 40 – 70% (Milford 1967; Skerman *et al.* 1988). It is susceptible to attack from Bean Fly (*Melanagromyza phaseolin*) at the seedling stage, to Phaseolus virus 2, root-knot nematode (*Meloidogyne javanica*) and to mildew (Skerman *et al.* 1988; Jones and 't Mannetje 1992a).

Macroptilium martii (Benth.) Marchal & Baudet

Macroptilium martii is an annual herbaceous plant with a trailing/scrambling habit. Leaves are trifoliate and, along with the stems, covered in fine, soft white hairs. Axillary inflorescences have paired orange-red flowers which give rise to paired pods with a curved hook at the tip and a prominent beak. The pods contain 2 – 5 kidney-shaped seeds, light brown or mottled grey in colour and 2 – 4 x 1 – 2 mm in size (Ossiya 1993; Amar 1996).

Found in Brazil, Bahia and Paraguay, *M. martii* is confined to dry areas receiving 380 – 664 mm of rainfall per year (Burt *et al.* 1979; Lewis 1987; Amar 1996). It has been found to grow on soils of sandy to clay texture, preferring deeper soils. Burt *et al.* (1979) indicated that the species was not found upon soils of low fertility and high acidity and suggested that it is probably best suited to more fertile soils or where fertiliser may be applied. Dry matter was found by Silva and Faria (1989) (cited by Amar 1996) to reach 2.56 t/ha on a podsolic soil low in P in Brazil, a yield almost 1 t/ha greater than that of Siratro. It is also indicated by Oliveria and Silva (1988) (cited by Ossiya 1993) to yield more heavily than either *Cajanus cajan* or *Clitoria ternatea,* however the quality of material produced is inferior with crude protein levels found to be approximately 10% as opposed to 20% and 24% respectively.

Macrotyloma axillare (E. Mey.) Verde
Synonyms: *Dolichos axillaris, Clitoria vividiflora*
Common names: Axillaris, Perennial Horse Gram, Archer Axillaris

A trailing and twining perennial herb, *M. axillare* has cylindrical stems with appressed hairs, trifoliate leaves, with bright green, ovate leaflets 1.1 – 7.5 x 0.7 – 4.2 cm in size. *Macrotyloma axillare* has a strong woody taproot with trailing stems. Greenish yellow flowers are borne on a short axillary raceme, the pod is slightly curved, linear-oblong 3 – 8 cm long containing 5 – 9 seeds. The seeds are smooth and hard with light or dark mottling (Davies and Hutton 1970; Anon. 1972e; Skerman *et al.* 1988; Staples 1992b).

Three varieties of *M. axillare* have been recognised: var. *axillare* and var. *glabrum* both of which have flowers 1.2 – 1.5 cm long, and var. *macranthum* with flowers 2 – 2.4 cm long. Cultivar Archer is indicated by Staples (1992b) to be close to var. glabrum and this variety. *M. axillare* var. glabrum cv. Archer has a natural distribution through central and southeast Africa, and has become naturalised in many small areas of eastern Australia and Papua New Guinea (Blumenthal and Staples 1993). It is a summer growing, short-day plant best adapted to areas receiving more than 1000 mm annual rainfall, on well drained soils (Anon. 1972e; Cameron 1986). It is not suited to heavy clays, infertile, acid soils, solodic soils, nor will it tolerate water logging or salinity (Staples 1992b). It has a good drought tolerance and is very heat tolerant (Luck and Douglas 1966).

Macrotyloma axillare has been found to compete well with weeds once established and has a moderate tolerance of grazing and trampling, but will not tolerate heavy grazing (Farinas 1966; Tutt and Luck 1969; Skerman *et al.* 1988; Staples 1992b). Parberry (1967b) obtained a dry matter yield of 15.5 t/ha under irrigation in the Kimberly region, while without irrigation yields of 3 – 4 t/ha were obtained. The N content of material produced by *M. axillare* was found to be 2% during the early wet season, falling to 1% during the dry season. Similarly crude protein was 11.9% during full growth, but fell to 6.2% when seeding (Parberry 1967a). Early growth has been reported to be unpalatable to stock which can aid its persistence in pasture (Skerman *et al.* 1988; Staples 1992b). It is reported by Staples (1992) to have a bitter taste, which may cause it to be rejected by stock until they become used to it. It may also taint the meat of lambs when fed as a large part of their diet for a long period of time and may taint milk under similar circumstances.

Neonotonia wightii (Wight and Arnott)
Synonyms: *Notonia wightii, Glycine javanica, Glycine wightii*
Common names: Glycine, Perennial Soy Bean

Neonotonia wightii has a natural distribution ranging from Africa to Asia, but it is now present in many humid tropical and sub-tropical regions of the world. It is a herbaceous twining or climbing plant with a strong taproot and a woody base with slender well branched stems with runners frequently rooting at the nodes. Under grazing, stems may arise from a crown below the soil surface. Leaves are trifoliate with ovate to elliptical leaflets that are glabrous to densely hairy on both sides. Racemes are 4 – 30 cm long and contain clusters of 20 – 150 white or violet flowers. The hairy pods are straight or slightly curved, bearing 3 – 8 seeds, which vary in colour and size depending on variety (Anon. 1972d; Bogdan 1977; Skerman *et al.* 1988; Pengelly and Benjamin 1992).

Neonotonia wightii is best adapted to areas receiving between 750 – 1500 mm annual rainfall and has a degree of drought tolerance. It prefers deep, friable, well drained soils with a pH above 6.0, but is not suited to very wet or waterlogged conditions (Pengelly and Benjamin 1992; Reynolds 1995). It combines well with grasses such as *Pennisetum purpureum, Panicum maximum, Melinis minutiflora, Chloris gayana* and *Setaria anceps,* but only lasted two years when grown with Signal grass (*Digitaria decumbens*) in Brazil (Skerman *et al.* 1988; Reynolds 1995). Initially establishment is slow, but after this period the species is reasonably persistent (Whiteman 1980). However due to its climbing habit it is susceptible to heavy grazing. It produces a highly nutritious and moderately palatable forage with Skerman *et al.* (1988) indicating that it compares favourably with the best quality Lucerne and Alfalfa hay. Concentrations of between 2 – 4.2% N and dry matter digestabilities of 55 – 61% have been reported (Holder 1967). *Neonotonia wightii* may produce up to 4 – 5 t of dry matter/ha/year when grown in a sward with grass, and up to 10 t/ha/year if grown in a pure stand (Pengelly and Benjamin 1992).

Pueraria phaseoloides (Roxb.) Benth.
Synonyms: *Pueraria javanica, Dolichos phaseoloides, Pueraria phaseoloides* var. *javanica*
Common names: Puero, Tropical Kudzu

Originating in the lowlands of East and Southeast Asia, *P. phaseoloides* is a very vigorous climbing perennial with hairy stems and leaves and sub-tuberous roots. Stems may extend 4.5 – 10 m, rooting at the nodes if in contact with moist soil and also forming lateral branches at the nodes. As a result a tangled mass of vegetation 60 – 75 cm thick may form within 8 – 9 months of sowing. Trifoliate leaves are borne on hairy petioles 2 – 13 cm long, with triangular-ovate, shallowly lobed leaflets. Flowers are mauve-deep purple and are produced on axillary racemes, 15 – 30 cm long, held above the plant. The straight or slightly curved pods contain 10 – 20 oblong-squarish seeds, roughly 3 x 2 mm in size, brown to black in colour (Skerman *et al.* 1988; Halim 1992a; Reynolds 1995).

Initially seedlings of *P. phaseoloides* are only moderately vigorous and may grow slowly for the first 3 or 4 months, however once established it is very vigorous and quickly smothers weeds and may climb fences and trees (Halim 1992a). Able to grow on a wide range of soils, with the exception of very heavy clays and coralline areas, *P. phaseoloides* prefers areas with a rainfall greater than 2500 mm per annum but can tolerate short dry periods as well as acidic and waterlogged soils (Skerman *et al.* 1988; Reynolds 1995). It grows well with the grasses *Brachiaria. subquadripara, M. minutiflora, Panicum maximum* and *P. purpureum* but is unable to persist with *B. decumbens* or *Digitaria. eriantha. Pueraria phaseoloides* is very palatable to stock and as a result it may be selectively grazed. It is moderately tolerant of defoliation and recovers well after lenient grazing and should be grazed in this manner to maintain botanical composition. Yields of up to 10 t/ha of dry matter have been obtained in the past in pure swards, while in conjunction with *Melinis minutiflora* a total dry matter yield of 22.8 t/ha was obtained with *P. phaseoloides* contributing 9.1 t/ha (Vicente-Chandler *et al.* 1953; Halim 1992a). The material produced by *P. phaseoloides* typically has N concentrations in the range of 2 – 4% (Dijkstra and Dirven 1962; Butterworth 1963; Halim 1992a).

Rhynchosia minima (L.) DC.
Synonyms: *Dolichos minimus, Glycine rhombea*
Common names: Rhynchosia, Burn Mouth Vine, Least Rhynchosia

A climbing or sub-erect perennial species that may be glabrous to slightly pubescent. Slender stems are numerous and may be up to 120 cm long. It has trifoliate leaves with ovate-rhomboid leaflets 0.5 – 3 x 0.5 – 3 cm in size, which are glabrous to velvety. The yellow flowers are held in a 6 – 12 flowered raceme. The pods contain 2 seeds, black when ripe and 1 – 1.5 x 0.4 – 0.6 mm in size (Skerman *et al.* 1988).

Rhynchosia minima tends to occur on heavier textured soils, particularly those high in lime and phosphorus, and has been found to grow in association with Mitchell grass (*Astrelba* spp.) and *Dicanthium sericrum* in the 450 – 750 mm rainfall area of Australia (Skerman *et al.* 1988). There have been mixed reports in relation to *R. minima's* palatability and probably due to the large number of ecotypes that exist. It was found to be readily eaten by cattle when young but became fibrous and coarse when mature (Hassell 1945). It was indicated by Beeston (1978) to be highly palatable while Boyland (1974) ranked its palatability as moderate. A crude protein level of 15.1% and a dry matter digestibility of 60% is given by Skerman *et al.* (1988), who also notes that it has a degree of tolerance of salinity.

Stylosanthes guianensis (Aubl.) Sw.
Synonyms: *Stylosanthes hispida, S. gracilis* var. *subviscosa, S. pohliana, Trifolium guianense*
Common names: Common Stylo, Stylo, Brazilian Lucerne

Naturally occurring from northern Argentina to Mexico, *S. guianensis* var. *guianensis* has been introduced into the tropics throughout the world. A semi-erect to erect herb or sub-shrub, *S. guianensis* is a summer growing species with a strong taproot and hairy, branched stems, which become woodier at the base with age. The leaves are trifoliate with elliptical leaflets between 15 – 55 mm. The yellow-orange flowers are borne in a loosely capitate, terminal or axillary spike. The hairy pods have one fertile joint and a very small beak, pale brown or purple in colour and are 2 – 3 x 1.5 – 2.5 mm in size (Skerman *et al.* 1988; Reid 1990; 't Mannetje 1992).

S. guianensis is particularly well suited to acid soils of low fertility and is able to withstand high Al and Mn concentrations, and performs well on coarser textured soils but not heavy clays (Skerman *et al.* 1988; 't Mannetje 1992). One of the main advantages of *S. guianensis* is its ability to grow on poor soils with a phosphorus requirement of only 0.17% (Andrews and Robins 1969a). Some authors suggest it is adapted to rainfalls ranging from 900 – 4000 mm per year and to have good drought tolerance (Skerman *et al.* 1988; Reynolds 1995), although ‘t Mannetje (1992) indicates that it is not drought tolerant, but all agree that it is able to withstand temporary waterlogging. It has been successfully grown with the grasses *Digitaria decumbens, Chloris gayana, Melinis minutiflora* and *Setaria anceps* but was shaded out by *Brachiaria decumbens, B. brizantha, Panicum maximum* and *P. coloratum,* and only lasted two years with *B. mutica* (Whiteman 1980). Once established *S. guianensis* is able to compete successfully with weeds due to its low palatability in the early stages of growth and its heavy seeding habit (Horrell 1963 cited by Skerman *et al.* 1988; Reynolds 1995). Yields of *S. guianensis* have reached up to 11 t/ha in pure stands while in mixed swards it has contributed from 2 – 6 t/ha varying with soil moisture and fertility (Gilchrist 1967; 't Mannetje 1992). *S. guianensis* is not adapted to heavy grazing and may become more prostrate under grazing. It was found by Grof and Harding (1968) that harvesting at a frequency of 18 weeks caused the lower stems to become woody with nearly the complete loss of the stand. Cattle will initially graze leafy material, then move lower down with each subsequent grazing until the woody parts of the plant are consumed and damage results as there are very few growing points on plants as they mature (Skerman *et al.* 1988). Crude protein levels in whole *S. guianensis* plants range from 12.1 – 18.1% with dry matter digestibility of 48.4% (Scaut 1959 cited by Skerman *et al.* 1988; Allen and Cowdry 1961).

Stylosanthes hamata (L.) Taub.
Synonyms: *Hedysarum hamatum, Stylosanthes procumbens*
Common names: Caribbean Stylo, Pencil Flower, Mother Segal

Native to the drier parts of the Caribbean Islands, the coastal areas of South and Central America, and southern Florida, *S. hamata* is a herbaceous annual or short lived perennial. Branching is non-determinate with a line of ascending whitish indentum changing sides at each internode but glabrous elsewhere. Leaves are trifoliate with narrowly elliptical-lanceolate leaflets with the central leaflet 16 – 26 x 3 – 6 mm in size. The inflorescence is terminal or axillary, indeterminate, bearing up to 8 – 14 flowers. Terminal inflorescences have 2 – 3 alternate spikes. Flowers are yellow with the standard having a reddish marking. The fruit is a lomentum that usually contains two fertile articles, medium to dark brown in colour, 6 –7 mm long, with a distinctly curved beak 3 – 4 mm long (Skerman *et al.* 1988; Edye and Topark-Ngarm 1992b).

Well adapted to the semi-arid and sub-humid tropics, *S. hamata* is suited to regions with short variable growing seasons. An annual rainfall of 700 – 900 mm is preferred although it will grow under rainfalls of 500 – 2000 mm per year, however a short pronounced dry season is required for optimum growth (Skerman *et al.* 1988). *Stylosanthes hamata* has good drought tolerance although it may drop leaves in order to ensure the survival of the crown and can avoid long dry seasons as hard seed (>97% when the average temperature is >24°C during seed formation), but this quickly breaks down when maximum diurnal soil temperatures reach 50 - 55°C just before the wet season (Edye and Topark-Ngarm 1992b). *Stylosanthes hamata* is able to grow on a wide range of soil types from sands to clay loams but not on heavy clays (Edye and Topark-Ngarm 1992b), while Skerman *et al.* (1988) indicates that soil requirements are fairly specific for each ecotype. It is particularly well suited to infertile, moderately acidic soils with very low phosphorus levels. Shaw *et al.* (1994) (cited by Amar 1995) found that a bicarbonate-extractable or weak acid extractable concentration of 8 ppm P was sufficient to obtain 80% of maximum growth of the cultivar Verano. However due to this ability to grow at very low levels of P, the application of P fertiliser or the provision of a supplement may be necessary to ensure adequate animal nutrition as the concentrations of P in herbage may fall below 0.12% (Edye and Topark-Ngarm 1992b). Nitrogen concentrations and in-vitro digestibility generally decline during the growing season with N concentrations in green leaves between 2.7 – 3.9% and whole plant material at flowering averaging 1.8%, with in-vitro digestibility from 33 – 57%. Yields of up to 10 t/ha of dry mater have been produced under high rainfalls and fertilisation, and it may comprise from 1 – 7 t/ha in mixed swards depending upon conditions (Edye and Topark-Ngarm 1992b). Able to withstand heavy grazing under which it may form a dense ground-hugging mat, *S. hamata* is more persistent under such conditions due to the reduction in competition from tall grasses (Skerman *et al.* 1988; Reid 1990).

Stylosanthes scabra Vog.
Synonyms: *Stylosanthes gloides, S. diarthra, S. plicata*
Common name: Shrubby Stylo

S. scabra is a shrubby, perennial legume, up to 2 m tall, with an erect to sub-erect habit, woody stems and a strong taproot. Stems are densely hairy, covered by short or long hairs with bristles and vary in colour from pale green to dark blue-green, brown or reddish. Leaves are trifoliate with elliptical to oblong, obtuse, mucronate leaflets, hairy on both surfaces, with the terminal leaflet 20 – 33 x 4 – 12 mm in size. The inflorescence is a broad, loosely formed, shortly elongated spike that occurs singly in leaf axils and is 1 – 3 cm long with several flowers each surrounded by a bract and 3 bracteoles. The fruit is a lomentum typically carrying two fertile seeds with a slightly curved beak and covered in short viscid hairs (Skerman *et al.* 1988; Edye and Topark-Ngarm 1992a).

S. scabra is a summer growing species that is very drought resistant and can survive long dry spells, and is useful in tropical areas receiving 600 – 1700 mm rainfall and having a short, variable growing season (Reid 1990). This is in part due to its deep taproot (up to 4 m long) and the ability of leaf tissue to withstand much lower water potentials than other species (Williams and Gardener 1984; Edye and Topark-Ngarm 1992a). It is very well adapted to infertile, moderately acidic, sandy surfaced soils that have very low P levels, especially solodics. *S. scabra* is able to grow on a wider range of soils than other stylos but it is not suited to heavy, black clays (Edye and Topark-Ngarm 1992a).

Once *S. scabra* is established it is very competitive and can successfully compete with most associated species. After grazing, regrowth occurs from buds along the aerial stems that are rarely removed due to their hard, woody nature. However when cut, the woody stems should not be cut too low as this will adversely affect regrowth and some plants will die, with regrowth occurring from buds or even slightly below ground level (Skerman *et al.* 1988; Edye and Topark-Ngarm 1992a). Yields of less than 1 t of dry matter/ha have been reported by Edye *et al.* (1984) to over 9 t/ha on solodic soils and red and yellow earths in high rainfall areas respectively. Material produced by *S. scabra* is described by Reid (1990) to be nutritious to stock, however Skerman *et al.* (1988) indicates that material grown on low fertility soils is very poor in quality. Leaves were found to contain 3% N, falling to 1.5% with age and the in-vitro digestibility from 70 to 50% (Edye and Topark-Ngarm 1992a).

Vigna luteola (Jacq.) Benth.
Synonyms: *Vigna marina, V. nilotica, V. bukombensis*
Common name: Dalrymple Vigna

A densely leafy, short-lived, climbing/trailing perennial, that is sparsely hairy and rooting at the nodes when in contact with moist soil. Leaves are trifoliate with ovate-lanceolate leaflets 2.5 – 10 cm in length and 1.5 – 5 cm wide. The many flowered axillary racemes contain yellow flowers 1.8 – 2.2 cm long. The pods are pendant, thin shelled, up to 5 cm long and 0.5 – 0.6 cm wide with waxy margins when dry, containing up to 6 brown to black seeds, 3 – 4 x 2 – 3 mm in size (Skerman *et al.* 1988; Reynolds 1995).

Vigna luteola is widely distributed in the tropics, preferring a rainfall of greater than 1250 mm and especially wet or swampy soils, as it is one of the best legumes for wet conditions (Bogdan 1977; Skerman *et al.* 1988). It will not tolerate dry conditions or drought. Friable soils allow *V. luteola* to root down well, but it does not have specific soil requirements and is also able to tolerate saline conditions (Hutton 1968). *V. luteola* has very vigorous seedling growth during the first year, which greatly aids establishment but after this period its performance may vary. It has been reported to make good growth with *Paspalum* and *Setaria* species, but does not tolerate heavy grazing or cutting. Material produced by *V. luteola* is very palatable to stock and has a crude protein range of between 12.1 – 19.9% (Andrews and Robins 1969b). One of the species' major problems is its susceptibility to insect attack, which includes leaf eating caterpillars and the bean fly (*Melanagromyza phaseloi*) that attacks seedlings (Skerman *et al.* 1988).

1.5 Conclusions

It is apparent that grazing livestock beneath tree plantations can result in several beneficial effects, including soil stabilisation, higher plantation yields through better weed control and nutrient cycling, an increased and diversified income and the accretion of nitrogen (Shelton 1991). The acceptance of tree-pasture systems in Australia has been hindered by the belief that productive pasture cannot be maintained beneath tree canopies. In order to address this, species of both grasses and legumes need to be identified that are productive and persistent beneath tree plantations and the levels of shade that are present in such systems

This study examines a range of legume species for some of the desirable qualities sought in a species for use in such systems. Most research in the past has focused upon species adapted to the wet tropics with much of the associated research conducted outside Australia. Secondly there has been very little work conducted on species adapted to the seasonally dry tropics where interest in establishing timber plantations has increased in recent years.

The objectives of the thesis were to examine the physiological and agronomic properties of a range of tropical pasture legumes under differing levels of shade, and to ultimately identify a number of legume species adapted to both the wet and the wet/dry tropics that would be suitable for use beneath tree plantations. The project aimed at identifying such species through examining the effects of differing shade levels upon plant characteristics such as above and below ground dry matter production, content of selected nutrients in leaves, root nodulation levels, seed production and properties, estimating plant shade adaptation via measurement of photosynthetic rates at a range of light intensities, performance of selected species under field conditions including dry matter production, pasture composition, and potential effects on soil moisture.

This thesis is divided into two sections, the first (Chapters 2 and 3) examine the performance of various species of legume adapted to both the wet and the wet/dry tropics beneath varying levels of shade under controlled conditions in shadehouse trials. The second section (Chapters 4 and 5) details the trialing of selected legume species under established tree plantations of varying age, in the wet and wet/dry tropics, to assess legume performances under field conditions. Conclusions drawn from the research are presented in Chapter 6.

Chapter 2 – Effects of shade on the comparative performance of forage legumes grown under glasshouse conditions- agronomic properties

2.1 Introduction

The major restraint 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 (1991) 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 grasses species, suited to the wet tropics. Very little information could be found relating to the shade tolerance of species of grass or 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 interested 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. Its 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 tolerant species tend to have greater longevity than those in high light environment 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

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

The aim of the shadehouse trials was to assess a selection of legume species, for which material was available, for the effects of shading upon a range of properties and their potential suitability for use beneath timber plantations. 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 the effects of shade on 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 following procedure was used for all pot trials, except for minor differences which will be noted where relevant.

Experimental site.

The experiment was conducted as a pot trial at the School of Tropical Biology, James Cook University, Townsville (19° 20’ S), which 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.

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). Levels were: control (no shade, approximately 40% shade relative to outside shadehouse), 63 (78% shade), 76 (86% shade) and 84% (90% shade) shade. The shade levels used in this study were heavy (78%) to very heavy (90%). From this point on levels of shade shall be expressed as a percentage of the control treatment, which will be refered to as “unshaded”even though it was only approximately 60% of outside sun. 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.

Figure 2.1 Maximum, minimum and mean air temperatures during trial period and long term average weather data. Graph constructed from data obtained from the Australian Bureau of Meteorology.

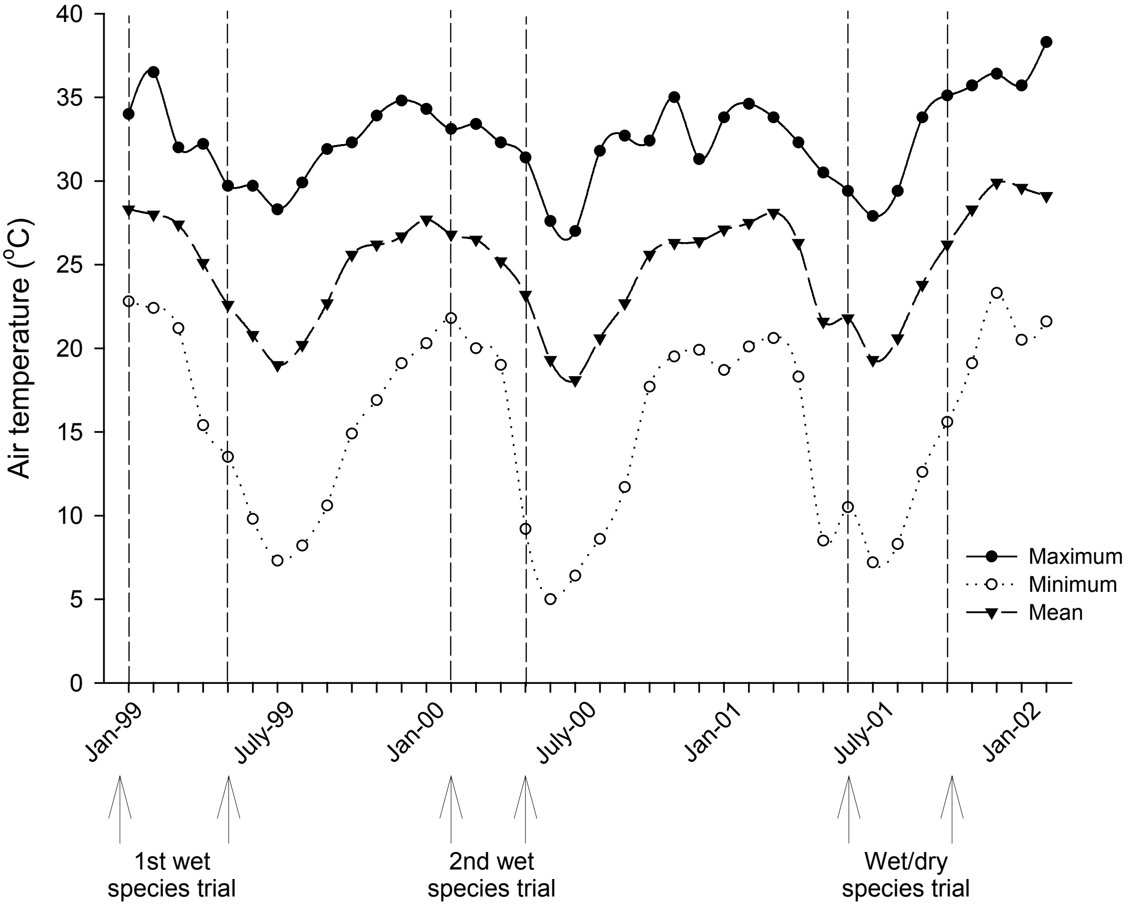

Table 2.1 Species of legumes tested for shade tolerance – species suited to the wet tropics tested in (a) January to May 2000, (b) tested in February to May 2001, and (c) the seasonal wet/dry tropics tested in June to October 2001.

(a)

First wet tropical species tested	**Cultivar/Accession**
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 tested	**Cultivar/Accession**
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. *paraguianensis* 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*.

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, shoot:root 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. Organic carbon was determined by Heanes (1984) method (Rayment and 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 and Higginson 1992).

Property	Concentration	SE	n
Organic matter	1.09	0.11	5
Total nitrogen (%)	0.291	0.020	15
Total phosphorus (%)	0.063	0.018	15
pH	5.44	0.06	15
Electrical conductivity (dSm^{-1})	0.517	0.019	15

The soil was passed through a 2mm 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 and 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 fertiliser “Thrive” (Yates Australia) at the rate of 8g 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.

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)

2.2.2 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, shoot:root 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 2mm 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 shoot:root ratio was determined (root mass divided by total above-ground biomass).

Leaf nitrogen and phosphorus content.

Leaf material (lamina and petiole) was hammer milled through a 2mm sieve and analysed for nitrogen and phosphorus using the methods of Anderson and 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 and Alley (1989), and phosphorus by adaptation of Murphy and Riley's (1962) single solution method (Anderson and 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 legume genotype and 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 Test (ISTA, 1985).

Seed from each species, under each light treatment, was pooled and then divided into four 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 mid- day 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) and 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 at*. (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_j' where "$n_i < 0.5(N+1) < n_j$".

Data for seed germination, seed production, size and number of seeds per pod were only obtained 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.

Statistical analysis

Data were analysed as a regression between shade blocks and by analysis of variance (ANOVA) within shade blocks with 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 varience.

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

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	-	-

2.3 Results

Summary of Results

Highly significant (P<0.0001) effects for, shade, species, shade x species interaction and shade regressions were found in all plant attributes with the exceptions of the species and interaction effect on shoot:root ratio, but these were still found to be significant (Tables 2.4 and 2.5) and number of days to first flower was not strongly affected in all categories. Where a ‘ – ‘ appears in a table it indicates that there was no result obtained for that specific field, usually due to the failure of any plants to have grown and/or survived until the trial’s end and these could not be included in any statistical analysis.

2.3.1 Above-ground Biomass

a) Effect of shade level

The shade treatments strongly affected yield of above-ground biomass in all trials with the greatest yields under full light (control, 0% shade) and the lowest beneath 84% shade. Figure 2.2 displays the overall relationship of above-ground dry matter production with increasing shade levels, with the two trials involving wet tropical species apparently more affected by shading than species adapted to the wet/dry tropics, showing a much greater decrease in production of above ground dry matter with increased shade.

b) Effect of legume genotype

First wet tropical species trial

Vigna luteola was the best overall producer of above-ground biomass, however it was not found to be statistically different from *D. intortum, C. mucunoides* or *M. axillare*. The species with the lowest yield across all light levels in the first trial was *D. canum*, but this was also not significantly different from three other species, *A. pintoi, D. ovalifolium* and *M. axillare* (Table 2.6).

Second wet tropical species trial

When averaged across all shade levels the greatest yields of above-ground biomass were produced by *P. phaseoloides*. Statistically *P. phaseoloides* was not significantly different from seven other species, with the second most productive species, *C. acutifolium,* averaging only 2.1g per plant less than *P. phaseoloides*. The lowest yielding species, *A. kretschmeri,* was also not statistically different from six other accessions. Many species were contained in more than one statistical grouping, with no clear boundary between high and low yielding species but instead a range of yields were found within the species examined (Table 2.6).

Wet/dry tropical species

Clitoria ternatea was clearly the greatest producer of above-ground biomass, with 63% more biomass than *A. stenosperma*, the second most productive species. This large difference in production was reflected in the statistical groupings, with *C. ternatea* significantly different from all other species (Table 2.6). There was a gradual decrease in yield among remaining species, with a large overlap in statistical groupings. The lowest overall yield of above-ground biomass was given by *D. virgatus,* however it was not statistically different from nine other species.

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.

	1st Wet Species Trial			**2nd Wet Species Trial**			**Wet/Dry Species Trial**		
Plant Attribute	**Shade**	**Species**	**Interaction**	**Shade**	**Species**	**Interaction**	**Shade**	**Species**	**Interaction**
Above-ground biomass	***	***	***	***	***	***	***	***	***
Root biomass	***	***	***	***	***	***	***	***	***
Total biomass	***	***	***	***	***	***	***	***	***
Shoot:root ratio	***	***	*	***	***	***	***	***	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)

Table 2.5 Summary of regression analysis of three shade house trials examining effects of shade on a range of properties in 35 accessions of tropical forage legume.

	1st Wet species Trial		**2nd Wet species Trial**		**Wet/dry Species Trial**	
Plant attribute	R Squared value	Significance	R Squared value	Significance	R Squared value	Significance
Above-ground biomass	0.5814	***	0.5445	***	0.3406	***
Root biomass	0.4300	***	0.4866	***	0.4047	***
Total biomass	0.5611	***	0.5642	***	0.3997	***
Shoot:root ratio	0.0732	**	0.0657	**	0.2035	***
Root nodulation	0.3045	***	0.6864	***	0.5413	***
Leaf N content	0.0947	***	0.4529	***	0.2451	***
Leaf P content	0.0160	n.s.	0.0662	***	0.0233	n.s.
Days to first flower	0.2120	*	0.0001	n.s.	0.1180	***

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

Figure 2.2 Regressions of overall production of above-ground biomass (means with standard errors), 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

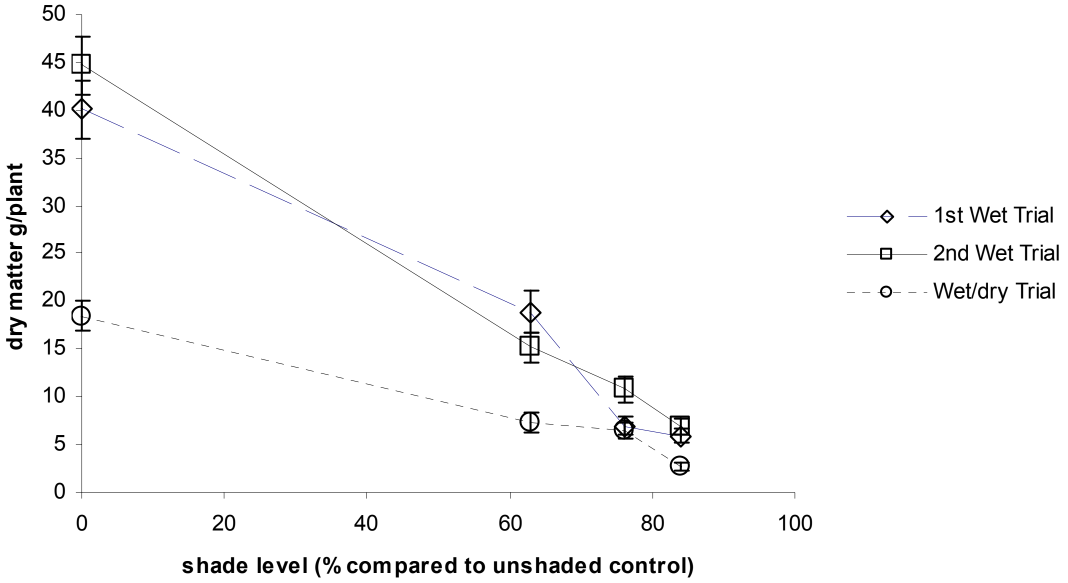

Table 2.6 Means, standard errors and LSD groupings of above-ground biomass (g per plant, oven dried at 70°c) production by (a) 7, (b) 14 and (c) 14 legume species grown under 4 shade levels, harvested 107, 103 and 119 days after planting respectively. n = 20, 16 and 16 respectively. Means in a column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

a)1st Trial

Species	**Above-ground biomass (g per plant)**
V. luteola	27.4 ± 5.4 a
D. intortum	24.4 ± 4.7 ab
C. mucunoides	24.0 ± 3.1 ab
M. axillare	17.9 ± 5.4 abc
D. ovalifolium	14.7 ± 3.5 bc
A. pintoi	10.1 ± 2.4 c
D. canum	9.7 ± 2.0 c
Probability	0.0052

b) 2nd Trial

Species	**Above-ground biomass (g per plant)**
P. phaseoloides	32.1 ± 5.7 a
C. acutifolium	30.0 ± 6.5 a
D. heterophyllum	28.8 ± 4.9 a
D. uncinatum	28.4 ± 4.2 ab
A. americana	26.4 ± 7.7 abc
C. pubescens	25.9 ± 4.5 abc
C. macrocarpum	20.3 ± 2.9 abcd
N. wightii	18.4 ± 5.5 abcde
S. guianensis	13.5 ± 5.6 bcde
A. villosa cv. Kret.	11.4 ± 4.1 cde
D. triflorum	10.3 ± 3.0 de
A. villosa	10.2 ± 5.9 e
F. congesta	4.8 ± 1.8 e
A. kretschmeri	3.2 ± 1.0 e
Probability	<0.001

c) 3rd Trial

Species	**Above-ground biomass (g per plant)**
C. ternatea	23.8 ± 3.8 a
A. stenosperma	15.1 ± 3.3 b
M. lathyroides	13.5 ± 1.8 bc
D. scorpiurus	12.8 ± 4.5 bcd
C. rotundifolia	9.8 ± 2.7 bcde
S. hamata	8.5 ± 3.2 bcde
R. minima	8.1 ± 1.8 bcde
M. atropurpureum	7.7 ± 1.0 cde
C. brasilianum	6.9 ± 1.0 de
A. paraguariensis	6.0 ± 1.8 de
C. pascuorum	5.7 ± 2.0 de
M. martii	5.6 ± 1.7 de
S. scabra	5.6 ± 1.8 e
D. virgatus	4.7 ± 0.9 e
Probability	<0.001

c) Interaction effects

First wet tropical species trial

A highly significant species by shade interaction was present. *Vigna luteola* was the best producer of above-ground biomass beneath full light (Table 2.7). Other species that performed well under full light included *D. intortum* and *M. axillare,* neither of which was found to be statistically different from *V. luteola*. *Arachis pintoi* was the lowest yielding of the species beneath full light but, despite being the lowest yielding species, plants were still large and growing well. Statistically *A. pintoi* was not significantly different from *D. canum*.

Statistical analysis revealed two clear groupings of species under 63% shade. The greatest yielding species remained *V. luteola* although the margin from the second highest yielding species, this time *C. mucunoides*, was only 2.4g. *A. pintoi* remained one of the lowest yielding species however it was noted that the plants grown beneath this shade level appeared to be in a much better condition than those grown under the control treatment.

Calopogonium mucunoides was the greatest producer of above-ground biomass under 76% shade followed by *D. intortum* and *V. luteola*. *Macrotyloma axillare,* however, experienced a large decrease in production, falling from having the third highest yield beneath 63% shade to having the lowest yield at 76% shade. *Macrotyloma axillare* clearly remained the lowest yielding species beneath 84% shade, despite not being statistically separate from three other low yielding species, *D. ovalifolium*>*D. canum*> *M. axillare*. *Calopogonium mucunoides* remained the best producer of above-ground biomass and was statistically the only species in the highest yielding LSD grouping beneath 84% shade. *Vigna luteola* gave the second highest yield of above-ground biomass, however it should be noted that the plants grown under 84% shade appeared sickly and weak. They had few leaves which had large necrotic patches. *Macrotyloma axillare* remained the lowest yielding species, with little change in yield from 76% shade and was statistically inseparable from *D. ovalifolium*>*A. pintoi*>*D. canum*.

Within species, full light gave the highest yields in all species and was the only treatment contained in the highest yielding LSD grouping, with the exception of *C. mucunoides* (Table 2.7 and Figures 2.2 a – d). *Calopogonium mucunoides* was the only species in which the 63% shade treatment was not statistically different from the control. In other species the 63% shade treatment was either contained in the second LSD grouping along with the 76% and 84% shade treatments (*A. pintoi, D. canum* and *D. ovalifolium*), or it was an intermediate grouping between the highest and the lowest yielding treatments (*D. intortum, M. axillare* and *V. luteola*). In all species the 76% and 84% shade treatments were not statistically different from one another.

Second wet tropical species trial

A highly significant shade by species interaction was present with the greatest yielding species under full sunlight being *C. acutifolium* followed by *A. americana* and *P. phaseoloides*. There was a gradual decline in the yields of the remaining species, with the lowest given by *A. kretschmeri*. Statistical analysis shows no clear groupings with five species contained in three LSD groupings (Table 2.8).

Pueraria phaseoloides was the highest yielding species under 63% shade but was not statistically separate from *D. uncinatum*> *D. heterophyllum*>*C. acutifolium*> *C. pubescens*> *C. macrocarpum*. Large reductions in yield were found in many species, with *A. americana* showing the greatest (53.8 g) while, *C. acutifolium, N. wightii* and *S. guianensis* also showed large reductions in yield (46.3, 47.7 and 42.8 g respectively). *Stylosanthes guianensis* produced only 4% of the dry matter yield under the control treatment. While *A. kretschmeri* appears to have the best production relative to full sunlight, this was not the case. The cuttings of *A. kretschmeri* used for this trial, failed to grow beneath full sunlight and 63% shade. While they did not die, they did not produce any significant amounts of new material. As a result the relative production of above-ground biomass under 63% shade relative to full sunlight appeared to be very large. Taking this into account *C. macrocarpum* and *D. uncinatum* were the species with the greatest yields relative to full sunlight (68.8% and 62.3% respectively). The lowest yielding species was *S. guianensis* that averaged 1.8 g dry matter per plant. *Aeschynomene villosa* had no surviving plants under this shade treatment by the time of harvest.

Individual species all experienced a reduction in yield with increased shading. With many species there was statistically no difference between yields of above-ground biomass under 76% and 84% shade, although in some cases the difference between the two treatments was quite pronounced (Table 2.8, Figure 2.2 e - h). *Aeschynomene villosa*, *Arachis kretschmeri* and *C. macrocarpum* displayed no significant difference in yields between any of the shade treatments. In the cases of *A. villosa* and *C. macrocarpum,* this was found despite large differences in yield between the control and one or more of the shade treatments.

Wet/dry tropical species

Under full sunlight *C. ternatea* was the most productive of the fourteen species adapted to the wet/dry tropics, but was not found to be statistically separate from *A. stenosperma*, the second most productive species (Table 2.9). The lowest yield of above-ground biomass under full light was given by *D. virgatus*, however it was not found to be statistically different from species which yielded up to 16.3 g per plant (*A. paraguariensis*). Eight of the fourteen species averaged yields between 16.6 and 10.5 g per plant. With the exception of *C. ternatea* and *D. virgatus* all remaining species belonged to two or more statistical groupings.

Clitoria ternatea was again the highest yielding species under 63% shade and statistically different from all other species. *Clitoria ternatea*'s production was nearly twice that of *M. lathyroides* the second most productive species,. The lowest yielding statistical grouping contained nine species, of which *S. hamata* produced the least above-ground dry matter, however only one plant of *S. hamata* had survived beneath 63% shade by the time of harvest. This failure to survive resulted in low numbers of replicates making statistical analysis of the species less reliable, however the death of plants of this species may be taken as an indication of a very poor adaptation to shading. This was further supported by the death of all plants of *S. hamata* beneath the 76% and 84% shade treatments.

Under 76% shade, C. *ternatea* and *M. lathyroides* remained the first and second greatest yielding species, respectively. Statistically no difference was detected between them. The statistical groupings of all species became less complicated than under the previous shade levels, with only three homogeneous groups detected. With the exception of *S. hamata* (no surviving plants), *S. scabra* yielded the lowest quantities of above-ground biomass. Again the statistical grouping with the lowest means contained a large number of species, with 10 other species displaying no significant difference to *S. scabra*. The highest yielding of these was *A. stenosperma*, the third highest yielding of the species tested under 76% shade.

The margin between *C. ternatea* and the second most productive species was much smaller than found in the other shade treatments (0.6 g per plant). *Arachis stenosperma* and *M. lathyroides* were the second and third best producers of above-ground dry matter beneath 84% shade, respectively. *Stylosanthes hamata* again had no surviving plants by the time of harvest, and *M. martii,* the second poorest yielding species, had only one surviving plant. No significant difference was found between any of the species beneath 84% shade (P = 0.1177), although some species clearly performed better than others, for example *C. ternatea, A. stenosperma* and *M. lathyroides* produced from ten to eleven times as much dry matter as *C. rotundifolia*.

Within species, increasing shade from 0% in the control treatment to 63% generally resulted in large decreases in the production of above-ground biomass (Table 2.9, Figure 2.3 i - l). Six species did not have significant differences in production between shade treatments, a larger number than in the previous two trials (0 and 2 species in the first and second wet tropical species trials respectively). There were also a number of marginally significant/non-significant species with probabilities close to 0.05 (*C. brasilianum, C, rotundifolia, M. atropurpureum* and *M. lathyroides* with P values of 0.0308, 0.0339, 0.0650 and 0.0614 respectively). In species where significant differences were present, the control treatment was, in all cases but one, the only shade treatment found in the highest yielding statistical grouping. *Centrosema brasilianum* was the exception to this with the control, 63% and 76% shade treatments contained in the first statistical grouping. Typically the three shade treatments were all contained in the second, lower yielding, statistical grouping even though in many cases the yields produced under 63% shade were many times that of the 84% shade treatment.

Table 2.7 Means, standard errors and LSD groupings of above-ground biomass (g per plant, oven dried at 70°c) produced by 7 forage legume species grown under 0 (control), 63, 76 and 82% shade (n = 5), harvested 107 days after planting. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly.

	Above-ground biomass (g per plant)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
V. luteola	61.1 ± 7.1 aA	32.7 ± 2.1 aB	7.9 ± 2.4 bC	7.7 ± 2.4 bC	<0.0001
D. intortum	52.5 ± 8.1 abA	24.6 ± 3.0 aB	9.8 ± 2.4 abC	7.4 ± 0.7 bC	0.0001
M. axillare	46.8 ± 3.6 abA	24.8 ± 5.7 aB	1.0 ± 0.2 cC	0.7 ± 0.2 cC	<0.0001
D. ovalifolium	38.4 ± 4.3 bcA	8.2 ± 0.6 bB	5.1 ± 1.0 bcB	5.2 ± 0.9 bcB	<0.0001
C. mucunoides	38.2 ± 4.6 bcA	30.3 ± 4.7 aA	13.4 ± 7.0 aB	12.6 ± 2.0 aB	0.0002
D. canum	24.2 ± 2.8 cdA	5.6 ± 0.5 bB	5.0 ± 0.6 bcB	4.0 ± 1.1 bcB	<0.0001
A. pintoi	20.6 ± 5.0 dA	6.7 ± 2.1 bB	4.3 ± 1.2 bcB	4.8 ± 1.4 bcB	0.0138
Probability	0.0001	<0.0001	0.0015	0.0032	

Table 2.8 Means, standard errors and LSD groupings of above-ground biomass (g per plant, oven dried at 70°c) produced by 14 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly.

	Above-ground biomass (g per plant)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. acutifolium	70.6 ± 6.3 aA	24.3 ± 5.8 aB	16.8 ± 3.3 aBC	8.3 ± 1.7 abC	<0.0001
A. americana	68.8 ± 5.6 abA	15.0 ± 3.7 bcB	6.4 ± 3.4 bB	4.3 ± 0.7 bcB	<0.0001
P. phaseoloides	66.6 ± 6.0 abA	29.4 ± 5.8 aB	21.5 ± 0.8 aBC	10.8 ± 2.3 aC	<0.0001
D. heterophyllum	58.9 ± 4.0 abcA	24.9 ± 2.6 aB	18.7 ± 2.9 aBC	11.3 ± 2.4 aC	<0.0001
N. wightii	56.1 ± 11.2 abcA	8.4 ± 1.2 cdB	15.1 ± 2.3 aB	3.5 ± 0.8 cB	<0.0001
C. pubescens	53.2 ± 6.9 bcA	23.3 ± 2.2 abB	16.9 ± 1.2 aBC	10.1 ± 1.5 aC	<0.0001
D. uncinatum	46.9 ± 2.7 cdA	29.2 ± 5.0 aB	16.5 ± 3.6 aC	11.0 ± 2.1 aC	0.0002
S. guianensis	44.6 ± 5.3 cdeA	1.8 ± 0.7 dB	0.8 ± 0.4 bB	0.4 ± 0.1 cB	<0.0001
C. macrocarpum	30.4 ± 6.5 def	20.9 ± 5.5 ab	19.8 ± 4.9 a	10.4 ± 0.7 a	0.0768
A. villosa cv. Kretschmer	30.3 ± 3.3 defA	2.7 ± 1.0 dB	1.0 ± 0.2 bB	-	<0.0001
D. triflorum	28.2 ± 5.6 efA	9.3 ± 1.9 cdB	2.1 ± 0.7 bB	1.6 ± 0.2 cB	<0.0001
A. villosa	22.0 ± 11.3 fg	1.7 ± 0.8 b	-	0.5 ± -	0.2363
F. congesta	14.6 ± 4.5 fgA	2.9 ± 1.7 dB	1.5 ± 0.3 bB	1.2 ± 0.5 cB	0.0069
A. kretschmeri	3.4 ± 0.2 g	3.1 ± 1.7 d	-	-	0.9136
Probability	0.0001	0.0001	0.0001	0.0001	

Table 2.9 Means, standard errors and LSD groupings of above-ground biomass (g per plant, 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly.

	Above-ground biomass (g per plant)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. ternatea	40.2 ± 4.1 aA	25.5 ± 3.9 aB	17.5 ± 3.9 aB	5.8 ± 2.5 C	0.0007
A. stenosperma	33.7 ± 3.0 abA	12.7 ± 1.2 bB	8.1 ± 1.0 bcB	5.2 ± 1.2 B	<0.0001
D. scorpiurus	28.1 ± 4.2 bcA	1.2 ± 0.6 dB	5.1 ± 0.4 cB	1.3 ± 0.3B	0.0036
C. rotundifolia	23.3 ± 7.9 cdA	8.4 ± 1.9 bcB	6.4 ± 1.8 cB	0.5 ± 0.3 B	0.0339
M. lathyroides	19.2 ± 0.9 cde	13.5 ± 1.7 b	14.0 ± 5.1 ab	4.9 ± 2.3	0.0614
C. pascuorum	16.6 ± 2.9 deA	1.6 ± 0.1 dB	1.5 ± 0.6 cB	1.1 ± 0.7 B	0.0002
A. paraguariensis	16.3 ± 4.3 defA	3.2 ± 0.8 cdB	3.2 ± 0.7 cB	2.1 ± 0.8 B	0.0033
S. scabra	13.2 ± 2.0 defA	1.9 ± 0.6 dB	0.8 ± 0.2 cB	0.9 ± 0.9 B	0.0008
R. minima	11.7 ± 1.9 def	8.8 ± 1.1 bc	2.4 ± - c	1.9 ± 1.8	0.1191
M. atropurpureum	11.4 ± 1.8 ef	6.4 ± 1.7 cd	7.5 ± 1.5 bc	4.3 ± 1.1	0.0650
C. brasilianum	10.7 ± 1.4 efA	6.6 ± 1.3 cdAB	7.4 ± 2.6 bcAB	3.2 ± 0.9 B	0.0308
M. martii	10.6 ± 1.5 efA	1.2 ± 0.9 dB	2.9 ± 2.6 cB	0.2 ± - B	0.0278
S. hamata	10.5 ± 3.2 ef	0.6 ± - d	-	-	0.2645
D. virgatus	6.7 ± 1.7 f	5.8 ± 1.5 cd	4.6 ± 2.4 c	1.0 ± 0.1	0.2300
Probability	<0.001	<0.001	0.0068	0.1177	

Figure 2.3 Plants from each shade treatment on the day of harvest.

a) *Arachis pintoi*

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b) *Calopogonium mucunoides*

Figure 2.3 cont.
c) *Macrotyloma axillare*

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d) *Vigna luteola*

Figure 2.3 cont.
e) *Desmodium heterophyllum*

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f) *Stylosanthes guianensis*

g) *Desmodium uncinatum*

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h) *Aeschynomene villosa* cv. Kretschmer

i) *Arachis stenosperma*

j) *Macrotilium lathyroides*

k) *Stylosanthes hamata*

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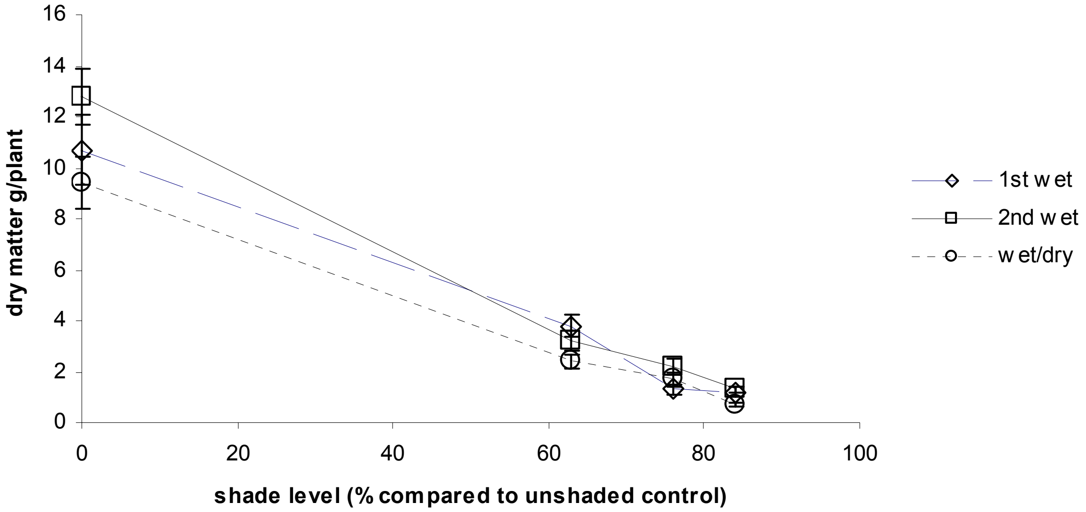
l) *Clitoria ternatea*

2.3.2 Root Biomass

a) Effect of shade level

In general the effects of both shade and species on the production of root material mirrored that found for above-ground biomass. The largest root systems were produced under full light (control) conditions, as would be suggested by the above-ground biomass results, described above. In all three trials the control treatment was substantially greater than the other shade treatments (Figure 2.4). Again the wet/dry species were less affected overall by shading than the wet species in their production of root biomass, however the difference was not as pronounced as was observed in the above-ground biomass.

Figure 2.4 Regressions of overall production of root biomass (means with standard errors), 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.



b) Effect of legume genotype

First wet tropical species

Individually *V. luteola* produced the greatest overall root biomass closely followed by *C. mucunoides*. *Arachis pintoi* had the lowest overall yield of root biomass but was not significantly different from four other species, *A. pintoi<D. canum<D. ovalifolium<M. axillare<D. intortum* (Table 2.10). Statistically however it was not considered significantly different from four other species *D. intortum, M. axillare, D. ovalifolium* and *D. canum*.

Second wet tropical species trial

Pueraria phaseoloides yielded the largest root biomass across all shade treatments, although it was not statistically separate from *D. uncinatum>C. pubescens> A. americana* (Table 2.10). *Aeschynomene americana* and the remaining species were all contained in the lowest yielding LSD group, with *A. kretschmeri* averaging the smallest root biomass of the species examined.

Wet/dry tropical species trial

With an average root biomass yield of nearly twice that of *D. scorpiurus, C. ternatea* was clearly the species with the largest overall root production (Table 2.10), although they were not found to be significantly different from one another. *Desmodium scorpiurus* and all remaining species were not found to differ significantly from one another, with the lowest overall production of root material given by *S. scabra*

Table 2.10 Means, standard errors and LSD groupings of root biomass (g per plant, oven dried at 70°c) production by (a) 7, (b) 14 and (c) 14 legume species grown under 4 shade levels, harvested 107 and 103 days after planting respectively. n = 20 and 16 respectively. Means in a column followed by the same letter are not significantly different.

(a) 1st Trial

Species	**Root biomass (g per plant)**
V. luteola	8.5 ± 2.4 a
C. mucunoides	7.0 ± 1.1 ab
D. intortum	4.3 ± 0.9 bc
M. axillare	4.3 ± 1.2 bc
D. ovalifolium	2.5 ± 0.6 c
D. canum	2.3 ± 0.4 c
A. pintoi	1.4 ± 0.4 c
Probability	0.0008

(b) 2nd Trial

Species	**Root biomass (g per plant)**
P. phaseoloides	11.0 ± 3.2 a
D. uncinatum	7.8 ± 3.2 a
C. pubescens	7.5 ± 1.6 ab
A. americana	6.7 ± 2.3 abc
D. heterophyllum	5.5 ± 1.5 bc
C. acutifolium	5.1 ± 1.1 bc
A. villosa	4.5 ± 3.1 bc
N. wightii	4.3 ± 1.0 bc
C. macrocarpum	3.6 ± 0.7 bc
A. villosa cv. Kret.	3.3 ± 1.2 bc
S. guianensis	2.7 ± 1.2 c
F. congesta	2.3 ± 0.9 c
D. triflorum	2.2 ± 0.7 c
A. kretschmeri	1.0 ± 0.3 c
Probability	0.004

(c) 3rd Trial

Species	**Root biomass (g per plant)**
C. ternatea	10.4 ± 3.2 a
D. scorpiurus	5.9 ± 2.8 a b
M. lathyroides	5.9 ± 1.1 b
A. stenosperma	4.7 ± 1.9 b
S. hamata	4.7 ± 2.1 b
R. minima	4.6 ± 1.6 b
M. atropurpureum	4.5 ± 0.9 b
C. rotundifolia	3.6 ± 1.6 b
C. pascuorum	3.6 ± 0.6 b
M. martii	2.6 ± 0.9 b
C. brasilianum	2.3 ± 0.6 b
A. paraguariensis	1.9 ± 0.5 b
D. virgatus	1.5 ± 0.4 b
S. scabra	1.3 ± 0.5 b
Probability	0.0044

c) Interaction effects

First wet tropical species trial

A highly significant interaction between species and shade level was detected with Table 2.11 showing mean root biomass and statistical groupings within shade treatments and species. Beneath the control and 63% shade treatments, *V. luteola* produced the greatest amounts of root material followed, in both cases, by *C. mucunoides*. At shade levels of 76% and 84%, *C. mucunoides* produced most root material, with little difference between the two treatments. Production of root material by *M. axillare* was severely reduced by 76% and 84% shade, falling from the third most productive species to one of the lowest. *Arachis pintoi* consistently had very low yields of root material across all light levels, being the lowest yielding species under all shade levels except 76%.

In all cases except *A. pintoi* and *M. axillare*, analysis within species gave the same LSD groupings. The control treatment was always the only treatment in the highest yielding LSD grouping, with the remaining shade treatments all contained within the second, and lowest yielding groups. *Macrotyloma axillare* was different from other species in that it had three LSD groupings with the 63% shade treatment as the second, intermediate yielding group, and the 76% and 84% shade treatments contained in the lowest yielding group. *Arachis pintoi was* the only species in which no significant difference in root biomass production was detected, despite a much larger yield under full light than under any of the shade treatments.

Second wet species trial

Interaction effects of shade by species on root biomass are shown in Table 2.12. *Pueraria phaseoloides* produced the largest root biomass of the 14 species tested under full sunlight, however it was not statistically different from *C. pubescens*. Statistical analysis of the control treatment found five LSD groupings in which the means were not significantly different. There was a gradual reduction in yield between the species, with a large amount of over-lap between LSD groups and many species occurred in three LSD groupings. *Arachis kretschmeri* yielded the smallest amount of root biomass under full sun followed by *D. triflorum*. However, these species were not statistically separate from the seven other of the lowest yielding species, *A. kretschmeri<D. triflorum<C.*

macrocarpum<*F. congesta*<*A. villosa* cv. Kretschmer<*S. guianensis*<*A. villosa*<*N. wightii*<*C. acutifolium*.

63% shade resulted in a decrease in root production by all species, with *P. phaseoloides* remaining the most productive. Statistical analysis revealed a large amount of overlap in LSD groupings but not to the extent of that found under full sun. The most productive grouping contained 3 species, *P. phaseoloides*> *D. uncinatum*>*C. pubescens.* The lowest yielding LSD group contained every species except those already mentioned, despite relatively large differences between some of the means, *D. heterophyllum* (3.9 g per plant) and *S. guianensis* (0.3 g per plant) for example. There were no surviving plants of *A. villosa* at the end of the trial.

Analysis of root production beneath 76% shade found clearer LSD groupings of species. *Centrosema pubescens* was the greatest producer of root material with *P. phaseoloides* and *D. uncinatum* producing similar amounts. *Stylosanthes guianensis* remained the lowest yielding species. *Arachis kretschmeri* plants failed to survive until the end of the trial.

Shading of 84% resulted in even lower yields with *C. pubescens* the most productive of the species. *Desmodium uncinatum* produced only marginally less than *C. pubescens*. *Aeschynomene villosa* yielded the lowest amount of root material of the species that survived. No *A. kretschmeri* or *A. villosa* cv. Kretschmer plants survived under 84% shade until the time of harvest.

Within species significant differences were found in all species except *A. villosa* and *A. kretschmeri*. Few plants of either species survived under the shaded treatments making statistical analysis difficult and less reliable. In all other remaining species save *N. wightii*, the statistical groupings were the same. The control treatment was the only treatment in the highest yielding grouping with the remaining 64%, 76% and 84% shade treatments all in the second, lower yielding, LSD group. *Neonotonia wightii* was the only species to differ with the 63% and 76% shade treatments forming an intermediate grouping.

Wet/dry species trial

The control treatment was found to contain five groups within which the means were not significantly different from one another (Table 2.13). *Clitoria ternatea* was the only species in the first, highest yielding group, clearly separated from the second highest yielding species (*A. stenosperma*) with a difference of over 8 g per plant. The lowest yielding group contained nine species with the mean yield of root biomass ranging from 9.9 to 3.0 g per plant (*C. pascuorum>R. minima>C. brasilianum>S. hamata>A. paraguariensis>M. martii>S. scabra>D. virgatus*).

Clitoria ternatea remained the most productive of the species under 63% shade, again being the only species in the highest yielding statistical grouping. The other two groupings divided the remaining species into a group with an intermediate yield, *M. lathyroides>M. atropurpureum>C. pascuorum>R. minima>A. stenosperma* and the lowest yielding group, *R. minima>A. stenosperma>D. virgatus>C. brasilianum>C. rotundifolia>A. paraguariensis>S. scabra>D. scorpiurus>M. martii>S. hamata.*

The production of root material beneath 76% shade displayed no significant differences between species (P = 0.2622). *Macroptilium lathyroides* replaced *C. ternatea* as the species with the largest root system, although there was a large amount of variation in the samples comprising the means for *M. lathyroides* and *M. martii,* as can be seen in the standard errors. The smallest, surviving root system was produced by *S. scabra,* with this figure obtained from only one surviving plant. No plants of *S. hamata* survived.

In contrast to the 76% shade treatment a significant difference was found between species grown under 84% shade (P = 0.0093). *Macroptilium atropurpureum* gave the greatest yield of root material followed by *M. lathyroides*, with no significant difference between the two species. A group with intermediate yield was detected comprising *M. lathyroides>C. ternatea>A. paraguariensis>D. scorpiurus*. Again no plants of *S. hamata* survived until the time of harvest and only one plant survived of the species *R. minima* and *M. martii*.

Within species, where significant differences were found, the statistical groupings all followed the same pattern. The control was always the treatment with the highest mean and also the only treatment contained in the first statistical grouping. The remaining three shade treatments were not found to be significantly different from one another, forming the second, lower yielding group. The species *D. virgatus, M. atropurpureum, M. martii, R. minima* and *S. hamata* were not found to have any significant differences between shade treatments, however they still displayed the pattern of decreasing biomass with increasing shade level.

Table 2.11 Means, standard errors and LSD groupings of root biomass (g per plant, oven dried at 70°c) produced by 7 forage legume species grown under 0 (control), 63, 76 and 84% shade (n = 5), harvested 107 days after planting. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly.

	Root biomass (g per plant)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
V. luteola	24.5 ± 4.3 aA	7.5 ± 0.7 aB	0.9 ± 0.4 bcB	1.1 ± 0.4 bB	<0.0001
C. mucunoides	13.9 ± 2.2 bA	6.2 ± 0.5 abB	3.5 ± 0.6 aB	3.6 ± 0.6 aB	0.0001
M. axillare	12.3 ± 1.3 bcA	5.1 ± 0.8 bB	0.19 ± 0.1 cC	0.4 ± 0.1 bC	<0.0001
D. intortum	9.4 ± 1.7 bcA	3.4 ± 0.5 cB	1.5 ± 0.4 bB	1.0 ± 0.1 bB	0.0004
D. ovalifolium	6.8 ± 0.9 cdA	1.1 ± 0.07 dB	0.8 ± 0.3 bcB	0.7 ± 0.1 bB	<0.0001
D. canum	5.5 ± 0.6 cdA	1.8 ± 0.1 dB	0.9 ± 0.2 bcB	1.0 ± 0.2 bB	<0.0001
A. pintoi	3.2 ± 1.0 d	0.9 ± 0.4 d	0.5 ± 0.07 bc	0.1 ± 0.01 b	0.0597
Probability	<0.0001	<0.0001	<0.0001	<0.0001	

Table 2.12 Means, standard errors and LSD groupings of root biomass (g per plant, oven dried at 70°c) produced by 14 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. A "–" indicates no surviving plants or not enough samples to calculate the s.e.

	Root biomass (g per plant)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
P. phaseoloides	29.0 ± 6.3 aA	9.0 ± 3.7 aB	4.5 ± 1.3 aB	1.5 ± 0.3 abcB	0.0009
C. pubescens	20.1 ± 4.6 abA	5.8 ± 1.5 abcB	4.5 ± 0.8 aB	2.5 ± 0.3 aB	0.0005
A. americana	19.4 ± 1.7 bA	2.6 ± 0.6 cdB	1.0 ± 0.3 bcB	0.8 ± 0.2 bc	<0.0001
D. uncinatum	15.7 ± 2.0 bcA	6.6 ± 1.0 abB	4.2 ± 1.1 aB	2.4 ± 1.2 abB	0.0004
D. heterophyllum	13.4 ± 4.3 bcdA	3.9 ± 0.8 bcdB	3.0 ± 0.4 abB	1.6 ± 0.5 abB	0.0114
C. acutifolium	12.1 ± 1.0 bcdeA	2.9 ± 0.8 bcdB	3.7 ± 1.3 aB	1.7 ± 0.2 abB	<0.0001
N. wightii	11.7 ± 1.7 bcdeA	3.0 ± 0.4 bcdB	3.3 ± 0.4 aB	0.8 ± 0.1 bcC	<0.0001
A. villosa	10.2 ± 6.2 cde	-	0.3 ± 0.1 c	0.1 ± - c	0.3346
S. guianensis	8.8 ± 2.1 cdeA	0.3 ± 0.1 dB	0.1 ± 0.06 cB	0.46 ± 0.2 bcB	0.0010
A. villosa cv. Kretschmer	8.7 ± 1.0 cdeA	0.7 ± 0.2 dB	0.3 ± 0.08 cB	-	<0.0001
F. congesta	7.8 ± 1.9 cdeA	1.1 ± 0.8 dB	0.5 ± 0.1 cB	0.3 ± 0.08 cB	0.0012
C. macrocarpum	7.3 ± 0.8 cdeA	2.7 ± 1.0 bcdB	3.1 ± 1.2 abB	1.4 ± 0.2 abcB	0.0046
D. triflorum	7.0 ± 0.3 deA	1.3 ± 0.4 cdB	0.4 ± 0.2 cB	0.3 ± 0.1 cB	<0.0001
A. kretschmeri	1.8 ± 0.5 e	0.8 ± 0.3 d	-	-	0.2647
Probability	<0.0001	<0.0006	<0.0001	<0.0089	

Table 2.13 Means, standard errors and LSD groupings of root biomass (g per plant, 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. A "–" indicates no surviving plants or not enough samples to calculate the s.e.

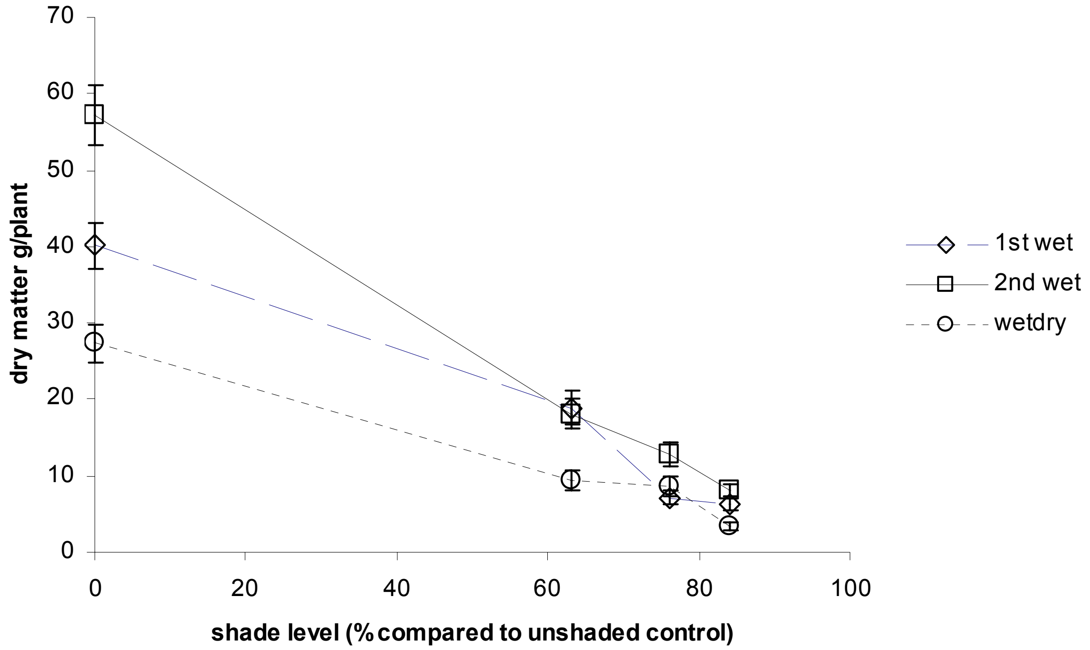
	Root biomass (g per plant)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. ternatea	24.7 ± 5.6 aA	7.7 ± 2.0 aB	3.4 ± 1.3 B	1.00 ± 0.51 bcB	0.0044
D. scorpiurus	16.4 ± 4.0 bA	0.4 ± 0.3 cB	1.1 ± 0.2 B	0.60 ± 0.30 bcB	0.0209
A. stenosperma	13.9 ± 3.9 bcA	2.2 ± 0.5 bcB	0.7 ± 0.3 B	0.47 ± 0.31 cB	0.0033
C. rotundifolia	11.9 ± 3.6 bcdA	1.3 ± 0.6 cB	0.8 ± 0.2 B	0.25 ± 0.50 cB	0.0066
M. lathyroides	11.8 ± 1.0 bcdA	4.7 ± 0.4 bB	4.6 ± 2.3B	1.73 ± 0.44 abB	0.0019
C. pascuorum	9.9 ± 2.4 bcdeA	2.8 ± 1.7 bcB	0.3 ± 0.07 B	0.30 ± 0.17 cB	0.0034
M. atropurpureum	8.1 ± 2.4 cde	3.7 ± 0.8 b	2.4 ± 0.5	2.55 ± 1.15 a	0.0765
R. minima	7.7 ± 2.2 cde	2.7 ± 0.8 bc	0.4 ± -	0.20 ± -	0.2930
C. brasilianum	6.3 ± 0.7 deA	1.4 ± 0.3 cB	1.0 ± 0.2 B	0.45 ± 0.17 cB	<0.0001
S. hamata	5.8 ± 2.4 de	0.3 ± - c	-	-	0.3809
A. paraguariensis	4.5 ± 1.0 deA	1.0 ± 0.2 cB	1.8 ± 1.3 B	0.73 ± 0.18 bcB	0.0295
M. martii	4.4 ± 0.3 de	0.3 ± 0.2c	3.6 ± 3.5	0.10 ± - c	0.3412
S. scabra	3.2 ± 1.0 e	0.5 ± 0.1 c	0.2 ± -	0.05 ± 0.05 c	0.0311
D. virgatus	3.0 ± 1.1 e	1.6 ± 0.6 c	0.9 ± 0.5	0.25 ± 0.05 c	0.0852
Probability	<0.0001	<0.0001	0.2622	0.0093	

2.3.3 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 regression analysis found highly significant (P<0.001) effects. Overall total plant biomass production, displayed results similar to above-ground and root biomass. The control treatment clearly produced the greatest yielding plants, with total plant biomass falling with increased shade levels (Figure 2.5). Again the wet/dry species were not affected to the extent of the two wet species trials, but the plants that were produced by the wet/dry species were generally smaller than those in the two wet species trials.

Figure 2.5 Regressions of overall production of total biomass (means with standard errors), 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.



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 biomass produced by *V. luteola*, with *A. pintoi* yielding only slightly more (Table 2.14).

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 2.14). *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 detailed later (see discussion). The lowest yielding statistical grouping contained a large range of yields (22.7 to 3.8 g per plant) with a total of eight species contained in the grouping.

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 2.14). 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).*

Table 2.14 Means, standard errors and LSD groupings of total plant biomass (g per plant, 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) 1st Trial

Species	**Mean Total biomass (g per plant)**
V. luteola	27.4 ± 5.38 a
D. intortum	23.6 ± 4.77 a
C. mucunoides	23.5 ± 3.01 a
M. axillare	18.4 ± 5.41 b
D. ovalifolium	14.3 ± 3.53 bc
A. pintoi	10.1 ± 2.43 cd
D. canum	9.73 ± 2.05 d
Probability	<0.001

(b) 2nd Trial

Species	**Mean Total biomass (g per plant)**
P. phaseoloides	43.1 ± 8.8 a
C. acutifolium	35.1 ± 7.5 ab
D. heterophyllum	34.0 ± 6.3 abc
A. americana	33.1 ± 9.9 abcd
D. uncinatum	33.1 ± 5.6 abcd
C. pubescens	32.9 ± 5.8 bcd
C. macrocarpum	22.7 ± 6.5 bcde
N. wightii	22.7 ± 3.6 bcde
S. guianensis	16.3 ± 6.7 cde
A. villosa	14.7 ± 9.0 de
A. villosa cv. Kret	14.6 ± 5.3 de
D. triflorum	12.6 ± 3.7e
F. congesta	7.1 ± 2.8 e
A. kretschmeri	3.8 ± 1.2 e
Probability	<0.004

(c) 3rd Trial

Species	**Mean Total biomass (g per plant)**
C. ternatea	35.4 ± 7.6 a
A. stenosperma	20.4 ± 5.4 b
M. lathyroides	19.3 ± 2.9 b
D. scorpiurus	18.1 ± 6.6 bc
C. rotundifolia	14.3 ± 4.9 bcd
S. hamata	13.1 ± 4.7 bcd
M. atropurpureum	12.2 ± 1.9 bcd
R. minima	11.4 ± 2.7 bcd
C. pascuorum	9.5 ± 3.3 cd
C. brasilianum	9.3 ± 1.5 cd
A. paraguariensis	8.4 ± 2.5 cd
M. martii	8.2 ± 2.8 cd
S. scabra	6.6 ± 2.3 cd
D. virgatus	6.3 ± 1.3 d
Probability	<0.0001

c) Interaction effects

First wet tropical species trial

Table 2.15 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 of 23.7g per plant (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. *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 2.16. 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*.

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 still 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 plant, while the highest yielding species in the low yielding group, *A. americana*, averaged only 7.4 g per plant. There were no surviving plants of *A. kretschmeri*.

Under the 84% shade level the six highest yielding species, the highest yielding LSD group, all produced within 3 g per plant 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 plant 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 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 2.17). 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 the 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*. No plants of *S. hamata* survived beneath this shade treatment.

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. The 63%, 76% and 84% shade treatments were always grouped together in the second statistical grouping. This statistical grouping of shaded treatments together often occurred 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 plant. Four species (*D. virgatus, M. martii, R. minima* and *S. hamata*) were found not to have any significant differences between shade treatments

Table 2.15 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 lower case letter and means in the same row followed by the same upper case letter do not differ significantly.

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

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Table 2.16 Means, standard errors and LSD groupings of total plant biomass production (g per plant, 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. A “–“ indicates no surviving plants or not enough samples to calculate the s.e.

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

Table 2.17 Means, standard errors and LSD groupings of total plant biomass (g per plant, 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. A "–" indicates no surviving plants or not enough samples to calculate the s.e.

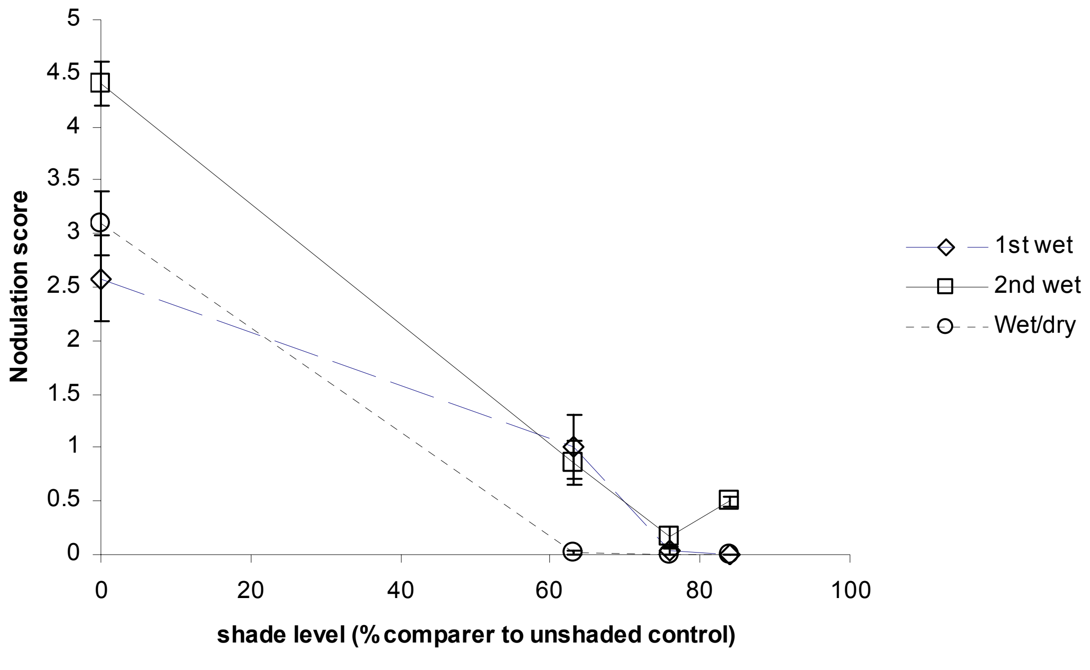
	Total plant biomass (g per plant)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. ternatea	65.0 ± 9.6 aA	31.2 ± 6.8 aB	21.0 ± 5.2 aB	4.1 ± 2.2 B	0.0039
A. stenosperma	47.6 ± 8.7 bA	14.9 ± 1.4 bcB	9.1 ± 1.7 bcB	5.7 ± 1.6 B	0.0005
D. scorpiurus	40.5 ± 6.8 bcA	1.6 ± 0.9 dB	6.2 ± 0.6 bcB	1.8 ± 0.6 B	0.0060
C. rotundifolia	34.2 ± 11.3 bcdA	8.4 ± 2.5 cdB	7.2 ± 2.0 bcB	1.0 ± - B	0.0454
M. lathyroides	31.1 ± 1.0 cdeA	18.2 ± 1.9 bB	18.2 ± 7.4 bB	6.6 ± 2.8 B	0.0195
C. pascuorum	26.5 ± 1.9 cdeA	2.9 ± 1.1 dB	1.8 ± 0.6 cB	1.4 ± 0.9 B	0.0001
A. paraguariensis	20.9 ± 5.2 defA	4.3 ± 1.0 dB	6.3 ± 2.7 bcB	2.8 ± 0.9 B	0.0070
M. atropurpureum	19.5 ± 3.5 defA	9.4 ± 1.7 cdB	9.9 ± 2.0 bcB	6.1 ± 2.3 B	0.0387
R. minima	17.3 ± 2.1 ef	11.5 ± 1.9 c	2.8 ± - bc	2.1 ± -	0.0671
C. brasilianum	17.0 ± 1.6 efA	8.0 ± 1.3 cdB	8.5 ± 2.9 bcB	3.6 ± 1.0 B	0.0010
S. scabra	16.5 ± 2.9 efA	2.4 ± 0.7 dB	1.0 ± 0.005 cB	1.0 ± 0.9 B	0.0017
M. martii	16.4 ± 1.3 ef	1.4 ± 1.1 d	6.5 ± 6.1 bc	0.3 ± -	0.0679
S. hamata	16.2 ± 4.6 ef	0.9 ± -	-	-	0.2329
D. virgatus	9.8 ± 2.9 f	7.4 ± 2.0 d	5.5 ± 2.9 bc	1.2 ± -	0.1919
Probability	<0.0001	<0.0001	0.0484	0.1946	

2.3.4 Root Nodulation

a) Effects of shade level

A distinct decline in root nodulation was observed with increasing shade levels. Nodulation was at its greatest in plants grown beneath full sunlight and almost entirely absent in plants grown under 76% and 84% shade (Figure 2.6). Scores greater than 0 under 76% and 84% shade were typically caused by low levels of nodulation on one or two plants, when the majority of plants had no nodulation.

Figure 2.6 Regressions of root nodulation level (means with standard errors), 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.



b) Effects of legume genotype

First wet tropical species trial

Overall *V. luteola* was the species with the greatest level of nodulation followed by *M. axillare* and *C. mucunoides,* although *V. luteola* was significantly different from *M. axillare* and *C. mucunoides* (Table 2.18). *Desmodium ovalifolium, D. canum* and *A. pintoi* failed to nodulate under any shade level.

Second wet tropical species trial

When averaged across all light levels, the three most prolific nodulating species belonged to the genus *Aeschynomene*. *Aeschynomene americana* averaged the highest level of nodulation followed by *A. villosa* cv. Kretschmer and *A. villosa* CPI 37235 (Table 2.18). Plants of *Arachis kretschmeri* failed to nodulate beneath any shade treatment, suggesting that the specific rhizobium necessary was not present in the soil.

Wet/dry tropical species trial

Six significantly different groups were detected among species. The group with the highest mean nodulation score contained only one species – *S. hamata* (Table 2.18). The average nodulation score of *S. hamata* was higher than other species due to the low number or absence of surviving plants beneath the 64, 76 and 84% shade treatments, which judging by effects on all other species, would have had much lower levels of nodulation, reducing the overall mean. The means of other species varied greatly from 2.0 (*D. scorpiurus*) to 0 (*D. virgatus* and *M. martii*).

Table 2.18 Means, standard errors and LSD groupings of mean root nodulation score (0 = none, 5 = most) 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) 1st Trial

Species	**Mean nodulation score**
V. luteola	2.50 ± 0.55 a
M. axillare	1.73 ± 0.56 b
C. mucunoides	1.57 ± 0.50 b
D. intortum	0.94 ± 0.42 c
D. ovalifolium	0.00 ± 0.00 d
D. canum	0.00 ± 0.00 d
A. pintoi	0.00 ± 0.00 d
Probability	<0.0001

(b) 2nd Trial

Species	**Mean nodulation score**
A. americana	2.2 ± 0.6 a
A. villosa cv. Kret	2.2 ± 0.7 a
A. villosa	2.0 ± 0.8 ab
D. triflorum	2.0 ± 0.6 ab
P. phaseoloides	2.0 ± 0.5 ab
C. acutifolium	1.5 ± 0.5 ab
D. heterophyllum	1.4 ± 0.5 ab
D. uncinatum	1.3 ± 0.6 ab
F. congesta	1.1 ± 0.5 abc
C. pubescens	1.0 ± 0.5 abc
N. wightii	1.0 ± 0.5 bc
C. macrocarpum	0.8 ± 0.4 bc
S. guianensis	0.8 ± 0.4 bc
A. kretschmeri	0.0 ± 0 c
Probability	<0.001

(c) 3rd Trial

Species	**Mean nodulation score**
S. hamata	2.80 ± 1.01
D. scorpiurus	2.00 ± 0.81
C. pascuorum	1.66 ± 0.71
C. ternatea	1.42 ± 0.62
C. brasilianum	1.25 ± 0.56
M. lathyroides	1.20 ± 0.54
A. stenosperma	1.07 ± 0.56
M. atropurpureum	1.00 ± 0.53
C. rotundifolia	0.66 ± 0.45
A. paraguariensis	0.38 ± 0.31
R. minima	0.25 ± 0.25
S. scabra	0.18 ± 0.18
D. virgatus	0.0 ± 0.0
M. martii	0.0 ± 0.0
Probability	0.0851

c) Interaction effects

First wet tropical species trial

Upon statistical analysis three groups of species were apparent beneath the control treatment (Table 2.19). *Vigna luteola, M. axillare* and *C. mucunoides* had the greatest nodulation (all with mean nodulation scores of 5) beneath full light, followed by *D. intortum* with an intermediate level of nodulation. *Desmodium ovalifolium, D. canum* and *A. pintoi* all failed to nodulate.

Macrotyloma axillare and *C. mucunoides* suffered substantial reductions in nodulation level when shade was increased to 63% and could no longer be statistically separated from species that failed to nodulate. *Vigna luteola* was the only species with a high level of nodulation.

76% shade resulted in no nodulation on roots of any plant of any species. Beneath 84% shade there was also no nodulation in any species with the exception of *V. luteola*. *Vigna luteola's* mean score of 0.2 resulted from a single individual with a few nodules, but it did not result in a significant difference from other species.

Calopogonium mucunoides, D. intortum, M. axillare and *V. luteola* all had highly significant ($P<0.001$) effects caused by shade level. All of these species had developed high levels of nodulation under the control treatment, but in each case, with the exception of *V. luteola*, shading of 63% or more caused a dramatic reduction (*C. mucunoides* and *M. axillare*) or complete absence (*D. intortum)* in root nodulation. *Vigna luteola* was unique in its maintenance of a high level of nodulation beneath 63% shade. However when shading was increased to 76% and 84%, nodulation was absent or greatly reduced, respectively. The mean nodulation score of 0.2 in *V. luteola* beneath 84% shade was cause by a single plant with a nodulation score of 1, with the remaining plants under 84% shade displaying no nodulation. *Arachis pintoi, D. canum* and *D. ovalifolium* all failed to nodulate under any of the treatments.

Second wet tropical species trial

The interaction effect between shade and species was only just significant ($P = 0.049$). The only significant differences found upon more detailed examination were between species in the control treatment. The LSD grouping with the highest mean nodulation scores contained every species except two – *S. guianensis* and *A. kretschmeri* (Table 2.20). *Stylosanthes guianensis* was contained in the second grouping along with three other species, whose mean nodulation score was less than five. Finally *A. kretschmeri* was the only species to fail to nodulate under full light and was the only species in the third and final grouping.

Under the 63, 76 and 84% shade treatments there were no significant differences detected. The average nodulation levels of each species fell substantially under 63% shade in comparison to full light, with *C. macrocarpum, C. pubescens, N. wightii, S. guianensis* and *A. kretschmeri* failing to nodulate at all. Species that did nodulate under 63% shade did not do so to the extent found under full sun. *Desmodium triflorum* was the highest of these, averaging a nodulation score of 3.0 compared to 5.0 under full light.

Aeschynomene americana and *P. phaseoloides* were the only species to nodulate beneath 76% shade with nodulation by both species at low levels. Under 84% shade *D. heterophyllum* was the only species to nodulate with a mean score of 0.5. However this score was a result of only one plant nodulating, with the other three *D. heterophyllum* plants failing to do so.

Nodulation was greatest under the control treatment in all species. Many species also continued to nodulate under the 63% and even the 76% shade treatments, although it was at much lower levels than found under the control treatment. With the exception of *D. uncinatum,* in all species where significant differences were found, the control treatment was statistically different from the other shaded treatments. In most cases the remaining shade treatments were not significantly different from one another. In contrast to the two earlier trials, eight species displayed nodulation beneath 63% shade, *D. triflorum* being the most notable of these. *Arachis kretschmeri* was the only species that failed to nodulate under any of the treatments.

Wet/dry tropical species trial

Significant differences were only detected under the control and 76% shade treatments. Beneath the control treatment many species had developed substantial levels of nodulation with *C. brasilianum, C. pascuorum, C. ternatea* and *D. scorpiurus* all averaging a nodulation score of 5 the highest level of nodulation (Table 2.21.) *Arachis paraguariensis, R. minima* and *S. scabra* all averaged relatively low levels of nodulation, while *D. virgatus* and *M. martii* did not nodulate at all.

Nodulation beneath 63% shade was entirely absent in the root systems of surviving plants, and also beneath 84% shade. Beneath 76% shade *A. paraguariensis* was the only species to have a mean nodulation level greater than 0, which was due to a single plant with a nodulation score of 1.

With the exception of *A. paraguariensis*, no nodulation was found in any species under any of the shaded treatments. Under the control treatment nodulation was prolific in species where it occurred.

Table 2.19 Means, standard errors and LSD groupings of mean root nodulation score (0 = none, 5 = most) of seven wet tropical forage legume species grown under four different shade levels (n = 5). Means in a column followed by the same lower case and mean in the same row followed by the same upper case letter do not differ significantly.

	Mean nodulation score				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
V. luteola	5.0 ± 0 aA	4.8 ± 0.20 aA	0.0 ± 0 aB	0.2 ± 0.2 aB	0.001
M. axillare	5.0± 0 aA	1.2 ± 0.5 bB	0.0 ± 0 aB	0.0 ± 0 aB	0.001
C. mucunoides	5.0 ± 0 aA	1.0 ± 0.5 bB	0.0 ± 0 aB	0.0 ± 0 aB	0.001
D. intortum	3.6 ± 0.9 bA	0.0 ± 0.0 bB	0.0 ± 0 aB	0.0 ± 0 aB	0.001
D. ovalifolium	0.0 ± 0 c	0.0 ± 0.0 b	0.0 ± 0 a	0.0 ± 0 a	-
D. canum	0.0 ± 0 c	0.0 ± 0.0 b	0.0 ± 0 a	0.0 ± 0 a	-
A. pintoi	0.0 ± 0 c	0.0 ± 0.0 b	0.0 ± 0 a	0.0 ± 0 a	-
Probability	<0.001	<0.001	No Result	0.524	

Table 2.20 Means, standard errors and LSD groupings of mean root nodulation score (0 = none, 5 = most) of 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly.

	Mean nodulation score				
Species	**Control**	**63 % Shade**	**76% Shade**	**84% Shade**	**Probability**
A. americana	5.0 ± 0 aA	1.7 ± 1.2 B	1.2 ± 0.9 B	0 ± 0 B	0.0172
A. villosa cv. Kretschmer	5.0 ± 0 aA	1.7 ± 1.2 B	0 ± 0 B	-	0.0018
A. villosa	5.0 ± 0 a	0 ± 0	0 ± 0	-	-
C. acutifolium	5.0 ± 0 aA	1.0 ± 1.0 B	0 ± 0 B	0 ± 0 B	<0.0001
C. pubescens	5.0 ± 0 aA	0 ± 0 B	0 ± 0 B	0 ± 0 B	<0.0001
D. heterophyllum	5.0 ± 0 aA	0.2 ± 0.2 B	0 ± 0 B	0.5 ± 0.5 B	<0.0001
D. triflorum	5.0 ± 0 aA	3.0 ± 1.1 B	0 ± 0 C	0 ± 0 C	<0.0001
N. wightii	5.0 ± 0 aA	0 ± 0 B	0 ± 0 B	0 ± 0 B	<0.0001
P. phaseoloides	5.0 ± 0 aA	2.0 ± 1.1 B	1.0 ± 1.0 B	0 ± 0 B	0.0025
F. congesta	4.6 ± 0.3 abA	0.3 ± 0.3 B	0 ± 0 B	0 ± 0 B	<0.0001
D. uncinatum	3.7 ± 1.2 abA	1.0 ± 1.0 AB	0 ± 0 B	0 ± 0 B	0.0491
C. macrocarpum	3.5 ± 0.6 abA	0 ± 0 B	0 ± 0 B	0 ± 0 B	<0.0001
S. guianensis	3.0 ± 1.2 bA	0 ± 0 B	0 ± 0 B	0 ± 0 B	0.0259
A. kretschmeri	0.0 ± 0 c	0 ± 0	0 ± 0	0 ± 0	-
Probability	<0.0003	<0.0673	<0.4018	<0.6973	

Table 2.21 Means, standard errors and LSD groupings of mean root nodulation score (0 = none, 5 = most) of 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly.

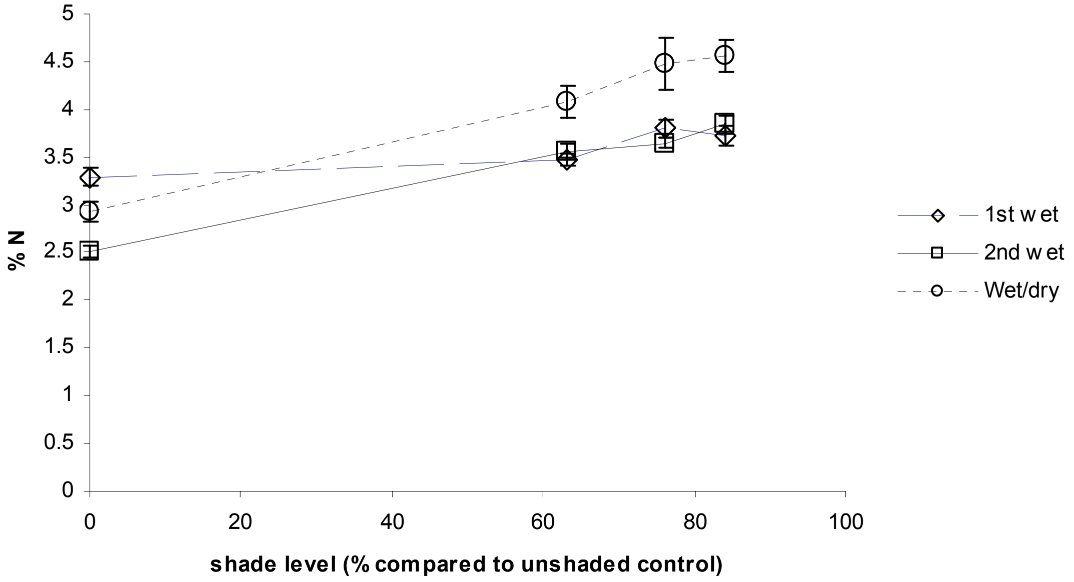
	Mean nodulation score				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. brasilianum	5.0 ± 0.0 aA	0.0 ± 0.0 B	0.0 ± 0.0 B	0.0 ± 0.0 B	<0.0001
C. pascuorum	5.0 ± 0.0 aA	0.0 ± 0.0 B	0.0 ± 0.0 B	0.0 ± 0.0 B	<0.0001
C. ternatea	5.0 ± 0.0 aA	0.0 ± 0.0 B	0.0 ± 0.0 B	0.0 ± 0.0 B	<0.0001
D. scorpiurus	5.0 ± 0.0 aA	0.0 ± 0.0 B	0.0 ± 0.0 B	0.0 ± 0.0 B	<0.0001
M. lathyroides	4.5 ± 0.5 aA	0.0 ± 0.0 B	0.0 ± 0.0 B	0.0 ± 0.0 B	<0.0001
A. stenosperma	3.8 ± 1.3 a	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0076
M. atropurpureum	3.8 ± 1.3 aA	0.0 ± 0.0 B	0.0 ± 0.0 B	0.0 ± 0.0 B	<0.0001
S. hamata	3.5 ± 0.9 ab	0.0 ± 0.0	0.0 ± 0.0	-	0.2006
C. rotundifolia	3.3 ± 1.7 abA	0.0 ± 0.0 B	0.0 ± 0.0 B	0.0 ± 0.0 B	0.0121
A. paraguariensis	1.3 ± 1.3 bc	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.4399
R. minima	0.5 ± 0.5 c	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.8766
S. scabra	0.5 ± 0.5 c	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5099
D. virgatus	0.0 ± 0.0 c	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	-
M. martii	0.0 ± 0.0 c	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	-
Probability	<0.0001	-	0.4429	-	

2.3.5 Nitrogen content of leaf material

a) Effects of shade level

In contrast to the declining levels of root nodulation with increasing shade, the N content of leaf material was found to increase with shade. Overall the highest concentrations of N were found in leaf material produced under the 76% and 84% shade treatments, with a clear decline in plants grown under full sun (Figure 2.7). The control treatment gave the lowest concentrations of N in all trials.

Figure 2.7 Regressions of leaf nitrogen content, with standard errors, 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.



b) Effects of legume genotype

First wet tropical species trial

Of the species tested, *D. canum* had the highest N content (3.96% N) and *D. ovalifolium* the lowest (3.05% N) (Table 2.22). The species *D. canum, M. axillare, V. luteola* and *C. mucunoides* were not significantly different from one another and contained the greatest overall concentrations of leaf N. *Desmodium ovalifolium* and *D. intortum* were both contained in the statistical grouping with the lowest average N concentration, with the species *V. luteola, C. mucunoides, A. pintoi* and *D. intortum* belonging to two statistical groupings.

Second wet tropical species trial

Aeschynomene americana contained the highest levels of leaf nitrogen, however it was not found to be statistically different from the species *D. triflorum* and *A. villosa* cv. Kretschmeri (Table 2.22). Lowest nitrogen levels were found in *P. phaseoloides*, which was not significantly different from the five other lowest nitrogen-containing species (*F. congesta>A. kretschmeri> N. wightii>C. acutifolium>S. guianensis)*.

Wet/dry tropical species trial

The greatest concentrations of leaf N were found in the species *A. stenosperma>D. virgatus>M. atropurpureum>C. ternatea*, which together formed the statistical grouping with the highest N concentrations (Table 2.22). *Stylosanthes hamata* and *M. martii* contained the lowest and second lowest concentrations of N respectively. These species were not found to be significantly different from eight others (*C. rotundifolia>M. lathyroides>C. pascuorum>S. scabra>D. scorpiurus>C. brasilianum>A. paraguariensis>R. minima*).

.

Table 2.22 Means, standard errors and LSD groupings of nitrogen concentration (%) of leaf material (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)1st Trial

Species	**Leaf nitrogen %**
D. canum	3.96 ± 0.16 a
M. axillare	3.88 ± 0.13 a
V. luteola	3.77 ± 0.11 ab
C. mucunoides	3.63 ± 0.09 ab
A. pintoi	3.46 ± 0.06 bc
D. intortum	3.23 ± 0.09 cd
D. ovalifolium	3.05 ± 0.05 d
Probability	<0.0001

b) 2nd Trial

Species	**Leaf nitrogen %**
A. americana	4.13 ± 0.19 a
D. triflorum	3.85 ± 0.17 ab
A. villosa cv. Kret.	3.70 ± 0.10 ab
A. villosa	3.65 ± 0.11 bc
D. heterophyllum	3.53 ± 0.17 bcd
D. uncinatum	3.45 ± 0.19 bcd
C. pubescens	3.37 ± 0.18 bcd
C. macrocarpum	3.35 ± 0.23 cd
F. congesta	3.17 ± 0.18 cde
A. kretschmeri	3.12 ± 0.19 cde
N. wightii	3.09 ± 0.16 cde
C. acutifolium	3.09 ± 0.24 de
S. guianensis	2.83 ± 0.18 e
P. phaseoloides	2.81 ± 0.13 e
Probability	<0.0001

c) 3rd Trial

Species	**Leaf nitrogen %**
A. stenosperma	4.95 ± 0.38 a
D. virgatus	4.93 ± 0.59 a
M. atropurpureum	4.29 ± 0.18 ab
C. ternatea	4.02 ± 0.49 ab
C. rotundifolia	3.97 ± 0.33 bc
M. lathyroides	3.96 ± 0.26 bc
C. pascuorum	3.45 ± 0.36 bc
S. scabra	3.62 ± 0.08 bc
D. scorpiurus	3.56 ± 0.19 bc
C. brasilianum	3.51 ± 0.24 bc
A. paraguariensis	3.40 ± 0.13 bc
R. minima	3.30 ± 0.35 bc
M. martii	2.74 ± 0.34 c
S. hamata	2.68 ± 0.21 c
Probability	0.0004

c) Interaction effects

First wet tropical species trial

The highest concentration of N under the control treatment was found in *D. canum*. It was the only species in the highest averaging statistical grouping (Table 2.23). *Vigna luteola* was the species with the second highest N concentration and, like *D. canum*, it was statistically different from all other species. The lowest concentration was found in *D. intortum,* however it was not found to be statistically different from *D. ovalifolium*.

Desmodium canum remained the species with the greatest concentration of N under 63% shade, and it was again statistically different from all other species. *Vigna luteola* was replaced by *M. axillare* as the species with the second greatest N concentration, followed by *A. pintoi*. *Desmodium ovalifolium* and *D. intortum* remained in the lowest statistical grouping beneath 63% shade, swapping positions as the species with lowest and second lowest N concentrations.

Growth beneath 76% shade resulted in the highest N concentrations being found in *M. axillare, V. luteola* and *D. canum,* with these species forming the first statistical group. The lowest concentrations of N were again found in *D. ovalifolium* and *D. intortum.*

Macrotyloma axillare remained the species with the highest N concentration under 84% shade, followed by *C. mucunoides*, which under the other shade levels, had not been one of the species with higher N levels. *Desmodium ovalifolium* remained one of the species with the lowest N concentrations, however *D. canum* was found to have even lower levels after a large decrease relative to other species.

Within species

A significant difference was detected between shade levels within all species except *D. ovalifolium*. Generally there was an increase in leaf N with increasing shade levels, however *D. canum* was the exception to this, showing the reverse. There were highly significant differences between shade levels in *V. luteola* but no trend was apparent. In all cases, except *D. canum* and *V. luteola,* the 76% and 84% shade treatments were not statistically different from one another, while the control treatment in most cases tended to be significantly different from the other treatments.

Second wet tropical species trial

A highly significant interaction effect was found between shade level and legume species. The control treatment generally gave the lowest nitrogen concentrations in leaf material. Table 2.24 shows LSD groupings of species beneath each shade level and groupings of shade levels within each species. The three species with the highest nitrogen content under full light all belonged to the *Aeschynomene* genus and also comprised the highest averaging LSD group. Of these *A. americana* had the highest nitrogen concentration, followed by *A. villosa* and *A. villosa* cv. Kretschmer. In total 6 separate LSD groupings were found beneath full light, with many species falling into two or more groupings, making clear separation into high, medium and low nitrogen content species difficult. *Centrosema macrocarpum* and *C. acutifolium* contained the two lowest levels of leaf nitrogen under full light.

Aeschynomene americana remained the species with the highest nitrogen content when grown under 63% shade. *Aeschynomene villosa* cv. Kretschmer also experienced an increase in nitrogen content, however it was not to the extent of *D. triflorum* and *D. heterophyllum,* which, under 63% shade, both experienced increases in leaf nitrogen content of over 1% in comparison to full sunlight. *Pueraria phaseoloides* was the species with the lowest mean nitrogen content, however it was not statistically different from species with mean nitrogen contents of up to 3.28% (*A. kretschmeri*< *S. guianensis*< *D. uncinatum*).

Leaf nitrogen contents were generally higher under 76% shade compared to 63% shade. However these increases were not as large as when shade was increased from 0% (control) to 63%. Four species (*A. americana, D. heterophyllum, N. wightii* and *F. congesta*) were found to have decreased nitrogen levels in comparison to 63% shade, with *N. wightii* the largest (-0.55%). Remaining species all had higher leaf nitrogen contents, with *D. triflorum* containing the highest nitrogen concentration. Despite decreased nitrogen contents, *A. americana* and *D. heterophyllum* still had some of the highest N concentrations of the species tested. *Pueraria phaseoloides* again contained the lowest N concentration but was still not significantly different from the four other lowest averaging species.

The deepest shade level of 84% gave the highest nitrogen levels. *Aeschynomene americana* once again had the highest nitrogen content of the 14 species (4.89%). It was also the only species in the highest averaging LSD group. *Pueraria phaseoloides* remained the species with the lowest N content, however it was not significantly different from *S. guianensis<N. wightii<F. congesta*.

Within species, seven species (*C. acutifolium, C. pubescens, D. heterophyllum, D. triflorum F. congesta, P. phaseoloides* and *S. guianensis*) displayed no significant difference between the 84%, 76% and 63% shade treatments, with only the control treatment in the second LSD grouping. As mentioned earlier, *A. americana, D. heterophyllum, N. wightii* and *F. congesta* all displayed decreases in leaf nitrogen content upon increasing shade from 63% to 76%. Of these species, no significant differences between shade levels were detected for *A. americana* and *A. kretschmeri*. *Desmodium heterophyllum* displayed no significant differences between the three shaded treatments. However *N. wightii* and *F. congesta,* were found to contain the highest levels of leaf nitrogen under 63% shade. In the case of *F. congesta* this level was not significantly different from either the 76% or 84% shade levels. *Neonotonia wightii* was unique in that the 63% shade treatment gave the highest levels of leaf nitrogen and that it was significantly different from the 76% shade but not 84%.

Wet/dry tropical species trial

Full light in the control treatment resulted in four statistical groupings. The group with the highest mean concentration of N contained the species *D. virgatus>M. atropurpureum>S. scabra>A. stenosperma>M. lathyroides>D. scorpiurus* (Table 2.29). The statistical grouping with the lowest mean N concentration also contained a large number of species (8) *C. ternatea<C. brasilianum<M. martii<S. hamata<C. rotundifolia<R. minima<C. pascuorum<A. paraguariensis*.

Desmanthus virgatus contained higher levels of N under 63% shade, as did all species except *M. martii*, however in relation to other species it had the fourth highest N concentration. *Arachis stenosperma* was the species with the greatest N concentration followed by *D. scorpiurus>C. pascuorum>D. virgatus>M. atropurpureum>R. minima*, all of which comprised the first statistical grouping. An intermediate group was found which contained every species except *A. stenosperma* (highest mean) and *M. martii* (lowest mean). A third grouping was detected which contained the two species with the lowest N concentrations *S. hamata* and *M. martii*.

No significant differences were found between species under 76% shade (P=0.1577). *Desmanthus virgatus* was once again the species with the greatest N concentration; with its mean approximately 1% greater than the species with the second highest mean, *C. ternatea*. Beneath this shade treatment many of the species were found to have lower N concentrations in their leaf tissue than under the 63% shade; *M. atropurpureum, S. scabra, A. stenosperma, D. scorpiurus, A. paraguariensis, C. pascuorum, R. minima, C. brasilianum*. The lowest N concentration was found in the species *R. minima*.

In contrast to the 76% shade treatment, a significant difference was found between species under 84% shade (P=0.0306). *Centrosema pascuorum* was found to have the greatest concentration of N, however this result was obtained from only one plant which produced enough leaf material for testing. In addition to *C. pascuorum* the LSD grouping with the highest means contained the species *A. stenosperma>M. atropurpureum>C. ternatea>M. lathyroides>M. martii>C. rotundifolia*. Lowest concentrations of N were found in the species *A. paraguariensis*.

Within species, eight were found not to have any significant differences between shade levels; *A. paraguariensis, C. rotundifolia, D. virgatus, M. atropurpureum, M. lathyroides, R. minima* and *S. hamata*. In species where significant differences were found there were no consistent form of statistical grouping as was found in previous trials. However the trend of increasing N content with increasing shade level was still clearly evident.

Table 2.23 Means, standard errors and LSD groupings of leaf nitrogen concentration (%), on a 70°c oven dry basis of 7 forage legume species grown under 0 (control), 63, 76 and 82% shade (n = 5), harvested 107 days after planting. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly.

	Leaf N (%)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
D. canum	4.31 ± 0.10 aB	4.03 ± 0.15 aA	4.14 ± 0.13 abA	3.02 ± 0.20 dA	<0.0001
V. luteola	3.66 ± 0.15 bB	3.19 ± 0.08 dC	4.25 ± 0.12 aA	3.97 ± 0.18 bcAB	0.0003
C. mucunoides	3.24 ± 0.12 cB	3.33 ± 0.15 cdB	3.87 ± 0.03 bcA	4.08 ± 0.04 bA	<0.0001
M. axillare	3.20 ± 0.05 cdC	3.68 ± 0.14 bB	4.32 ± 0.12 aA	4.62 ± 0.28 aA	0.0006
A. pintoi	3.10 ± 0.10 cdB	3.56 ± 0.03 bcA	3.58 ± 0.07 ceA	3.61 ± 0.01 cA	0.0004
D. ovalifolium	2.85 ± 0.16 de	3.16 ± 0.04 d	3.05 ± 0.02 f	3.14 ± 0.05 d	0.1007
D. intortum	2.63 ± 0.08 eB	3.35 ± 0.06 cdA	3.37 ± 0.13 efA	3.56 ± 0.12 cA	<0.0001
Probability	<0.0001	<0.0001	<0.0001	<0.0001	

Table 2.24 Means, standard errors and LSD groupings of leaf nitrogen concentration (%), on a 70ºc oven dry basis of 14 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. A "–" indicates no surviving plants or not enough samples to calculate the s.e.

	Leaf N (%)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
A. americana	3.76 ± 0.36 a	4.29 ± 0.28 a	3.96 ± 0.40 ab	4.89 ± 0.24 a	0.3101
A. villosa	3.65 ± 0.11 a	-	-	-	-
A. villosa cv. Kretschmer	3.40 ± 0.09 abB	3.93 ± 0.11 bcdA	3.96 ± 0.09 abcA	-	0.0114
D. triflorum	2.78 ± 0.17 bcB	3.99 ± 0.09 abA	4.31 ± 0.11 aA	4.32 ± 0.07 bA	<0.0001
A. kretschmeri	2.76 ± 0.01 bc	3.09 ± 0.09 fg	3.53 ± 0.80 bcd	-	0.4104
D. uncinatum	2.67 ± 0.30 cdB	3.28 ± 0.25 efgB	4.05 ± 0.04 abA	4.13 ± 0.16 bcA	0.0045
D. heterophyllum	2.39 ± 0.14 cdeB	3.95 ± 0.08 abcA	3.82 ± 0.09 abcA	3.97 ± 0.11 cdA	<0.0001
C. pubescens	2.27 ± 0.31 cdeB	3.64 ± 0.14 bcdeA	3.66 ± 0.10 bcA	3.90 ± 0.10 cdA	0.0002
P. phaseoloides	2.14 ± 0.32 cdeB	2.85 ± 0.10 gA	3.01 ± 0.07 eA	3.23 ± 0.14 fA	0.0079
N. wightii	2.06 ± 0.29 defC	3.64 ± 0.05 bcdeA	3.07 ± 0.14 cdeB	3.35 ± 0.08 fAB	<0.0001
F. congesta	2.01 ± 0.17 defB	3.59 ± 0.09 bcdefA	3.48 ± 0.06 bcdeA	3.50 ± 0.01 efA	<0.0001
S. guianensis	2.00 ± 0.18 efB	3.22 ± 0.06 efgA	3.23 ± 0.01 bcdeA	3.29 ± 0.06 fA	0.0003
C. macrocarpum	1.96 ± 0.24 efC	3.48 ± 0.22 cdefB	3.77 ± 0.23 abcAB	4.17 ± 0.05 bcA	<0.0001
C. acutifolium	1.51 ± 0.10 fB	3.45 ± 0.24 defA	3.63 ± 0.13 bcA	3.76 ± 0.03 deA	<0.0001
Probability	<0.0001	<0.0001	<0.0025	<0.0001	

Table 2.25 Means, standard errors and LSD groupings of leaf nitrogen concentration (%), on a 70ºc oven dry basis of 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. A "–" indicates no surviving plants or not enough samples to calculate the s.e.

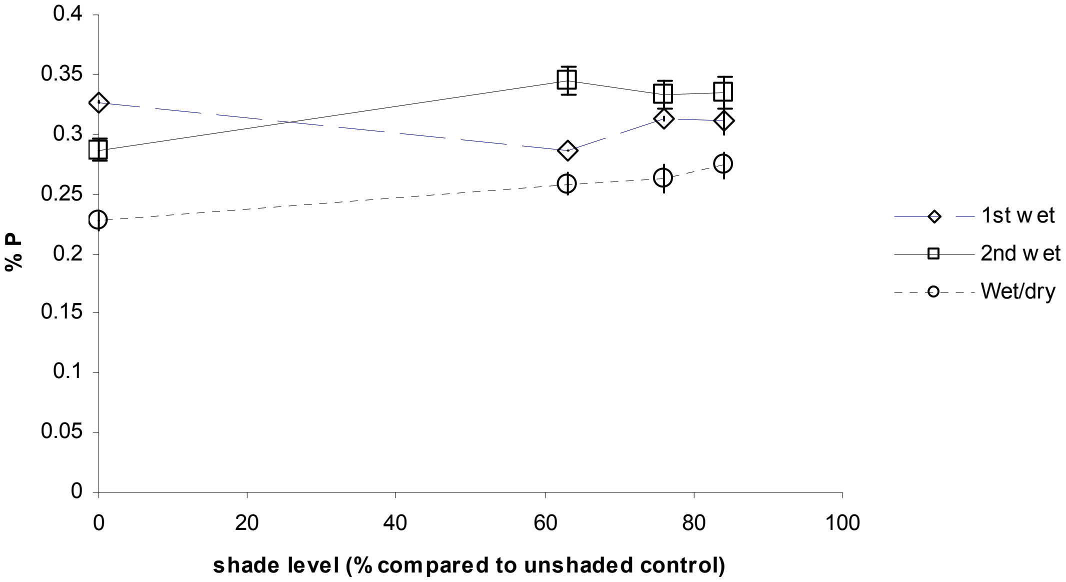
	Leaf N (%)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
D. virgatus	3.89 ± 0.53 a	4.78 ± 0.21 ab	6.85 ± 2.24	4.22 ± 0.26 bc	0.3177
M. atropurpureum	3.75 ± 0.35 ab	4.23 ± 0.29 ab	4.18 ± 0.18	5.23 ± 0.40 ab	0.0509
S. scabra	3.43 ± 0.07 abA	3.88 ± 0.09 bA	3.40 ± 0.14 B	3.69 ± 0.21 cAB	0.0362
A. stenosperma	3.17 ± 0.43 abcB	5.67 ± 0.69 aA	5.57 ± 0.50 A	5.56 ± 0.61 aA	0.0208
M. lathyroides	3.16 ± 0.23 abc	3.51 ± 0.66 b	4.51 ± 0.32	4.89 ± 0.25 abc	0.0551
D. scorpiurus	3.12 ± 0.03 abcD	4.93 ± - abA	3.51 ± 0.06 C	3.83 ± 0.02 cB	<0.0001
A. paraguariensis	2.88 ± 0.14 bcd	3.79 ± 0.20 b	3.31 ± 0.21	3.58 ± 0.25 c	0.0648
C. pascuorum	2.79 ± 0.15 cdC	4.90 ± 0.68 abAB	3.85 ± 0.36 BC	6.17 ± - aA	0.0105
R. minima	2.76 ± 0.48 cd	4.21 ± 0.60 ab	2.72 ± -	3.68 ± - c	0.3940
C. rotundifolia	2.76 ± 0.56 cd	4.01 ± 0.80 b	4.62 ± 0.16	4.38 ± 0.45 abc	0.2103
S. hamata	2.56 ± 0.23 cd	3.17 ± - bc	-	-	0.3218
M. martii	2.55 ± 0.31 cd	1.66 ± 0.47 c	3.31 ± -	4.52 ± - abc	0.0563
C. brasilianum	2.07 ± 0.24 dB	4.06 ± 0.32 bA	3.98 ± 0.25 A	3.91 ± 0.25 cA	0.0005
C. ternatea	2.06 ± 0.19 dC	3.72 ± 0.38 bBC	5.87 ± 1.35 A	5.16 ± 0.59 abAB	0.0102
Probability	0.0030	0.0196	0.1557	0.0306	

2.3.6 Phosphorus content of leaf material

a) Effects of shade level

A significant correlation regression ($r^2 = 0.0662$, $P < 0.001$) was detected only in the second wet species trial . Within this trial there was an overall increase in the P content of leaf material under the shade treatments compared to the control (Figure 2.8). In the remaining two trials there was no statistical relationship between shade level and leaf P content; although the wet/dry species trial displayed an increase in P content with shade it was not statistically significant.

Figure 2.8 Regressions of leaf phosphorus content, with standard errors, 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.



b) Effects of legume genotype

First wet tropical species trial

A total of six statistical groupings were found among the seven species tested. Overall *M. axillare* contained the highest levels of phosphorus and was significantly different from all other species (Table 2.25). *Desmodium ovalifolium* was found to have the lowest level of phosphorus, closely followed by *D. canum*, with no significant difference between these two species.

Second wet tropical species trial

Stylosanthes guianensis and *A. americana* contained the highest concentrations of phosphorus, but despite a relatively large difference between means (0.037%) the species were not significantly different (Table 2.26. The species with the lowest mean was *C. acutifolium*, with a mean phosphorus content of less than half that of *S. guianensis*. *Centrosema acutifolium* was significantly different from all other species and as such was the only species in the lowest yielding statistical group.

Wet/dry tropical species trial

Of the species best suited for the wet/dry tropics, the highest concentrations of phosphorus were found in the species *C. rotundifolia* and *S. scabra*, together forming the first statistical grouping (Table 2.26). There was a gradual decrease in phosphorus content in remaining species, with the lowest concentration found in *A. paraguariensis.* However this species was not significantly different from five others; *D. scorpiurus>C. pascuorum>R. minima>S. hamata>M. martii>A. paraguariensis*.

Table 2.26 Means, standard errors and LSD groupings of P concentrations (%) of leaf material (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)1st Trial

Species	Leaf P (%)
M. axillare	0.419 ± 0.025 a
V. luteola	0.335 ± 0.016 b
D. intortum	0.325 ± 0.006 bc
C. mucunoides	0.296 ± 0.008 cd
A. pintoi	0.292 ± 0.006 de
D. canum	0.266 ± 0.002 ef
D. ovalifolium	0.261 ± 0.004 f
Probability	<0.0001

b) 2nd Trial

Species	Leaf P (%)
S. guianensis	0.434 ± 0.023 a
A. americana	0.397 ± 0.012 ab
N. wightii	0.375 ± 0.023 bc
A. villosa cv. Kret.	0.360 ± 0.015 bc
C. macrocarpum	0.355 ± 0.019 bc
A. kretschmeri	0.355 ± 0.005 bc
F. congesta	0.351 ± 0.020 c
D. uncinatum	0.351 ± 0.015 c
P. phaseoloides	0.297 ± 0.009 d
A. villosa	0.293 ± 0.003 d
C. pubescens	0.281 ± 0.013 d
D. triflorum	0.264 ± 0.005 d
D. heterophyllum	0.259 ± 0.017 d
C. acutifolium	0.218 ± 0.008 e
Probability	<0.0001

c) 3rd Trial

Species	Leaf P (%)
C. rotundifolia	0.344 ± 0.018 a
S. scabra	0.300 ± 0.015 ab
A. stenosperma	0.271 ± 0.006 bc
M. lathyroides	0.265 ± 0.010 bc
C. brasilianum	0.261 ± 0.011 bc
M. atropurpureum	0.259 ± 0.013 bc
D. virgatus	0.257 ± 0.024 bcd
C. ternatea	0.253 ± 0.012 cde
D. scorpiurus	0.237 ± 0.015 cdef
C. pascuorum	0.214 ± 0.014 def
R. minima	0.204 ± 0.028 ef
S. hamata	0.202 ± 0.015 f
M. martii	0.192 ± 0.028 f
A. paraguariensis	0.191 ± 0.012 f
Probability	<0.0001

Interaction effects

First wet tropical species trial

A highly significant difference (P<0.001) was detected between species under the control treatment (Table 2.27). *Macrotyloma axillare* had the highest mean phosphorus concentration, followed by *D. intortum,* although there was a significant difference between the species. *Desmodium ovalifolium* contained the lowest concentrations of phosphorus under full light and together with *D. canum*, the species with the second lowest concentration, it formed the statistical grouping with the lowest means.

Macrotyloma axillare remained the species with the greatest phosphorus concentration under 63% shade, however it was not significantly different from the species *D. intortum>A. pintoi>V. luteola*. The species with the lowest concentration continued to be *D. ovalifolium*, with the lowest grouping containing the species *V. luteola>D. canum>C. mucunoides>D. ovalifolium*.

Much clearer statistical groupings were found beneath 76% shade. *Macrotyloma axillare* and *V. luteola* contained the greatest concentrations of phosphorus, and together formed the first statistical grouping. Remaining species belonged to the second statistical grouping, with *D. ovalifolium* continuing to have the lowest levels of phosphorus, although the margin was small between it *D. canum* and *A. pintoi*.

Under 84% shade, as found in under all other shade treatments, *M. axillare* contained the highest phosphorus concentrations, while the lowest were found in *D. canum*, however this was not statistically different from the species with the second lowest phosphorus concentration; *D. ovalifolium*, which had contained the lowest levels in all previous treatments.

Within species, only four of seven were found to have significant differences between shade treatments, *C. mucunoides, D. intortum, M. axillare* and *V. luteola*. *Calopogonium mucunoides* and *D. intortum* both contained statistically higher phosphorus concentrations beneath the control treatment than under any of the shaded treatments, with no significant differences found between any of the shaded treatments. *Macrotyloma axillare* and *V. luteola* displayed the opposite trend to *C. mucunoides* and

D. intortum, with the highest concentrations of phosphorus in both species found beneath the 76% and 84% shade treatments. In the case of *M. axillare,* these shade treatments were not significantly different from one another or the control treatment, with the lowest phosphorus concentration found in leaf material produced under 63% shade. The situation with *V. luteola* was somewhat clearer with the highest concentrations again found under the 76% and 84% shade treatments. The second statistical grouping contained the 84%, control and 63% shade treatments.

Second wet tropical species trial

Under the three shaded treatments (63, 76 and 84% shade) the greatest phosphorus levels were present in *S. guianensis*, followed by *N. wightii* (63 and 84% shade) or *A. americana*, neither of which were statistically different from *S. guianensis*. Beneath the control treatment, *S. guianensis* was the species with the fifth highest P concentration, however it was not significantly different from the four species with higher P levels, *D. heterophyllum> A. americana> A. villosa* cv. Kretschmer>*A. kretschmeri>S. guianensis* (Table 2.28). *Desmodium heterophyllum* was noteworthy as under the control treatment it contained the highest levels of P, however when it was grown under shaded conditions it was either the species with the lowest P levels (63 and 84% shade) or the second lowest (76% shade). *Centrosema acutifolium* was another species that had very low levels of P compared to the other species under all treatments.

Within species the highest levels of P were typically found beneath the shaded treatments. In several species the levels of P increased with shading (*C. macrocarpum* and *C. pubescens*), but more commonly the greatest level of P was found beneath the 63% shade treatment. *Desmodium uncinatum, F. congesta, N. wightii* and *P. phaseoloides* all had the highest concentrations of P present under 63% shade, although the 63% shade treatment was not found to be significantly different from other shade treatments in any of the species. However two species, *D. heterophyllum* and *D. triflorum*, did not follow this pattern and contained the greatest P levels under the control treatment, with P levels falling with increasing shade. The control treatment for *D. heterophyllum* was statistically different from any of the shaded treatments, while no statistical differences were found between any of the treatments in *D. triflorum*.

Wet/dry tropical species

Chamaecrista rotundifolia contained the highest levels of leaf P under all shade treatments with the exception of 63% shade, where *S. scabra* contained a greater P concentration although the margin between the two species was very small (0.001%) with no significant difference detected between them (Table 2.29). Beneath the control treatment only two statistical groupings were found with both groups containing all species bar those with the highest and lowest values (*C. rotundifolia* and *R. minima* respectively). No significant difference was detected between species grown beneath 76% shade, despite substantial differences between the species with highest and lowest P concentrations (*C. rotundifolia* and *A. paraguariensis* respectively). Shading of 84% resulted in four statistical groupings with the species *C. rotundifolia>S. scabra* forming the group with the greatest average P concentration and *C. ternatea>C. pascuorum>D. virgatus>M. martii* the group with the lowest.

Four of the fourteen species tested (*C. rotundifolia, S. scabra, M. lathyroides* and *R. minima*) were found to have significant differences between shade treatments within species. Results within these species displayed no clear trend, aside from a general increase in P concentrations beneath the shaded treatment than under the control. Some species in which significant differences were not detected (*D. scorpiurus, C. brasilianum* and *M. atropurpureum*) had greater concentrations of P under the control treatment than most of the shade treatments. In some species the concentration of P appeared to follow no pattern at all (*M. martii, C. pascuorum, A. stenosperma*).

Table 2.27 Means, standard errors and LSD groupings of leaf phosphorus concentrations (%), on a 70ºc oven dry basis of 7 forage legume species grown under 0 (control), 63, 76 and 82% shade (n = 5), harvested 107 days after planting. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly.

	Leaf P (%)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
M. axillare	0.482 ± 0.006 aA	0.323 ± 0.030 aB	0.462 ± 0.069 aA	0.358 ± 0.024 aA	0.0195
D. intortum	0.356 ± 0.007 bA	0.313 ± 0.003 aB	0.299 ± 0.003 bB	0.325 ± 0.012 bcB	0.0012
C. mucunoides	0.345 ± 0.014 bA	0.259 ± 0.010 cB	0.292 ± 0.010 bB	0.289 ± 0.014 cdB	0.0009
V. luteola	0.313 ± 0.011 cB	0.285 ±0.014 abcB	0.392 ± 0.042 aA	0.357 ± 0.024 bAB	0.0493
A. pintoi	0.290 ± 0.006 cd	0.308 ± 0.011 ab	0.271 ± 0.011 b	0.295 ± 0.020 cd	0.3576
D. canum	0.279 ± 0.004 de	0.267 ± 0.005 bc	0.269 ± 0.004 b	0.258 ± 0.005 d	0.2016
D. ovalifolium	0.262 ± 0.007 e	0.248 ± 0.007 c	0.263 ± 0.013 b	0.270 ± 0.006 d	0.3477
Probability	<0.0001	0.0050	0.0003	<0.0001	

Table 2.28 Means, standard errors and LSD groupings of leaf phosphorus concentrations (%), on a 70ºc oven dry basis of 14 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. A "–" indicates no surviving plants or not enough samples to calculate the s.e.

	Leaf P (%)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
D. heterophyllum	0.367 ± 0.017 aA	0.205 ± 0.010 hC	0.222 ± 0.004 fBC	0.242 ± 0.011 fB	<0.0001
A. americana	0.365 ± 0.013 aB	0.415 ± 0.018 bcA	0.437 ± 0.014 abA	0.350 ± 0.020 cdB	0.0150
A. villosa cv. Kretschmer	0.365 ± 0.006 a	0.330 ± 0.010 ef	0.395 ± 0.075 bc	-	0.3455
A. kretschmeri	0.360 ± 0.010 a	0.352 ± 0.007 def	0.355 ± 0.015 cd	-	0.8714
S. guianensis	0.340 ± 0.014 aB	0.477 ± 0.037 aA	0.495 ± 0.005 aA	0.475 ± 0.025 aA	0.0131
A. villosa	0.293 ± 0.003 b	-	-	-	-
D. uncinatum	0.280 ± 0.004 bB	0.397 ± 0.022 bcdA	0.350 ± 0.020 cdA	0.386 ± 0.016 bcA	0.0021
C. macrocarpum	0.277 ± 0.015 bc	0.360 ± 0.031 cde	0.385 ± 0.038 bc	0.400 ± 0.041 bc	0.0891
D. triflorum	0.272 ± 0.008 bc	0.260 ± 0.014 gh	0.265 ± 0.005 ef	0.260 ± 0.017 e	0.8713
P. phaseoloides	0.270 ± 0.023 bc	0.335 ± 0.020 ef	0.280 ± 0.007 e	0.305 ± 0.010 de	0.0719
F. congesta	0.236 ± 0.012 cdB	0.410 ± 0.005 bcdA	0.360 ± 0.015 cA	0.396 ± 0.018 bcA	<0.0001
N. wightii	0.213 ± 0.017 deB	0.427 ± 0.011 abA	0.400 ± 0.017 bcA	0.420 ± 0.014 abA	<0.0001
C. pubescens	0.270 ± 0.014 de	0.300 ± 0.020 fg	0.302 ± 0.004 de	0.312 ± 0.020 de	0.0027
C. acutifolium	0.185 ± 0.018 e	0.230 ± 0.014 h	0.212 ± 0.014 f	0.245 ± 0.006 f	0.0579
Probability	<0.0001	<0.0001	<0.0001	<0.0001	

Table 2.29 Means, standard errors and LSD groupings of leaf phosphorus concentrations (%), on a 70ºc oven dry basis, of 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. A "–" indicates no surviving plants or not enough samples to calculate the s.e.

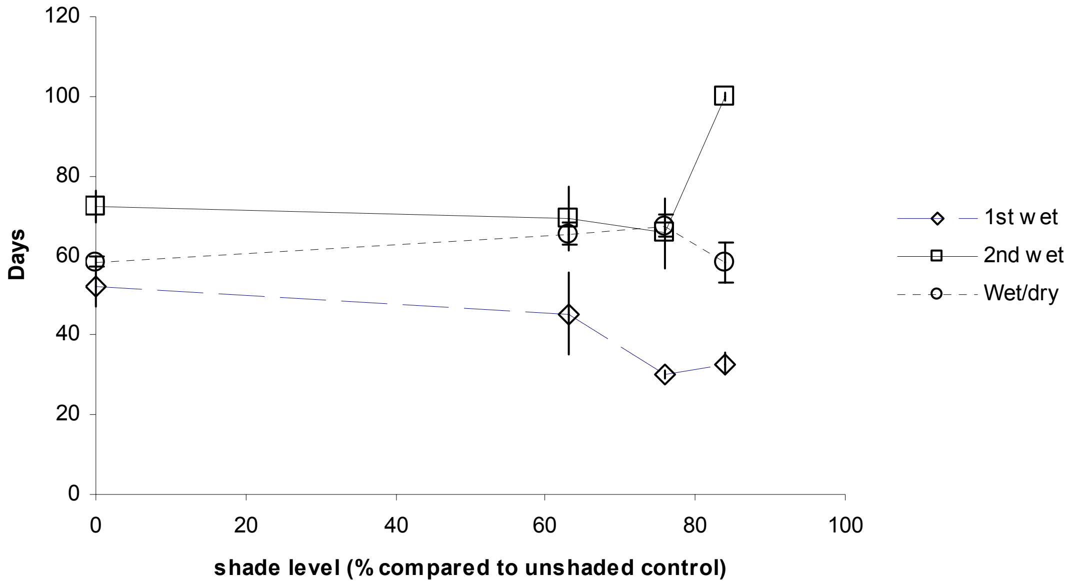
	Leaf P (%)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. rotundifolia	0.274 ± 0.031 aB	0.350 ± 0.028 aAB	0.346 ± 0.021 AB	0.433 ± 0.036 aA	0.0463
C. brasilianum	0.272 ± 0.040 a	0.260 ± 0.013 b	0.259 ± 0.019	0.253 ± 0.024 cd	0.9624
A. stenosperma	0.259 ± 0.011ab	0.248 ± 0.013 bc	0.276 ± 0.013	0.294 ± 0.004 bc	0.0787
M. atropurpureum	0.259 ± 0.034 ab	0.237 ± 0.015 bc	0.296 ± 0.013	0.240 ± 0.040 cd	0.3983
D. scorpiurus	0.250 ± 0.012 ab	0.242 ± - bc	0.205 ± 0.077	0.241 ± 0.017 cd	0.8030
S. scabra	0.247 ± 0.011 abB	0.351 ± 0.014 aA	0.266 ± 0.005 B	0.340 ± 0.016 abA	0.0010
M. lathyroides	0.234 ± 0.021 abB	0.242 ± 0.008 bcB	0.290 ± 0.011 A	0.306 ± 0.018 bcA	0.0194
C. ternatea	0.218 ± 0.027 ab	0.263 ± 0.001 b	0.253 ± 0.032	0.286 ± 0.018 bcd	0.2500
D. virgatus	0.207 ± 0.022 ab	0.255 ± 0.023 b	0.325 ± 0.083	0.241 ± 0.033 cd	0.3966
M. martii	0.205 ± 0.037ab	0.106 ± 0.041 c	0.245 ± 0.089	0.205 ± - cd	0.4736
S. hamata	0.200 ± 0.018 ab	0.208 ± - bc	-	-	0.8709
C. pascuorum	0.200 ± 0.021 ab	0.248 ± 0.016 bc	0.193 ± 0.033	0.259 ± - bcd	0.4219
A. paraguariensis	0.189 ± 0.019 ab	0.191 ± 0.036 c	0.173 ± 0.013	0.232 ± 0.001 cd	0.5782
R. minima	0.137 ± 0.013 bC	0.295 ± 0.006 abA	0.246 ± - AB	0.182 ± - dBC	0.0109
Probability	0.0401	<0.0001	0.0974	0.0045	

2.3.7 Days to first flower

a) Effect of shade level

The effects of shade level on the time to opening of the first flower varied between experiments. In the first wet tropical species trials the general effect of shading appeared to shorten the time to production of the first flower (Figure 2.9). While in the second wet tropical trial no relationship between shading and time to first flower production could be determined. In the wet/dry tropical species trial, shading of 63% and 76% increased the time to flowering, while beneath 84% shade, flowering time was decreased and no significant relationship was detected. Due to the low numbers of plants flowering beneath the shaded treatments, and not all species flowering beneath all shade treatments, these results should be viewed with caution.

Figure 2.9 Regressions of days to first flower, with standard errors, 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.



b) Effect of legume genotype

First wet tropical species trial

Only four species of legume flowered during the trial with *M. axillare* having the greatest time until the opening of the first flower (Table 2.30), although it was not statistically different from *D. canum*. *Arachis pintoi* was the fastest flowering species, doing so in less than approximately half the time taken by other species. Statistically *A. pintoi* was significantly different from all other species.

Second wet tropical species trial

At total of six species flowered during the course of the trial with the earliest flowering found to be *D. heterophyllum*. Despite having a mean time to first flower of 10 days less than that of the second earliest flowering species, *A. villosa*, *D. heterophyllum* was not significantly different from that species (Table 2.30). The species with the greatest time to first flower was *C. acutifolium*, however it was not statistically separate from *C. pubescens* or *D. triflorum*.

Wet/dry tropical species trial

In contrast to the other trials all species, save *A. paraguariensis*, flowered before harvesting. The quickest of these was found to be *A. stenosperma,* which flowered an average of 46 days after planting (Table 2.30), and was significantly different from all other species. The longest time to flowering was given by *C. ternatea*, taking over twice as long as *A. stenosperma*, however a number of other species averaged a similar amount of time and were not significantly different from *C. ternatea* or one another (*C. rotundifolia>R. minima>D. virgatus)*. A total of six groups in which means were not significantly different were found showing a gradual decrease in the time to flowering among the species.

Table 2.30 Means, standard errors and LSD groupings of days to first flower 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 and 16 respectively. Means in a column followed by the same letter are not significantly different. A – indicates no flowering plants.

(a) 1st Trial

Species	**Days to first flower**
M. axillare	73.6 ± 5.2 a
D. canum	66.4 ± 2.1 ab
V. luteola	60.0 ± - b
A. pintoi	31.4 ± 1.1 c
C. mucunoides	-
D. intortum	-
D. ovalifolium	-
Probability	<0.0001

(b) 2nd Trial

Species	**Days to first flower**
C. acutifolium	95.5 ± 1.2 a
C. pubescens	89.5 ± 2.5 ab
D. triflorum	83.7 ± 5.9 ab
A. villosa cv. Kret.	73.7 ± 1.3 bc
A. villosa	62.2 ± 0.9 cd
D. heterophyllum	52.8 ± 3.5 d
A. americana	-
A. kretschmeri	-
C. macrocarpum	-
D. uncinatum	-
F. congesta	-
N. wightii	-
P. phaseoloides	-
S. guianensis	-
Probability	<0.0001

(c) 3rd Trial

Species	**Days to first flower**
C. ternatea	76.8 ± 3.4 a
C. rotundifolia	74.5 ± 5.7 ab
R. minima	69.7 ± 3.2 abc
D. virgatus	69.0 ± 2.3 abc
S. scabra	66.0 ± 5.2 bcd
C. brasilianum	64.5 ± 1.5 cd
M. lathyroides	63.8 ± 1.4 cd
M. martii	58.5 ± 1.4 de
D. scorpiurus	58.4 ± 1.5 de
M. atropurpureum	57.9 ± 2.0 de
S. hamata	57.5 ± 7.3 de
C. pascuorum	55.7 ± 1.1 e
A. stenosperma	46.0 ± 3.5 f
A. paraguariensis	-
Probability	<0.0001

c) Interaction effects

First wet tropical species

No significant interaction effects between shade and species were detected. Average times to the opening of the first flower under each shade level are displayed in Table 2.31. *Arachis pintoi* was the only species to flower under all shade treatments, with shade having no easily recognized effect upon time to flowering. *Macrotyloma axillare* was the only other species to flower beneath any treatment other than the control. Flowering by *M. axillare* was 10 days later under 63% shade than under the control treatment. However only one plant flowered beneath the control treatment, and the standard error of the mean for the 63% shade treatment was quite large in comparison to the others.

Second wet tropical species trial

With the exception of 84% shade there were significant differences between species within each shade treatment. No significant differences were found between species beneath 84% shade, as *D. triflorum* was the only species to flower (Table 2.32). Under the control treatment *D. heterophyllum* was the fastest flowering species, followed by *A. villosa* and *D. triflorum*. The greatest time to flowering was found in *C. acutifolium,* followed by *C. pubescens* and *A. villosa* cv. Kretschmer, neither of which was significantly different from *C. acutifolium*.

Under the 63% shade treatment only three species flowered, with the quickest of these being *D. heterophyllum*. *Centrosema acutifolium* and *D. triflorum* were much slower flowering in comparison, taking almost twice as long.

There were only three flowering species under 76% shade, with the quickest species again being *D. heterophyllum*. *Aeschynomene villosa* was the second fastest, followed by *D. triflorum*. All species were significantly different from one another.

Within species

Only one species, *D. triflorum*, was found to have a significant difference between shade treatments. Three of the species that flowered under treatments other than the control (*C acutifolium, D. triflorum* and *A. villosa*) displayed an increase in time to flowering with shading. This was most apparent in *D. triflorum* with an increase in time to flowering found with each increase in shade level resulting in a total of 36 days longer to flower under 84% shade than under the control. All of the shaded treatments, 63%, 76% and 84% shade, were not found to have any significant differences between one another, while the control was statistically different from all other treatments. *Desmodium heterophyllum* was the only species to display a decrease in time to flowering with shading.

Wet/dry tropical species trial

Beneath the control treatment *C. pascuorum* was the fastest flowering species and statistically it was different from all other species (Table 2.33). The longest time to flowering was given by *C. ternatea*, with a mean of over 70 days. *Clitoria ternatea* was contained in the LSD grouping with the highest means along with *R. minima* and *D. virgatus*. A total of six separate groupings were detected, with a large amount of overlap and all species, save four, contained in two groupings.

Clitoria ternatea remained one of the latest flowering species under 63% shade, with only *Chamaecrista rotundifolia*, taking longer to flower, and both species were not significantly different from one another. *Centrosema pascuorum* remained the fastest flowering species, but was only marginally faster than *A. stenosperma*, which averaged only 0.2 days more than *C. pascuorum*. Both of these species were contained in the same LSD grouping, and the next fastest species, *M. martii*, flowering 8.5 days later. A total of eight groups in which the means were not significantly different from one another were detected, showing a gradual change in the times to flowering between the species.

Under 76% shade *S. scabra* took the greatest time to flower followed by *C. rotundifolia*>*A. stenosperma*>*C. ternatea*>*R. minima*>*D. virgatus*, all of which were contained in the statistical grouping with the greatest means. *Centrosema pascuorum* remained the fastest flowering species, doing so in almost half the time of *S. scabra.* It was also the only species in the lowest averaging LSD group.

Beneath 84% shade many species failed to flower, with only six of the fourteen species flowering during the trial. *Clitoria ternatea* was clearly the slowest to flower, and statistically different from all other species. *Macroptilium lathyroides*>*C.*

brasilianum>M. atropurpureum>M. martii were not found to be significantly different from one another, and formed the middle statistical grouping. As beneath other shade treatments, *C. pascuorum* flowered in the shortest amount of time and was significantly different from all other species.

Within species

Of the fourteen species examined, only four (*C. ternatea, A. stenosperma, M.* atropurpureum and *S. hamata*) were found to have significant differences between shade treatments. However a trend was apparent of greater times to flowering with increased levels of shade. Within species, where significant differences were found, statistical groupings were varied. The 63 and 76% shade treatments of *C. ternatea* were not significantly different from one another, while the control and the 84% shade level were significantly different from all other treatments. Within *A. stenosperma* the control and 63% shade treatments were not statistically different from one another, while 76% shade was different from the other two treatments. *Macroptilium atropurpureum* also contained two statistical groupings, with the group having the larger means comprised of the treatments of 84%, 76% and 63% shade. The second grouping was formed from the control and the 63% shade treatments. Within *S. hamata* the control and 63% shade treatments were significantly different from one another.

Table 2.31 Means and standard errors of the time to first flower of 7 forage legume species (trial 1) grown under 0 (control), 63, 76 and 82% shade (n = 5), harvested 107 days after planting. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly. A – indicates no flowers were produced. * Note – no LSD test was possible within the control treatment due to only one plant of several species flowering.

	Days to first flower (days)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
A. pintoi	33.0 ± 2.8	29.5 ± 2.0 a	30.0 ± 0.9	32.8 ± 2.7	0.6090
V. luteola	60 ± -	-	-	-	-
D. canum	66.4 ± 2.1	-	-	-	-
M. axillare	67.0 ± -	77.0 ± 7 b	-	-	-
C. mucunoides	-	-	-	-	-
D. intortum	-	-	-	-	-
D. ovalifolium	-	-	-	-	-
	<0.0001*	0.0010	-	-	

Table 2.32 Means, standard errors and LSD groupings of the time to first flower of 14 forage legume species (trial 2) grown under 0 (control), 63, 76 and 82% shade (n = 4), harvested 103 days after planting. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly. A – indicates no flowers were produced or not enough samples to calculate the s.e.

	Time to first flower (days)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. acutifolium	96.0 ± 1.5 a	94.0 ± - a	-	-	0.5799
C. pubescens	89.5 ± 2.5 ab	-	-	-	n.r.
A. villosa cv. Kretschmer	73.5 ± 1.3 bc	-	-	-	n.r.
D. triflorum	64.0 ± 3.6 cdA	87.6 ± 8.8 aB	99.0 ± - aB	100.0 ± 1.0 B	0.0412
A. villosa	61.0 ± 0.0 cd	-	63.5 ± 1.5 b	-	0.2375
D. heterophyllum	56.7 ± 9.1 d	49.7 ± 1.2 b	51.0 ± 0.0 c	-	0.7081
A. americana	-	-	-	-	-
A. kretschmeri	-	-	-	-	-
C. macrocarpum	-	-	-	-	-
D. uncinatum	-	-	-	-	-
F. congesta	-	-	-	-	-
N. wightii	-	-	-	-	-
P. phaseoloides	-	-	-	-	-
S. guianensis	-	-	-	-	-
Probability	0.0017	0.0066	0.0029	n.r.	

Table 2.33 Means, standard errors and LSD groupings of the time to first flower of 14 forage (wet/dry tropical) legume species grown under 0 (control), 63, 76 and 82% shade (n = 4), harvested 119 days after planting. A – indicates no flowers were produced or not enough samples to calculate the s.e. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly.

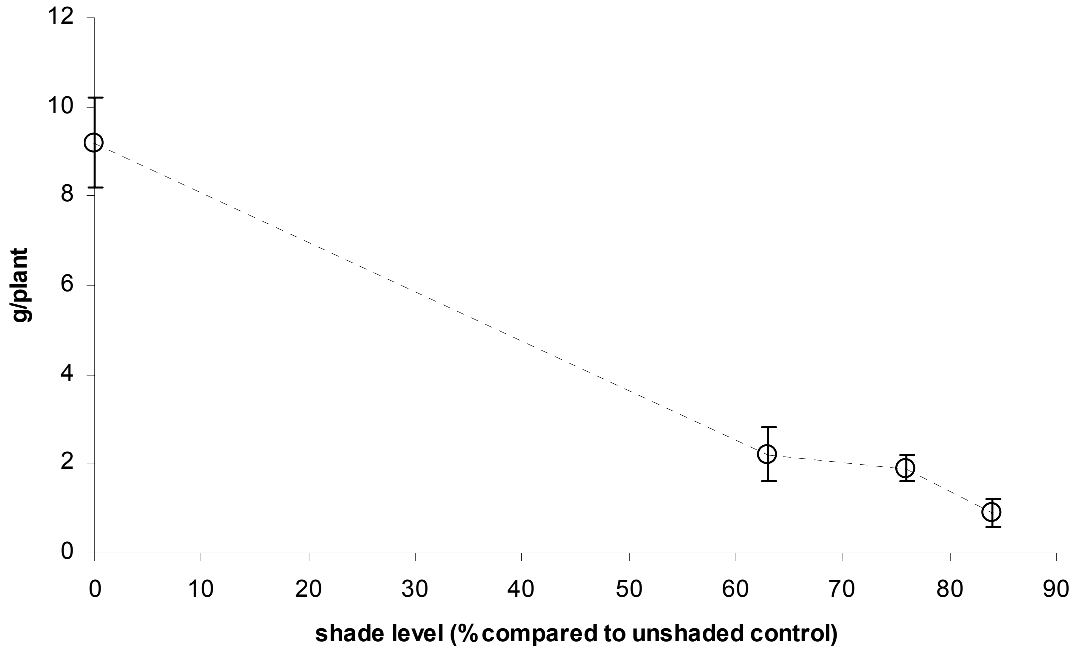
	Time to first flower (days)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. ternatea	70.7 ± 0.8 aC	89.5 ± 3.5 abC	76.0 ± - abB	105.0 ± - aA	0.0014
R. minima	68.6 ± 4.3 a	73.0 ± - cd	74.0 ± - abc	-	0.8007
D. virgatus	65.7 ± 1.4 ab	78.0 ± - c	73.0 ± - abcd	-	0.0586
M. lathyroides	61.7 ± 1.6 bc	65.0 ± 2.0 def	67.0 ± 4.0 bcde	71.0 ± - b	0.2395
C. rotundifolia	61.5 ± 0.5 bc	92.0 ± 2.0 a	82.3 ± 1.0 ab	-	0.2344
C. brasilianum	61.0 ± 0.6 bc	66.0 ± 3.1 de	67.0 ± 1.0 bcde	68.0 ± - b	0.3969
S. scabra	61.0 ± 1.9 bc	-	86.0 ± - a	-	-
M. martii	65.5 ± 3.0 cd	58.0 ± 1.5 fg	61.5 ± 0.5 de	62.0 ± 0.0 b	0.4233
D. scorpiurus	54.5 ± 2.2 de	61.6 ± 1.3 ef	60.3 ± 2.8 e	-	0.1129
A. stenosperma	53.7 ± 1.4 deB	49.5 ± 1.5 ghB	76.0 ± - abA	-	0.0030
M. atropurpureum	52.5 ± 0.3 deB	59.0 ± 4.0 efBA	64.0 ± 3.0 cdeA	65.5 ± 0.5 bA	0.0226
S. hamata	50.3 ± 2.3 eB	79.0 ± - bcA	-	-	0.0255
C. pascuorum	43.7 ± 0.6 f	49.3 ± 0.9 h	44.0 ± 2.0 f	46.7 ± 2.9 c	0.2640
A. paraguariensis	-	-	-	-	-
Probability	<0.0001	<0.0001	<0.0017	<0.0012	

2.3.8 Production of seed

a) Effect of shade level

A decrease in the amount of seed produced was observed under the shade treatments. The greatest amount of seed was produced under the control treatment, which yielded over ten times that of 84% shade (Figure 2.10). A highly significant regression (r^2 = 0.4680, $P < 0.001$) was found between shade level and seed production.

Figure 2.10 Regressions of seed production, with standard errors, of 14 species of wet/dry tropical forage legume grown beneath four shade levels, 119 days after planting. N = 56.



b) Effect of legume genotype

No significant difference was found between the legume genotypes, despite large differences in overall production between some species (Table 2.34). The greatest yield of seed was given by *C. brasilianum* followed by *C. ternatea*>*C. pascuorum*>*M lathyroides*. *Chamaecrista rotundifolia* gave the lowest yield of seed, while *D. virgatus* and *R. minima* only produced 0.3 g per plant more.

c) Interaction effects

Three statistical groupings were found beneath the control treatment. The group with the highest yields contained the species *C. pascuorum*, *C. brasilianum* and *M. lathyroides* (Table 2.35). *Centrosema pascuorum* and *C. brasilianum* produced very similar amounts of seed, with a difference between the two species of only 0.3 g per plant. The second group, with an intermediate yield of seed, contained the species *M. lathyroides>M. atropurpureum>M. martii>C. ternatea*. Of the species which produced seed, *Chamaecrista rotundifolia* was the lowest yielding, however it was not statistically different from the two other low yielding species *D. virgatus* and *R. minima*.

Shading of 63% resulted in large decreases in seed production by all species however, the high yielding species under the control treatment were the most affected. Statistically no difference was found between species under 63% shade, despite the best yielding species, this time *C. brasilianum*, producing approximately 40 times the mass of seed of the poorest yielding species, *C. rotundifolia*. *Centrosema pascuorum* suffered the largest reduction in yield (15.2 g per plant or 3.7% of its former yield), although *C. rotundifolia* underwent a similar larger relative reduction in yield (3.8% of former yield).

Table 2.34 Means, standard errors and LSD groupings of seed production of 14 forage legume species grown under 0 (control), 63, 76 and 82% shade, with seed harvested up to 119 days after planting. A – indicates no seed was produced or not enough samples to calculate the s.e. Means in a column followed by the same lower case letter do not differ significantly.

Species	**Seed production (g per plant)**
C. brasilianum	7.4 ± 1.8
C. ternatea	6.7 ± 1.6
C. pascuorum	6.6 ± 2.3
M. lathyroides	5.7 ± 1.7
M. martii	4.4 ± 1.2
M. atropurpureum	3.8 ± 1.1
D. virgatus	1.9 ± 1.2
R. minima	1.9 ± 1.1
C. rotundifolia	1.6 ± 0.9
Probability	0.2921

Table 2.35 Means, standard errors and LSD groupings of seed production (g per plant) produced by 14 forage legume species grown under 0 (control), 63, 76 and 82% shade (n = 4), with seed harvested up until 119 days after planting. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly.

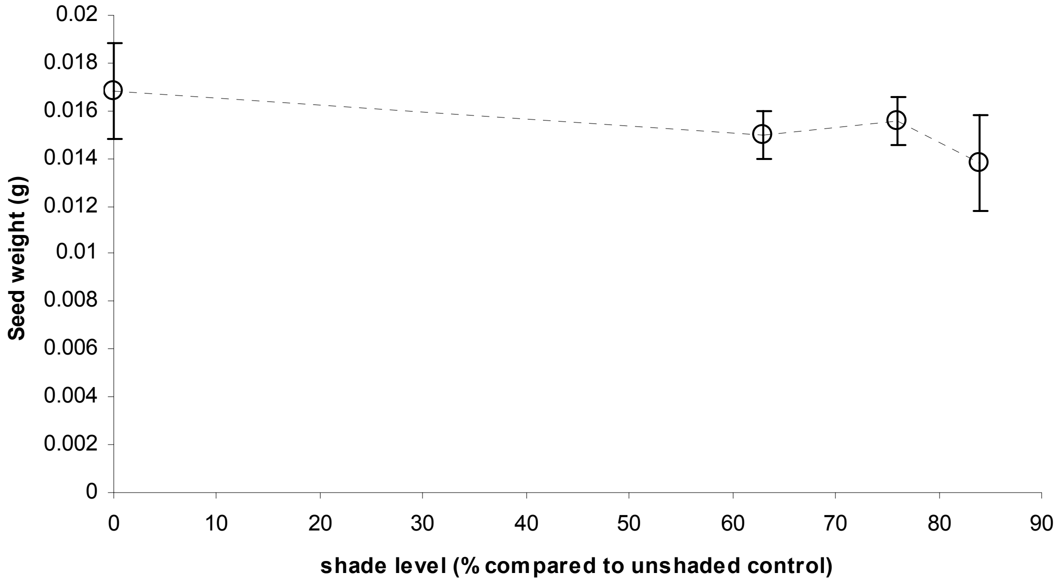
	Seed production (g per plant)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. pascuorum	15.8 ± 1.6 aA	0.6 ± 0.3 B	1.7 ± 0.4B	1.1 ± - bB	0.0001
C. brasilianum	15.5 ± 2.9 aA	4.0 ± 2.0 B	3.9 ± 0.8 B	2.7 ± - aB	0.0102
M. lathyroides	11.4 ± 1.6 abA	3.1 ± 0.7 B	0.7 ± 0.3 B	0.9 ± - bB	0.0058
M. atropurpureum	9.1 ± 1.7 bA	1.8 ± 0.8 B	2.0 ± 0.4 B	0.6 ± 0.2 bB	0.0019
M. martii	8.2 ± 0.7 bcA	2.6 ± - B	1.9 ± 1.0 B	0.2 ± 0.04 bB	0.0027
C. ternatea	6.7 ± 1.6 bc	-	-	-	-
D. virgatus	3.2 ± 1.8 c	0.2 ± -	0.09 ± -	-	0.6323
R. minima	3.1 ± 1.6 c	0.4 ± -	0.07 ± -	-	0.6088
C. rotundifolia	2.7 ± 1.7 c	0.1 ± -	1.0 ± -	-	0.7522
A. paraguariensis	-	-	-	-	-
A. stenosperma	-	-	-	-	-
D. scorpiurus	-	-	-	-	-
S. hamata	-	-	-	-	-
S. scabra	-	-	-	-	-
Probability	0.0002	0.6917	0.0733	0.0448	

2.3.9 Seed size

a) Effect of shade level

No significant differences were detected in average seed weight across shade levels (P>0.4044). Seeds were largest beneath the control treatment (Figure 2.11) while the smallest seeds were produced under the 84% shade treatment. The 63% and 76% shade treatments produced seeds of intermediate size.

Figure 2.11. Regressions of seed production, with standard errors, of 14 species of wet/dry tropical forage legume grown beneath four shade levels, 119 days after planting. N = 56.



b) Effect of legume genotype

A highly significant difference between legume genotypes was detected with the largest seeds produced by *C. ternatea*, followed by *C. brasilianum>C. pascuorum>M. atropurpureum>R. minima>M. lathyroides> M. martii>D. virgatus>C. rotundifolia*. A large number of statistical groupings were found (7) reflecting the range of seed sizes found in the different species (Table 2.36).

Table 2.36 Means, standard errors and LSD groupings of average seed weight of 14 forage legume species grown under 0 (control), 63, 76 and 82% shade, with seed harvested up to 119 days after planting. A – indicates no seed was produced or not enough samples to calculate the s.e. Means in a column followed by the same lower case letter do not differ significantly.

Species	**Mean seed weight(g)**
C. ternatea	0.0411 ± 0.0010 a
C. brasilianum	0.0242 ± 0.0099 b
C. pascuorum	0.0203 ± 0.0023 c
M. atropurpureum	0.0154 ± 0.0051 d
R. minima	0.0140 ± 0.0023 de
M. lathyroides	0.0102 ± 0.0012 ef
M. martii	0.0078 ± 0.0003 fg
D. virgatus	0.0049 ± 0.0007 g
C. rotundifolia	0.0045 ± 0.0003 g
Probability	<0.0001

c) Interaction effects

A highly significant (P<0.0001) interaction between shade treatment and species was detected. Within shade treatments significant differences were detected in the control, 63% and 76% shade treatments. *Clitoria ternatea* produced the largest seeds under the control treatment, with seeds almost twice the weight of the second largest species *C. pascuorum*. Statistically *C. ternatea* was different from all other species, while both *Centrosema* species were contained in the grouping with the second greatest mean (Table 2.37). The seeds with the lowest weight belonged to *C. rotundifolia,* however this species was not significantly different from *M. martii* or *D. virgatus.* The largest seeds beneath 63% shade were produced by *C. brasilianum* although it was not significantly different from the species *C. pascuorum* and *R. minima*. Statistical groupings displayed more overlap between species under 63% shade than the control treatment, with all species except *C. brasilianum, D. virgatus* and *C. rotundifolia* contained in more than one grouping. Four species, *M. martii>M. lathyroides>C. rotundifolia>D. virgatus* were contained in the statistical grouping with the lowest means, despite *M. martii* and *M. lathyroides* producing seeds approximately twice the size of *D. virgatus*. *Clitoria ternatea* failed to produce any seed under 63% shade. *Centrosema brasilianum* also produced the largest seeds under 76% shade, followed by *C. pascuorum* and *M. atropurpureum*, all of which were not significantly different from one-another. Similarly *D. virgatus, C rotundifolia, M. martii* and *M. lathyroides* to producede the smallest seeds with no statistical difference between the species. No significant difference was found between species beneath 84% shade. The only species to produce seed beneath this level of shade were *C. pascuorum, C. brasilianum, M. atropurpureum, M. lathyroides* and *M. martii* with *C. brasilianum* and *M. martii* producing the largest and smallest seeds respectively.

Within species, *D. virgatus* was the only species to have a significant difference between shade levels. Seeds produced by *D. virgatus* were largest under the control treatment and became smaller under shade levels up to 76% where seeds weighed approximately a third of those produced under full sun. *Centrosema pascuorum* also displayed a decrease in seed size with shading, although this was not statistically significant. Remaining species did not display any clear trends in seed size with shading. Seed sizes for the species under certain shade levels were derived from only one seed-producing plant and, as such, these results should be viewed with this in mind (*R. minima, M. martii, D. virgatus, C. rotundifolia* – 63% and 76% shade, *R. minima, D. virgatus, C. rotundifolia* – 76% shade, *C. brasilianum, M. lathyroides* – 84% shade).

Table 2.37 Means, standard errors and LSD groupings of average seed weight (g) produced by 14 forage legume species grown under 0 (control), 63, 76 and 82% shade (n = 4), with seed harvested up until 119 days after planting. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly.

	Mean seed weight (g)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. ternatea	0.0411 ± 0.0010 a	-	-	-	-
C. pascuorum	0.0249 ± 0.0012 b	0.0204 ± 0.0030 ab	0.0203 ± 0.0039 ab	0.0109 ± 0.0109	0.2813
C. brasilianum	0.0244 ± 0.0005 b	0.0232 ± 0.0024 a	0.0240 ± 0.0023 a	0.0278 ± -	0.7689
M. atropurpureum	0.0149 ± 0.0009 c	0.0149 ± 0.0005 bcd	0.0165 ± 0.0009 abc	0.0154 ± 0.0018	0.7295
R. minima	0.0136 ± 0.0037 c	0.0179 ± - abc	0.0110 ± - bcd	-	0.7867
M. lathyroides	0.0111 ± 0.0030 cd	0.0084 ± 0.0007 de	0.0095 ± 0.0007 cd	0.0129 ± -	0.7712
M. martii	0.0069 ± 0.0005 de	0.0093 ± - cde	0.0086 ± 0.0002 cd	0.0079 ± 0.0007	0.1658
D. virgatus	0.0060 ± 0.0002 deA	0.0042 ± - eAB	0.0022 ± - dB	-	0.0331
C. rotundifolia	0.0043 ± 0.0007 e	0.0046 ± - e	0.0048 ± - cd	-	0.9191
A. paraguariensis	-	-	-	-	-
A. stenosperma	-	-	-	-	-
D. scorpiurus	-	-	-	-	-
S. hamata	-	-	-	-	-
S. scabra	-	-	-	-	-
Probability	<0.0001	0.0031	0.0138	0.4523	

2.3.10 Seed germination

Table 2.38 summarizes the statistical results of the germination trial. Significant to highly significant differences were found between legume genotypes, shade levels and interactions, for all seed parameters save the effects of shade level and shade by genotype interaction for the percentage of non-viable seed.

Table 2.38 Statistical summary of germination trial of seeds produced by legumes under 4 levels of shade.

Seed Parameters	Genotype	Shade level	Interaction
Time to 50% germination	***	***	***
Readily germinated seeds	***	***	***
Hard seeds	***	*	***
Non-viable seeds	***	n.s.	*

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

a) Effect of shade level

The overall percentage of readily germinable seed, was found to increase when seed was produced under shaded conditions. The shaded treatments of 84%, 76% and 63% shade were not significantly different from one another (Table 2.39), with the greatest percentage of readily germinable seed present in the 84% shade treatment. The control treatment gave approximately one third the level of readily germinable seed of 84% shade, and along with 63% shade was contained in the second statistical grouping.

Percentages of hard seed were generally higher in seed produced under the unshaded control and the 63% shade treatment than from the 76% and 84% shade treatments. The greatest and lowest percentages of hard seed were found in the control and 76% shade treatment respectively with a difference between the two of 9.9%. Statistically the control and 63% shade treatments were not different from one another as were the 63%, 76% and 84% shade treatments.

Levels of non-viable seed were generally lower with increasing levels of shade. However no statistical differences were detected between the treatments, despite quite a large difference in non-viable seed between 84% shade and the other three treatments.

The time to 50% germination was quickest in seed from 63% shade and longest in seed produced under the control. No real trends could be observed.

Table 2.39 Means, standard errors and LSD groupings of time to 50% germination (days), % readily germinable seed, % hard seed and % non-viable seed of 8 forage legume species grown under 0 (control), 63, 76 and 82% shade, with seed harvested up to 119 days after planting. A – indicates no seed was produced or not enough samples to calculate the s.e. Means in a column followed by the same lower case letter do not differ significantly.

Shade level	Readily germinable seed (%)	Hard seed (%)	Non-viable seed (%)	Time to 50% germination
Control	10.5 ± 2.7 b	76.2 ± 3.4 a	13.2 ± 3.1	11.3 ± 1.3 a
63%	17.0 ± 3.6 ab	70.8 ± 4.8 ab	12.1 ± 2.7	6.6 ± 0.8 ab
76%	22.8 ± 4.9 a	66.3 ± 4.5 b	10.7 ± 2.5	7.1 ± 1.2 b
84%	29.3 ± 6.9 a	68.2 ± 7.2 b	2.4 ± 1.0	10.4 ± 1.4 ab
Probability	0.0305	0.0190	0.1205	0.0170

b) Effect of legume genotype

Overall *Centrosema pascuorum* had the greatest percentage of readily germinable seed (Table 2.40), followed by *M. atropurpureum* and *M. lathyroides*. These three species contained substantially greater levels of readily germinable seed than the remaining species, and they were all found to be significantly different from all other species. The lowest levels of germinable seed were found in *M. martii,* which along with the species *D. virgatus, R. minima, C. rotundifolia* and *C. brasilianum* were all contained in the statistical grouping with the lowest means.

Hard seededness was at its highest level in *M. martii* which, along with the species *C. brasilianum>M. lathyroides>D. virgatus>R. minima*, comprised the statistical grouping with the highest means. *Centrosema pascuorum* had the lowest level of hard seed of the species examined, which was approximately one-third that of *M. martii*, and significantly different from all other species.

Approximately one-third of seed produced by *Chamaecrista rotundifolia* proved to be non-viable, and was the highest level found in any of the species tested. The smallest amounts of non-viable seed were found in the species *M. lathyroides<M. atropurpureum<C. brasilianum<M. martii* all of which were contained in the statistical grouping with the lowest means.

The quickest overall time to 50% germination of seed was found in *M. lathyroides*, taking slightly over three days. Statistically *M. lathyroides* did not take significantly longer than the species *M. martii* and *R. minima* to reach 50% germination. The greatest time was taken by *C. brasilianum*, which took just under 16 days for 50% of the readily germinable seed to germinate. Statistically it could not be separated from the *C. rotundifolia*, which averaged just under 12 days to 50% germination.

Non-viable seed

No real trends of the production of non-viable seed with shade level could be found. Table 2.58. The greatest overall level of non-viable seed was found in *C. rotundifolia*, which was the only species in the statistical grouping with the highest mean. *Rhynchosia minima, D. virgatus* and *C. pascuorum* formed an intermediate grouping with the lowest levels of non-viable seed present in *M. lathyroides*, however it was not statistically different from *M. atropurpureum<C. brasilianum<M. martii<C. pascuorum.*

Table 2.40 Means, standard errors and LSD groupings of time to 50% germination (days), % readily germinable seed, % hard seed and % non-viable seed of 8 forage legume species grown under 0 (control), 63, 76 and 82% shade, with seed harvested up to 119 days after planting. A – indicates no seed was produced or not enough samples to calculate the s.e. Means in a column followed by the same lower case letter do not differ significantly.

	Readily germinable seed (%)	**Hard seed (%)**	**Non-viable seed (%)**	**Time to 50% germination**
Centrosema pascuorum	48.5 ± 3.2 a	32.5 ± 4.5 c	9.0 ± 3.0 bc	9.5 ± 0.7 b
Macroptilium atropurpureum	36.7 ± 3.9 b	60.6 ± 3.9 b	2.6 ± 0.7 c	8.6 ± 0.7 bc
Macroptilium lathyroides	17.7 ± 2.7 c	80.4 ± 2.9 a	1.8 ± 0.5 c	3.2 ± 0.2 d
Centrosema brasilianum	5.9 ± 1.3 d	87.7 ± 1.9 a	6.3 ± 1.0 c	15.9 ± 1.8 a
Chamaecrista rotundifolia	3.5 ± 1.6 d	64.4 ± 6.5 b	32.0 ± 5.9 a	11.8 ± 4.5 ab
Rhynchosia minima	2.9 ± 1.8 d	78.9 ± 5.2 a	18.1 ± 4.8 b	7.3 ± 1.0 bcd
Desmanthus virgatus	2.8 ± 1.2 d	80.3 ± 5.8 a	16.8 ± 5.2 b	8.5 ± 1.6 bc
Macroptilium martii	2.3 ± 0.6 d	90.5 ± 3.2 a	7.1 ± 3.3 c	5.3 ± 1.9 d
Probability	<0.0001	<0.0001	<0.0001	<0.0001

c) Interaction effects

Readily germinable seed

Highly significant interaction effects between legume genotype and shade level were found for all seed parameters save non-viable seed, for which a significant interaction was found (0.05>P>0.01). *Centrosema pascuorum* produced the highest levels of readily germinable seed under three of the four shade treatments (control, 63% and 76%). Under these three shade treatments *C. pascuorum* clearly had the greatest levels of readily germinable seed, in each case being significantly different from all other species (Table 2.41). The second greatest levels of readily germinable seed were found in *M. atropurpureum*, under the control, 63% and 76% shade treatments and the greatest beneath 84% shade. Under the control, the remaining species had relatively low levels of readily germinable seed, with the greatest of these, *M. lathyroides,* having 6.7% of its seeds germinate in the first 28 days. A general increase in readily germinable seed was observed in seed produced beneath 63% shade, with the seed of several species, *M. atropurpureum, M. lathyroides* and *C. brasilianum* having nearly twice the level of readily germinable seed found in the control treatment. Further increases in readily germinable seed were found in some species (*C. pascuorum, M. atropurpureum* and *M. lathyroides*) grown under 76% shade. Only four species produced seed under 84% shade, with *M. atropurpureum* and *C. pascuorum* having the greatest levels of readily germinable seed.

Five significant differences were found between shade levels within species. Of these *C. pascuorum*, *M. atropurpureum, D. virgatus* and *M. lathyroides* displayed marked increases in the percentage of readily germinable seed with shade. *Centrosema pascuorum* displayed increases with shading up to 76% shade. Beneath the 84% shade treatment the level of readily germinable seed fell back to the same amount as was found in the control treatment, from which it was not significantly different. The remaining species, *C. brasilianum,* where a significant a difference was found, did not display any trend between readily germinable seed and shade treatment.

Hard seed

The amount of hard seed produced beneath the control treatment was greatest in the species *M. martii>M. lathyroides>C. brasilianum>M. atropurpureum,* all of which were not significantly different from one another (Table 2.42). The lowest level of hard seed under the control treatment was found in *C. pascuorum*, which also had the lowest levels of hard seed under 63% and 76% shade. Shading of 63% caused a slight reduction in the production of hard seed in most legume species. Just over 95% of seed produced by *Macroptilium martii* was hard, showing little difference from the control, however it was no longer the species with the greatest level of hard seed. The level of hard seed produced by *Desmanthus virgatus* under 63% shade increased by over 20%, to become the species with the greatest percentage of hard seed. Statistically the two species were not significantly different from one another or from *R. minima*. Decreases in hard seed were found in the species *M. martii, M. lathyroides, M. atropurpureum* and *D. virgatus,* upon increasing shade to 76%. The greatest fraction of hard seed was found in *C. brasilianum* and the lowest in *C. pascuorum.* Beneath 84% shade the highest percentage of hard seed was produced by *C. brasilianum* and *M. martii*, and the lowest by *M. atropurpureum* and *C. pascuorum*.

Within species significant differences were found in only four of the eight seed producing species. *M. atropurpureum* displayed a decrease in the percentage of hard seed with increasing shade, while the remaining three species did not display any clear trends. *Centrosema pascuorum* underwent a decrease under 63% and 76% shade but the percentage of hard seed rose sharply under 84% shade to a similar level to the control.

Non-viable seed

Table 2.43 displays the percentages of non-viable seed produced by each species under the varying shade treatments. Beneath the control and 63% shade treatments *Chamaecrista rotundifolia* contained the greatest fraction of non-viable seed beneath the control and 63% shade treatments. Under the control treatment, *C. rotundifolia* was not significantly different from two other species (*R. minima* and *D. virgatus*), but beneath 63% shade it was significantly different from all other species. *Macroptilium lathyroides* and *M. atropurpureum* produced the lowest fractions of non-viable seed beneath the control treatment and all other treatments, with little change in the values. Increasing shade from 0% (control) to 63% resulted in a decrease in non-viable seed in some species (*R. minima, D. virgatus* and *M. martii*), while others experienced an increase (*C. rotundifolia, C. brasilianum, C. pascuorum, M. atropurpureum* and *M. lathyroides*), although some of the increases were very small. No significant difference was detected between species beneath 76% shade, with both decreases and increases found in comparison to 63% shade. *Desmanthus virgatus* and *M. martii* both experienced large increases in the fraction of non-viable seed (approximately 9 and 15 times that found beneath 63% shade respectively). Similarly no significant difference was found between species beneath 84% shade. Beneath 84% shade *Centrosema brasilianum* was unique, producing no non-viable seed. Remaining species had low levels of non-viable seed, with the greatest of these being *C. pascuorum* with a mean of 3.7%.

Centrosema brasilianum and *C. pascuorum* were the only species in which significant differences were detected between shade levels. Within *C. brasilianum* the absence of any non-viable seed beneath 84% shade resulted in it being statistically different from other shade treatments, between which there was little difference. *Centrosema pascuorum* experienced a large increase in the amount of non-viable seed beneath 63% shade, which was significantly different from other shade treatments, which had much lower levels of non-viable seed. Species that did not have significant differences between shade treatments also had large variations with no pattern visible.

Time to 50% germination

Significant differences were found between species under all shade treatments (Table 2.44). No clearly discernable pattern was evident, with most species experiencing substantial changes in time to 50% germination with shading. *Macroptilium lathyroides* was the quickest of the species under the control treatment with 50% of readily germinable seeds germinated between days 3 and 4. The greatest time was found in *C. rotundifolia*, taking just over 19 days to 50% germination. Statistically the species were divided into three groups. The group with the shortest times contained the species *M. lathyroides<R. minima<M. atropurpureum<D. virgatus*. While the species *C. rotundifolia>C. brasilianum>M. martii>C. pascuorum* averaged the greatest time to 50% germination. Five species (*C. rotundifolia, C. brasilianum, M. martii, C. pascuorum* and *M. lathyroides*) had their time to 50% germination decreased by shading of 63% in comparison to full sun. Of these, *C. rotundifolia* underwent the greatest decrease taking, on average, 15.4 days less than under full sun to reach 50% germination. Seeds of *C. brasilianum* produced under 63% shade took longest for 50% germination, followed by *R. minima*. The fastest germinating species was *M. martii,* which germinated 11.3 days earlier compared to the control treatment, although it was only marginally faster than *M. lathyroides* which had not had its germination speed affected to any great extent by 63% shading. Shading of 76% resulted in the time to 50% germination of *C. brasilianum* substantially increasing to a level comparable with the control treatment. *Centrosema brasilianum* was clearly the slowest germinating species under 76% shade taking 9.4 days longer than the second slowest species *D. virgatus*. *Centrosema brasilianum* was significantly different from all other species, with remaining species all contained in the second statistical grouping. *Chamaecrista rotundifolia* was the earliest germinating species with 50% of its readily germinable seeds germinated after one day. Remaining species had 50% germination times similar to those found under 63% shade. Both *M. atropurpureum* and *C. pascuorum* took longer to reach 50% germination when produced under 84% shade. The time taken by *C. pascuorum* increased in comparison to 76% shade, rising to a level similar to that found in the control treatment. *Macroptilium atropurpureum* increased in its time to 50% germination taking longer under 84% shade than any other treatment. A similar effect was found in *C. brasilianum*, which beneath 84% shade took the longest time to 50% germination of any species under any shade treatment.

With the exception of *M. martii,* results within species also displayed little or no pattern. *Macroptilium martii* displayed a clear trend of decreasing time to 50% germination with increased levels of shading. Statistically the differences were highly significant, with the control significantly different from the remaining shade treatments. The only other species in which a significant difference was detected between shade treatments was *C. pascuorum*, however no real trend was apparent with the control and 84% shade treatments giving the greatest times to 50% germination and both treatments contained in the first statistical grouping. *Macroptilium lathyroides* was the only species in which the time to 50% germination remained relatively constant under the different shade treatments.

d) Germination curves

In each species the germination of seed with respect to time can be seen in Figures 2.12 a – h. In some graphs, particularly those with low levels of seed germination, differences (if any) between shade treatments are not clear. However in the species *C. brasilianum, M. atropurpureum* and *M. lathyroides* the differences in germination between shade treatments is clearly apparent. In these species seed produced under shaded conditions tended to have a greater percentage of germinated seed right from the beginning of the trial. In the species *C. brasilianum* and *M. atropurpureum* seed germination continued throughout the entire 28-day period, although very slowly at some points, particularly in *C. brasilianum*. *Macroptilium lathyroides,* however, had little or no further germination after approximately 9 days regardless of shade treatment. In the remaining species there was either too much variation for the curves to be of much use (*C. rotundifolia, R. minima* and *M. martii*), or no clear trend was apparent in relation to shade treatment (*D. virgatus* and *C. pascuorum*).

Table 2.41 Means, standard errors and LSD groupings of percent readily germinable seed of 8 forage legume species grown under 0 (control), 63, 76 and 82% shade, with seed harvested up to 119 days after planting. A – indicates no seed was produced or not enough samples to calculate the s.e. Means in a column followed by the same lower case letter do not differ significantly.

	Readily germinable seed (%)				
Species	**Control**	**63% shade**	**76% shade**	**84% shade**	*Probability*
Centrosema pascuorum	48.2 ± 2.6 aC	61.5 ± 4.4 aB	75.3 ± aA	48.7 ± 3.7 bC	0.0003
Macroptilium atropurpureum	17.5 ± 0.6 bD	31.7 ± 2.9 bC	40.0 ± bB	57.7 ± 1.3 aA	<0.0001
Macroptilium lathyroides	6.7 ± 1.5 cC	18.2 ± 1.6 cB	28.2 ± cA	-	<0.0001
Chamaecrista rotundifolia	4.5 ± 0.8 cd	5.0 ± 5.0 de	1.0 ± e	-	0.5971
Centrosema brasilianum	2.2 ± 0.2 cB	13.0 ± 1.3 cdA	6.0 ± deB	1.4 ± 1.4 cB	0.0006
Rhynchosia minima	2.2 ± 1.3 c	3.5 ± 3.5 e	-	-	0.7398
Macroptilium martii	1.5 ± 0.5 c	3.2 ± 0.7 e	2.0 ± de	2.5 ± 2.5 c	0.8406
Desmanthus virgatus	1.0 ± 0.0 cB	0.0 ± 0.0 eB	7.5 ± dA	-	0.0102
Probability	<0.0001	<0.0001	<0.0001	<0.0001	

Table 2.42 Means, standard errors and LSD groupings of percent hard seed of 8 forage legume species grown under 0 (control), 63, 76 and 82% shade, with seed harvested up to 119 days after planting. A – indicates no seed was produced or not enough samples to calculate the s.e. Means in a column followed by the same lower case letter do not differ significantly.

	Hard seed (%)				
Species	**Control**	**63% shade**	**76% shade**	**84% shade**	*Probability*
Macroptilium martii	95.0 ± 2.5 a	95.3 ± 0.8 a	76.7 ± 10.3 ab	95.0 ± 2.8 a	0.0885
Macroptilium lathyroides	92.0 ± 1.2 abA	79.7 ± 2.9 bB	69.5 ± 1.8 abC	-	0.0001
Centrosema brasilianum	89.7 ± 1.5 abcB	78.7 ± 1.6 bC	86.5 ± 1.4 aB	98.6 ± 1.4 aA	<0.0001
Macroptilium atropurpureum	80.7 ± 1.1 abcA	63.8 ± 3.0 cB	58.6 ± 2.6 bB	39.3 ± 1.3 bC	<0.0001
Desmanthus virgatus	74.2 ± 10.2 bcd	97.5 ± 2.5 a	69.3 ± 10.4 ab	-	0.0957
Rhynchosia minima	72.2 ± 5.2 cd	85.7 ± 8.2 ab	-	-	0.2191
Chamaecrista rotundifolia	56.7 ± 13.7 de	52.5 ± 6.3 c	84.0 ± 6.9 a	-	0.0903
Centrosema pascuorum	49.1 ± 3.0 eA	13.4 ± 5.7 dB	19.9 ± 2.0 cB	47.5 ± 4.7 bA	0.0001
Probability	0.0002	<0.0001	<0.0001	<0.0001	

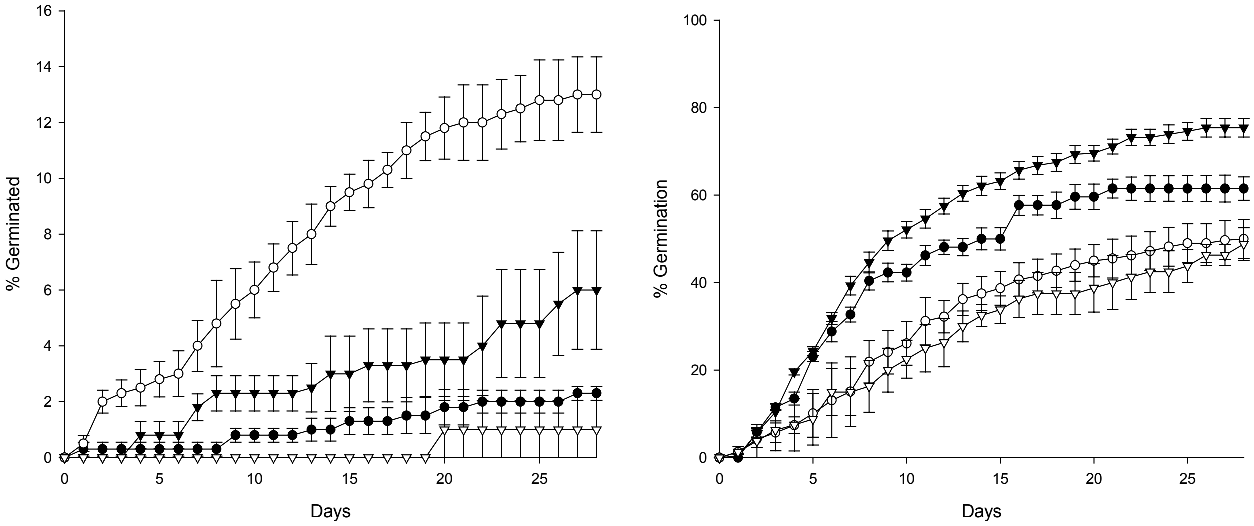
Table 2.43 Means, standard errors and LSD groupings of percent non-viable seed of 8 forage legume species grown under 0 (control), 63, 76 and 82% shade, with seed harvested up to 119 days after planting. A – indicates no seed was produced or not enough samples to calculate the s.e. Means in a column followed by the same lower case letter do not differ significantly.

	Non-viable seed (%)				
Species	**Control**	**63% shade**	**76% shade**	**84% shade**	*Probability*
Chamaecrista rotundifolia	38.7 ± 13.3 a	42.5 ± 4.7 a	15.0 ± 6.5	-	0.1178
Rhynchosia minima	25.5 ± 5.0 ab	10.7 ± 6.8 c	-	-	0.1333
Desmanthus virgatus	24.7 ± 10.2 ab	2.5 ± 2.5 c	23.1 ± 9.2	-	0.1506
Centrosema brasilianum	8.0 ± 1.4 bcA	8.2 ± 1.3 cA	7.5 ± 1.3 A	0.0 ± 0.0 B	0.0038
Macroptilium martii	3.5 ± 2.1 c	1.4 ± 1.4 c	21.2 ± 10.8	2.5 ± 2.5	0.0902
Centrosema pascuorum	2.7 ± 1.3 cB	25.0 ± 7.9 bA	4.6 ± 1.3 B	3.7 ± 2.4 B	0.0082
Macroptilium atropurpureum	1.7 ± 0.8 c	4.4 ± 1.6 c	1.3 ± 0.8	2.9 ± 2.0	0.4555
Macroptilium lathyroides	1.2 ± 0.6 c	2.0 ± 1.4 c	2.2 ± 0.6	-	0.7543
Probability	0.0011	<0.0001	0.0742	0.6978	

Table 2.44 Means, standard errors and LSD groupings of estimated time to 50% germination (days) of seed produced by 8 forage legume species grown under 0 (control), 63, 76 and 82% shade, with seed harvested up to 119 days after planting. A – indicates no seed was produced or not enough samples to calculate the s.e. Means in a column followed by the same lower case letter do not differ significantly.

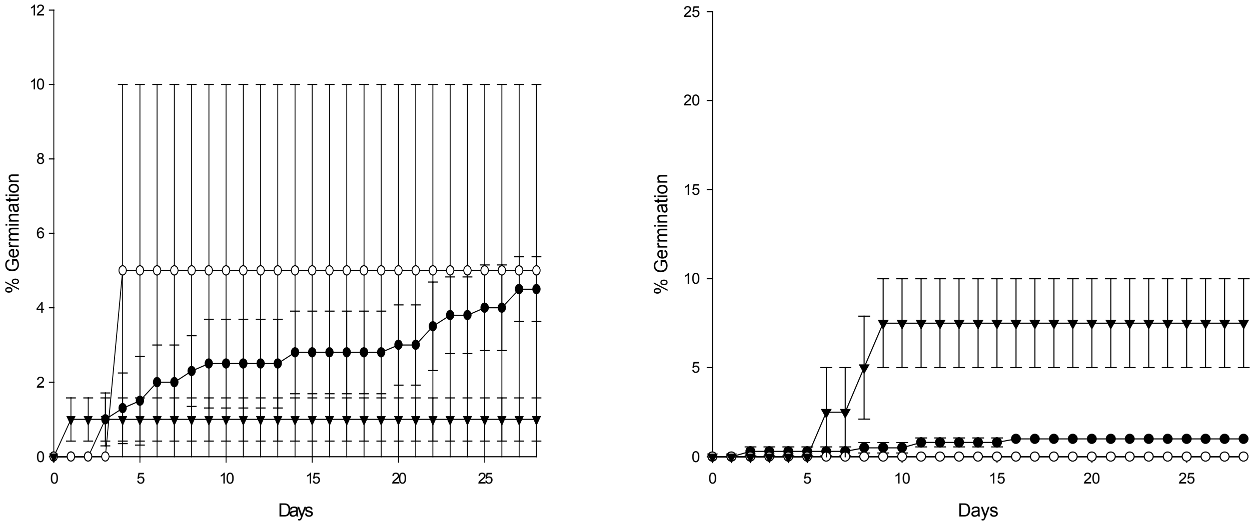
	Time to 50% germination (days)				
Species	**Control**	**63% shade**	**76% shade**	**84% shade**	*Probability*
Chamaecrista rotundifolia	19.2 ± 5.3 a	3.8 ± - cd	1.0 ± 0.0 b	-	0.1595
Centrosema brasilianum	18.8 ± 2.9 a	11.8 ± 0.6 a	17.0 ± 4.2 a	20.0 ± - a	0.3858
Macroptilium martii	13.5 ± 2.5 abA	2.2 ± 0.6 dB	1.7 ± 0.4 bB	1.0 ± - cB	0.0042
Centrosema pascuorum	12.0 ± 0.4 abA	6.9 ± 0.9 bcB	6.9 ± 0.2 bB	11.6 ± 0.7 bA	0.0001
Desmanthus virgatus	9.2 ± 2.9 bc	-	7.6 ± 0.8 b	-	0.6734
Macroptilium atropurpureum	7.1 ± 0.8 bc	8.3 ± 1.2 b	7.4 ± 0.9 b	11.7 ± 1.7 b	0.0813
Rhynchosia minima	6.4 ± 0.7 bc	10.0 ± - ab	-	-	0.1252
Macroptilium lathyroides	3.4 ± 0.6 c	2.6 ± 0.3 d	3.6 ± 0.3 b	-	0.3080
Probability	0.0025	<0.0001	0.0005	0.0143	

Figure 2.12 Changes over time in mean germination rates and standard errors of seed produced under control (0%shade), 63%, 76% and 84% shade, at 32°C under a 12/12 hour day/night cycle for 28 days. N =4



a) *Centrosema brasilianum*

b) *Centrosema pascuorum*

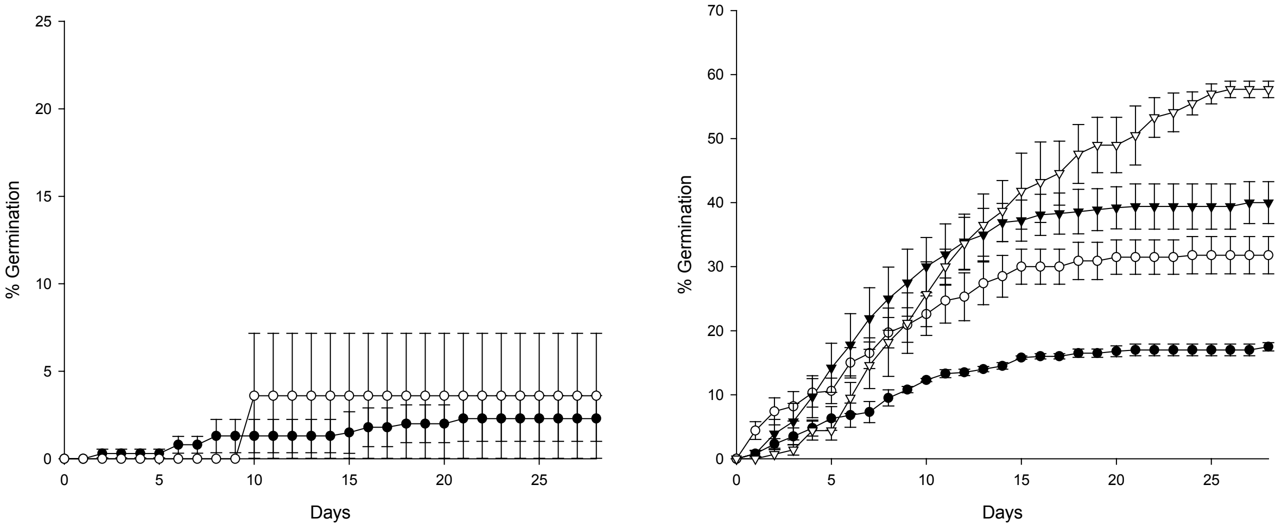


c) *Chamaecrista rotundifolia*

d) *Desmanthus virgatus*

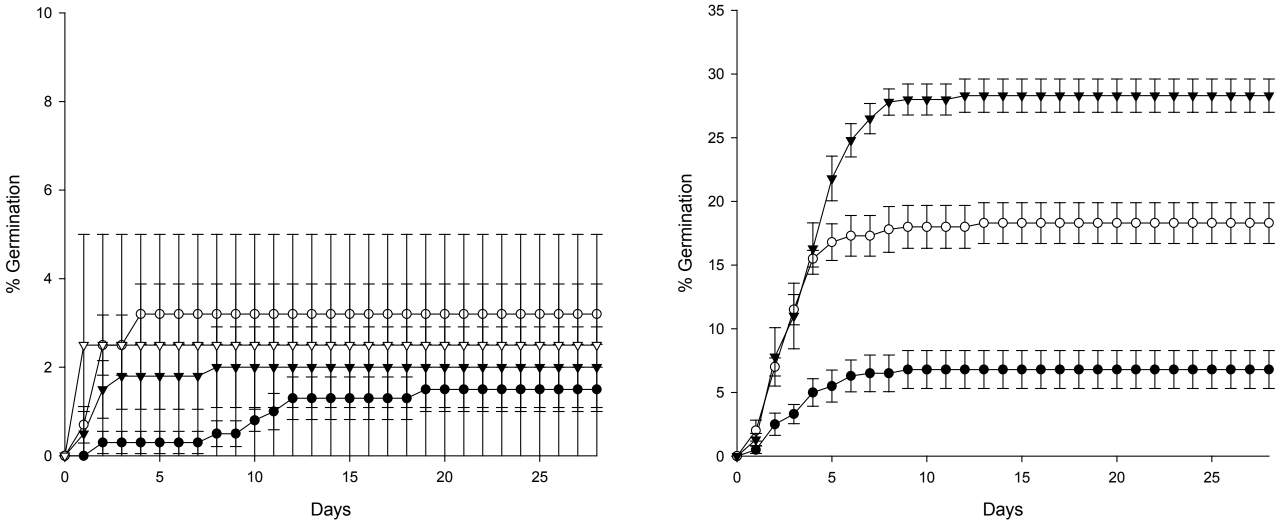
—●— Control
—○— 63% Shade
—▼— 76% Shade
—▽— 84% Shade

Figure 2.12 cont.



e) *Rhynchosia minima*

f) *Macroptilium atropurpureum*



g) *Macroptilium martii*

h) *Macroptilium lathyroides*

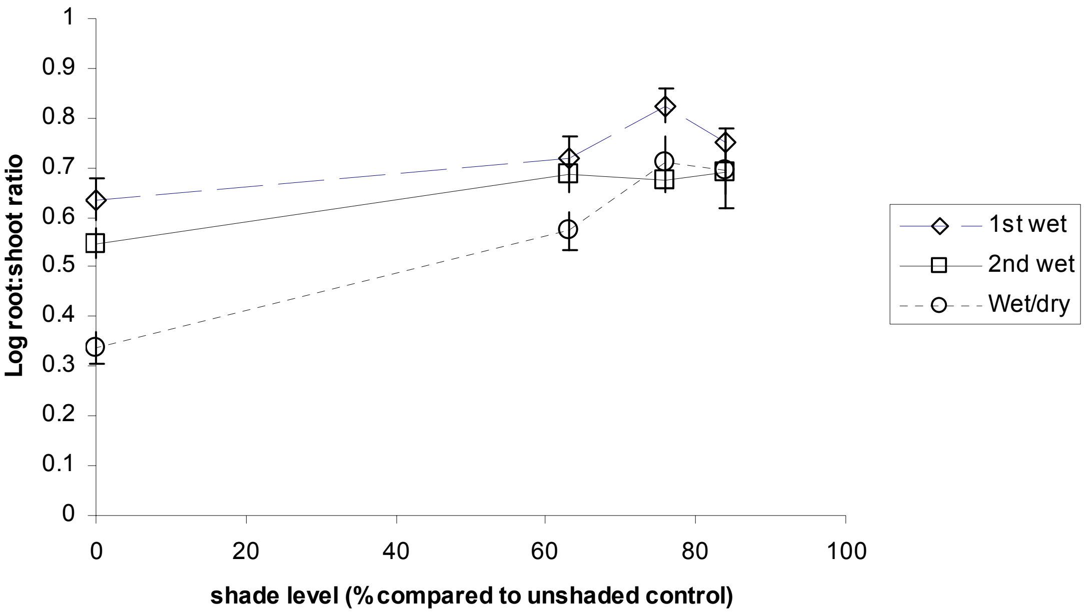
—●— Control
—○— 63% Shade
—▼— 76% Shade
—▽— 84% Shade

2.3.11 Shoot:root ratio

a) Effect of shade level

Shade significantly increased the shoot:root ratio in each trial (Figure 2.13). The wet tropical species from both trials were found to have significant relationships with shade levels (P values of 0.0026 and 0.004 respectively), while the wet/dry species trial had a highly significant relationship ($P<0.0001$).

Figure 2.13 Regressions of log root:shoot ratios, with standard errors, 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.



b) Effect of legume genotype

1st wet tropical species trial

Arachis pintoi allocated the greatest proportion of its resources into the production of shoot material of the species examined, although it was not significantly different from *D. ovalifolium* and *D. intortum* which had similar shoot:root ratios (Table 2.45). The lowest shoot:root ratio was present in *C. mucunoides,* that was less than half of *A. pintoi*.

2nd wet tropical species trial

Statistical analysis revealed extensive overlap of species, with all species bar two, contained in two or more statistical groupings (Table 2.45). The two species present in only one statistical grouping were *D. heterophyllum* and *F. congesta*, with the highest and lowest shoot:root ratios, respectively. Seven statistical groupings were found in which the means were significantly different from one another, but the large amount of overlap between species indicates no distinctly different groupings. The group with the greatest mean contained the species *D. heterophyllum>C. macrocarpum>C. acutifolium>D. triflorum>A. americana*. Similarly the grouping with the lowest mean also contained a large number of species *F. congesta<A. kretschmeri<A. villosa* cv. Kretschmer<*C. pubescens<N. wightii<S. guianensis*.

Wet/dry tropical species

Arachis stenosperma was the species with the greatest shoot:root ratio which was substantially greater than that of *S. scabra* the second greatest, although they were not significantly different from one another (Table 2.45). In contrast, the grouping of the species with the lowest shoot:root ratios contained a large number of species (*M. atropurpureum<S. hamata< M. lathyroides<M. martii<A. paraguariensis<D. scorpiurus<C. pascuorum<C. ternatea<R. minima*). No clear differences between species were present as all save *A. stenosperma* and *M. atropurpureum* belonged to 2 or 3 statistical groupings.

Table 2.45 Means, standard errors and LSD groupings of the log of shoot:root ratio of (a) 7, (b) 14 and (c) 14 legume species grown under 4 shade levels, harvested 107 and 103 days after planting respectively. n = 20 and 16 respectively. Means in a column followed by the same letter are not significantly different. Numbers in parenthesis are the untransformed shoot:root ratio means.

(a) 1st Trial

Species	**Log of shoot:root ratio**
A. pintoi	0.873 ± 0.041 a (7.99)
D. ovalifolium	0.834 ± 0.032 ab (7.17)
D. intortum	0.824 ± 0.038 ab (7.11)
V. luteola	0.731 ± 0.071 bc (7.12)
M. axillare	0.717 ± 0.063 bc (6.01)
D. canum	0.613 ± 0.034 cd (4.36)
C. mucunoides	0.557 ± 0.028 d (3.76)
Probability	<0.0001

(b) 2nd Trial

Species	**Log of shoot:root ratio**
D. heterophyllum	0.803 ± 0.045 a (6.88)
C. macrocarpum	0.785 ± 0.042 ab (6.49)
C. acutifolium	0.768 ± 0.061 abc (6.98)
D. triflorum	0.745 ± 0.054 abcd (6.29)
A. americana	0.671 ± 0.036 abcde (4.90)
P. phaseoloides	0.652 ± 0.065 bcde (5.45)
A. villosa	0.630 ± 0.083 cdef (4.84)
D. uncinatum	0.630 ± 0.053 cdef (4.72)
S. guianensis	0.600 ± 0.086 defg (4.77)
N. wightii	0.518 ± 0.043 efg (4.08)
C. pubescens	0.574 ± 0.043 efg (4.01)
A. villosa cv. Kret	0.518 ± 0.054 efg (3.59)
A. kretschmeri	0.451 ± 0.086 fg (3.10)
F. congesta	0.448 ± 0.042 g (2.96)
Probability	<0.0001

(c) 3rd Trial

Species	**Log of shoot:root ratio)**
A. stenosperma	0.940 ± 0.130 a (16.2)
S. scabra	0.700 ± 0.086 ab (6.34)
C. rotundifolia	0.664 ± 0.089 bc (5.57)
C. brasilianum	0.635 ± 0.089 bc (5.78)
D. virgatus	0.621 ± 0.060 bc (4.78)
R. minima	0.553 ± 0.113 bcd (4.40)
C. ternatea	0.543 ± 0.084 bcd (4.35)
C. pascuorum	0.498 ± 0.114 bcd (4.56)
D. scorpiurus	0.460 ± 0.090 bcd (3.39)
A. paraguariensis	0.441 ± 0.071 cd (3.12)
M. martii	0.435 ± 0.090 cd (3.08)
M. lathyroides	0.420 ± 0.049 cd (2.88)
S. hamata	0.339 ± 0.140 cd (2.66)
M. atropurpureum	0.300 ± 0.061 d (2.22)
Probability	0.0001

c) Interaction effects

1st wet tropical species trial

Significant differences were detected between species in three of the four treatments with no significant difference found beneath 76% shade (Table 2.46). Under the control treatment the species *A. pintoi, D. intortum* and *D. ovalifolium* were all contained in the first statistical grouping, and remained so beneath the 63 and 84% shade treatments, with the species *M. axillare* (63% shade) and *V. luteola* and *M. axillare* (84% shade). Species with the lowest transformed means included *V. luteola* and *C. mucunoides*, however their rankings did not remain constant across all shade treatments. *Vigna luteola* was the species with the lowest yield under the control treatment but beneath 76 and 84% shade it was found to have the greatest and the fourth greatest transformed mean, respectively.

Within species, *D. canum, C. mucunoides* and *V. luteola* were found to contain significant differences between shade treatments. Of these the species only *V. luteola* displayed a clear trend with as the shoot:root ratio increased with shading. *Calopogonium mucunoides'* results were somewhat confused with the 84% shade treatment not found to be significantly different from the control. In the case of *D. canum* the greatest shoot:root ratio was found beneath in the 76% shade and control treatments. The species *A. pintoi, D. intortum* and *D. ovalifolium* all displayed a slight increase in shoot:root ratio under the shaded treatments however it was not found to be statistically significant. *Macrotyloma axillares'* shoot:root ratio also increased beneath the shaded treatments, however it was not as apparent as in other species with the 84% shade treatment having only a slightly greater ratio than the control.

2nd wet tropical species trial

Under the control treatment *C. acutifolium* allocated the greatest fraction of resources to the production of shoot material, although it plus *S. guianensis>D. heterophyllum>N. wightii>C. macrocarpum>D. triflorum>A. americana>A. villosa* were not statistically different (Table 2.47). Similarly the grouping with the lowest transformed means contained a large number of species *F. congesta<A. kretschmeri<P. phaseoloides<C. pubescens<A. villosa<D. uncinatum*. A large amount of overlap was present in many of the species, of which some belonged to up to four statistical groupings. *Centrosema acutifolium* remained the species with the greatest transformed mean beneath 63%

shade, but again it was not significantly different from a large number of other species (*C. acutifolium>D. triflorum>C. macrocarpum>D. heterophyllum>S, guianensis>A. americana*). *Flemingia congest* no longer had the lowest shoot:root ratio, but it was still present in the lowest statistical grouping along with six other species (*N. wightii<A. villosa* cv. Kretschmer*<F. congesta<P. phaseoloides<C. pubescens<D. uncinatum*). Similar to the control treatment many species belonged in a large number of statistical groupings (5 species were present in 4 statistical groupings). The 76% shade treatment was not found to have any significant differences between species although the probability was close to the 0.05 threshold (P = 0.0615). A substantial difference between some species was present, for example a difference of 0.357 was present between the species with the greatest and lowest transformed means, *C. macrocarpum* and *F. congesta* respectively. Under this shade treatment several of the species which previously hade lower transformed means of shoot:root ratio were among the highest (*A. villosa, P. phaseoloides*). The most notable change beneath 84% shade was present in *S. guianensis*, which was the lowest ranked species beneath this shade treatment, which had a transformed mean of –0.100, and was statistically different from all other species. The greatest transformed means were found in the species *D. uncinatum>C. macrocarpum>D. heterophyllum>P. phaseoloides>D. triflorum>A. americana>A. villosa>C. acutifolium*. Once again there was a large amount of overlap present with all save three species contained in 2 or more statistical groupings.

Within species, five were found to have significant differences between shade treatments (*S. guianensis, C. macrocarpum, D. uncinatum, F. congesta* and *P. phaseoloides*). *Flemingia congesta, C. macrocarpum* and *P. phaseoloides* displayed clear increases in shoot:root ratio beneath the shade treatments, while *D. uncinatum* did show a general increase the control, 63 and 76% shade treatments were not significantly different from one another. In contrast *S. guianensis* displayed a trend of decreasing shoot:root ratio with shading however the control, 63 and 76% shade treatments were not significantly different from one another, while the 84% shade treatment mean was much lower than the previous three. Of the species in which no significant differences were found *D. heterophyllum, D. triflorum, A. americana, A. villosa, C. pubescens, A. krestschmeri* and *S. hamata* all tended to increase in shoot:root ratio beneath shaded treatments, while the species *N. wightii* and *A. villosa* cv. Kretschmer did not display any clear trends.

Wet/dry tropical species trial

No significant differences were detected between species beneath the control or any of the shade treatments. Beneath the control the greatest transformed mean was given by *S. scabra* and the lowest by *M. atropurpureum* (Table 2.48). Beneath 63% shade *S. scabra* was no longer the species with the greatest transformed mean, ranking seventh of the species. *Chamaecrista rotundifolia* had the greatest transformed mean under 63% shade although the margin between it and *A. stenosperma* was small (0.022). *Macroptilium atropurpureum* continued to have the lowest shoot:root ratio. *Chamaecrista rotundifolia* and *Arachis stenosperma* remained the two species with the greatest shoot:root ratios although *A. stenosperma* had greatest transformed mean beneath 76% shade. *Macroptilium martii* replaced *M. atropurpureum* as the lowest ranking species. Shading of 84% resulted in *A. stenosperma* remaining as the species with the greatest transformed mean, while *C. rotundifolia* fell to seventh. *Macroptilium atropurpureum* had the lowest transformed mean, which was less than half that of the second lowest species, *M. martii*.

The majority of species (*A. stenosperma, D. virgatus, R. minima, S. hamata, C. rotundifolia, C. pascuorum, C. ternatea, D. scorpiurus, C. brasilianum* and *M. lathyroides*) were found to display an increase in shoot:root ratio with shading, while *A. paraguianensis* appeared to under go a decrease in shoot:root ratio with shading. The remaining species, *S. scabra* and *M. martii,* did not show any clear trend.

Table 2.46 Means, standard errors and LSD groupings of the log of shoot:root ratio of 7 forage legume species grown under 0 (control), 63, 76 and 82% shade (n = 5), harvested 107 days after planting. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly. Numbers in parenthesis are the untransformed shoot:root ratio means.

	Log shoot:root ratio (untransformed data mean)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
A. pintoi	0.853 ± 0.046 a (7.30)	0.859 ± 0.073 a (7.44)	0.891 ± 0.210 (9.81)	0.895 ± 0.0313 a (7.91)	0.9814
D. intortum	0.759 ± 0.044 a (5.86)	0.857 ± 0.105 a (8.04)	0.844 ± 0.070 (7.32)	0.850 ± 0.081 a (7.36)	0.7781
D. ovalifolium	0.758 ± 0.037 a (5.80)	0.864 ± 0.051 a (7.51)	0.810 ± 0.137 (7.16)	0.896 ± 0.061 a (8.20)	0.4501
D. canum	0.643 ± 0.020 bAB (4.41)	0.474 ± 0.028 cC (3.00)	0.757 ± 0.066 A (6.00)	0.580 ± 0.077 bBC (4.02)	0.0146
M. axillare	0.550 ± 0.040 bc (3.59)	0.730 ± - ab (5.32)	0.892 ± 0.153 (9.35)	0.600 ± 0.050 ab (4.00)	0.1820
C. mucunoides	0.444 ± 0.024 cdC (2.80)	0.665 ± 0.066 bA (4.58)	0.597 ± 0.047 AB (4.05)	0.513 ± 0.032 bBC (3.28)	0.0131
V. luteola	0.414 ± 0.040 dC (2.63)	0.642 ± 0.066 bcBC (4.58)	1.02 ± 0.137 A (12.5)	0.848 ± 0.147 aAB (8.76)	0.0065
Probability	<0.0001	0.0019	0.2223	0.0162	

Table 2.47 Means, standard errors and LSD groupings of the log of shoot:root ratio of 14 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. Numbers in parenthesis are the untransformed shoot:root ratio means.

	Log shoot:root ratio (untransformed data mean)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
C. acutifolium	0.765 ± 0.764 a (5.89)	0.952 ± 0.154 a (11.2)	0.715 ± 0.121 (5.88)	0.639 ± 0.129 abcd (4.98)	0.3375
S. guianensis	0.714 ± 0.079 aA (5.78)	0.765 ± 0.038 abcdA (5.89)	0.644 ± 0.082 A (4.62)	-0.100 ± 0.039 eB (0.79)	0.0001
D. heterophyllum	0.731 ± 0.147 a (6.46)	0.825 ± 0.110 abc (7.31)	0.785 ± 0.022 (6.13)	0.868 ± 0.062 ab (7.61)	0.7877
N. wightii	0.666 ± 0.063 ab (4.73)	0.441 ± 0.109 e (3.02)	0.647 ± 0.017 (4.44)	0.600 ± 0.092 cd (4.27)	0.2485
C. macrocarpum	0.600 ± 0.057 abcB (4.08)	0.832 ± 0.063 abcA (6.94)	0.842 ± 0.088 A (7.38)	0.877 ± 0.045 aA (7.62)	0.0430
D. triflorum	0.580 ± 0.085 abcd (4.03)	0.894 ± 0.093 ab (8.44)	0.720 ± 0.067 (5.43)	0.786 ± 0.150 abcd (7.24)	0.2411
A. americana	0.549 ± 0.055 abcd (3.63)	0.740 ± 0.065 abcd (5.69)	0.692 ± 0.064 (5.10)	0.733 ± 0.0671 abcd (5.74)	0.1787
A. villosa cv. Kret.	0.541 ± 0.086 abcd (3.72)	0.429 ± 0.142 de (3.59)	0.521 ± 0.067 (3.45)	-	0.9441
D. uncinatum	0.482 ± 0.080 bcdeB (3.18)	0.648 ± 0.045 bcdeB (4.52)	0.597 ± 0.032 B (3.97)	0.936 ± 0.171 aA (9.32)	0.0259
A. villosa	0.452 ± 0.145 bcde (3.20)	0.580 ± - cde (3.80)	-	0.815 ± - abc (4.54)	0.3698
C. pubescens	0.405 ± 0.102 bcde (2.68)	0.642 ± 0.093 bcde (4.69)	0.595 ± 0.073 (4.13)	0.610 ± 0.060 bcd (4.20)	0.2749
P. phaseoloides	0.382 ± 0.066 cdeB (2.49)	0.635 ± 0.148 bcdeAB (5.10)	0.732 ± 0.120 A (5.99)	0.857 ± 0.063 abcA (7.43)	0.0458
A. kretschmeri	0.298 ± 0.092 de (2.03)	0.527 ± 0.106 cde (3.64)	-	-	0.2485
F. congesta	0.247 ± 0.039 eB (1.78)	0.532 ± 0.098 cdeA (3.56)	0.485 ± 0.040 A (3.09)	0.514 ± 0.077 dA (3.37)	0.0470
Probability	0.0027	0.0314	0.0615	0.0002	

Table 2.48 Means, standard errors and LSD groupings of the log of shoot:root ratio of 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 lower case letter and means in a row followed by the same upper case letter do not differ significantly. Numbers in parenthesis are the untransformed shoot:root ratio means.

	Log shoot:root ratio (untransformed data mean)				
Species	**Control**	**63% Shade**	**76% Shade**	**84% Shade**	**Probability**
S. scabra	0.663 ± 0.102 (5.03)	0.408 ± 0.100 (4.00)	0.779 ± 0.451 (9.56)	0.948 ± 0.249 (10.39)	0.5744
A. paraguariensis	0.546 ± 0.078 (3.63)	0.496 ± 0.086 (3.32)	0.272 ± 0.256 (2.20)	0.375 ± 0.223 (2.97)	0.6601
A. stenosperma	0.463 ± 0.131 (3.41)	0.777 ± 0.099 (6.28)	0.946 ± 0.009 (8.83)	1.020 ± 0.200 (11.61)	0.0697
M. martii	0.424 ± 0.002 (2.66)	0.684 ± 0.052 (4.86)	0.230 ± 0.348 (2.27)	0.371 ± - (2.35)	0.4344
D. virgatus	0.401 ± 0.073 (2.63)	0.618 ± 0.081 (4.36)	0.816 ± 0.102 (7.10)	0.659 ± 0.159 (5.13)	0.0747
R. minima	0.326 ± 0.116 (2.26)	0.539 ± 0.077 (3.51)	0.772 ± - (5.92)	1.043 ± - (11.0)	0.1168
S. hamata	0.322 ± 0.179 (2.68)	0.408 ± - (2.56)	-	-	0.8453
C. rotundifolia	0.275 ± 0.076 B (1.93)	0.799 ± 0.139 B (7.03)	0.874 ± 0.049 B (7.62)	0.586 ± - AB (3.85)	0.0086
C. pascuorum	0.247 ± 0.187 (2.39)	0.518 ± 0.632 (7.47)	0.723 ± 0.133 (5.93)	0.518 ± 0.159 (3.70)	0.4958
C. ternatea	0.243 ± 0.069 C (1.82)	0.493 ± 0.031 BC(3.13)	0.746 ± 0.064 AB (5.69)	0.916 ± 0.213 A (9.25)	0.0030
D. scorpiurus	0.240 ± 0.151 (1.97)	0.632 ± 0.219 (4.84)	0.680 ± 0.060 (4.83)	0.399 ± 0.141 (5.13)	0.2601
C. brasilianum	0.231 ± 0.068 B (1.76)	0.664 ± 0.133 A (5.25)	0.789 ± 0.121 A (6.64)	0.763 ± 0.162 A (6.36)	0.0154
M. lathyroides	0.214 ± 0.050 B (1.67)	0.455 ± 0.045 A (2.90)	0.612 ± 0.077 A (4.28)	0.393 ± 0.102 AB (2.61)	0.0099
M. atropurpureum	0.182 ± 0.093 (1.61)	0.305 ± 0.180 (2.33)	0.486 ± 0.057 (3.14)	0.159 ± 0.063 (1.45)	0.1830
Probability	0.1355	0.6555	0.0924	0.0762	

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 under shade treatments. 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 (Eriksen and Whitney 1981; Chen 1993; Amar 1996; Devkota *et al.* 2001; Peri *et al.* 2001; Varella *et al.* 2001b).

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 above-ground dry matter is expressed as a percentage of production under the control, the potential shade tolerance of species is easier to ascertain (Tables 2.49). Species producing approximately one-fifth or more of their yield under the control treatment beneath 84% shade included *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 (Section 2.3.1), 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 and 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 and 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 maintain 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 and 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 will be discussed later, 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 shade-adapted plant and in some cases to perform better under light to moderate shading than under full sun. Fisher and 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 20cm. *Arachis pintoi* is generally regarded as being shade-tolerant (Cook 1992; Fisher and 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 and Sumolang 1990; Ng 1990; Rika *et al.* 1990; Stur 1990; Kaligis *et al.* 1994b). *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, 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 (1992b) 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 and 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 and 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 (*Stylosanthes guianensis*) (Ludlow 1980). However Reynolds (1995) found that its growth beneath coconuts in Western Samoa and Zanzibar was poor.

Macrotyloma axillare and *V. 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 suggesting that nutritive value to stock and persistence, in particular, may be serious problems under shaded conditions. *Macrotyloma axillare* was one of the worst affected species by shade with dry matter production declining to very low levels beneath 76% and 84% shade. *Macrotyloma axillare* had the second lowest relative yield of any species examined that survived beneath 84% shade. According to Reynolds (1995), little is know 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 under taken by Stur (1990). *Macrotyloma axillare* is reported by Staples (1992c) 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 and 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 and 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, *C. 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*). *Centrosema macrocarpum* maintained the greatest proportion of its yield under full light than any other species, save *C. mucunoides* under 63% 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 (1992c) 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 and Stur (1999) indicated that it had potential as a cover crop beneath trees.

Production of above-ground biomass by *P. phaseoloides* was amongst the best of all species having the greatest of all yields under 63 and 76% shade and the third greatest beneath the control and 84% shade. Relative yields were good but not as great as some species. The results obtained here clearly indicate *P. phaseoloides* as a species well suited to growth beneath shaded conditions. Reynolds (1995) indicates that *Pueraria phaseoloides* has slow to germination and early growth, but once established grows rapidly and this trial was no exception. It is widely used as a cover-crop beneath coconut and oil palm plantations (Halim 1992a) and is sometimes used as a pioneering legume along with *C. mucunoides, C. pubescens* and a grass (Reynolds 1995), where its growth can be so vigorous it is used to suppress weeds. As such a vigorous climber it may be a potential weed in young plantations where it may smother young or small trees and even the grass component of pasture. Its is indicated by Reynolds (1995) to be fairly shade tolerant and to grow well beneath coconuts and Skerman *et. al.* (1988) states that it tolerates partial shade. Halim (1992a), however, indicates it as being highly shade tolerant. The growth of *P. phaseoloides* may be such that it may suppress accompanying grasses (Steel *et al.* 1980a) even beneath 50% shade (Halim 1992a). It was also noted by Steel *et al.* (1980a) that under shade in particular *P. phaseoloides* appears to be poorly accepted by cattle. As a result of its vigorous growth and poor palatability to stock careful management of will be required in order to prevent the smothering of trees and grasses by *P. phaseoloides*.

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 1992a). *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 and 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 5.7g 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 shade-tolerant by a number of sources (Schultze-Kraft 1986; Skerman *et al.* 1988; Stur 1990; Wong 1991; Reynolds 1995) with Hacker and Teitzel (1992) suggesting that it is one of the most shade-tolerant legumes. Kaligis and 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 and 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 (*Brachyiaria 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 and 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 (Ludlow 1980; Eriksen and Whitney 1982), with Gutteridge and Whiteman (1978) noting that it behaved more as a short-term pioneer species. *Flemingia congesta* has been noted to tolerate shade (Budelman and Siregar 1992), however it did not perform as well as many other species. As the species typically grows into a woody deep-rooting shrub 1 – 4 m tall it may have been restricted in growth by the pots, as even the plants in the control treatment were not particularly large. The results obtained in this trial however do not indicate a large degree of shade tolerance, however its was certainly not as adversely affect as some 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. However when light was reduced to 20%, both *A. americana* cv. Glenn and CPI 56283 had much lower yield rankings (Stur 1991). Beneath light transmission of 73% PAR initial yields of *A. americana* were found by Kaligis and 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 38.15%. It appears 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 and 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 and 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 *D. 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 suggests 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 and 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). *Desmodium 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 *A. 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 *C. ternatea*, which gave the best actual 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. The relative production of *C. ternatea* 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 in shaded situations due to its high actual production. Several other of the plant's properties will have to be borne in mind when considering *C. ternatea* 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 in turn cause its failure to persist (Skerman *et al.* 1988). *Clitoria ternatea* does not appear to have been widely tested for its performance under shade. Sanchez and Ibrahim (1991) found *C. ternatea* 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 PARs of 100, 27, 8, 6 and 3%. 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, 60th and 53rd 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*, save *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. *Macroptilium 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. *Macroptilium atropurpureum* is indicated by Skerman *et al.* (1988) to grow reasonably well in shade, but to prefer abundant sunlight. More specific information is given by Eriksen and 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. atropurpureums'* 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 in response to shade the lower parts of the plant can become woody in response to shade, and that it is not unduly suppressed by the absence of light, 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 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 given 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 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 and estimated 73% PAR (Kaligis and 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 *M. 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 *D. 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 and Sumolang (1991), while Rika *et al.* (1991)*l.* 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 had 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

22nd, 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 nut 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 provided ground cover, although it was indicated that it could be evaluated as a cover crop for tropical fruit groves.

Due to the mixture of species (*D. virgatus, D. pubescens* and *D. leptophyllus*) used in the cultivar marketed as *D. virgatus* cv. Jabiru, 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. Jabirus' 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 2.49 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

Wet tropical species	**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

Wet/dry tropical species	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	-

2.4.3 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. 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 organic soil 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 (Ludlow 1980; Eriksen and Whitney 1981; Wilson *et al.* 1986; Shelton *et al.* 1987; Wilson and Wild 1995). Reduction in nodulation and N fixation in legumes when grown in shade has been noted in the past (Chu and Robertson 1974; Lie 1974; Wong and Wilson 1980; Eriksen and Whitney 1982; Sundram *et al.* 1986; Bacanamwo and Harper 1997). Fixation of N has been found to be directly related to the supply of surplus assimilate to nodules (Othman *et al.* 1988; Humphreys 1991) and therefore it can be expected that shading that 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 or absence of root nodulation by shade 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 (Wong and Wilson 1980; Wilson *et al.* 1986; Humphreys 1994). It is known that when grown under shaded conditions tropical grasses may under-go an increase in N content and dry matter yield if soil N is limiting to growth under full light. This effect was shown by Wilson and Wild (1991) to reside in the soil 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 and 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 a 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 discernable. Within the wet/dry species tested results were also mixed with some species increasing P concentrations with shade (*C. rotundifolia, A. stenosperma, S. scabra, M. lathyroides, C. ternatea* and *D. virgatus*), and others decreases with shading (*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 (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. This may have implications in seed production with earlier flowering cultivars/accessions desirable in certain situations in order produce seed before unfavourable conditions can effect 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 (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 to 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 in the past to be decreased by shading during the reproductive stage in cereals such as rice (Venkateswarlu and Maddulety 1976), cotton seed (Eaton and Ergle 1954), grain legumes such as Peas (Meadly and Milbourn 1971) Cowpea (Summerfield *et al.* 1976), grasses (de Oliveira and 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 (Gifford *et al.* 1973; Fisher 1975). Similarly de Oliveira and 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 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 however it was present in different species than had increased amounts of readily germinable seed (*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 discernable 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 (Ludlow *et al.* 1974; Lange *et al.* 1981; Wong *et al.* 1985a, 1985b; Samarakoon *et al.* 1990a; Wilson and Ludlow 1991; Amar 1996; Atwell *et al.* 1999). 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 roots 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 and Ludlow 1991). Under full light regrowth after defoliation has been found to be more dependant upon residual leaf area than upon stored reserves (Humphreys and Robinson 1966) but Wilson and 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 anchoring the plants in the ground.

2.5 Conclusions

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

1. Decrease the production of above and below-ground plant matter although the extent of this decrease varied substantially between species.
2. Decrease the level of root nodulation and hence potentially decrease the amount of N 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.
3. Concentrations of leaf N was found to increase with shading, possibly due to the same reasons as given for decreased nodulation.
4. Concentrations of leaf P in response to shade were irregular between species, with both increases and decreases found in plants grown under shade.

5. Length of time until the production of the first flower was generally longer in plants grown beneath shade, suggesting that shading prolongs vegetative growth.
6. Production of seed was greatly diminished under shade, however the weight of seeds produced did not appear to be less than those under the control treatment.
7. Amounts of readily germinable seed were greater in some species when seed was produced under the shade treatments in comparison to that of 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.
8. Shoot:root ratio was increased by shading as was expected, with the shoot system fraction increasing at the expense of the root system, with excessive increases in the shoot:root ratio potentially leading to problems with water stress, recovery after defoliation and uprooting by stock.

The species *A. pintoi, D. 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 there prostrate or trailing/scrambling habit. Species recommended for wet/dry tropical areas include *M. lathyroides* and *A. stenosperma*. Other species which can be recommended for use, but have other issues that may have implications upon their suitability, include *C. macrocarpum, C. mucunoides, C. pubescens, P. phaseoloides, C. acutifolium* and *N. wightii* (wet tropics), *M. atropurpureum, C. ternatea* and *C. 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. The second issue with climbing species is that of persistence, with climbing/twining species not 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 site factors such as soil pH, drainage etc.

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 fields 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.

Chapter 3 - Light response curves and physiological measurements

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 lower levels of adaptability (Atwell *et al.* 1999). Plants may be divided, based upon their photosynthetic characteristics into two broad categories; C_3 species, which include temperate grasses and legumes, most broad leaf plants and tropical legumes, with plants in this group using the Calvin pathway of CO_2 fixation, and C_4 species which includes improved and most native grasses of tropical and subtropical areas, with these plants utilizing the C_4 pathway of CO_2 fixation (Ludlow 1978).

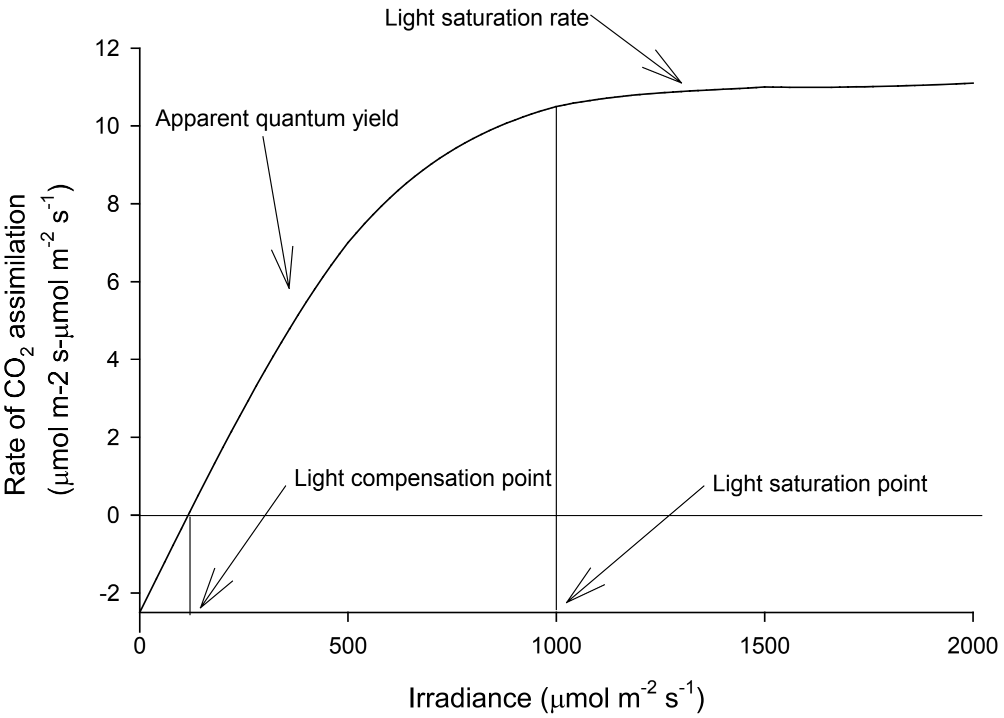
Low light intensities limit photosynthesis and therefore impose stresses upon plants through lower net carbon gain and plant growth (Lambers *et al.* 1998). It is estimated that only about 1% of visible light striking the leaf is utilized by photosynthesis, with the energy of photons hitting various pigments in the chloroplasts collected by chlorophyll molecules, in light-harvesting protein complexes, transferred by the Hill reaction to electrons (Nilsen and Orcutt 1996). Plant responses to low light intensities can be at the structural or the biochemical level (Lambers *et al.* 1998). 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 curve has general properties which 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, due to light being the limiting factor (Nilsen and 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 and Orcutt 1996). The light intensity where CO_2 assimilation is balanced by CO_2 loss due to respiration is known as the “compensation point”, below which there is insufficient light to compensate for respiratory CO_2 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 and 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 (Boardmean 1977; Ludlow 1978; Nilsen and Orcutt 1996; Lambers *et al.* 1998). The photosynthesis of sun-plants will decrease substantially beneath shade compared to full light, as shown by Ward and Woolhouse (1986). However 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 and Ludlow 1991). As a result 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 aims of the experiment detailed in this chapter were to attempt to determine if there was a correlation between physiological and agronomic results and potential of physiological measurements for the determination of shade tolerance or adaptation in selected pasture legumes.

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

Plants upon which these measurements were made were taken from the pot trials detailed in Chapter 2, section 2.1.1. For species that failed to survive beneath shaded treatments (*Aeschynomene villosa* cv. Kretschmer and *Stylosanthes hamata*), plants were later grown beneath the control and 84% shade treatments in order for measurements to be made. Despite repeated attempts, no seedlings of *Aeschynomene villosa* or cuttings of *Arachis kretschmeri* survived under the 84% shade treatment long enough to reach a suitable size.

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 CO_2 uptake was measured were 0, 5, 10, 20, 40, 60, 100, 500, 800, 1000 and 1500 $\mu mol/m^2/s$ (micro-mols of quanta per square metre per second), with these levels maintained automatically within the auger-head by the machine. 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-m), and critical points of light curves displayed in Table 3.1. The closeness of curves from the control and 84% shade, suggests shade adaptation, while large differences between curves indicates sun 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 four categories;

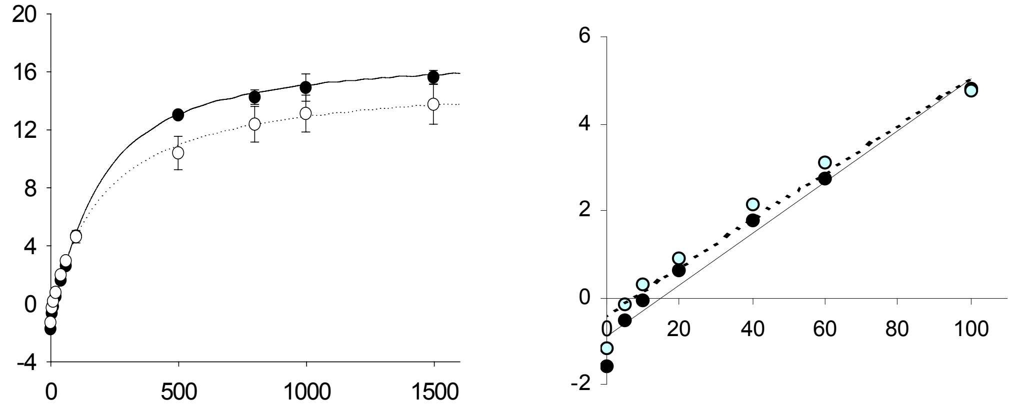
a) Species that had substantial differences between light response curves from the control and 84% shade treatment, yet yielded well under the shaded treatments (*D. heterophyllum, C. acutifolium, C. macrocarpum, P. phaseoloides, M. atropurpureum* and *M. lathyroides*)

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*)

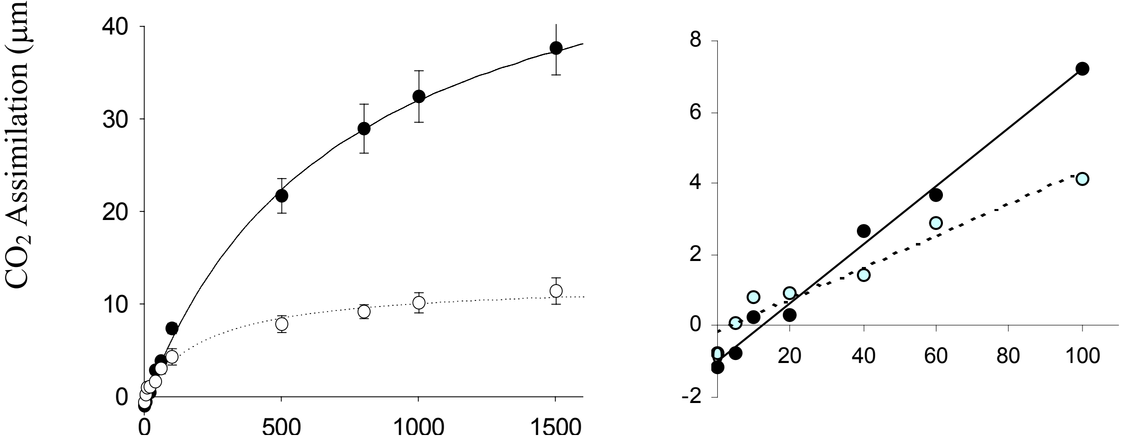
c) Species in which there were substantial differences between the light response curves of the 84% shade and the control treatment, and which also had poor yields beneath the shaded treatments (*A. americana, A. villosa* cv. Kretschmer, *D. scorpiurus, F. congesta, M. axillare, M . martii, S. guianensis, 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*).

Figure 3.2 Light response curves (CO_2 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 and 84% shade treatments. Error bars indicate the standard error. Solid circles denote plants grown under the control treatment and hollow circles plants grown under 84% shade.

a) *Arachis pintoi*



b) *Aeschynomene americana*



c) *Aeschynomene villosa* cv. Kretschmer

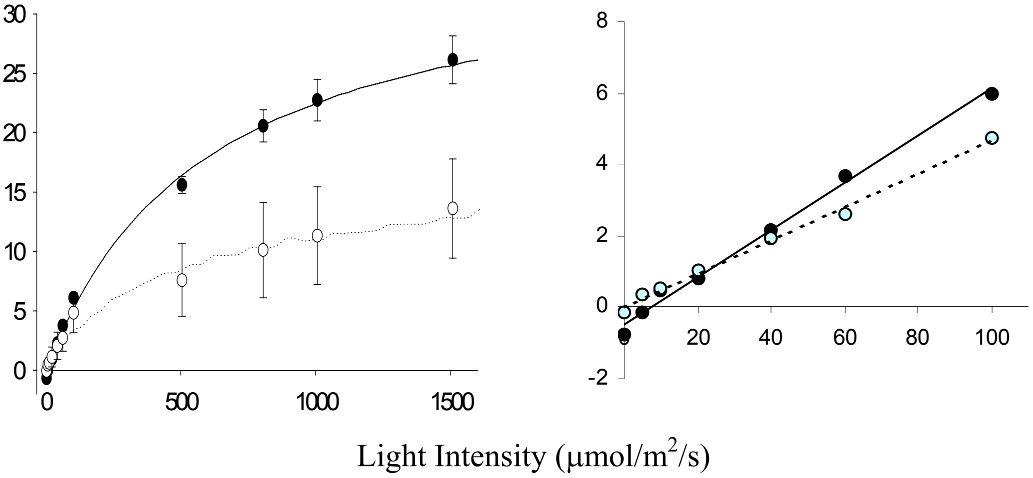
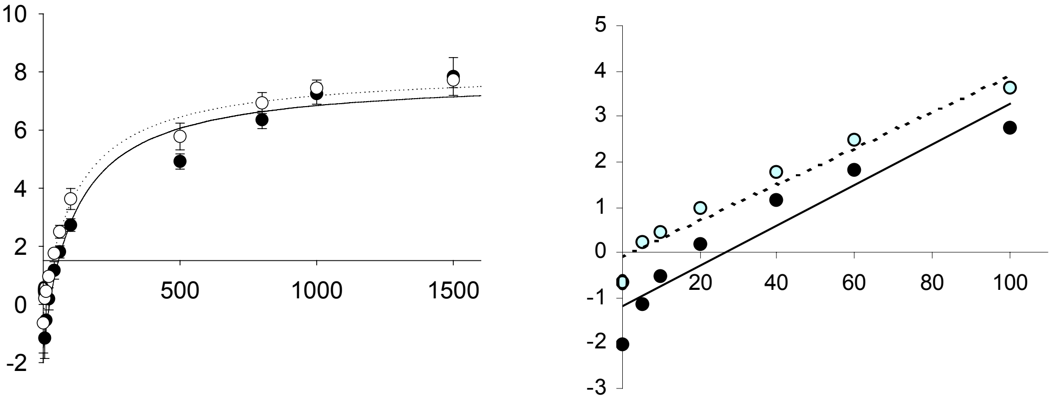
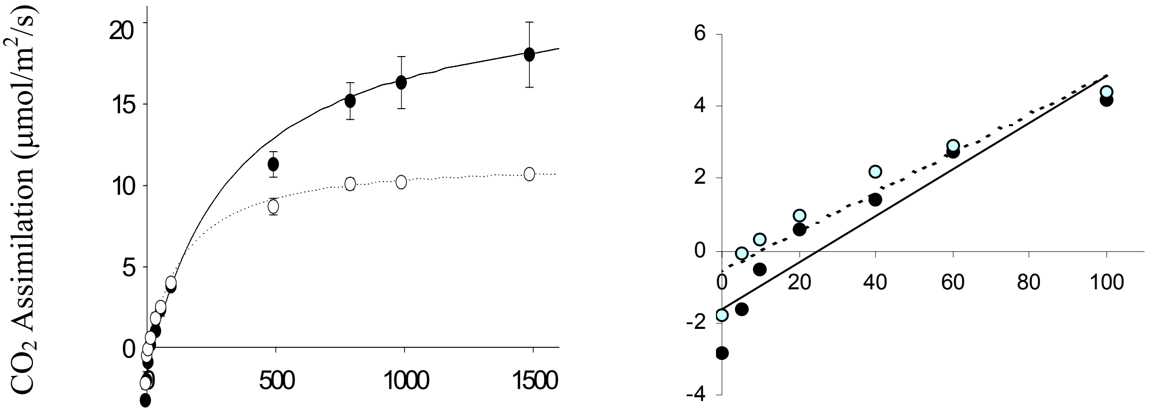


Figure 3.2 cont.

d) *Calopogonium mucunoides*



e) *Desmodium canum*



f) *Desmodium intortum*

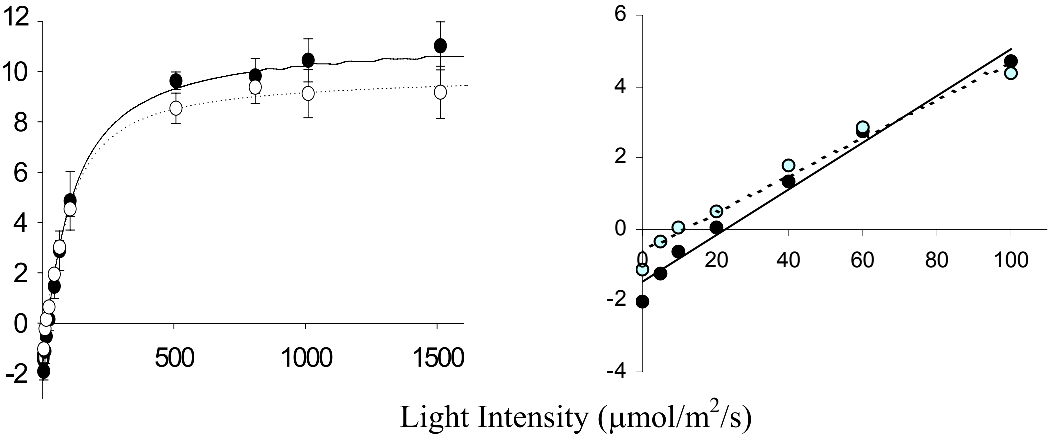
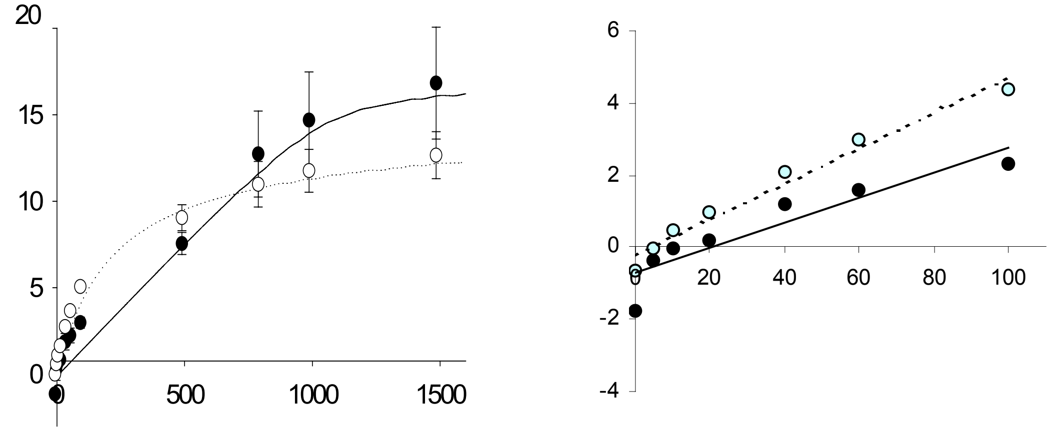
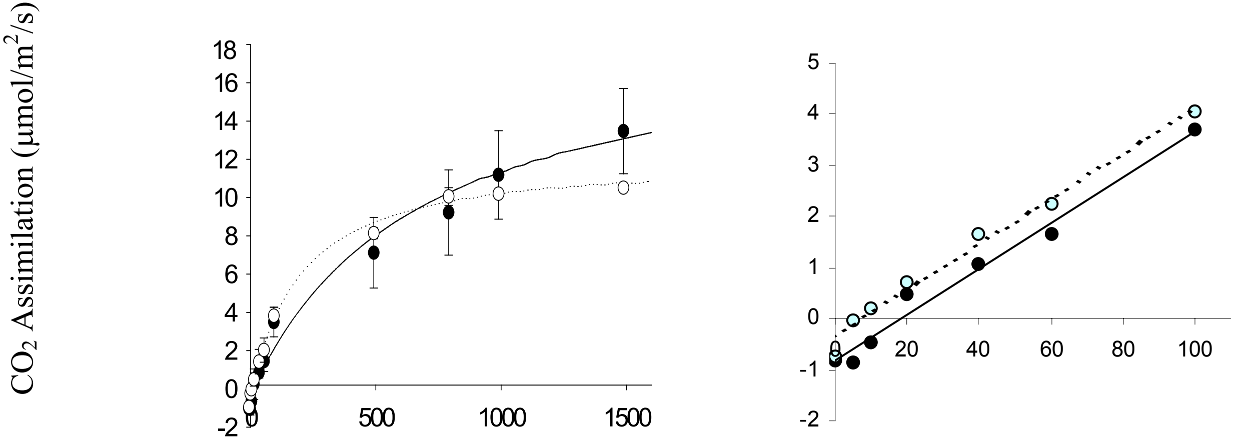


Figure 3.2 cont.

g) *Desmodium ovalifolium*



h) *Desmodium triflorum*



i) *Desmodium uncinatum*

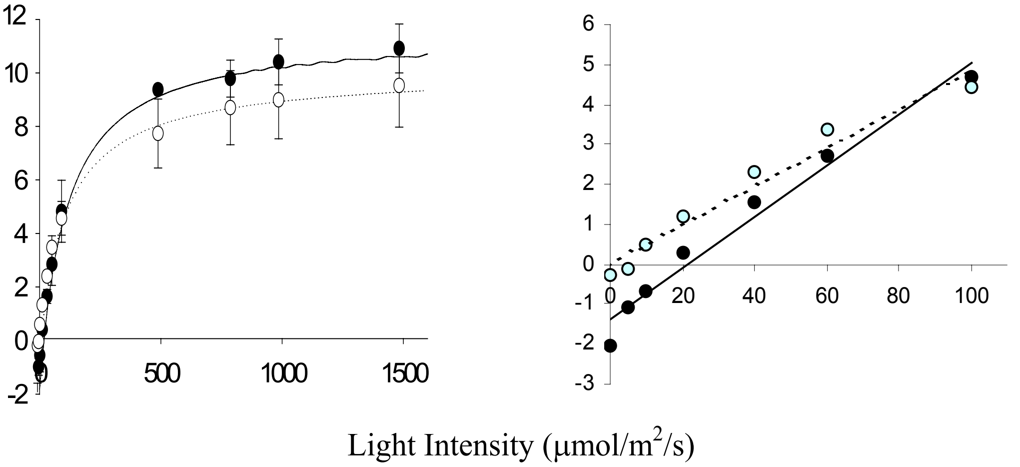
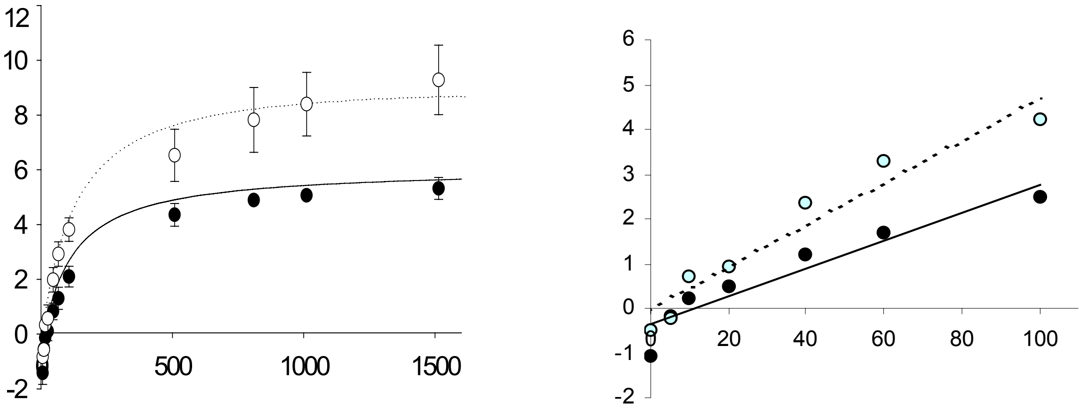
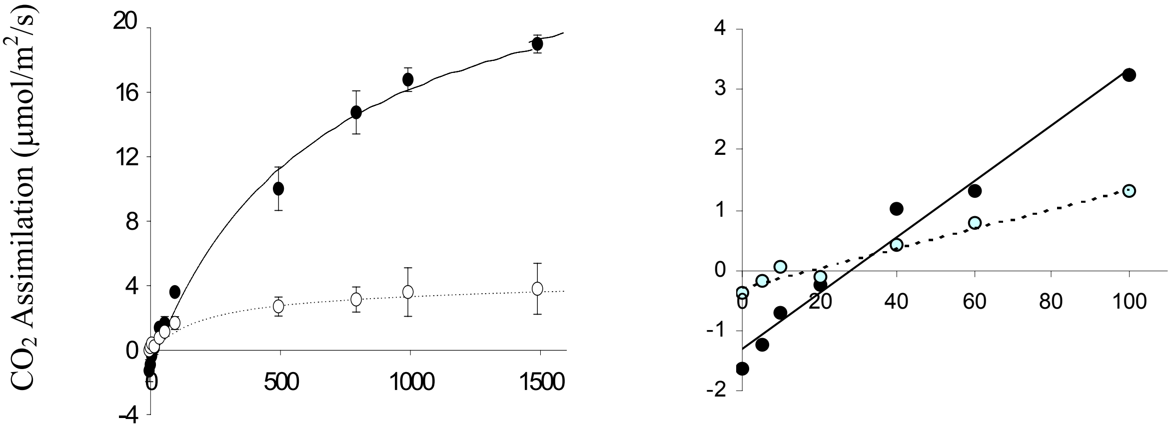


Figure 3.2 cont.

j) *Desmodium heterophyllum*



k) *Desmodium scorpiurus*



l) *Centrosema acutifolium*

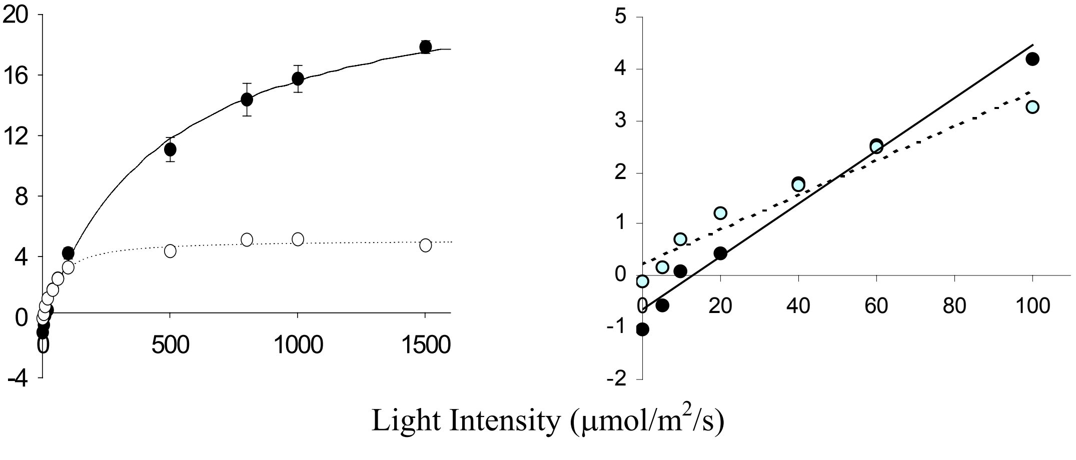
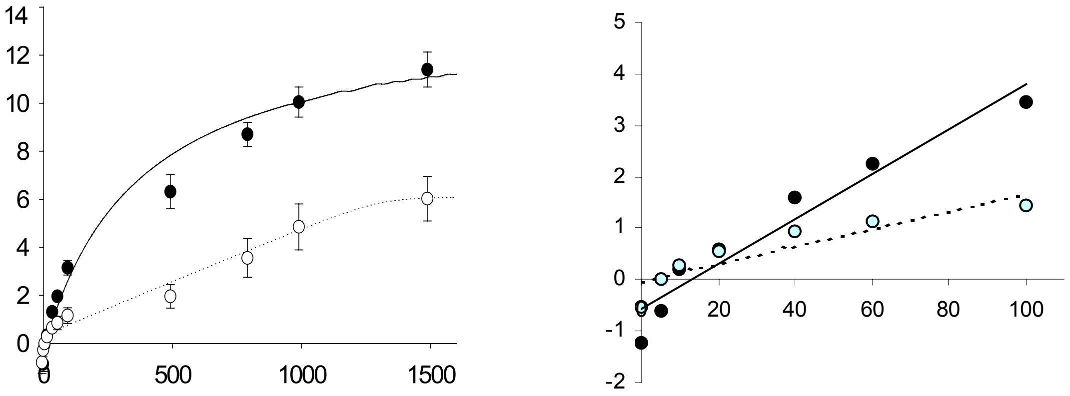
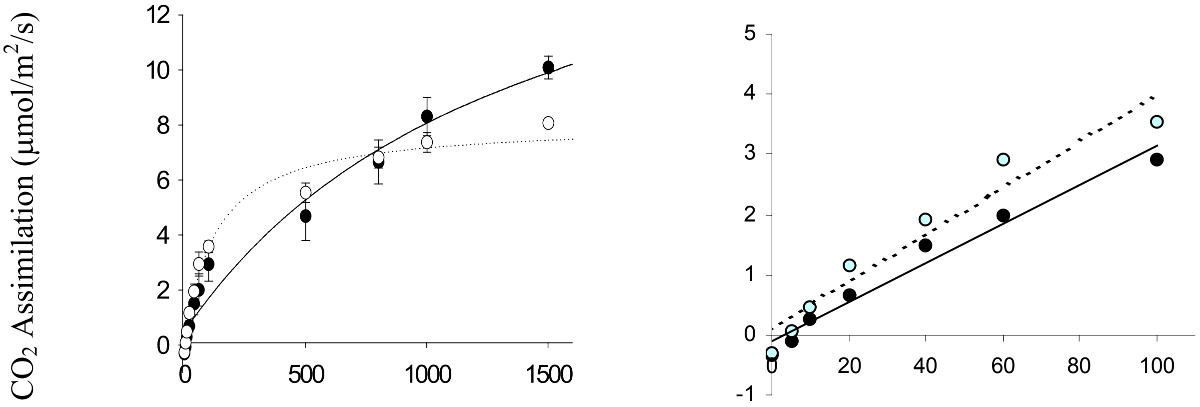


Figure 3.2 cont.

m) *Centrosema macrocarpum*



n) *Centrosema pubescens*



o) *Flemingia congesta*

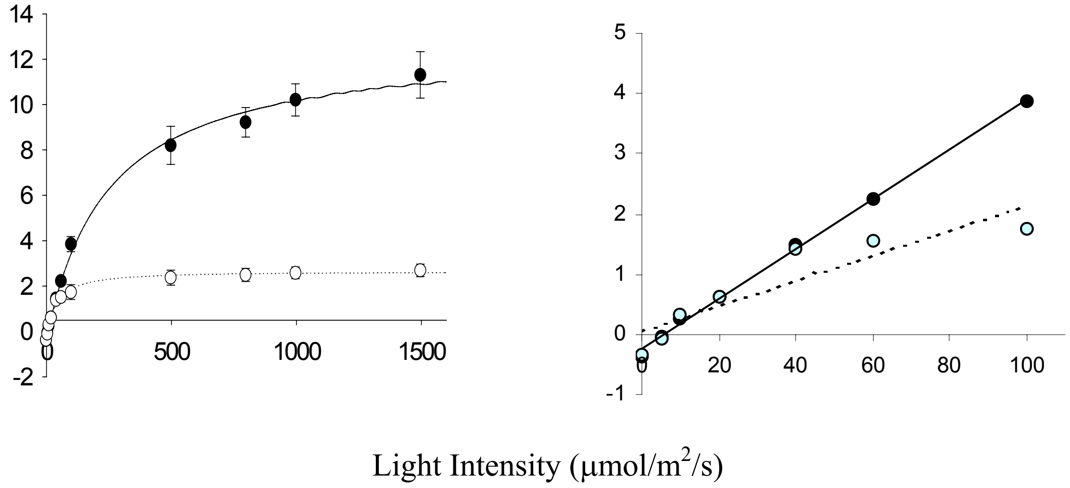
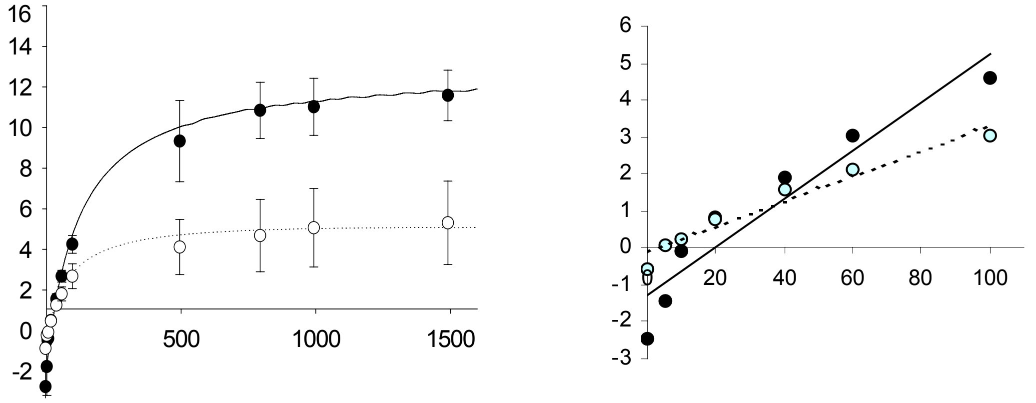
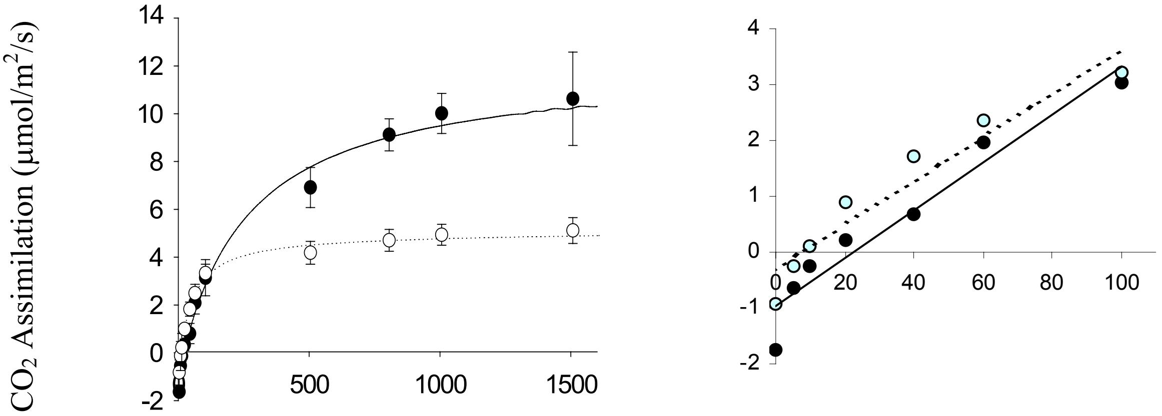


Figure 3.2 cont.

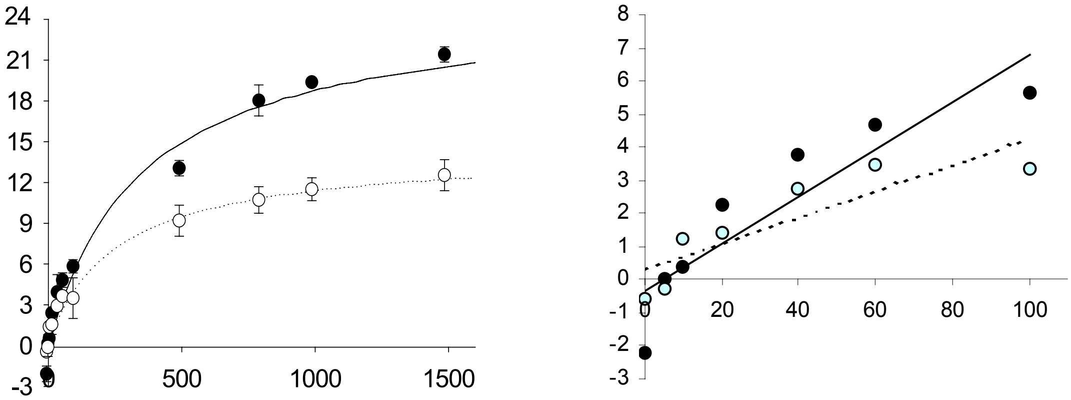
p) *Macrotyloma axillare*



q) *Pueraria phaseoloides*



r) *Stylosanthes guianensis*



Light Intensity (µmol/m^2/s)

Figure 3.2 cont.

s) *Vigna luteola*

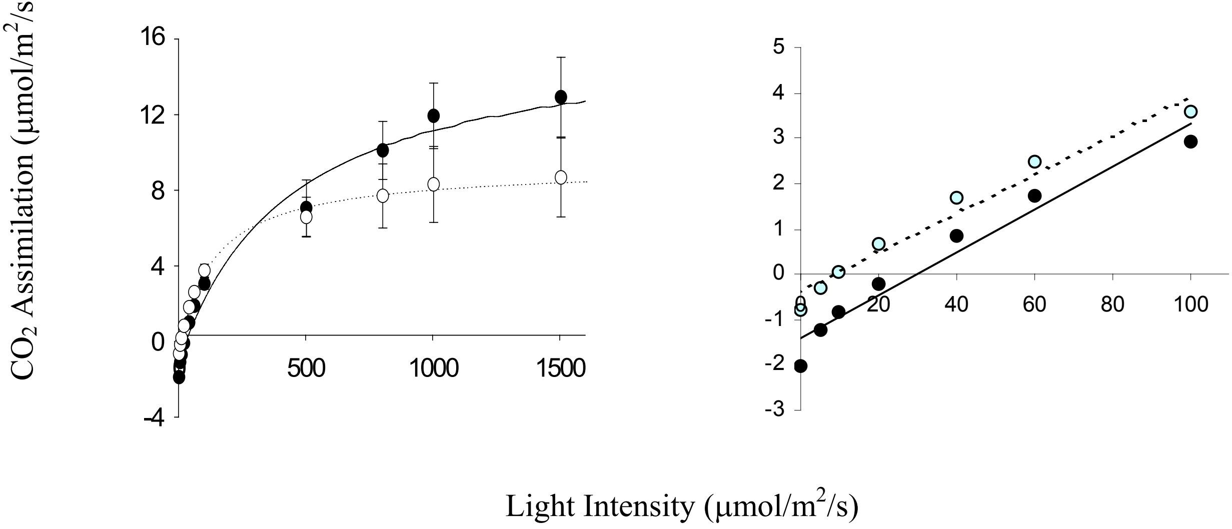
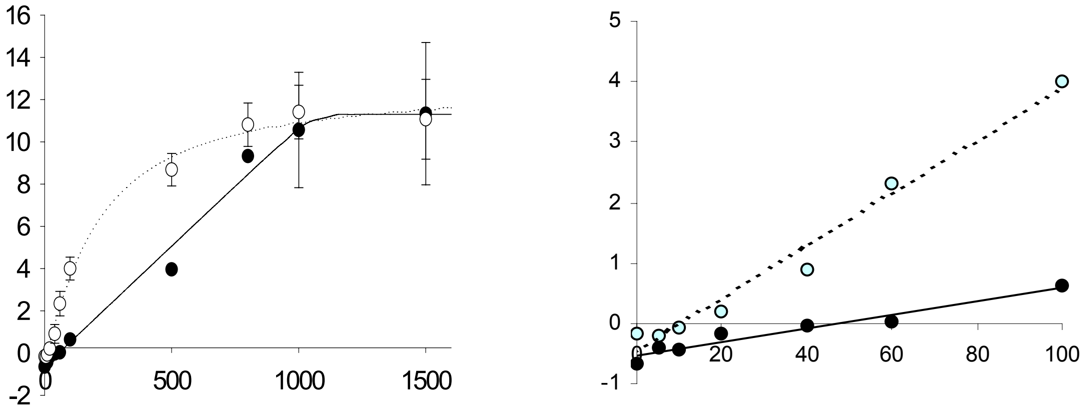
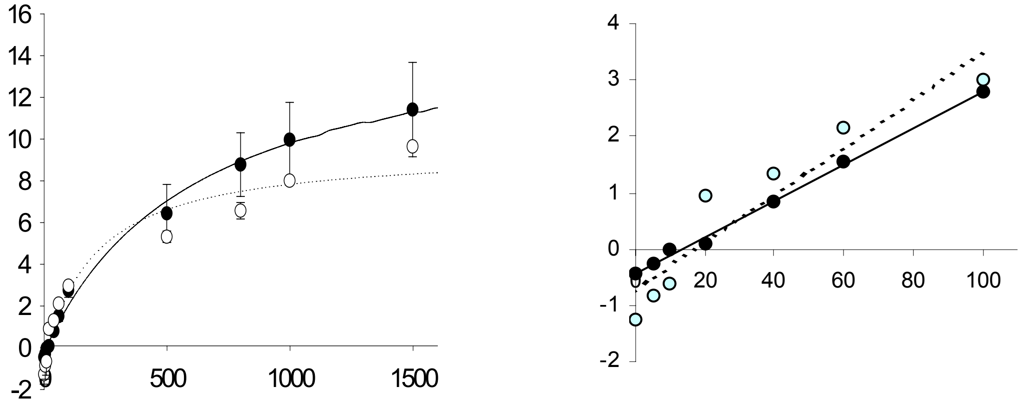


Figure 3.3 Light response curves (CO_2 assimilation vs. light intensity) and line of best fit of the initial linear section of the curve of 13 species of tropical forage legume, adapted to the wet/dry tropics, grown beneath control and 84% shade treatments. Error bars indicate the standard error. Solid circles denote plants grown under the control treatment and hollow circles plants grown under 84% shade.

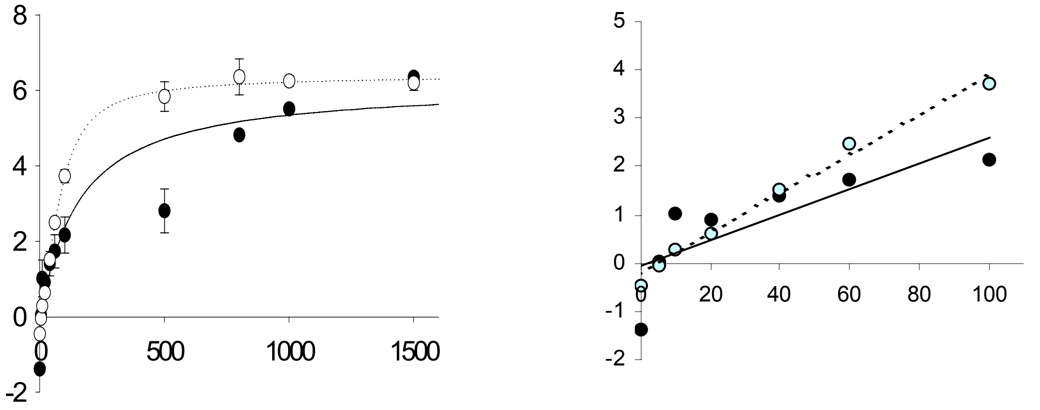
a) *Arachis paraguariensis*



b) *Arachis stenosperma*



c) *Centrosema brasilianum*

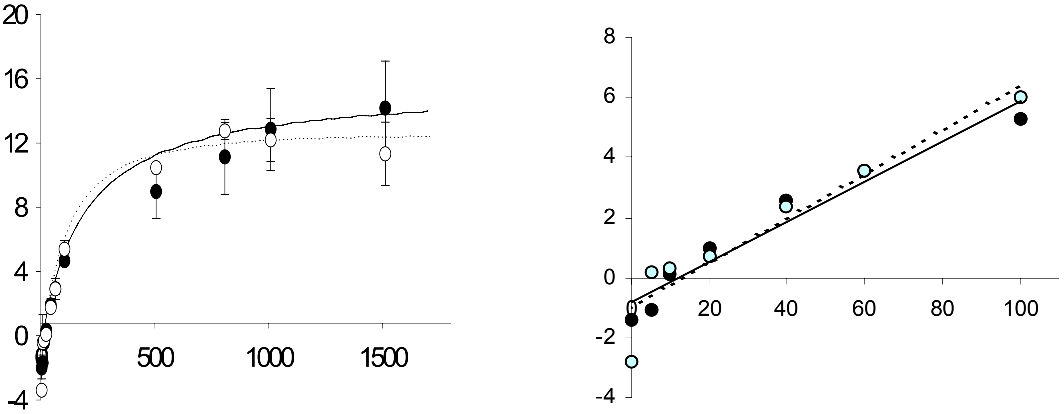


CO_2 Assimilation (μmol/m^2/s)

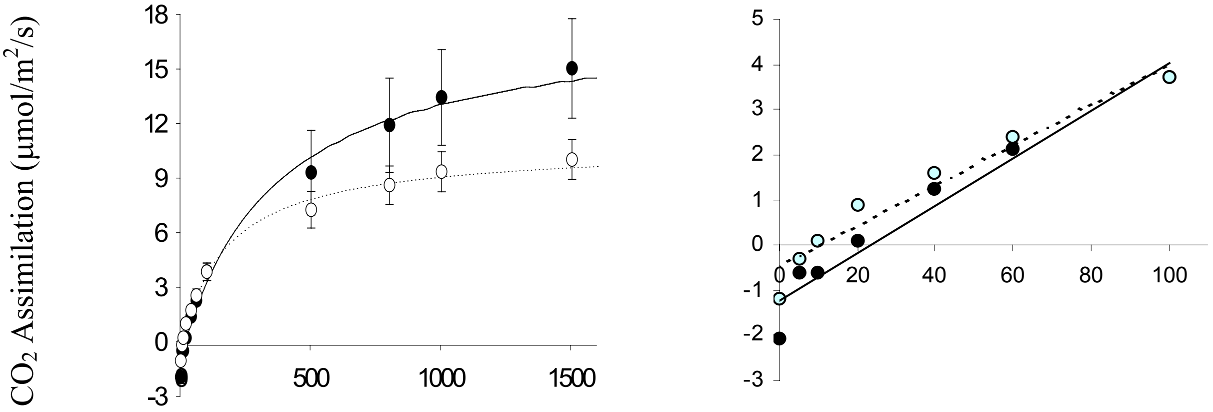
Light Intensity (μmol/m^2/s)

Figure 3.3 cont.

d) *Centrosema pascuorum*



e) *Chamaecrista rotundifolia*



f) *Clitoria ternatea*

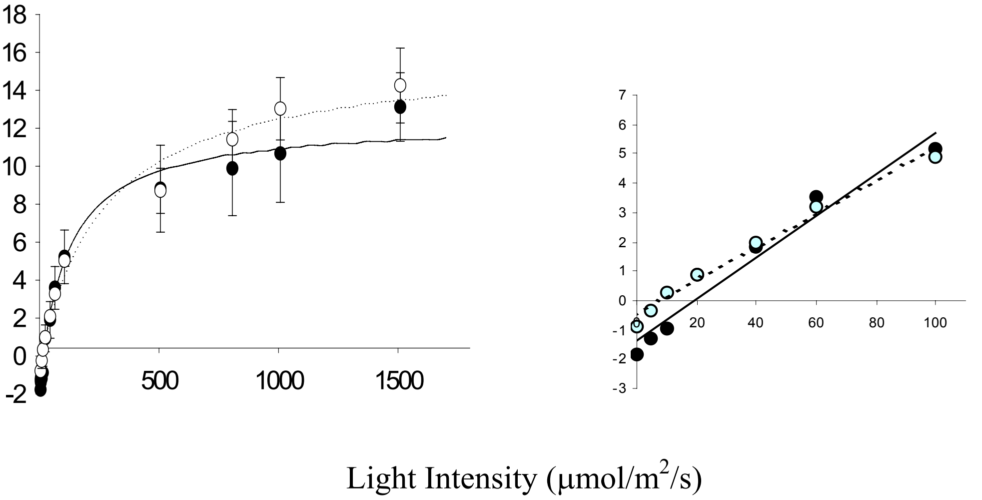
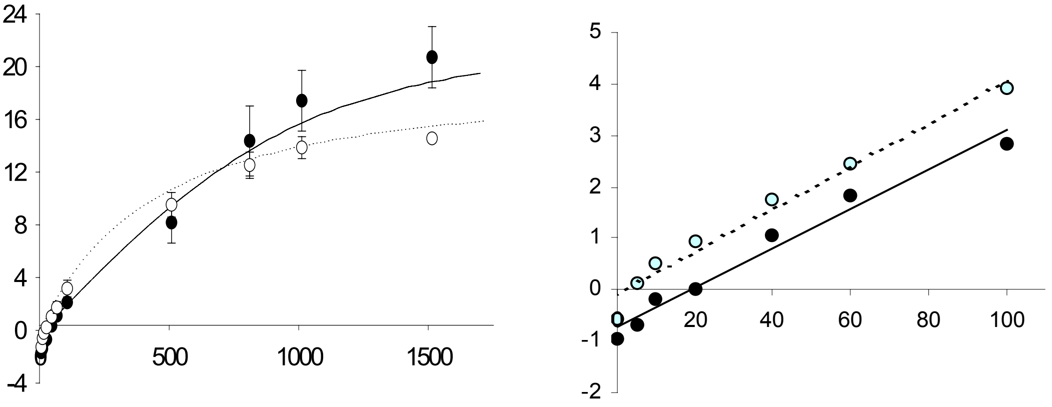
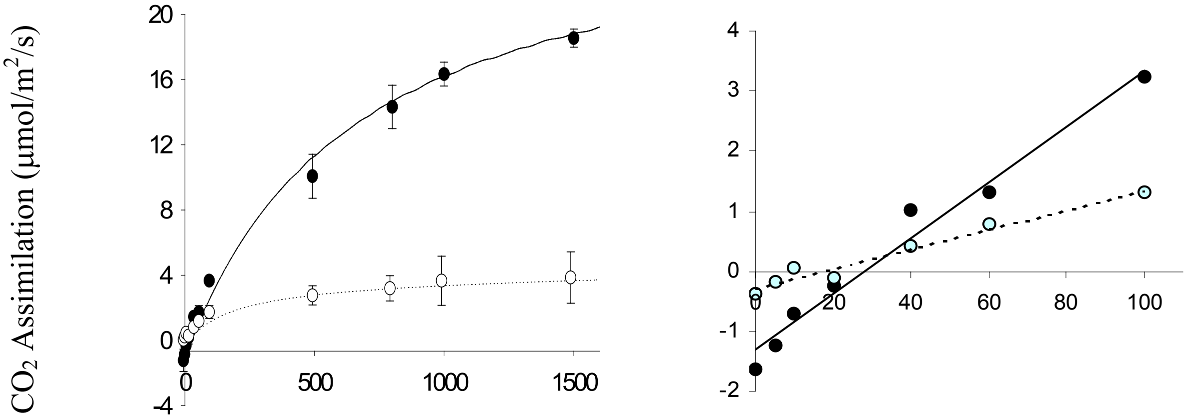


Figure 3.3 cont.

g) *Desmanthus virgatus*



h) *Desmodium scorpiurus*



i) *Macroptilium atropurpureum*

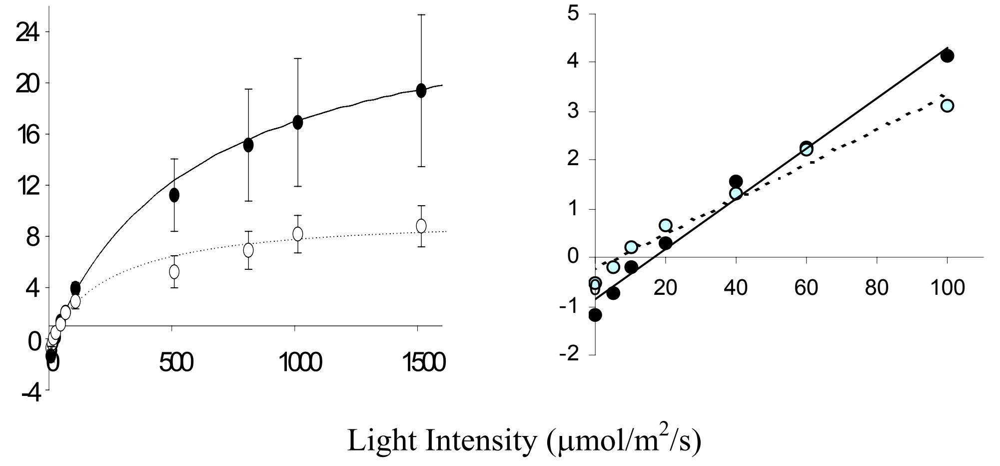
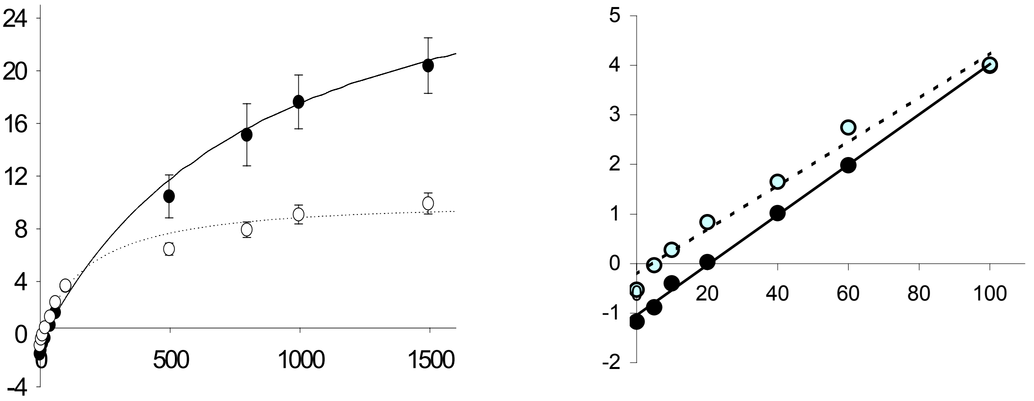
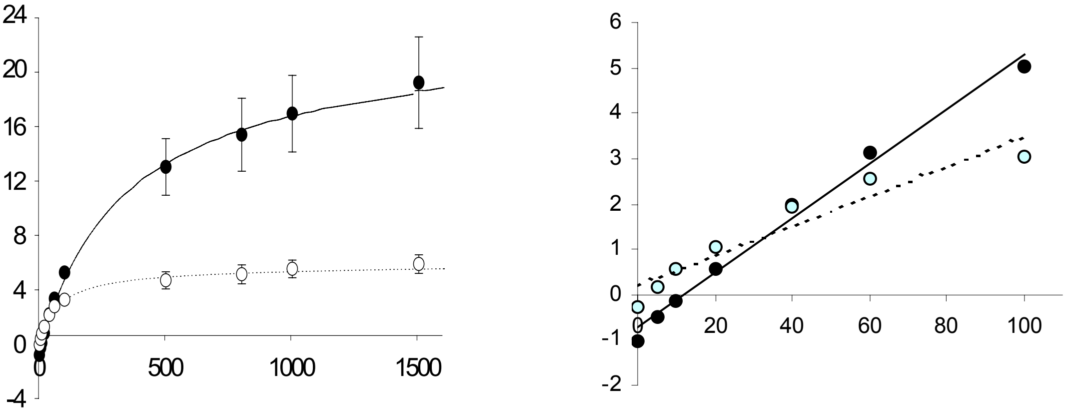


Figure 3.3 cont.

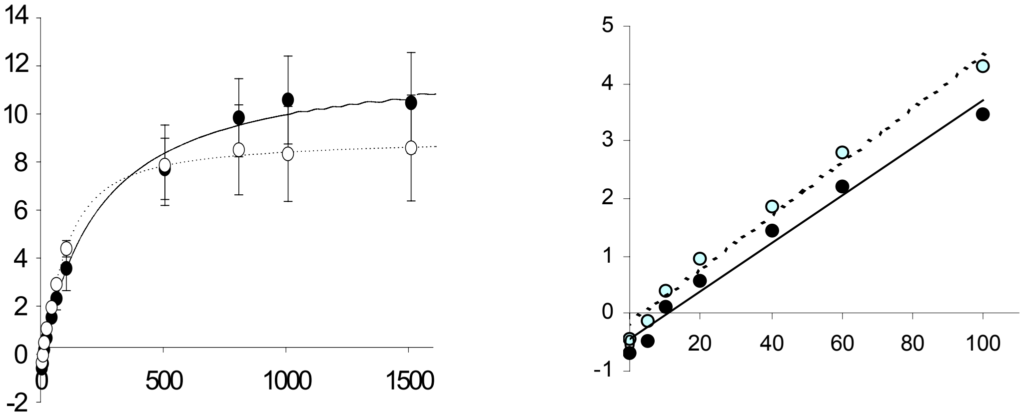
j) *Macroptilium lathyroides*



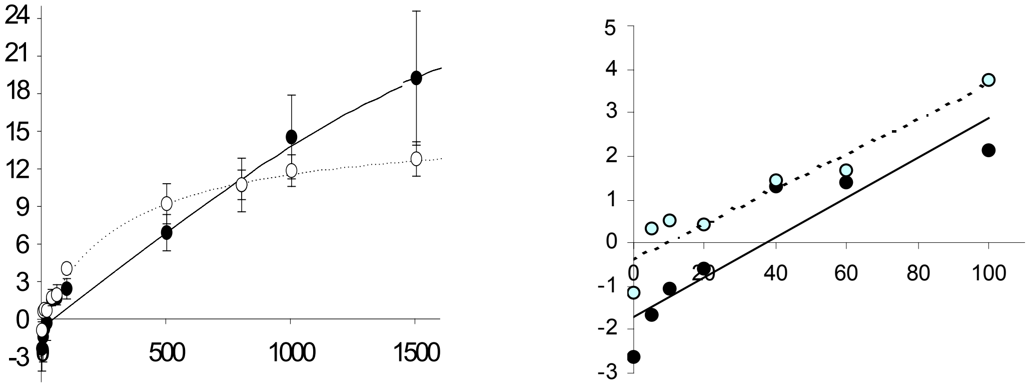
k) *Macroptilium martii*



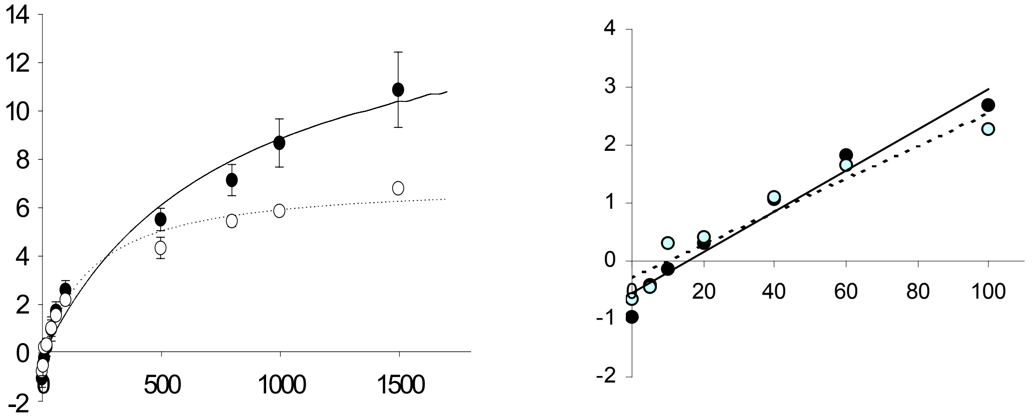
l) *Rhynchosia minima*



m) *Stylosanthes hamata*



n) *Stylosanthes scabra*



Estimates of the apparent quantum efficiency, compensation point, light saturation point and light saturation rates of plants were inconsistent and varied between shade treatments in many species (Table 3.2). The species *A. stenosperma, C. brasilianum, C. pubescens, C. rotundifolia, D. canum, D. heterophyllum* and *V. luteola* all experienced increases in quantum efficiency when grown under 84% shade compared to full sun. However the majority of species displayed the opposite, and unexpected, result of decreasing quantum efficiency for plants grown under 84% shade. These species were *A. americana, A. villosa* cv. Kretschmer, *C. acutifolium, C. pubescens, D. intortum, D. uncinatum, M. atropurpureum, M. lathyroides, M. martii, M. axillare* and *S. guianensis.* A small number of species maintained similar quantum efficiencies beneath both treatments; *A. pintoi, C. mucunoides, C. pascuorum* and *D. triflorum.* Results were obtained for a number of species for which the apparent quantum efficiencies appeared to be much less than in other species and are not thought to be reliable figures. Such results were obtained for the species *A. paraguariensis, C. macrocarpum, D. virgatus, D. ovalifolium, D. scorpiurus, F. congesta, S. hamata* and *S. scabra*.

Most species had lower compensation points when grown under 84% shade than under full light, as was expected. However there were still several species for which dubious values were found, either being too high in comparison to other species (*C. pascuorum*) or very low (*A. villosa* cv. Kretschmer and *D. uncinatum*).

The light intensities at which photosynthesis reached its maximum capacity (light saturation point) generally displayed a decrease in plants grown under 84% shade in comparison to full light. There were several species for which the light intensity at which maximum photosynthesis was reached was unusually high, in comparison to the majority of species, with all of the high results found in plants grown in full sun (*A. paraguariensis, C. pubescens, D. virgatus, D. ovalifolium* and *S. hamata*).

Maximum rates of photosynthesis were generally lower in plants grown under 84% shade, as would be expected, although in the species *D. heterophyllum* and *A. paraguariensis* the maximum rates was found to be greater in shaded plants, while in the species *C. pascuorum, C. brasilianum, A. pintoi* and *C. mucunoides* there was little difference between 84% shade and full sun.

Table 3.1 Equations of lines of best fit and R^2 values for linear parts of light response curves

	Equation of the line of best fit		**R^2**	
Wet tropical species	**Control**	**84% shade**	**Control**	**84% shade**
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. Kretschmer	$y = 0.0659x - 0.4657$	$y = 0.0464x + 0.0241$	0.9937	0.9947
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 3.1 cont.

	Equation of the line of best fit		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

Table 3.2 Apparent quantum efficiencies, light compensation points, light saturation points and light saturation rates of photosynthesis

Species	**1/Apparent quantum efficiency**		**Light compensation point (μ mols $m^{-2} s^{-1}$)**		**Light saturation point (μ mols $m^{-2} s^{-1}$)**		**Light saturation rate (μ mols $m^{-2} s^{-1}$)**	
	Control	**84% shade**	**Control**	**84% shade**	**Control**	**84% shade**	**Control**	**84% shade**
A. americana	12.2	22.2	12.4	3.7	733	217	56.3	12.3
A. pintoi	16.8	12.5	14.2	8.3	261	215	18.3	16.5
A. paraguariensis	88.5	22.8	46.9	10.8	1100	269	11.9	13.3
A. stenosperma	31.2	19.4	7.8	14.4	626	214	16.2	10.3
A. villosa cv. Kretschmer	15.2	21.5	7.0	0.5	593	491	36.0	15.9
C. acutifolium	19.6	30.2	12.7	7.2	470	85	23.5	4.9
C. brasilianum	37.7	18.5	5.1	6.8	154	132	6.4	6.7
C. macrocarpum	22.8	58.1	13.0	1.9	374	1256	14.2	6.1
C. mucunoides	22.5	14.7	18.7	4.2	135	127	9.3	8.3
C. pascuorum	14.9	8.3	188	138	188	138	16.5	15.3
C. pubescens	31.2	25.5	3.2	2.0	1366	214	18.2	8.2
C. rotundifolia	19.0	14.5	19.7	9.9	368	173	19	11.2
D. virgatus	26.0	22.1	13.7	3.2	1130	479	23.8	21.5
D. canum	15.5	10.5	21.5	9.8	345	148	24	13
D. heterophyllum	31.8	20.9	11.6	1.2	122	131	6.7	10.1
D. intortum	15.3	13.2	17.9	11.7	145	150	13.1	10.5
D. ovalifolium	28.7	16.7	8.9	4.2	1099	207	16.9	13.3

Table 3.2 cont.	**1/Apparent quantum efficiency**		**Light compensation point (μ mols m^{-2} s^{-1})**		**Light saturation point (μ mols m^{-2} s^{-1})**		**Light saturation rate (μ mols m^{-2} s^{-1})**	
	Control	**84% shade**	**Control**	**84% shade**	**Control**	**84% shade**	**Control**	**84% shade**
D. scorpiurus	21.4	62.5	28.2	16.8	797	195	29.8	3.9
D. triflorum	22.1	22.3	18.4	7.8	672	210	19.4	13.0
D. uncinatum	15.5	20.4	21.3	0.4	129	118	13.3	10.2
F. congesta	24.1	47.6	5.6	2.1	256	41.7	13.0	3.0
M. atropurpureum	19.3	27.6	16.5	6.5	600	272	27.9	10.2
M. lathyroides	19.7	22.4	20.7	4.9	873	195	32.9	11.1
M. martii	16.5	30.3	12.1	5.7	351	75	23.4	5.7
M. axillare	15.3	14.0	15	5.5	136	91	14.7	6.1
P. phaseoloides	23.2	25.2	22.8	7.9	268	56	13.1	5.8
S. guianensis	14.0	25.3	4.4	7.4	345	247	25.4	13.9
S. hamata	21.9	20.4	48.1	8.11	1731	323	26.3	15.4
S. scabra	28.3	26.7	8.5	8.9	774	212	15.9	7.6
V. luteola	21.1	13.9	27.8	8.9	460	143	17.5	9.6

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, D. uncinatum* and *R. minima* all suggest a degree of shade adaptation as plants from the control treatment were not able to increase their photosynthetic capacity compared to that of plants grown under 84% shade. According to Wilson and 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 outlined in 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.

Where large differences between the light response curves of the control and 84% shade treatments were present (*D. heterophyllum, C. acutifolium, C. macrocarpum, P. phaseoloides, M. atropurpureum* and *M. lathyroides*), in addition to the production of substantial amounts of dry matter under the more heavily shaded treatments, it suggests that these species have the capacity to become shade-acclimated rather than shade-tolerant. Typically sun plants have their capacity for photosynthesis greatly reduced under shaded conditions (Ward and Woolhouse 1986), however the rate of photosynthesis may still be greater than that of shade-tolerant species (Wilson and 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, indicates 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 as such appear to be poorly suited for use under shaded conditions.

Estimates of the important physiological points of the light curves proved in many cases to vary substantially between plants grown under full sun and those grown beneath 84% shade. The apparent quantum efficiency appeared to be the most inconsistent, with many species displaying a decrease in apparent quantum efficiency where an increase was expected beneath the 84% shade treatment, as all plants have the ability to acclimate to shade some extent (Lambers 1998). It is not known what caused these unexpected results, however the frequency of this phenomenon may suggest that some other unidentified factor was influencing photosynthetic efficiency beneath the shaded treatment in many species.

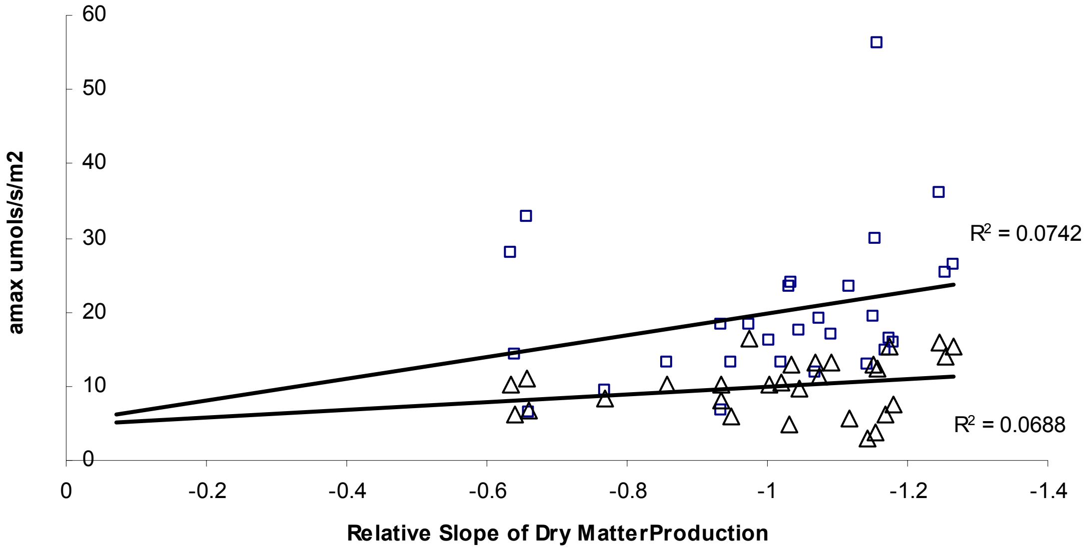
Light compensation points and light saturation points gave more consistent results with most species undergoing a decrease in the intensity of light required to balance CO_2 loss from respiration with CO_2 fixation from photosynthesis. Such a decrease is one method by which plants typically acclimate to environments with reduced light intensities (Nilsen and Orcutt 1996; Lambers *et al.* 1998). The results obtained do not correlate well with the results found in Chapter 2, as there appears to be no relationship between increases or decreases in apparent quantum efficiency and performance under shade. For example *D. heterophyllum* and *C. brasilianum* both displayed increases in apparent quantum efficiency and both yielded well under the shaded treatments, while *D. intortum, D. uncinatum* and *C. pubescens* also yielded well under shaded treatments but displayed decreases in apparent quantum efficiency. Furthermore, *D. triflorum*, *A. pintoi* and *C. mucunoides* displayed no substantial differences in apparent quantum efficiency between the control and 84% shade treatments and are all known to have a degree of shade tolerance.

Light compensation points largely decreased under 84% shade compared to full sun, however there was still no clear relationship between either changes in light compensation points, or light compensation point values, and species performance. Ludlow (1978) indicates that dark respiration rates and light compensation points of leaves developed under shade are reduced but their photochemical efficiencies remain unchanged, resulting in only marginally higher photosynthetic rates at low light levels compared with previously unshaded leaves. Normally species adapted to high light environments would be expected to require higher light intensities to balance carbon dioxide release from photorespiration and dark respiration with fixation from photosynthesis. The higher rates of dark respiration in sun leaves is likely to be due to a greater demand for respiratory energy for maintenance of the greater numbers of leaf cells, the greater protein content per cell and for the export of photosynthetic products from the leaf (Lambers *et al.* 1998).

A similar situation was found in the light saturation points, with most species undergoing a decline in the light intensity at which the maximum photosynthetic rate was reached. Large increases in the maximum photosynthetic (A_{max}) rate indicate species adapted to high light environments, as shade plants are unable to adapt to high light intensities with an increase in A_{max} (Wilson and Ludlow 1991). Using A_{max} values, the species *A. americana, A. villosa* cv. Kretschmer, *D. canum, D. scorpiurus, C. acutifolium, C. macrocarpum, F. congesta, M. axillare, P. phaseoloides, S. guianensis, V. luteola, M. atropurpureum, M. lathyroides, M. martii, R. minima* and *S. scabra* all appear to be sun plants due to the large increases of A_{max} in plants grown under full sun compared to those under 84% shade.

When A_{max} values were plotted against the slope of the relative yields of dry matter a general relationship between the two became apparent, however the relationship was not strong in either plants grown under full sun or 84% shade, with R^2 values of 0.0742 and 0.0688 respectively (Figure 3.4). It was apparent that as the relative slope of dry matter production increased, so too did the rate of maximum photosynthesis. This indicates that when a species underwent a larger decrease in relative dry matter production it tended to be accompanied by a higher rate of maximum photosynthesis. This suggests that the results from Chapters 2 and 3 have similarities with each other but fall short of strongly supporting each other. A stronger correlation was found in plants grown under full sun than under 84% shade.

Figure 3.4 Slope of the line of best fit of relative yield of above-ground biomass vs. maximum rate of photosynthesis for all plants grown under full sun and 84% shade. Squares denote plants grown under full sun and triangles those grown under 84% shade.



3.5 Conclusions

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, D. uncinatum* and *R. minima* displayed similarity between the 84% shade and the control treatment that suggests a degree of shade tolerance or adaptation. When these results are viewed in conjunction with the production of dry matter (Chapter 2) not all of these species display equal potential for forage production beneath shaded conditions. Of these species several (*A. stenosperma, D. uncinatum, D. intortum, C. ternatea* and *C. mucunoides*) were also able to produce substantial quantities of dry matter under the control treatment.

In some species (*D. heterophyllum, C. acutifolium, C. macrocarpum, P. phaseoloides, M. atropurpureum* and *M. lathyroides*) there were large differences between light response curves of plants grown under the control and the 84% shade treatment, yet production of dry matter was substantial under the more heavily shaded treatments, indicating that these species are not shade-adapted but have the ability to become shade-acclimated, as sun plants will have their capacity for photosynthesis greatly reduced under shade, but their rate of photosynthesis may still be greater than that of shade tolerant species (Ward and Woolhouse 1986; Wilson and Ludlow 1991).

The measurement of important points on the light curves, such as apparent quantum efficiency, light compensation point, light saturation point and light saturation rates, did not prove to be particularly helpful in distinguishing shade tolerant or acclimated plants from sun plants with little ability to acclimate to shaded conditions. However, there was a correlation between the slope of relative above-ground dry matter yield and A_{max} values ($P = 0.6187$ and $P = 0.2282$ for the Control and 84% shade treatments respectively), although it was not strong enough to allow predictions about a plant's agronomic or physiological performance from either set of measurements.

Chapter 4 - Performance of selected legumes beneath established tree plantations

4.1 Introduction

The 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 and 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 and Rao 1991).

In many developing countries landowners have traditionally grazed livestock beneath tree plantations, particularly oil palm, coconut and rubber (Ismail and 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 (anon. date unknown).

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 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).

The following trials aimed to assess the potential of selected legume species for use beneath timber plantations under field conditions. Three field trials were established to examine growth and persistence of tropical forage legume species under existing tree plantations of varying ages. 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, including 4 accessions of *Arachis*, under young African Mahoganies planted at 2 different densities on the James Cook University campus, in Townsville.

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

4.2.1 Materials and methods

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 between trees within rows and 4.5 m between tree rows. Weather data is shown in Figures 4.1 and 4.2 and taken from the nearest Australian Bureau of Meteorology weather station located at Innisfail.

Table 4.1 Major nutrients in the fine earth fraction (<2mm) of the soil Bingil series krasnozem. Organic carbon was determined by Heanes (1984) method (Rayment and Higginson 1992), total nitrogen after wet oxidation with sulphuric acid and hydrogen peroxide as described by Anderson & Ingram (1989), acid extractable phosphorus after Rayment and Higginson (1992) and soil pH and electrical conductivity on a 1:5 soil/water suspension (Rayment and Higginson 1992). n = 5.

Depth (cm)	Organic C (%)	Total N (%)	Acid extractable P (mg/kg)	Exchangeable K (me/100g)	pH 1:5 (H_2O)
0-10	0.16	0.21	59.7	0.081	5.7
10-20	0.16	0.18	45.5	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

Figure 4.1 Maximum and minimum mean air temperatures at Babinda from Jan 2000 to October 2002. Data obtained from the Australian Bureau of Meteorology.

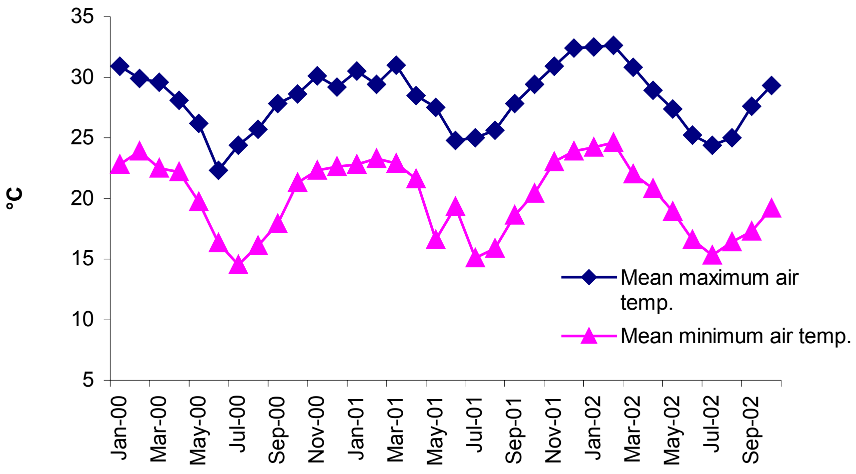
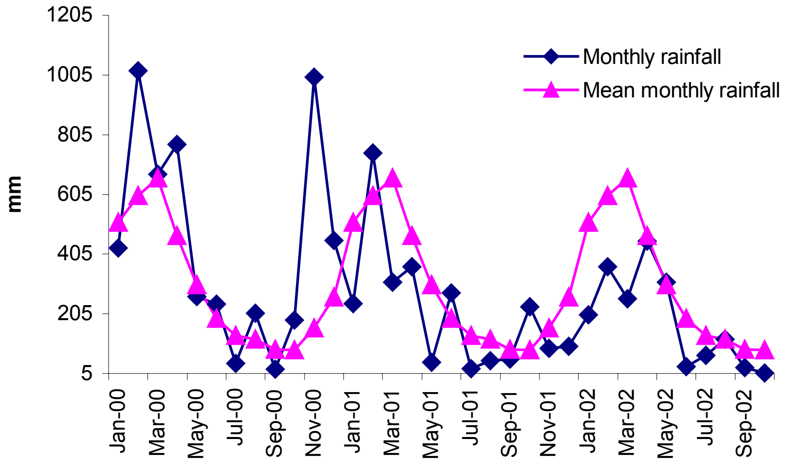


Figure 4.2 Monthly and long term mean of rainfall at Babinda from Jan 2000 to October 2002 Data obtained from the Australian Bureau of Meteorology.



Trial establishment

Seed was planted on the 19th of September 2000, between adjacent *E. pellita* trees, which had had any other living plant material removed. Four furrows were dug in the soil, from tree base to tree base, spaced 50cm apart, and a seed planted every 10 cm along each furrow, and covered with soil to a depth of approximately 5 – 10 mm. 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.

Trail 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 5cm above ground level, or in the case of *Arachis pintoi* to within 5cm of the centre of the plant. After harvesting plots were weeded by hand and the harvested legume 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.

Shade levels were estimated beneath the tree canopy using a Li-cor 1000 data logger. Readings were taken every 10 minutes beginning at 5am and continuing until dark Quantum sensors were placed at the mid point between trees in a row and an unshaded control obtained by placing one in an adjacent field. Shade levels were estimated at each sampling date to be 47% (December 2000), 51% (April 2001) and 60% (July 2002) of the unshaded control.

4.2.2 Results

Statistical summary of results

Significant to highly significant effects were found across all dates and in all attributes (Table 4.2), with the exception of individual plant size at the first sampling after establishment (December 2000).

Table 4.2 Summary of statistical results

Attribute	**Dec 2000**	**April 2001**	**Dec2001**	**July 2002**
Yield (t/ha)	n.r.	**	***	***
Plant size (g/plant)	n.r.	*	***	***
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 4.3). 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. As time increased so did the area of ground covered by *A. pintoi* and *S. guianensis*. 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. *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 4.4). 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 moderate levels of dry matter, with yields increasing in subsequent harvests. 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 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 4.5), with no statistical difference between the two species found. By December 2001, the average yield of *A. pintoi* was almost twice that of *S. guianensis,* the species with the second largest plants. 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 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 4.6). The cultivars *A. villosa* cv. Reid and *A. villosa cv.* Kretschmer, initially had high numbers of surviving plants, 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 4.3 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 ± 2.5 a	30.0 ± 5.4 a	38.1 ± 2.3 b	35.6 ± 9.2 a
A. villosa cv. Reid	15.6 ± 2.3 a	16.9 ± 2.1 b	3.1 ± 0.6 c	0.0 ± 0.0 c
S. guianensis	13.1 ± 2.1 ab	32.2 ± 1.5 a	46.2 ± 4.6 a	16.9 ± 3.8 b
A. villosa cv. Kretschmer	7.5 ± 1.0 bc	6.8 ± 0.6 cd	0.6 ± 0.6 c	0.0 ± 0.0 c
A. americana	3.7 ± 2.9 c	15.0 ± 5.3 bc	1.8 ± 1.2 c	0.6 ± 0.6 c
A. villosa	2.5 ± 1.4 c	3.7 ± 1.6 d	0.6 ± 0.6 c	0.0 ± 0.0 c
P value	0.0002	<0.0001	<0.0001	<0.0001

Table 4.4 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 ± 0.061a
A. americana	0.106 ± 0.040 ab	0.194 ± 0.032 b	0.0005 ± 0.005 b
S. guianensis	0.096 ± 0.012 bc	0.230 ± 0.036 b	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 ± 0.014 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 4.5 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 establishment.

	Mean plant weight (g)		
Species	**April 2001**	**Dec 2001**	**July 2002**
A. pintoi	4.48 ± 1.40 a	8.17 ± 1.5 a	7.80 ± 1.55 a
A. americana	4.27 ± 1.6 a	0.40 ± 0.40 b	0.11 ± 0.10 b
A. villosa	1.34 ± 1.02 b	0 ± 0 c	0 ± 0 b
A. villosa cv. Reid	1.20 ± 0.19 b	0.06 ± 0.03 c	0 ± 0 b
S. guianensis	1.18 ± 0.20 b	4.10 ± 1.04 b	5.84 ± 1.01 a
A. villosa cv. Kretschmer	0.24 ± 0.05 b	0.03 ± 0.03 c	0 ± 0 b
P value	0.0110	<0.0001	<0.0001

Table 4.6 Mean, standard error and LSD groupings of the number of plants per metrer 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 ± 0.62 ab	0.17 ± 0.04 c	0.00 ± 0.00 b
A. pintoi	1.57 ± 0.29 bc	1.80 ± 0.05 bc	1.45 ± 0.11 b	1.75 ± 0.04 a
A. villosa cv. Kretschmer	1.47 ± 0.21 bc	1.42 ± 0.04 bc	0.05 ± 0.05 c	0.00 ± 0.00 b
A. villosa	0.67 ± 0.19 c	0.40 ± 0.17 c	0.07 ± 0.05 c	0.00 ± 0.00 b
A. americana	0.62 ± 0.17 c	0.83 ± 0.24 bc	0.02 ± 0.02 c	0.09 ± 0.05 b
P value	0.0053	0.0046	<0.0001	<0.0001

4.2.3 Discussion

Of the species tested *Arachis pintoi* was clearly the best performing, consistently yielding greater quantities of dry matter than other species and also maintaining a good level of ground cover. The relatively consistent yield of dry matter over time indicates the suitability of the species for use in shaded situations, while the maintenance of ground cover indicates its potential for reducing erosion in exposed situations. What is not reflected in the data presented was the spread of the species beyond trial plots. By the second sampling date (April 2002) plants were already beginning to send stolons beyond the trial plots, with the distance of these increasing as time progressed, even being found in adjacent plots by July 2002. Work in the past has indicated that *A. pintoi* is a potentially useful species for shaded conditions (Cook 1992; Fisher and Cruz 1994; Humphreys 1994; Mendra *et al.* 1995; Reynolds 1995), and results obtained here concur.

Stylosanthes guianensis initially performed poorly yielding little dry matter however by December 2001 it yielded useful levels of dry matter, although not to the same extent as *A. pintoi. Stylosanthes guianensis* provided good ground cover at times but not consistently, suggesting that it may not be well suited for controlling erosion beneath tree plantations. Plants of *S. guianensis* tended to be smaller than those of *A. pintoi* and much of their weight composed of woody stem material. There was no evidence of *S. guianensis* spreading beyond its trial plot as was found with *A. pintoi.* The final yield of dry matter was unexpected as prior work in Chapters 2 and 3 indicated *S. guianensis* to be unsuited for use under shade, similar findings have been reported in the past (Ludlow 1980; Eriksen and Whitney 1982), while other work suggests shade tolerance (Gregor 1972; Mannetje 1992). The observation by Gutteridge and Whiteman (1978) that *S. guianensis* behaved as a short term pioneer species may explain the results obtained in this trial. However it is unlikely that shade level was the cause of the initial poor performance of *S. guianensis* followed by a much better yield in the final harvest, as shade levels beneath the tree canopy would be expected to increase with time resulting in a further decrease in yield. Germination of hard seed resulting in more plants establishing in the plots was not responsible as the mean number of plants per metre in plots fell as time progressed. Results here suggest that *S. guianensis* may be suitable for use in young, lightly shaded plantations but other work previously mentioned, indicates that it will not produce useful amounts of dry matter or even persist under heavy shade.

All species of *Aeschynomene* performed poorly at the first harvest with yields declining in subsequent harvests. *Aeschynomene americana* was the only species of *Aeschynomene* to yield any useful quantities of dry matter but only in the first two harvests with virtually no plant material produced in the third harvest. Ground cover provided by the species similarly declined from low initial levels to virtually nothing by the final harvest in all species of *Aeschynomene*. All species of *Aeschynomene* examined in this trial clearly appear to be unsuited for use beneath tree plantations. In the past *A. americana* has not been found to perform well under shade. Previous work has hinted that may not be suited for use under shaded conditions (Kaligis and Sumolang 1991; Rika *et al.* 1991; Stur 1991). When this is viewed in light with results from chapters 2 and 3 it is apparent that *A. americana* is not a suitable species for growth beneath timber plantations.

Aeschynomene villosa cv. Kretschmer, Reid and CPI 37235 had similarly poor performances. Literature regarding the shade tolerance of these species is scarce but results obtained in Chapters 2 and 3 indicated the intolerance of *A. villosa* cv. Kretschmer and *A. villosa* CPI 37235 to shade complement the results of this trial.

4.2.4 Conclusions

Arachis pintoi appears to be a species well suited for use beneath plantations, showing excellent growth and spreading beyond its original plots. 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 as previous work had not indicated that it would not be suited to use under tree plantations. However 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, *Aeschynomene villosa* cv. Reid, *Aeschynomene villosa* 37235 and *Aeschynomene villosa* cv. Kretschmer are not recommended for use in shaded conditions.

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

4.3.1 Materials and methods

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 College of Tropical Agriculture, near Clare, located approximately 65 kms ("as the crow" flies") south of Townsville (19° 47' S, 147° 13' E). The soil at the site was a Mottled yellow podzolic soil 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). Temperature and rainfall during the trial are shown in Figures 4.3 and 4.4.

Table 4.7 Major nutrients in the fine earth fraction (<2mm) of the topsoil (0 - 10 cm) of the trial site. Organic carbon was determined by Heanes (1984) method (Rayment and Higginson 1992), total nitrogen after wet oxidation with sulphuric acid and hydrogen peroxide as described by Anderson & Ingram (1989), acid extractable phosphorus after Rayment and Higginson (1992) and soil pH on a 1:5 soil/water suspension (Rayment and Higginson 1992).

Property	**Mean ± s.e.**
pH (n = 4)	6.2 ± 0.2
Organic C % (n = 90)	4.9 ± 0.08
Total N % (n = 90)	0.09 ± 0.002
Acid extractable P mg P kg-1 (n = 90)	86.8 ± 2.3

Figure 4.3 Maximum and minimum mean air temperatures at Ayr in 2000. Data obtained from the Australian Bureau of Meteorology.

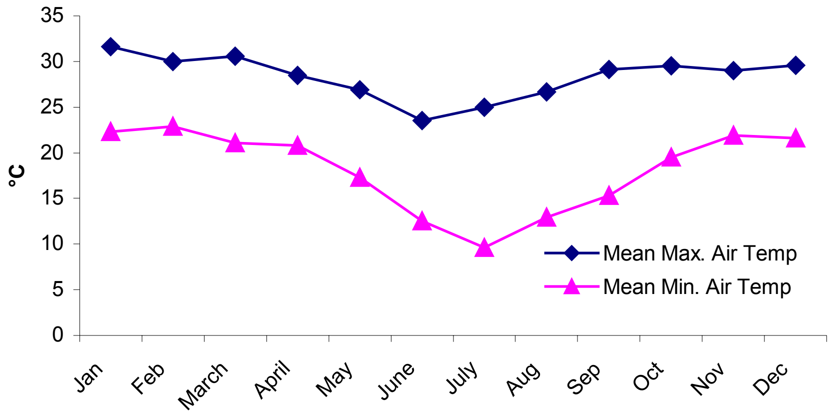
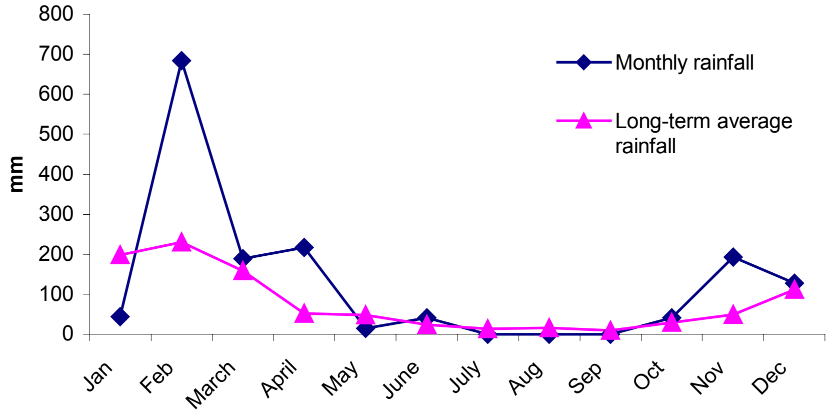


Figure 4.4 Monthly rainfall during 2000 and the long term monthly average. Data obtained from the Australian Bureau of Meteorology.



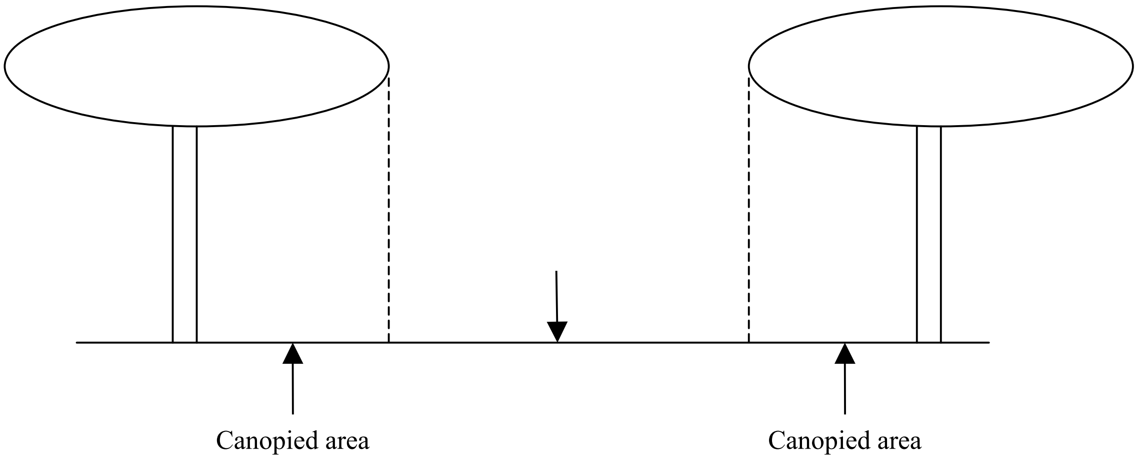
Trial establishment

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. Lines began and finished 0.5m from the base of the tree and were spaced 50 cm apart. Between each pair of trees one species of legume was sown along each line, with one seed planted every 10 cm at a depth of approximately 1 cm for larger seeded species (*C. ternatea, C. brasilianum* and *C. pascuorum*) and approximately 5mm or less for smaller seeded species (*S. hamata, S. scabra, C. rotundifolia* and *D. virgatus*) 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; *Clitoria ternatea* cv. Milgarra*,* *Centrosema brasilianum* cv. Ooloo and *C. pascuorum* cv. Cavalcade, *Stylosanthes hamata* cv. Verano, *S. scabra* cv. Seca, *Chamaecrista rotundifolia* cv. Wynn and *Desmanthus virgatus* cv. Jaribu each replicated four times per position treatment. The number of seeds sown of each species in the canopied or inter-canopied areas (see Trial sampling and data collection for definitions of these areas) varied due to the different lengths of these sections as a result of differing distances between trees and varying extents of canopy cover between adjacent trees. A control plot was established on nearby open ground in the same manner as already described, with the exception of each plot being 4m 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 (Skerman *et al.* 1988; Clements 1992; Edye and Topark-Ngarm 1992a; Jones 1992; Staples 1992a; Cameron and Lemke 1997).

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 4.5)

Figure 4.5 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 the tree canopy from the trunk to the canopy edge).

Dry matter was harvested on the 24th of October 2000 (30 weeks after planting) by placing a 0.5 x 0.5m quadrat in the centre of each location (control, canopied and inter-canopied), and harvesting plant material down to 10 cm above ground level in the case of more erect species such as *D. virgatus*, and to within 10 cm of the base of the plants 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/Radiometre/Photometre, (model LI-180) at midday on a clear day at the mid point of each treatment. Measurements were taken from the mid points of each treatment with eight replicates. Shade levels were determined to be as follows; June 2000, inter canopy 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).

4.3.2 Results

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 4.8). 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.

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 4.9). 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 4.8 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)**		
Effect	Yield t/ha	Ground cover	No. of plants/m	Yield t/ha	Ground cover	No. of 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)

Table 4.9 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 ± 3.9 a	8.0 ± 1.4
Canopied area	18.6 ± 2.5 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 4.10), 18.4% more than *C. brasilianum*, the species with the second greatest ground coverage. *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 coverage 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 4.10 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 ± 1.8 b	20.5 ± 1.8 a
Centrosema pascuorum	22.7 ± 5.2 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 inter-canopied and canopied locations and *C. ternatea* the most in the control treatment (Table 4.11). 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.

In June, the greatest ground cover within species was in the inter-canopy areas, (Table 4.11), followed by the canopied areas in all species except *C. brasilianum and C. rotundifolia*, which had their second greatest ground coverage 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 4.13). *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 inter-canopied areas.

Table 4.11 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 lower case letter and means in a row followed by the same upper case 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 ± 4.5 aB	27.5 ± 5.0 a	58.7 ± 6.4 aA	13.1 ± 4.3 ab	48.7 ± 4.6 aA	15.0 ± 4.6 ab	0.0018	0.2177
Centrosema brasilianum	22.5 ± 3.1 a	22.5 ± 5.0 ab	31.8 ± 4.8 b	19.3 ± 2.5 a	21.2 ± 2.1 c	20.6 ± 3.7 a	0.1084	0.8595
Chamaecrista rotundifolia	11.2 ± 3.9 b	11.2 ± 8.7 bc	12.5 ± 3.9 c	8.1 ± 2.1 bc	7.5 ± 1.5 d	9.3 ± 1.5 bc	0.5531	0.8284
Stylosanthes hamata	3.7 ± 2.6 bc	5.0 ± 0.1 c	8.7 ± 4.6 c	8.1 ± 1.2 bc	7.5 ± 1.5 d	7.5 ± 1.7 cd	0.4173	0.4635
Centrosema pascuorum	2.5 ± 1.6 cB	1.2 ± 1.2 c	41.2 ± 6.3 bA	0.0 ± 0.0 d	37.5 ± 7.7 bA	0.0 ± 0.0 e	<0.0001	0.1278
Stylosanthes scabra	2.5 ± 1.6 cB	2.5 ± 2.5 c	10.6 ± 2.3 cA	6.2 ± 2.6 bcd	7.8 ± 0.7 dA	5.0 ± 1.0 cde	0.0417	0.4635
Desmanthus virgatus	1.2 ± 1.2 c	0.0 ± 0.0 c	4.3 ± 1.8 c	1.2 ± 0.0 cd	3.4 ± 1.0 d	0.6 ± 0.6 d e	0.2652	0.5283
Probability	<0.0001	0.0146	<0.0001	0.0001	<0.0001	0.0001		

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 4.12). 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.

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 4.13). 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.

c) Interaction effects

Within locations

Under control and inter-canopy locations, *C. brasilianum* was the most productive of the species, followed in both cases by *C. ternatea* and *C. rotundifolia* (Table 4.14). 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 yielding 50% or less of their above-ground biomass. 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 4.14). 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 4.12 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.

Location	**Yield (kg/ha)**
Control	488.8 ± 201.7 a
Inter-canopy area	122.9 ± 38.8 b
Canopied area	82.6 ± 22.7 b
Probability	**0.0030**

Table 4.13 Means, standard errors and LSD groupings 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 ± 92.9 b
C. rotundifolia	118.8 ± 46.8 bc
S. hamata	62.7 ± 16.9 bc
S. scabra	40.7 ± 12.4 c
C. pascuorum	10.8 ± 10.8 c
D. virgatus	0.0 ± 0.0 c
Probability	**<0.0001**

Table 4.14 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 the 24th of October 2000. Means in a column followed by the same lower case letter and means in a row followed by the same upper case 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 ± 105.9 bA	278.3 ± 137.6 abB	228.9 ± 81.0 aB	0.0489
Chamaecrista rotundifolia	252.1 ± 207.4 c	119.0 ± 67.0 abc	52.0 ± 19.1 b	0.3326
Stylosanthes hamata	156.6 ± 7.9 cA	36.3 ± 11.3 bcB	42.2 ± 12.9 bB	0.0011
Centrosema pascuorum	54.2 ± 54.2 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 ± 15.6 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 4.15). 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 4.15 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 a b	0.36 ± 0.07
Canopied area	1.11 ± 0.08 b	0.23 ± 0.04
Probability	**0.0169**	**0.1439**

b) Effect of species

Table 4.16 displays the overall means and statistical groupings of plants per metre for each species. At the initial June sampling *C. ternatea* had the greatest 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. Remaining species clearly had smaller means than the previous 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 4.16 Mean, standard error and LSD groupings of the mean number of plants per metre of ground sown of tropical forage legumes grown 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 ± 0.16 b	0.006 ± 0.006 d
Centrosema brasilianum	1.46 ± 0.11 c	0.45 ± 0.07 b
Stylosanthes hamata	0.77 ± 0.11 d	0.30 ± 0.07 bc
Stylosanthes scabra	0.68 ± 0.07 d	0.16 ± 0.04 cd
Chamaecrista rotundifolia	0.45 ± 0.04 d	0.25 ± 0.05 c
Desmanthus virgatus	0.44 ± 0.005 d	0.07 ± 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

June 2000

Under the control treatment *Clitoria ternatea* had the greatest abundance. *Clitoria ternatea* had nearly double the number of plants per metre of the next species, *C. pascuorum*, and was statistically different from all other species (Table 4.17). *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 given by *S. scabra* and *C. rotundifolia*. The numbers of plants per metre in the inter-canopy area were slightly lower than those found in the control plot. *Clitoria ternatea* remained the species with the greatest abundance, 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. 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 numbers of plants per metre under all treatments with the control significantly different from the other two treatments.

October 2000

Legume abundance was much lower during October 2000, with no species having an average of greater than 1 plant per metre. 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. The lowest number of plants per metre was found in the species *D. virgatus* of which no plants 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*. *Clitoria 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 of were found beneath the canopied areas, although the difference between there and the other two locations was small (0.03 plants/m).

Table 4.17 Means, standard errors and LSD groupings mean number of plants per metre of seven species of tropical forage legume under canopied, inter-canopied and clear (control) areas beneath a 12-year-old *Khaya senegalensis* plantation sampled on the 8th of June and the 24th of October 2000. Means in a column followed by the same letter do not differ significantly. Means in a column followed by the same lower case letter and means in a row followed by the same upper case letter do not differ significantly.

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 ± 0.22 aA	0.65 ± 0.03 a	2.85 ± 0.21 aB	0.91 ± 0.10 a	2.33 ± 0.27 aB	0.54 ± 0.11 a	0.0005	0.0869
Centrosema pascuorum	2.75 ± 0.17 b	0.03 ± 0.03 b	1.97 ± 0.25 b	0 ± 0 e	1.89 ± 0.22 a	0 ± 0 d	0.2651	0.1278
Centrosema brasilianum	2.31 ± 0.37 bA	0.25 ± 0.12 bB	1.61 ± 0.12 bAB	0.65 ± 0.07 abA	1.29 ± 0.16 bB	0.36 ± 0.09 abB	0.0448	0.0424
Desmanthus virgatus	0.75 ± 0.14 c	0 ± 0 b	0.46 ± 0.05 d	0.08 ± 0.08 de	0.38 ± 0.08 d	0.09 ± 0.06 cd	0.1661	0.7269
Stylosanthes hamata	0.56 ± 0.15 c	0.25 ± 0.06 b	0.62 ± 0.08 cd	0.39 ± 0.18 bc	0.88 ± 0.19 bc	0.24 ± 0.01 bc	0.4880	0.6948
Chamaecrista rotundifolia	0.37 ± 0.07 cAB	0.18 ± 0.12 b	0.61 ± 0.11 cdA	0.35 ± 0.09 cd	0.36 ± 0.04 dB	0.17 ± 0.09 bcd	0.0481	0.3835
Stylosanthes scabra	0.37 ± 0.16 cA	0.15 ± 0.15 b	0.46 ± 0.13 dA	0.15 ± 0.05 cde	0.59 ± 0.09 cdB	0.18 ± 0.06 bcd	0.0450	0.9516
Probability	**<0.0001**	**0.0225**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0009**		

4.3.3 Discussion

The greater levels of dry matter production in the control treatment were almost certainly due to the greater levels of light than was present in the canopied or inter-canopied areas. Of the species tested it was clear that *C. brasilianum* and *C. ternatea* were the best yielding species with similar yields under canopied locations, however the larger yields of *C. brasilianum* at inter-canopy and control treatments, suggest that *C. brasilianum* may be a more versatile species than *C. ternatea,* with a better ability to increase production in response to increased light levels. Of the remaining species *Chamaecrista rotundifolia* was the next best performing species, however its yields did not approach those of either *C. brasilianum* or *C. ternatea*. The poor performance of this species under the inter-canopy and canopied areas suggests a poor shade adaptation or tolerance and hence unsuitability for use under timber plantations. *Stylosanthes hamata, S. hamata, C. pascuorum* and *D. virgatus* all performed poorly in comparison, with *D. virgatus* failing to establish at the site, possibly due to the site being unsuitable for the species, while *C. pascuorum* yielded poorly in control plots, the failure of any plants to survive in the inter-canopy and canopied plots suggests an unsuitability for use in such situations. Yields of *S. scabra* were similar under all treatments but were still very low. Low yields of *S. scabra* beneath the inter-canopy and canopied areas would have been expected as results in Chapters 2 and 3 suggested it is not a species that performs well under shaded conditions. *Stylosanthes hamata* was another species to have its yields decreased in inter-canopied and canopied plots compared to the control treatment indicating poor shade tolerance as has been found in the past (Stur 1991; Evans *et al.* 1992).

Ground cover initially displayed results which were not expected, with the greatest level of ground cover found in the inter-canopy and canopied treatments rather than in the control treatment as was expected due to higher light levels. A possible reason for this is the level of competition from surrounding grass and weeds. Grass and weed growth was much more vigorous in control plots and occupied a much greater fraction of ground than under the inter-canopied and canopied plots. However by October 2000 this difference had been reversed with the greatest levels of ground cover provided by the legume species found in the control plots and the lowest beneath inter-canopied and canopied plots. By this point in time much of the grass had died and the legumes were the only plants in each plot remaining green. Levels of ground cover in the inter-canopied and canopied plots were lower than the control plots at this largely because of the greater levels of legume growth in the control plots, as reflected in the dry matter yields.

Individually *C. ternatea* and *C. brasilianum* were the species providing the greatest levels of ground cover. The level of ground cover did not change in either species in the control treatment however beneath the inter-canopied and canopied treatments the ground-cover of each species decreased in the time between samplings, save *C. brasilianum* in canopied plots which also remain at roughly the same level. The decease in ground cover can almost certainly be attributed to the shedding of leaves by *C. ternatea* in response to water stress while the greater levels of ground cover given by *C. brasilianum* in canopied and inter-canopied plots at the October 2000 sampling are due to its greater level of growth and ability to remain green during the dry season (Skerman *et al.* 1988).

Numbers of plants per metre was also affected by growth in inter-canopied, canopied and control plots, but only at the June 2000 sampling date. At this date there was a decline in the number of plants per metre from the control plots to the inter-canopied plots to the canopied plots. Higher numbers of plants in control plots were possibly a result of higher light levels allowing seedlings to establish more successfully than under the two shaded treatments. The decrease in plant number by October 2000 was present in all treatments and had reduced plants numbers to between 11% and 27% of their former values. Reasons for plant death in this period could be many, such as water stress, disease, insect attack etc., however the much greater rate of plant mortality in control plots is likely to be a result of increased competition with grasses and weed species due to greater levels of plant growth, which was, in turn, a result of higher light levels than in the two shaded treatments. Of the species tested *C. ternatea* consistently had greater numbers of plants per metre than other species at all dates and locations followed by *C. pascuorum* in June 2000 and by *C. brasilianum* in October 2000. The large decrease in plant numbers (and dry matter yields) of *C. pascuorum* between June and October 2000 is likely to be a result of the annual nature of the species which regenerates aggressively with the onset of wet season rains (Skerman *et al.* 1988).

4.3.4 Conclusions

The yield of dry matter was clearly decreased by the presence of trees, 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 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 under 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.

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

4.4.1 Materials and methods

Experimental site

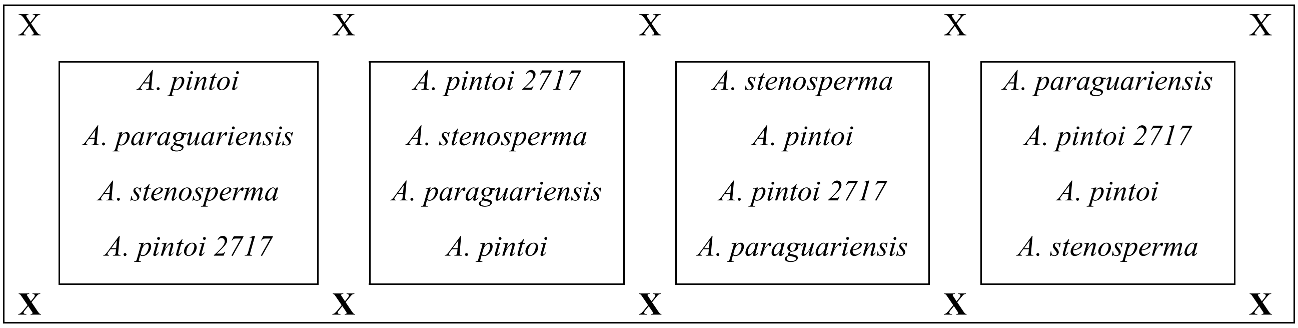
This trial was conducted on land located on the Townsville campus of James Cook University. African mahogany (*Khaya senegalensis*) seedlings were planted on the 16th of August 1999. Trees were planted in two separate blocks at spacings of 1 x 1m and 1.5 x 1.5m. Tree density and establishment date were chosen in order to ensure that a suitable level of shade was present beneath tree canopies. When trees were aged 15 months the trial was established (7th November 2000), by marking four furrows between trees. Furrows began 20 and 45cm from the base of the trees the 1 x1m and the 1.5 x 1.5m spacings respectively. Species examined in the trial were;

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

Arachis paraguiariensis ssp. *paraguiariensis* 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. paraguiariensis* ssp. *paraguiariensis* 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 rainfall.

Beneath the trees, species of *Arachis* were sown both on the edge of the tree plot where edge effects were expected to be present and in the centre, with each species replicated four times at the edge and the centre locations at each 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. Furrows were 60cm in length with 20cm between lines. Seed/cuttings of the six species tested were planted every 10cm 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 (see Figure 4.6).

Figure 4.6 Location of species relative to one another. X's represent individual trees.



The soil upon which the trial was conducted belonged to the Black series (Murtha 1982) and which 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 4.18

Sampling and data collection

Data were collected from 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 recorded and plant material harvested to within 10cm of the base of the plant for prostrate species or to 10cm 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 weight 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 5am and continuing until dark. Quantum sensors were placed in the open, in the central and edge parts of both tree densities, approximately 15cm above ground level and above any under story-vegetation. Results were summed and expressed as a percentage of the open area (Table 4.19).

Table 4.18 Major nutrients in the fine earth fraction (<2mm) of the trial site soil. Organic carbon was determined by Heanes (1984) method (Rayment and 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 and Higginson 1992). * Data obtained from (Murtha 1982).

Horizon	**Depth (cm)**	**pH (H_20)**	**Total N %**	**Avaliable P (mg/kg)**	**K***	**Na* (me/100g)**	**Ca***	**Sat. %***
A1	0-10	6.3	1.47	29	0.83	3.73	12.9	81
B	10-50	5.8	0.54	23	0.16	0.24	6.1	94

Table 4.19 Shade levels (percentage of full sun in the open) in the open and at 2 different locations in two densities of *Khaya senegalensis* on three harvesting dates.

Location	**March 2001**	**November 2001**	**April 2002**
1 x 1 m 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	0	0	0

4.4.2 Results

Statistical summary of results

Highly significant differences were present between legume species, in all attributes across all sampling dates (Table 4.20). 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 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 4.21), 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 decline in subsequent harvests, most notably in the control treatment where no yield was recorded by April 2002. November 2001 was the sampling date with the lowest yields for all 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 on all sampling dates and *A. pintoi* ATF 2717 on 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 4.23). Beneath all tree densities and 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. The species *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.

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 4.22). Despite the absence of a statistical difference between tree densities the fraction of ground covered by *A. pintoi* cv. Amarillo was greater at 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. The other species with no significant differences between tree densities, *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 finally 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 4.25). *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 (1.5 x 1.5 m March 2001). By March 2002 only *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 four cases; *A. stenosperma* November 2001 and April 2002, *A. pintoi* ATF April 2002 and *A. pintoi* cv. Amarillo April 2002 (Table 4.24). 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 4.20 Statistical summary of results

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

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

Table 4.21 Dry matter production (grams) by six accessions of legume under open conditions and beneath two densities of *Khaya senegalensis*, on three sampling dates. Means in a column followed by the same lower case 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	27.4 ± 17.0 a	5.3 ± 2.4 b	55.9 ± 25.9 a	91.8 ± 25.3 a	16.0 ± 1.9 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 ± 4.2 ab	10.7 ± 1.1 a	55.3 ± 9.4 a	39.3 ± 4.7 b	15.3 ± 1.3 a	50.2 ± 6.8 b	367.7 ± 77.0 a	22.7 ± 3.6 a	147.4 ± 39.4 a
A. stenosperma	8.1 ± 1.9 bc	1.4 ± 0.9 b	7.2 ± 1.7 b	40.4 ± 5.1 b	2.3 ± 0.9 b	6.2 ± 1.5 c	144.5 ± 21.3 bc	8.5 ± 0.2 b	0 ± 0 b
A. pintoi ATF 2717	7.5 ± 2.1 c	3.1 ± 1.1 b	8.6 ± 3.5 b	17.7 ± 2.5 c	3.8 ± 1.0 b	2.2 ± 1.2 c	81.5 ± 23.8 cd	11.7 ± 2.7 b	0 ± 0 b
A. pintoi cv. Amarillo	4.1 ± 1.2 c	4.1 ± 1.6 b	4.3 ± 1.8 b	10.8 ± 2.4 c	4.5 ± 1.5 b	1.9 ± 0.7 c	18.4 ± 11.2 d	5.3 ± 2.6 b	0 ± 0 b
C. rotundifolia	0.5 ± 0.4 c	0.9 ± 0.9 b	0.0 ± 0.0 c	5.4 ± 3.2 c	2.7 ± 2.7 b	0 ± 0 c	13.0 ± 13.0 d	8.5 ± 3.9 b	0 ± 0 b
P	0.0124	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Table 4.22 Ground cover (%) by six accessions of legume under open conditions and beneath two densities of *Khaya senegalensis*, on three sampling dates. Means in a column followed by the same lower case 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	100.0 ± 0.0 a	67.5 ± 7.5 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 ± 0.0 b
1.5 x 1.5 m	90.0 ± 7.0 a	45.0 ± 2.8 b	81.2 ± 6.2	70.0 ± 5.0 b	42.5 ± 3.6 a	41.8 ± 5.2 b	72.5 ± 6.5 a	6.2 ± 2.6 b	20.0 ± 5.1 ab
1 x 1 m	62.5 ± 10.3 b	15.0 ± 5.0 c	57.5 ± 21.7	55.0 ± 6.8 b	30.0 ± 2.6 b	57.5 ± 6.5 b	50.0 ± 5.9 b	3.7 ± 2.6 b	28.7 ± 7.4 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 ± 0.0 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 ± 3.2 b	10.0 ± 2.7 b	7.5 ± 1.3 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 ± 5.9 c	8.7 ± 2.9 b	33.7 ± 9.2 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 4.23 Ground cover of six accessions of legume under open conditions and beneath two densities of *Khaya senegalensis*, on three sampling dates.

	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 ± 4.4 b	25.0 ± 8.8 abc	81.2 ± 7.6 ab	12.5 ± 4.1 b	10.0 ± 3.4 cd	95.0 ± 5.0 a	12.5 ± 6.3 b	0.0 ± 0.0 c
A. paraguariensis	55.0 ± 6.8	30.0 ± 2.6 a	57.5 ± 6.5 a	70.0 ± 5.0 ab	42.5 ± 3.6 a	41.8 ± 5.2 b	92.5 ± 2.5 a	52.5 ± 8.5 a	90.0 ± 7.0 b
A. pintoi ATF 2717	50.0 ± 7.0	8.7 ± 2.9 b	33.7 ± 9.2 cd	66.2 ± 3.2 b	10.0 ± 2.7 b	7.5 ± 1.3 d	95.0 ± 2.8 a	27.5 ± 6.3 b	0.0 ± 0.0 c
A. stenosperma	50.0 ± 5.9	3.7 ± 2.6 b	28.7 ± 7.4 bcd	72.5 ± 6.5 ab	6.2 ± 2.6 b	20.0 ± 5.1 c	87.5 ± 6.3 a	20.0 ± 0.0 b	0.0 ± 0.0 c
C. rotundifolia	15.0 ± 8.6	2.5 ± 2.5 b	0.0 ± 0.0 d	25.0 ± 15.0 c	7.5 ± 7.5 b	0.0 ± 0.0 d	35.0 ± 20.2 b	20.0 ± 7.5 b	0.0 ± 0.0 c
P	0.0684	>0.0001	0.0054	0.0002	<0.0001	<0.0001	0.0007	0.0001	<0.0001

Table 4.24 Number of plants of six accessions of legume under open conditions and beneath two densities of *Khaya senegalensis*, on three sampling dates. Means in a column followed by the same lower case 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	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 ± 0.0 a	0.0 ± 0.0 b
1.5 x 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 ± 0.3 b	2.1 ± 0.2 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 ± 0.3 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 2717**			***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 ± 0.0 b	2.7 ± 0.2	3.0 ± 0.7	0.0 ± 0.0 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 ± 0.3 a	2.0 ± 0.3	1.2 ± 0.3	1.1 ± 0.2 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 ± 0.2 a	2.1 ± 0.3	1.6 ± 0.4	2.0 ± 0.4 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	-

Table 4.25 Number of plants of six accessions of legume under open conditions and beneath two densities of *Khaya senegalensis*, on three sampling dates.

	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 ± 0.8 ab	2.5 ± 0.9 a	3.0 ± 0.6 ab	2.7 ± 0.8 ab	2.7 ± 0.5 a	3.2 ± 0.5 a	3.5 ± 0.5 a	3.3 ± 0.2 a
A. stenosperma	2.9 ± 0.2 a	0.5 ± 0.4 c	1.7 ± 0.3 a	3.0 ± 0.4 a	0.8 ± 0.3 d	2.1 ± 0.2 ab	2.7 ± 0.2 ab	3.0 ± 0.0 a	0.0 ± 0.0 b
A. paraguariensis	2.2 ± 0.3 ab	2.6 ± 0.2 a	2.2 ± 0.2 a	2.4 ± 0.2 abc	2.8 ± 0.1 a	2.2 ± 0.3 ab	1.7 ± 0.2 bc	3.0 ± 0.0 a	3.0 ± 0.0 a
A. pintoi ATF 2717	2.1 ± 0.3 ab	1.6 ± 0.4 ab	2.0 ± 0.4 a	2.0 ± 0.3 bc	1.2 ± 0.3 cd	1.1 ± 0.2 c	2.7 ± 0.2 ab	3.0 ± 0.7 a	0.0 ± 0.0 b
A. pintoi cv. Amarillo	1.8 ± 0.5 b	1.1 ± 0.3 bc	1.4 ± 0.2 a	1.9 ± 0.2 c	1.8 ± 0.2 bc	1.6 ± 0.3 bc	2.2 ± 0.2 ab	1.0 ± 0.4 b	0.0 ± 0.0 b
C. rotundifolia	1.3 ± 0.6 b	0.2 ± 0.2 c	0.0 ± 0.0 b	0.8 ± 0.5 d	0.2 ± 0.2 d	0.0 ± 0.0 d	1.0 ± 0.6 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

4.4.3 Discussion

Production of dry matter was greatest in *C. ternatea* and *A. paraguariensis* both in control plots and under the two tree densities. The good performance of both species under all treatments suggests a degree of shade tolerance, and hence a potential for use in agroforestry systems. Growth beneath both the 1 x 1 m and 1.5 x 1.5 m tree spacings resulted in lower levels of dry matter production in these two species relative to the control treatment. However the April 2002 sampling saw the failure of any species save *C. ternatea* and *A. paraguariensis* to survive in control plots. Possible reasons for the failure of *A. stenosperma, A. pintoi* cv. ATF 2717, *A. pintoi* cv. Amarillo and *C. rotundifolia* to survive in the control treatment include an increased level of water stress due to greater water demands as a result of receiving direct light. The decline in dry matter production in each species at each location at the November 2001 sampling is a result of low levels of growth during the dry season since the last harvest. However *C. ternatea and A. paraguariensis* were the only species to recover and yield useful quantities of dry matter by the April 2002 sampling date after wet season rains. Remaining species failed to recover to the same extent both under the two tree densities and the control. *Arachis pintoi* cv. Amarillo and *C. rotundifolia* both failed to perform well at any stage of the trial under any of the treatments. The failure of these species to establish properly in control plots suggests that the site or climate may be unsuitable, as was anticipated in the case of *A. pintoi* cv. Amarillo due to its preference for wetter tropical climates. The poor performance of many species under the control treatment suggests that some factor other than light was limiting to plant growth at the final harvest and was more pronounced in control plots than beneath either tree density. Results appear to support this with yields of dry matter falling in *A. stenosperma, A. pintoi* cv. ATF 2717, *A. pintoi* cv. Amarillo and *C. rotundifolia* as time increased, with yields in the final April 2002 harvest greatest under the 1 x 1 m treatment followed by the 1.5 x 1.5 m treatment. The availability of soil moisture is likely to be the reason for these results as shade has been noted in the past to reduce evaporative demand, with soil moisture availability maintained at a higher level than in the open through the effects of reduced evaporation from the soil (through shade and a layer of leaf litter) and lower rates of transpiration from pasture plants (Wilson and Ludlow 1991). However if such an effect were present then it must have been large enough to out weight the effects of competition between the trees and legumes for soil moisture, which would not have been present in the control plots. *Clitoria ternatea* and *A. paraguariensis* must have been sufficiently drought tolerant as light appeared to be the limiting resource for their growth in this trial.

The numbers of plants surviving reflected the production of dry matter with the numbers of surviving plants generally declining with the progression of time. Tree density did not appear to have any consistent effects upon the number of surviving plants. The only clear effects of tree density upon the number of surviving plants was in the final sampling where no live plants of *A. stenosperma, A. pintoi* cv. Amarillo*, A. pintoi* ATF 2717 or *C. rotundifolia* were found beneath in control plots. *Clitoria ternatea* and *A. paraguariensis* generally had the greatest numbers of surviving plants particularly at the finial sampling date, reflecting the better overall performance of these species.

As would be expect ground cover also reflected the production of dry matter by each species with *C. ternatea* and *A. paraguariensis* clearly providing the greatest levels of ground cover, particularly at the final sampling date. Increasing tree density reduced the level of ground cover provided by these two species as would be expected due to the lower levels of growth by the two species under the 1.5 x 1.5 m and the 1 x 1 m tree densities. In remaining species tree density also reduced the level of ground cover in the first and second samplings, when it is likely that light not water was the limiting factor to growth. The final harvest the greatest levels of ground cover produced under the 1 x 1 m tree spacing followed by the 1.5 x 1.5 m spacing.

It is possible that shade initially decreased between March 2001 and November 2001 and then increased again in April 2002 due to the effects of tree leaf loss in the dry season. As *Khaya senegalensis* is a semi-deciduous species, losing some of its leaves in response to water stress, it is probable that the trees in this trial had done so by the November 2001 sampling date, causing the levels of shade found beneath the trees to be less than would otherwise be expected. Shade levels would then be expected to increase with the rains of the wet season and the flush of new growth that accompanies them.

4.4.4 Conclusions

Clitoria ternatea and *A. paraguariensis* appear to be the most suitable of the species examined for use in agroforestry systems, producing 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*.

4.5 General conclusions and summary

The following general conclusions were drawn from 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.

Chapter 5 – 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 tropics of Queensland in 1988, following World Heritage listing of these forests. 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 and 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 and Rose 1990), with the possibility of water becoming the limiting resource in the seasonally dry tropics during the dry season rather than light.

The majority of work in the past examining the suitability, largely 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. Recently increasing areas of plantations of the tree species *Khaya senegalensis*

(African mahogany) have been established around Townsville and Charters Towers (Collins and Sexton, *pers com.*), although little information is available regarding suitable forage species for growth beneath plantations in the seasonally dry tropics. In order to address this, a trial was established to examine the performance, under field conditions, of 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

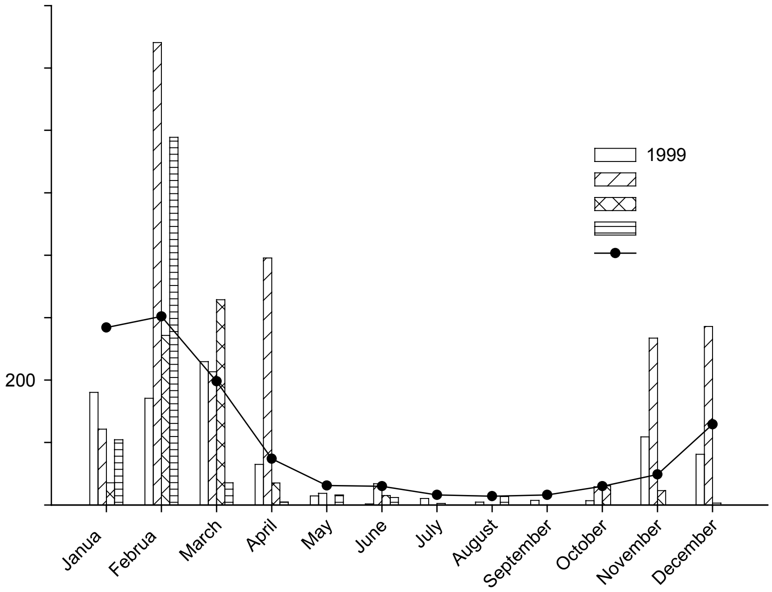
The trial was established upon a cleared plot of land on the Townsville campus of James Cook University. Prior to clearing, vegetation on the site was an Ironbark (*Eucalyptus drepanophylla)* woodland with an understory dominated by Chinee Apple (*Zizyphus mauritiana*) and Guinea Grass (*Panicum maximum*). 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 previously in Table 4.3

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 100g 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 (m) 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 the four species of legume, *Clitoria ternatea* cv. Milgarra, *Chamaecrista rotundifolia* cv. Wynn, *Centrosema brasilianum* cv. Ooloo or *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.

Temperatures and rainfall during the trial are shown in Figures 2.1 (Chapter 2) and 5.1 below.

Figure 5.1 Rainfall (mm) recorded at James Cook Universities Townsville campus from January 1999 to August 2002.



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 sealable plastic bags and the moisture content determined as a percentage based on weight according to the method of Rayment and 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 x 0.5 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 the 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 under-taken 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. Statistical analysis was conducted as a one-way ANOVA analysis to detect differences between legume species at a given tree density with sown legume species as the treatment with four replications. However an appropriate statistical analysis method for use between tree densities could not be found due to the lack of true replication, for which additional Nelder wheels would need to have been established. Instead data was viewed as a regression in order to assess species performance beneath differing tree densities.

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).

5.3.2 Soil moisture content

The content of 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 5.1 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

5.3.3 Pasture production and composition

Calibration Curves

When actual yields were plotted against estimated yields in calibration curves and a line of best fit added significant relationships were found (Table 5.6). Due to the good correlations between the estimated and actual yields the use of this technique was deemed suitable.

August 2001

Total dry matter production

Dry matter production was strongly depressed by the higher densities of trees present in the centre of the wheel (Table 5.3a), to the extent that no pasture growth was present under the highest tree density. Beneath 366, 1467, and 10270 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. Between species at each tree density there were no statistical differences detected.

Legume yield

With the exception of *C. ternatea,* the yield of remaining legume species decreased substantially as tree density increased, with the greatest yield given by *C. rotundifolia* under 259 trees/ha and the lowest by all four species which failed to produce any dry matter under 20541 trees/ha (Table 5.3b). 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 in comparison to the other three species under 259, 366, 543, 855 and 1467 trees/ha, but had the greatest legume component yield of any species beneath 10270 trees/ha. *Centrosema brasilianum* consistently produced the greatest or second greatest amounts of legume material under all tree densities except 10270 trees/ha. The only significant difference between species was present under 1467 stems/ha with *C. brasilianum* yielding significantly more than other species.

Grass yield

No significant differences between species were found with the growth of grasses severely depressed by higher tree densities (Table 5.3c). The production of dry matter by grasses was much greater than that of either legumes or broadleaf weeds. Under densities of 10277, 2282 and 259 stems/ha sectors sown with *C. brasilianum* gave the greatest yields of grass with *C. ternatea* and *C. rotundifolia* yielding the most under remaining densities. Grass production in *S. hamata* sectors was never greater than all other species but was the lowest under only one density (543 stems/ha). Beneath tree densities of 10270, 2282, 1467, 855 and 366 stems/ha grass production was lowest in sectors sown with *C. rotundifolia.* There was no grass growth under 20541 stems/ha.

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 and failing to grow beneath 20541 trees/ha (Table 5.3d). The species of legume sown did not appear to have any clear effects 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 and 1467 trees/ha, with *S. hamata* having the greatest under 259, 366 and 855 trees/ha. Beneath the higher densities of 2282 and 10270 stems/ha sectors sown with *C. brasilianum* contained the greater quantities of weeds. Statistically there was no difference between legume species under any tree density.

November 2001

Total dry matter production

Levels of dry matter production at the November 2001 sampling were slightly higher than found in August 2001 under lower tree densities. Beneath tree densities 259, 366, 543 and 855 stems/ha, little difference was present between sectors sown with different legume species (Table 5.4a). No species treatment consistently produced either the greatest or lowest yields of dry matter, with no pattern apparent. No plant growth was present under 20541 stems/ha nor were there any significant differences.

Legume yield

Centrosema brasilianum was conspicuous in its production of approximately twice the dry matter of other species beneath 259 and 366 trees/ha (Table 5.4b). It continued to produce the greatest amount of dry matter under remaining tree densities, although the margin between it and remaining species was not as large. At tree densities, of 1467, 855, 543 and 259 stems/ha *S. hamata* was the legume with the lowest yields. Statistical differences were found between species under 2282 and 1467 stems/ha where *C. brasilianum* and *C. rotundifolia* were not significantly different as were *C. rotundifolia* and *S. hamata.* At 366 stems/ha *C. brasilianum* was significantly greater than other species.

Grass yield

Grass was easily the greatest producing component of the pasture across all legume species. A substantial drop in grass yield was present beneath 2282 trees/ha in all legume treatments (Table 5.4c). Yields remained low as density increased until 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. No statistical differences were present.

Weed yield

The growth of broadleaf weeds was quite varied between sectors sown with different legume species, under the same tree densities (Table 5.4d). 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. Significant differences were found under densities of 2282 and 366 stems/ha.

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 (Table 5.5a). 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*. A significant difference was found under 10270 stems/ha with *C. rotundifolia* and *S. hamata* not differing from one another in the highest grouping while *S. hamata, C. brasilianum* and *C. ternatea* comprised the lower yielding group.

Legume yield

Yields of leguminous dry matter (Table 5.5b) 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. Only one significant difference was found under 855 stems/ha with *C. ternatea* and *S. hamata* forming the higher yielding group and *S. hamata, C. brasilianum* and *C. rotundifolia* forming the lower yielding group.

Grass yield

Grass clearly produced most of the pasture dry matter in all legume sectors (Table 5.5c) with no statistical differences found between legume species. The highest and lowest yields of grass were not consistently found in any legume treatment. In contrast to previous sampling dates there was a small yield of grass under 20541 trees/ha in the *C. ternatea* treatment, where previously no grass growth had occurred.

Weed yield

No statistical differences were found in weed growth between legume species. 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 (Table 5.5d). While *S. hamata* had the greatest quantity of weeds and 1467 and 855 stems/ha there was no clear pattern apparent between weed growth and sown legume species.

Table 5.2 Moisture content (% based upon weight, mean ± 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**			**November 2001**			**February 2002**		
(stem/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

Table 5.3 Means and standard errors of total, legume, grass and weed dry matter yields (kg/ha) for the August 2001 sampling. Means in a column followed by the same lower case letter are not significantly different.

a) Total dry matter yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	0 ± 0	339 ± 52 a	868 ± 225 a	1039 ± 247a	810 ± 71	1053 ± 135	1216 ± 189	1035 ± 117
C. brasilianum	0 ± 0	400 ± 77 a	920 ± 138 a	920 ± 143 a	865 ± 137	991 ± 122	1439 ± 159	1503 ± 153
C. rotundifolia	0 ± 0	77 ± 19 b	210 ± 31 b	399 ± 40 b	675 ± 71	1225 ± 186	1097 ± 177	1555 ± 222
S. hamata	0 ± 0	128 ± 29 b	271 ± 95 b	372 ± 41 b	804 ± 148	814 ± 78	1189 ± 123	1232 ± 149
P value	-	<0.0001	<0.0001	0.0010	0.6827	0.2015	0..5075	0.1606

b) Legume yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	0 ± 0	204 ± 34 a	67 ± 23 b	97 ± 17 b	70 ± 10 a	133 ± 36 b	136 ± 34	87 ± 16
C. brasilianum	0 ± 0	43 ± 7 b	119 ± 24 a	240 ± 39 a	248 ± 42 a	207 ± 39 b	347 ± 69	269 ± 62
C. rotundifolia	0 ± 0	14 ± 5 b	14 ± 8 c	67 ± 18 bc	112 ± 28 b	350 ± 75 a	267 ± 58	388 ± 106
S. hamata	0 ± 0	60 ± 21 b	20 ± 7 bc	30 ± 11 c	90 ± 41 b	157 ± 29 b	233 ± 48	142 ± 34
P value	-	<0.0001	<0.0001	<0.0001	<0.0001	0.0090	0.0562	0.0055

c) Grass yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	0 ± 0	91 ± 31 b	761 ± 227 a	770 ± 225 a	557 ± 74	648 ± 120	795 ± 183	766 ± 12
C. brasilianum	0 ± 0	268 ± 68 a	717 ± 138 a	664 ± 148 a	482 ± 105	607 ± 110	753 ± 142	851 ± 146
C. rotundifolia	0 ± 0	28 ± 7 b	140 ± 26 b	239 ± 37 b	450 ± 75	650 ± 157	591 ± 169	840 ± 194
S. hamata	0 ± 0	53 ± 20 b	192 ± 73 b	267 ± 38 b	480 ± 152	537 ± 75	610 ± 115	729 ± 140
P value	-	<0.0001	<0.0001	0.0090	0.9073	0.9034	0.7296	0.9304

d) Weed yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	0 ± 0	47 ± 15	40 ± 15	170 ± 50 a	184 ± 37	271 ± 80	284 ± 57	182 ± 3
C. brasilianum	0 ± 0	90 ± 42	68 ± 21	50 ± 17 b	145 ± 32	177 ± 57	337 ± 95	235 ± 70
C. rotundifolia	0 ± 0	32 ± 18	52 ± 17	67 ± 24 b	112 ± 35	227 ± 57	238 ± 59	328 ± 70
S. hamata	0 ± 0	13 ± 5	60 ± 23	103 ± 23 ab	233 ± 44	120 ± 25	347 ± 68	363 ± 53
P value	-	0.1611	0.7599	0.0430	0.1257	0.3020	0.6851	0.1124

Table 5.4 Means and standard errors of total, legume, grass and weed dry matter yields (kg/ha) for the November 2001 sampling. Means in a column followed by the same lower case letter are not significantly different.

a) Total dry matter yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	0 ± 0	17 ± 10	123 ± 43	302 ± 66 b	919 ± 90	1117 ± 188	1521 ± 74	1631 ± 166
C. brasilianum	0 ± 0	37 ± 37	208 ± 16	481 ± 75 a	871 ± 120	1134 ± 165	1328 ± 173	1929 ± 175
C. rotundifolia	0 ± 0	0 ± 0	169 ± 45	270 ± 28 b	957 ± 194	1291 ± 92	1514 ± 222	1484 ± 136
S. hamata	0 ± 0	8 ± 5	301 ± 71	436 ± 56ab	969 ± 183	1093 ± 51	1457 ± 168	1587 ± 119
P value	-	0.1974	0.2979	0.0426	0.9435	0.8082	0.8572	0.3653

b) Legume yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	0 ± 0	8 ± 6	16 ± 12 ab	60 ± 16 ab	97 ± 27	164 ± 39	151 ± 76 b	241 ± 32
C. brasilianum	0 ± 0	0 ± 0	28 ± 5 a	78 ± 10 a	166 ± 42	205 ± 58	493 ± 124 a	454 ± 101
C. rotundifolia	0 ± 0	0 ± 0	0.7 ± 0.7 b	24 ± 10 bc	97 ± 33	165 ± 45	139 ± 47 b	215 ± 71
S. hamata	0 ± 0	5 ± 4	2 ± 2 b	19 ± 9 c	83 ± 34	118 ± 28	174 ± 55 b	182 ± 31
P value	-	0.2485	0.0001	0.0016	0.1373	0.2743	<0.0001	0.0069

c) Grass yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	0 ± 0	8 ± 5	104 ± 42	201 ± 52	706 ± 89	791 ± 141	1179 ± 145	1012 ± 164
C. brasilianum	0 ± 0	37 ± 37	144 ± 34	385 ± 69	644 ± 75	875 ± 97	779 ± 97	1246 ± 190
C. rotundifolia	0 ± 0	0 ± 0	142 ± 52	224 ± 30	745 ± 150	971 ± 63	1223 ± 220	1101 ± 166
S. hamata	0 ± 0	2 ± 1	294 ± 77	350 ± 46	704 ± 147	853 ± 50	984 ± 103	1088 ± 106
P value	-	0.0981	0.1996	0.0615	0.9525	0.8653	0.2471	0.8454

d) Weed yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	0 ± 0	0.7 ± 0.7	1 ± 1	41 ± 12	116 ± 30	163 ± 38	192 ± 21 ab	380 ± 128
C. brasilianum	0 ± 0	0 ± 0	34 ± 13	18 ± 8	61 ± 35	52 ± 31	55 ± 32 b	230 ± 114
C. rotundifolia	0 ± 0	0 ± 0	3 ± 2	20 ± 9	115 ± 49	154 ± 85	153 ± 53 ab	173 ± 53
S. hamata	0 ± 0	0.5 ± 0.5	5 ± 5	66 ± 23	181 ± 63	121 ± 29	298 ± 84 a	319 ± 58
P value	-	0.3893	0.0038	0.0153	0.0864	0.0680	0.0006	0.0602

Table 5.5 Means and standard errors of total, legume, grass and weed dry matter yields (kg/ha) for the February 2002 sampling. Means in a column followed by the same lower case letter are not significantly different.

a) Total dry matter yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	17 ± 17	85 ± 29 b	516 ± 75	1540 ± 510	2184 ± 446	2018 ± 279	2364 ± 517	3132 ± 209
C. brasilianum	0 ± 0	106 ± 63 b	475 ± 191	1126 ± 299	1587 ± 317	2189 ± 249	2479 ± 324	2300 ± 649
C. rotundifolia	0 ± 0	348 ± 45 a	714 ± 136	1761 ± 441	1635 ± 459	2093 ± 509	2487 ± 921	2298 ± 282
S. hamata	4 ± 4	254 ± 84 ab	471 ± 117	1020 ± 112	1443 ± 70	1908 ± 104	1826 ± 55	1724 ± 226
P value	0.4744	0.0180	0.6630	0.3743	0.4803	0.9514	0.6822	0.1409

b) Legume yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	14 ± 14	50 ± 10	89 ± 37 a	208 ± 33	290 ± 39	521 ± 101	299 ± 140	427 ± 200
C. brasilianum	0 ± 0	13 ± 10	69 ± 40 ab	135 ± 46	107 ± 56	254 ± 64	403 ± 81	276 ± 136
C. rotundifolia	0 ± 0	21 ± 21	6 ± 4 c	151 ± 122	94 ± 46	385 ± 281	239 ± 142	122 ± 32
S. hamata	4 ± 4	48 ± 20	13 ± 10 bc	117 ± 57	204 ± 50	198 ± 70	225 ± 154	188 ± 25
P value	0.4921	0.3649	0.0213	0.5689	0.0662	0.1483	0.5139	0.0929

c) Grass yield

	Tree Density (stems/ha)							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	3 ± 3	35 ± 17	413 ± 60	1280 ± 509	1673 ± 391	1362 ± 220	1658 ±477	2243 ± 376
C. brasilianum	0 ± 0	45 ± 17	377 ± 137	965 ± 268	1314 ± 343	1747 ± 309	1746 ± 220	1887 ± 349
C. rotundifolia	0 ± 0	218 ± 93	593 ± 165	1487 ± 452	1495 ± 442	1555 ± 385	1922 ± 101	1988 ± 719
S. hamata	0 ± 0	163 ± 65	409 ± 137	712 ± 206	1016 ± 123	1574 ± 58	1422 ± 180	1236 ± 146
P value	0.3976	0.0612	0.7662	0.4404	0.6522	0.9163	0.8996	0.4333

d) Weed yield

	Tree Density							
Species	20541	10270	2282	1467	855	543	366	259
C. ternatea	0 ± 0	3 ± 3	13 ± 1	45 ± 28	221 ± 115	128 ± 19	406 ± 143	477 ± 331
C. brasilianum	0 ± 0	1 ± 1	28 ± 16	25 ± 17	165 ± 72	187 ± 58	329 ± 202	175 ± 83
C. rotundifolia	0 ± 0	106 ± 82	115 ± 41	122 ± 17	45 ± 9	154 ± 54	325 ± 124	188 ± 89
S. hamata	0 ± 0	42 ± 40	48 ± 26	190 ± 115	222 ± 94	135 ± 48	172 ± 56	299 ± 97
P value	-	0.1698	0.0591	0.0209	0.2862	0.9068	0.4180	0.1998

Table 5.6 R-squared and P values of the line of best fit on three sampling dates for actual yield vs. estimated yield of legume, grass and weed components of the pasture.

	August 2001		**November 2001**		**February 2002**	
	R^2	**P**	**R^2**	**P**	**R^2**	**P**
Weeds	0.9194	<0.001	0.9593	<0.001	0.7244	<0.001
Legume	0.8589	<0.001	0.844	<0.001	0.8949	<0.001
Grass	0.9167	<0.001	0.9196	<0.001	0.857	<0.001

5.4 Discussion

5.4.1 Shade levels

Beneath the higher tree densities (20541 and 10270 trees/ha) shade levels were very heavy in August 2001, however in the subsequent November and February recordings the level of shade was found to have decreased. These results initially appear to contrast with what would be expected, as it is well know 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 (Santhirasegaram 1966; Payne 1985; Chen 1989). 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; Wilson and Ludlow 1991; Reynolds 1995) 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 and Ludlow 1991). It is recognized that the shade levels recorded here would be expected to be lowest values, as measurements were taken from the mid-point between trees and shade levels would be expected to increase as distance to the tree base decreased. 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

Soil moisture content during the August 2001 sampling was 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 the November sampling while the sampling taken in February 2002 found very high levels of soil moisture that was a result of very heavy rainfall several days prior to sampling (in excess of 500mm). 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 soil moisture levels, 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 the top 10 cm of soils at different tree densities in November 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 50cm 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 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 and 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 cause 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. When a linear line of best fit is used to describe dry matter production (Figure 5.2 a-c) it can be seen that it does not provide a good fit (low R^2 values, see Table 5.7). However when an exponential line of best fit is used then R^2 values were increased substantially. Therefore it can be said that increasing tree density exponentially decreased the production of dry matter. Similar relationships between tree density and understorey 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.* (1989a) 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 5.7 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	Linear	Exponential
August 2001	0.7266	0.9753
November 2001	0.4656	0.9958
February 2002	0.6471	0.9828

5.4.4 Legume yield

The yield of the legume component of the pasture was decreased substantially by high tree density. In August 2001 *C. 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. *Clitoria 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 this (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, 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 *Chamaecrista rotundifolia* allowed much of the individual plants to avoid 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.

Centrosema brasilianum was the greatest yielding species at densities of 2282, 1467, 855 and 366 trees/ha at the August sampling which the ability of *C. brasilianum* to remain green during periods of water stress is likely to have played a large role. Yields of *C. ternatea* were greater during November 2001 than in the previous harvest. An unusually high yield was found beneath 10270 trees/ha in August and 2282 trees/ha in November. This suggests favourable 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.* (1989a), 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 allowing greater amounts of the species to avoid defoliation. By November 2001 *C. brasilianum* was easily the best performing species at 259 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 at that date.

The performance of *C. rotundifolia* was good under the tree densities 259 and 543 tees/ha at the August sampling, but it did not perform noticeably better than any other species of legume under remaining tree densities. *Chamaecrista 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). At the August sampling it performed better that *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. hamatas'* 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

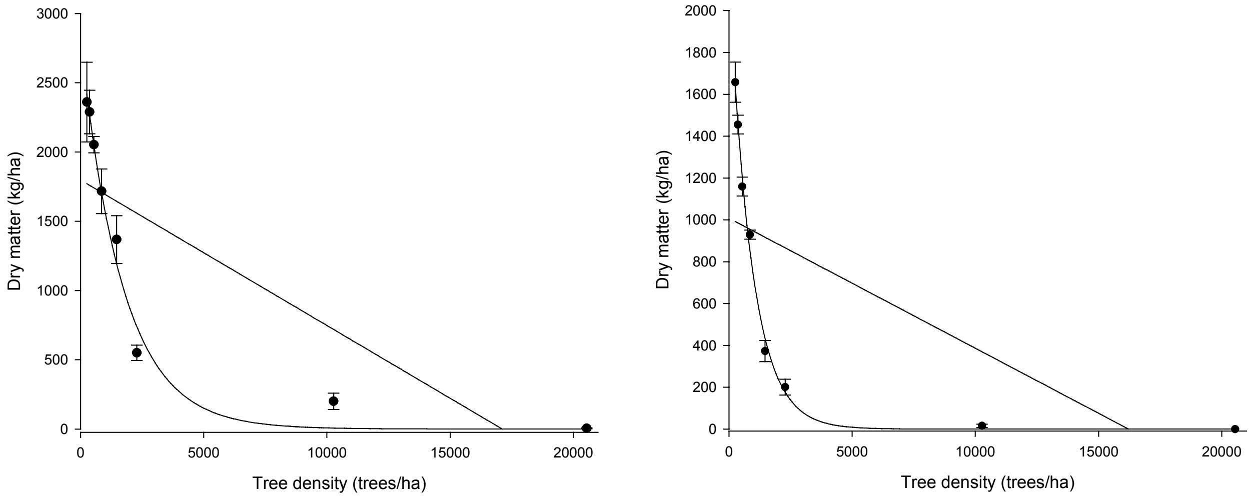
Grasses were clearly the dominant component of the pasture, with Guinea grass (*Panicum maximum*) composing the major part of grass material, with yields declining markedly with increasing tree density. Grass yields were not consistently greater in any legume treatment in the August and November samplings, however at the February 2002 sampling the greatest yields of grass were found in the *C. rotundifolia* treatment under densities of 10270, 2282, 1467 and 366 stems/ha. The greater yields of grass present in February 2002 were a result of the rainfall received during the previous three months and increased temperatures. 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 support 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.

5.4.5 Weed yield

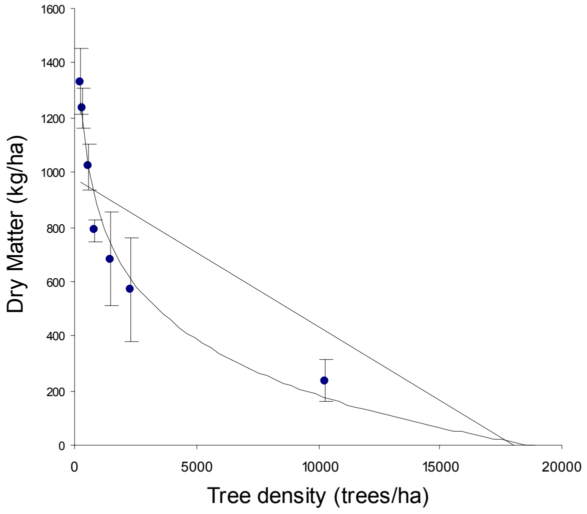
The yield of broadleaf weeds decreased with increasing tree density. Only at the November sampling could a clear effect of sown legume species be seen on the content of weeds. Sectors sown with *C. brasilianum* contained noticeably lower amounts of weed dry matter than other species of sown legume at 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 the decrease in weed growth as a result of increased growth and competition from *C. brasilianum*, however if this was the case it would be expected that grass yields would also have been depressed but this was not the case.

Figure 5.2 Average total dry matter production (kg/ha) of forage beneath eight densities of *Khaya senegalensis* on three dates with linear and logarithmic lines of best fit. Error bars depict the standard error of the mean.

a) August 2001 b) November 2001



c) February 2002



5.5 Conclusions

From the trial 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 tree growth continued and to stabilize around 855 trees/ha or less.

Soil moisture was also found to be lower at higher tree densities during the August sampling as a result of competition between trees. While the November sampling indicated that the small mount 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 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.

The legumes species *C. ternatea* was the best performing legume at the February sampling when conditions for growth where favorable, however, issues connected with defoliation 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 defoliation 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 the other grass species, such as *Urochloa mosambicensis,* contributing very small amounts of dry matter and only tended to be present under lower tree densities.

Weed growth was also decreased by tree density although 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.

Chapter 6 – General conclusions and new directions

6.1 Conclusions from shade-house trials

Shading was found to influence many of the properties measured although the effects were not always consistent across species.

- A decrease in the production of both above and below-ground plant material was observed with shading.
- The extent of root nodulation was decreased by shading and may affect the amount of N_2 fixation.
- N concentrations in leaf material were found to increase with shade and may have been caused by the same reasons listed for decreased nodulation.
- Concentrations of leaf P was found to respond inconsistently between species grown under shade, with both increases and decreases observed.
- Time taken to the production of the first flower were generally longer in plants grown under shade.
- A greatly decreased production of seed was found in plants grown under shade, however the weight of individual seeds was not affected.
- Shading increased the amount of readily germinable seed in some species compared to the control, along with accompanying decreases in levels of hard seed under shade. Shading did not affect levels of non-viable seed. The time taken to 50% germination was significantly faster in several species when seed was produced under shade.
- Shoot:root ratios decreased under shade, with the shoot system increasing at the expense of the root system.
- Physiological measurements did not prove to be particularly helpful in identifying suitable species, however overall light response curves did give an indication of species tolerance or ability to acclimate to shaded conditions.

Of the species examined *Arachis pintoi, Desmodium heterophyllum* and *D. uncinatum* are recommended for use under shaded conditions in wet tropical areas due to their shade tolerance, good production of dry matter under full sun and shade, and due to their prostrate/scrambling habit. In the wet/dry tropics *Macroptilium lathyroides* and

Arachis stenosperma are recommended for the same reasons. Species that were found to have good-shade tolerance or acclimation, but had other qualities which detract from their value for agroforestry systems, included *Centrosema macrocarpum, C. pubescens, C. acutifolium, C. mucunoides, Pueraria phaseoloides* and *Neonotonia wightii* (wet tropics), *Macroptilium atropurpureum, Clitoria ternatea* and *Centrosema brasilianum* (wet/dry tropics). All of these species have a climbing habit, some of which are particularly vigorous (*C. mucunoides, N. wightii* and *P. phaseoloides*). In plantations species with climbing habits have the potential to smother young or small trees and should not be sown beneath trees unless the landowner is prepared to put in extra management to control climbing species such as through controlled grazing regimes or slashing. A second issue arising with climbing species is their persistence as they are not as tolerant of defoliation as prostrate species. In order to avoid the decline and possible loss of the legume component from the pasture, appropriate grazing strategies would have to be adopted. Other site factors should be taken into account when selecting a legume for use beneath a timber plantation such as soil properties, climate and rainfall patterns.

Physiological measurements alone were found to be insufficient to predict the performance of a species under shade, as some species were shade-tolerant rather than shade-adapted, and when examined solely on physiological properties would not appear suitable for use under shade. However, when viewed in conjunction with agronomic results it was possible to use the light response curves for a species to determine if it was shade-tolerant or shade-adapted and to give an indication of how the plant would perform under full sun. Plants that were found to be shade-tolerant tended to produce high levels of dry matter under full sun as well as performing well under shade. However, shade-adapted plants did not produce well under full sun although they did do well under shaded conditions. The maximum rate of photosynthesis when plotted against relative production of dry matter displayed some correlation but not enough to allow strong predictions of a plant’s suitability for use under shade.

The effects of shade upon available N in the soil in shadehouse trials was unclear, but it appeared that the amounts of available N were sufficient for plant growth under heavy shade levels as suggested by plants’ low nodulation levels. However under field conditions plants may still need to nodulate to meet N requirements as the legumes will be competing with trees, grasses and weeds for soil N.

Additional research is required to continue examining the potential of new species, particularly those adapted to the wet/dry tropics, while long term field trials are necessary to more accurately determine the performance of species under field conditions. The response of species to defoliation under shade is an important factor that needs to be investigated both under controlled and field conditions, as does the compatibility of suitable legume species with shade tolerant grasses in order to assess long-term persistence. The reduction in plant nodulation under shade also requires further examination to identify specific causes.

6.2 Conclusions from field trials

Beneath a 5-year-old plantation of mixed species at Babinda, *Arachis pintoi* and *Stylosanthes guianensis* showed the greatest promise of six non-climbing legume accessions, as they were the only species showing significant ground cover and biomass production 22 months after planting. *Arachis pintoi* did particularly well and was beginning to spread well beyond its initial plots by the end of the trial, while the good performance of *S. guianensis* was unexpected, but much of the dry matter it produced was woody stem material.

For species suited to the seasonally dry tropics, trials were conducted under a 12-year-old African Mahogany (*Khaya senegalensis*) plantation near Clare and under new plantings of *Khaya*, less than 3 years of age in Townsville. *Clitoria ternatea* and *Centrosema brasilianum* performed best, however legume growth beneath trees was depressed compared to growth under open conditions. The results suggest that *C. ternatea* and *C. brasilianum* are shade-tolerant rather than shade-adapted and may be suited for use in plantations, although their climbing habits may be cause for concern among young trees. The remaining species examined in the trial (*C. pascuorum, S. hamata, S. scabra, C. rotundifolia and D. virgatus)* did not perform well and would not be recommended for use in plantations.

It was concluded from the Nelder Wheel trial, conducted in Townsville, that production of forage 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 very heavy beneath higher tree densities, but decreased as tree density fell and stabilised around 855 trees/ha or less.

Due to competition between trees, soil moisture was found to be lower under higher tree densities during the August sampling. Measurements taken at the November sampling indicated that the small amount of rainfall received in the period between samplings did not infiltrate beyond the top 10 cm, while soil moisture levels decreased at greater depths. The increased levels of soil moisture present in the top 10 cm of soil at this time were likely due to shading by the 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 received prior to sampling.

Centrosema brasilianum proved to be the best species for use during the early period of the growing season (November), while *Clitoria ternatea* was the best performing species in February when conditions for growth were more favourable. However 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 may prove useful in plantations that are frequently slashed or grazed. *Stylosanthes hamata* appears to be the least suitable of the species examined for use under tree plantations, while *C. ternatea* and *C. brasilianum* appear 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.

Higher tree densities also decreased weed growth 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 dynamic nature of the pasture beneath trees in the seasonally dry tropics is apparent in the differences in yields and legume performance between sampling dates, and highlights the importance of sampling date to detect changes in pasture growth, particularly in the transitional periods of the seasonally dry tropics. Results also suggest that water stress, not shade, may be the limiting factor for pasture growth at certain times of the year in the seasonally dry tropics, with higher tree densities causing increased competition for available water. As a result of continued changes in performance relative to legume treatment, tree density and time of year, the results obtained here indicate the need for long-term trials with more intensive monitoring in order to form a clearer picture of legume and pasture performance beneath trees over time.

Table 6.1 summarises the results for each species tested in each trial. The far right hand column indicates, according to the results obtained in this study, if the species is shade-tolerant, shade-adapted or neither. Shade-tolerant species appear to be more versatile than those that are shade-adapted as shade- adapted species are unable to adapt to high light levels (Wilson and Ludlow 1991), while species that are shade-tolerant may become shade-acclimated and still have greater rates of photosynthesis than shade-adapted plants while being able to increase photosynthesis under higher light levels.

Table 6.1 Summary of assessment for each species tested across all trials

Species	**Shade house and physiological trials**		**Field Trials - suitable for use under field conditions**				**Shade-adapted or shade-tolerant**
	Agronomic performance under shade Chap. 2.	Physiological measurements. Shade-tolerant Chap. 3.	Mixed rainforest species/*E. pellita* Chap 4.2	12 year old *Khaya senegalensis* Chap. 4.3	15 month old *Khaya senegalensis* Chap. 4.4	Nelder wheel trial Chap. 5	
A. americana	Poor	No	Poor	-	-	-	No
A. kretschmeri	Poor	-	-	-	-	-	No
A. paraguariensis	Unknown	Unknown	-	-	Excellent	-	Unknown
A. pintoi	Excellent	Yes	Excellent	-	Poor	-	Shade-adapted
A. stenosperma	Good	Yes	-	-	Poor	-	Shade-adapted
A. villosa	Poor	-	Poor	-	-	-	No
A. villosa cv. Kret.	Poor	No	Poor	-	-	-	No
C. acutifolium	Fair	No	-	-	-	-	Shade-tolerant
C. brasilianum	Excellent	Yes	-	Excellent	-	Excellent	Shade-adapted
C. macrocarpum	Excellent	No	-	-	-	-	Shade-tolerant
C. mucunoides	Excellent	Yes	-	-	-	-	Shade-adapted
C. pascuorum	Poor	Yes	-	Poor	-	-	Shade-adapted
C. pubescens	Excellent	Unknown	-	-	-	-	Unknown
C. rotundifolia	Poor	No	-	Poor	Poor	Poor	No
C. ternatea	Excellent	Yes	-	Excellent	Excellent	Excellent	Shade-adapted
D. canum	Good	Yes	-	-	-	-	Shade-adapted
D. heterophyllum	Excellent	No	-	-	-	-	Shade-tolerant
D. intortum	Excellent	Yes	-	-	-	-	Shade-adapted
D. ovalifolium	Good	Unknown	-	-	-	-	

Species	**Shade house and physiological trials**		**Field Trials - suitable for use under field conditions**				**Shade-adapted or shade-tolerant**
	Agronomic performance under shade Chap. 2.	Physiological measurements. Shade tolerant Chap. 3.	Mixed rainforest species/*E. pellita* Chap 4.2	12 year old *Khaya senegalensis* Chap. 4.3	15 month old *Khaya senegalensis* Chap. 4.4	Nelder wheel trial Chap. 5	
D. scorpiurus	Poor	No	-	-	-	-	No
D. triflorum	Excellent	Yes	-	-	-	-	Shade-adapted
D. uncinatum	Excellent	Yes	-	-	-	-	Shade-adapted
D. virgatus	Poor	Yes	-	Poor	-	-	No
F. congesta	Poor	No	-	-	-	-	No
M. atropurpureum	Excellent	No	-	-	-	-	Shade-tolerant
M. axillare	Poor	No	-	-	-	-	No
M. lathyroides	Excellent	No	-	-	-	-	Shade-tolerant
M. martii	Good	No	-	-	-	-	No
P. phaseoloides	Excellent	No	-	-	-	-	Shade-tolerant
R. minima	Poor	Yes	-	-	-	-	No
S. guianensis	Poor	No	Good	-	-	-	No
S. hamata	Poor	Unknown	-	Poor	-	Poor	No
S. scabra	Poor	No	-	Poor	-	-	No
V. luteola	Poor	No	-	-	-	-	No

6.3 Further Research

Sixteen species of legume that show promise for use beneath trees in silvo-pastoral systems have been identified by this study, however many of the species identified as being either shade tolerant or productive under shaded conditions have a climbing/twining habit that can cause concern in tree plantations, particularly in respect to the smothering of young or small trees. When the climbing species are discarded the remaining species for the wet tropics are *D. intortum, A. pintoi, D. ovalifolium, D. canum, D. heterophyllum* and *D. uncinatum*, while *A. stenosperma* and *M. lathyroides* show potential for the seasonally dry tropics. Climbing species still may be used beneath older plantations or where a higher level of pasture management is acceptable to help prevent smothering of trees through the frequency and intensity of grazing or defoliation.

Further research should continue testing additional legume species under shade, and examine appropriate grazing regimes for the control of climbing legumes in tree plantations, in order to broaden the potential range of legumes suitable for use in such situations. Research is also required to examine the long-term persistence, response to defoliation and productivity of species identified in this study as tree plantations age and shade levels increase. Compatibility with shade tolerant grasses is an important issue that has seen relatively little attention but will have important effects upon the persistence and productivity of both the grass and legume components of the pasture.

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