



Regrowth performance of tropical forage legumes on infertile soils

Andi L. Amar¹ , Ross J. Coventry², Robert A. Congdon² and Christopher P. Gardiner³

¹Faculty of Animal Husbandry and Fisheries, Universitas Tadulako, Palu 94117 Sulawesi Tengah, Indonesia.

²Tropical Plant Sciences, School of Marine and Tropical Biology, James Cook University, Townsville Qld 4811, Australia

³School of Veterinary and Biomedical Science, James Cook University, Townsville Qld 4811, Australia

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(✉) Corresponding Author: Andiamar85@gmail.com

Abstract

Survival, herbage yield and nutrient use efficiency of ten tropical forage legumes were compared in pot trials using two soil types (red and yellow kandosols), widespread in Australia's tropical rangelands, over a period of 22 months. Over this period, plants of *Centrosema brasilianum* cv. Ooloo, *Desmodium virgatus*, *Macropodium bracteatum* (93.8%), *Stylosanthes scabra*, *S. hamata* (87.5%) and *D. pubescens* (68.8%) survived best. *Arachis paraguariensis* (37.5%), *A. triseminalis*, *M. martii* (25.0%) and *C. pascuorum* (18.8%) were less successful. The highest herbage yields were consistently produced by *C. brasilianum*, followed by *M. bracteatum* and the *Stylosanthes* cultivars. The annual species, *C. pascuorum* and *M. martii* gave high yields in the first 3 9-weekly harvests. The *Stylosanthes* cultivars produced most root nodules, followed by *A. paraguariensis*, *C. pascuorum*, *C. brasilianum* and *M. martii*. *D. pubescens*, *D. virgatus*, *M. martii*, *A. triseminalis* and *C. brasilianum* had the highest nitrogen-use efficiencies, whilst *C. brasilianum* and the two *Stylosanthes* cultivars had the highest phosphorus-use efficiencies. All of the legumes increased the nitrogen content of the two soils significantly, especially *S. hamata*, *A. paraguariensis*, *C. brasilianum*, *M. martii* and *M. bracteatum*. Most of the legumes show promise for use in low-fertility tropical pastures, particularly *C. brasilianum* and *M. bracteatum*.

Keywords: Pasture Legumes, Low Fertility, Soils, Rangelands.

Introduction

The extensive grazing rangelands of tropical Australia are based on soils of low fertility (Cannon and Coventry, 1989; Ash et al., 2011; Reid et al., 2022), and productivity depends on the use of pasture legumes to enhance protein content of forage (Kebede et al., 2016; Garcia-Favre et al., 2022; Almeida dos Santos et al., 2022; Tulu et al., 2023). Soil nutrients are depleted over time by growing plants if nutrients or fertiliser are not added to the growing medium. In this study, a pot trial was used to compare the ability of a range of legume genotypes to survive and produce herbage when subjected to regular harvesting and depletion of nutrients on two different soils which are widespread in tropical Australia. This process provides a useful method to detect the legume differences in response to low fertility soils as was initiated in the earlier study (Amar et al., 2016), and the further depletion

of soil nutrients when the plants were subjected to regular harvesting in a Regrowth Study described here.

Nutrient-use efficiencies of the different legumes were compared, and were mainly determined as the ratio of biomass production over the biomass nutrient content (Chisholm and Blair 1988, Elliott and White 1994). Soil nutrient (N and P) changes during the study were used to help in the estimation of the nitrogen contribution and phosphorus-use efficiency of the legumes studied.

Many studies have shown that phosphorus plays an important role in leguminous plants, particularly in relation to their nitrogen-fixing ability. Cassman et al. (1993) suggested that potential nitrogen inputs to soils from nitrogen fixed by legumes mainly depend on soil phosphorus levels. Gunawardena et al. (1993) found increases in nitrogen fixed by soybean (*Glycine max* cv. Chippewa) as a result of

phosphorus applications, and [Sanginga \(1992\)](#) found increases in the number and biomass of nodules in *Leucaena* cultivars and *Gliricidia* with increasing rates of phosphorus application. In the latter case, however, ([Sanginga et al., 1995](#)) found that the percentage and amount of nitrogen fixed by *Gliricidia sepium* increased only with application of 20 kg P/ha, and not at 40 and 80 kg P/ha.

Hence, of the macronutrients, phosphorus is more likely to limit growth of legumes, as they are able to fix and use atmospheric nitrogen ([Cassman et al., 1993](#)), so a phosphorus-use efficiency index was used in this study to compare the genotypes in terms of units of nitrogen content per unit of phosphorus in the herbage. This approach is thought to be useful to give an indication of the phosphorus-use among the legumes in terms of N/P ratio of the above-ground parts of the plants.

Materials and methods

Experimental site

This ‘Regrowth Performance study’ was a continuation of the earlier study on seed quality ([Amar et al., 2016](#)) discussed in Part 1 of this series, using ten species of tropical forage legumes ([Table 1](#)). The 160 plants which were harvested in the previous study carried out at CSIRO were transferred to a shade house at the James Cook University, and their growth was monitored for another 72 weeks with regular harvesting at 9-week intervals. The daily maximum temperatures in the shade house during the study period over 16 months ranged from 16.0° to 42.0 °C and the daily minimum temperatures from 4.0° to 26.0 °C.

Experimental design

The pots were re-arranged into a randomized block design, with 8 replicates on 4 mesh benches. Every week the pots were rotated within each block to minimise any differences in growth due to the pot positions. They were watered daily with tap water (0 to 100 mL/pot) depending on the weather. Cutting of the plant shoot regrowth was done every 9 weeks to examine herbage production, and the numbers of surviving plants were recorded. The pots were individually weighed after each of 8 harvests, and water added to guarantee that the water contents were returned to field capacity at the onset of the next growth period ([Amar et al., 2016](#)).

After each harvest, the herbage was dried in a forced-draught oven at 70 °C to a constant weight. Originally, it was proposed to continue this study as long as the plants survived and grew, however, it was terminated after a 16 month period (the eighth harvest), due to time limitations for the course of study. At the final harvest, two soil sub-samples were collected from each pot of the surviving plants, by vertically inserting a 5 cm polyvinyl chloride pipe with a diameter of 1.5 cm, and removing approximately 1 cm of the surface soil. Sub-samples from each pot of the same plant-soil combination were mixed

and bulked into 4 replicated samples for soil nitrogen and phosphorus analysis. There were 40 soil samples for nutrient analysis (derived from 10 legume genotypes x 2 soil types x 2 soil samples for each plant-soil combination) to quantify the nutrient changes during the 22 months of growth of the different legume genotypes from the beginning of the early growth study to the completion of this ‘Regrowth Performance Study’.

Due to difficulties in separating the nodules, which were very small in some cases, they were not measured or weighed, despite these attributes often being determined by other workers. Similar information can be obtained, however, by visually scoring the nodule number on a scale from 0 to 5 ([Peoples et al., 1989](#)). After collecting the soil samples, the roots of the surviving plants were washed, the level of root nodulation was scored between 0 and 5, where 0= no nodules, 1 = 1 to 5 nodules, 2 = 6 to 10 nodules, 3 = 11 to 15 nodules, 4 = 16 to 20 nodules, and 5 = more than 20 nodules. Notes were taken on nodule size and health. The roots were washed and the root biomass was then determined after drying at 70 °C.

Herbage yields from the second, fourth, sixth, and eighth harvests were analysed for total nitrogen (N) and phosphorus (P) to estimate the nutrient-use efficiencies of the legumes. These 4 harvests were chosen to identify any trends in nutrient-use efficiency as the nutrients in the soil were depleted with time. The second and the last harvests represent the peak herbage yields. The fourth harvest represents the lowest herbage yield in winter, and the sixth harvest relates to plant growth in spring, which was harvested as temperatures became warmer.

The nutrient-use efficiencies (‘NUE’ for nitrogen; ‘PUE’ for phosphorus) were calculated using the formula of [Chisholm and Blair \(1988\)](#) and [Elliott and White \(1994\)](#): $NUE = \frac{\text{Total shoot biomass yield}}{\text{nutrient content of the biomass}}$.

Here, the “total shoot biomass yield” and “nutrient content of the biomass” refer only to the above-ground parts of the plants for 2 reasons. Firstly, the above-ground biomass is the main component of herbage for animal feed, and the authors consider this to be the best measure of nutrient-use efficiency for forage production. Secondly, the plants were grown and harvested several times, and their nutrient-use efficiencies were determined and compared after 4 periods of regrowth. However, the roots were harvested once only, at the end of the experiment, to allow the estimation of the total plant biomass. This method of determining nutrient-use efficiency, though questionable for use in grain crops, is thought to be appropriate and useful in forage plants ([Woodend and Glass 1993](#)).

To determine phosphorus-use efficiency, the following formula was used:

$$PUE_N = \frac{\text{Total herbage N}}{\text{total herbage P}}$$

Where, PUE_N is P-use efficiency for N content of the herbage,

or, the N/P ratio of the herbage produced

The data obtained from this study were subjected to an analysis of variance using a computer statistical package (Statistix version 4.1). Significant effects were compared by the least significant differences method (LSD, P<0.05).

Results and discussion

The experimental results show that total herbage yields, phosphorus-use efficiencies, nutrient changes in the soils, and herbage phosphorus concentration were significantly influenced by genetic and edaphic interactions. These parameters will be discussed in terms of interaction effects, while discussion of the others will be based on the main effects. To provide more information on the differences between genotypes, yields at each harvest of 9-week regrowth are compared among the legumes following the discussion of total herbage yields within each genus.

The effects of legume genotype

Plant survivorship

The numbers of surviving plants differed between legume genotypes (Table 1). There were no significant effects of either soil type or the interaction term. The mean percentages of the surviving legumes were 63.8% and 62.5% on the Red and Yellow Kandosols, respectively.

The highest percentages of surviving plants among the accessions were for *C. brasilianum*, *D. virgatus*, *M. bracteatum*, both *Stylosanthes* cultivars, and *D. pubescens*, which were not significantly different from one another. The lowest survivorship was found in *A. paraguayensis*, *A. triseminalis*, *M. martii*, and *C. pascuorum*, but *A. paraguayensis* did not differ significantly from *D. pubescens*.

Table 1. Plant survival of different legume genotypes subjected to 1 harvest after 6 months establishment, and 8 subsequent harvests at 9-week intervals. Means in a column followed by the same lower case letter are not significantly different

Comparisons	Original no. of plants	Surviving plants (%)
<i>S. scabra</i> cv. Seca	16	87.5 a
<i>S. hamata</i> cv. Verano	16	87.5 a
<i>A. paraguayensis</i>	16	37.5 bc
<i>A. triseminalis</i>	16	25.0 c
<i>C. brasilianum</i> cv. Ooloo	16	93.8 a
<i>C. pascuorum</i>	16	18.8 c
<i>D. pubescens</i>	16	68.8 ab
<i>D. virgatus</i>	16	93.8 a
<i>M. bracteatum</i>	16	93.8 a
<i>M. martii</i>	16	25.0 c
s.e.		15.43

There was no difference in survivorship between genotypes when compared within each of the *Stylosanthes*, *Arachis*, and *Desmanthus* genera, but the perennial species, *C. brasilianum* and *M. bracteatum*, survived better than their annual counterparts, *C. pascuorum* and *M. martii*, respectively. This trend matches the expected behaviour of perennial and annual species. In the case of the stylos, however, the perennial Seca and the annual-biennial Verano had the same survival percentages.

Herbage yields within each genus and at each harvest

Most of the genera displayed different total herbage yields between genotypes, except within the *Desmanthus* accessions (Table 2). Three other trends were recognised: the annual-biennial Verano outyielded the perennial Seca; the perennial *C. brasilianum* and *M. bracteatum* gave greater herbage yields than their annual counterparts, *C. pascuorum* and *M. martii*, respectively; and *A. paraguayensis* produced more herbage than *A. triseminalis* (both are perennials).

Herbage yields of the different legumes at each harvest are listed in Table 3. *C. brasilianum* consistently produced the highest yields, followed by *M. bracteatum* and the *Stylosanthes* cultivars. However, it is noteworthy that the annual species - *C. pascuorum* in particular and *M. martii* - produced high herbage yields at the first 3 harvests (at 1 year old).

Table 2. The effect of different legume genotypes on the herbage yields within each genus. Means in a column, within each legume genus, followed by the same lower case letter are not significantly different.

Legume genotypes	Herbage yield (g/plant)
<i>S. scabra</i> cv. Seca	16.4 a
<i>S. hamata</i> cv. Verano	18.7 b
s.e.	0.91
<i>A. paraguayensis</i> CPI 91419	9.1 a
<i>A. triseminalis</i> CPI 911423	5.4 b
s.e.	1.44
<i>C. brasilianum</i> cv. Ooloo	27.4 a
<i>C. pascuorum</i> CPI 55697	15.8 b
s.e.	1.44
<i>D. pubescens</i>	10.3 a
<i>D. virgatus</i>	8.7 a
s.e.	1.02
<i>M. bracteatum</i> CPI 55770	19.3 a
<i>M. martii</i> CPI 55783	12.7 b
s.e.	2.02

Root biomass and nodulation

There was no significant influence of soil factors on root biomass and nodule number. *C. brasilianum* and *A. paraguayensis* produced the highest root biomass, followed by *M. bracteatum*, *D. virgatus* and *C. pascuorum*, with both

Stylosanthes cultivars, Seca and Verano producing the least root biomass (Table 4).

Both stylos were very similar in root biomass and root nodulation, while *A. paraguariensis* had consistently higher values for both root characteristics compared to *A. triseminalis* (Table 4). Mean root biomass of *C. brasilianum* was significantly greater than *C. pascuorum*, but their root nodulation scores were similar. *D. virgatus* had significantly higher root biomass than *D. pubescens*, but they also had similar root nodulation scores. *M. bracteatum* also produced more root biomass than *M. martii*, but they were not different in root nodulation scores.

Based on the interpretation of root nodulation score by Sykes et al. (1988), the *Stylosanthes* cultivars were found to have the

most prolific root nodulation, followed by *A. paraguariensis*, *C. pascuorum*, *C. brasilianum* and *M. martii*. These genotypes can be classed as having ‘good’ root nodulation performance (Peoples et al., 1989, Sykes et al., 1988), and may make a considerable contribution of nitrogen to the soil. *M. bracteatum* and *D. pubescens* may fix enough nitrogen for their own needs; and the others showed poor nodulation and may not be self-sufficient for nitrogen.

Nevertheless, a reliable conclusion could not be drawn, since the genotypes producing the highest number of nodules, namely the *Stylosanthes* cultivars and *A. paraguariensis*, produced very small nodules whose colouration could not be observed.

Table 3. Comparison of mean herbage yields at different harvesting dates produced by pasture legumes grown on Kandosol soils (n=16, derived from 8 replicates x 2 soil types). Means in a column followed by the same lower case letter are not significantly different.

Legume	Herbage yield (g/plant) at each harvest of 8-week regrowth (date of harvest), and temperature regimes during regrowth							
	15-01-95 ‘warm’	19-03-95 ‘warm’	21-05-95 ‘warm’	23-07-95 ‘intermediate’	23-09-95 ‘cool’	24-11-95 ‘intermediate’	25-01-96 ‘warm’	29-03-96 ‘warm’
<i>S. scabra</i> cv. Seca	3.33 bc	4.49 c	2.40 c	0.62 b	0.54 c	1.19 b	1.53 bc	2.34 bc
<i>S. hamata</i> cv. Verano	3.60 b	5.87 b	3.25 b	0.58 bc	0.55 c	1.34 b	1.36 bc	2.14 c
<i>A. paraguariensis</i> CPI 91419	2.08 d	2.73 d	0.64 e	0.28 ef	0.58 bc	1.02 bc	1.01 cde	0.78 ef
<i>A. triseminalis</i> CPI 91423	1.46 ef	1.91 e	0.68 e	0.20 f	0.15 d	0.35 d	0.40 f	0.27 f
<i>C. brasilianum</i> cv. Ooloo	4.71 a	6.84 a	5.16 a	0.87 a	1.37 a	2.30 a	2.42 a	3.77 a
<i>C. pascuorum</i> CPI 55697	4.17 a	6.43 ab	3.13 b	0.39 de	0.13 d	0.39 d	0.60 ef	0.58 ef
<i>D. pubescens</i>	1.72 de	2.81 d	1.66 de	0.45 cd	0.49 c	0.93 bc	1.03 cde	1.23 d
<i>D. virgatus</i>	0.95 f	1.80 e	1.14 e	0.38 de	0.44 c	1.09 b	1.26 cd	1.61 cde
<i>M. bracteatum</i> CPI 55770	3.32 bc	6.32 ab	2.28 cd	0.52 bcd	0.82 b	1.21 b	1.87 ab	2.94 b
<i>M. martii</i> CPI 55783	2.84 c	3.87 c	2.84 bc	0.42 de	0.45 c	0.62 cd	0.76 def	0.88 def
s.e.	0.28	0.34	0.32	0.08	0.13	0.22	0.28	0.37

Table 4. Pairwise comparisons of mean root biomass and nodulation of the legumes grown on different soils, at the completion of the study, based on the number of surviving plants. Means in a column followed by the same lower case letter do not differ significantly.

Comparison between genotypes	No. of plants Surviving	Mean root biomass		Mean nodulation	
		(g/plant)	s.e.	(score: 0 to 5)	s.e.
<i>S. scabra</i> cv. Seca	14	2.02 d	0.27	5.00 a	0
<i>S. hamata</i> cv. Verano	14	2.13 d	0.18	5.00 a	0
<i>A. paraguariensis</i>	6	4.61 a	0.30	4.67 b	0.21
<i>A. triseminalis</i>	4	1.52 e	0.04	1.25 e	0.47
<i>C. brasilianum</i>	15	4.69 a	0.61	4.40 bc	0.19
<i>C. pascuorum</i>	3	3.05 c	0.04	4.67 b	0.33
<i>D. pubescens</i>	11	1.76 e	0.15	3.09 cd	0.53
<i>D. virgatus</i>	15	3.43 b	0.28	2.33 d	0.56
<i>M. bracteatum</i>	15	3.46 b	0.19	3.73 c	0.26
<i>M. martii</i>	4	2.40 d	0.40	4.00 bc	0.70

Although the *Stylosanthes* cultivars scored the best root nodulation, most of the genotypes showed good root nodulation, except for *D. virgatus* and *A. triseminalis*. Only accessions of *Centrosema* and *Macroptilium* produced some nodules greater than 1 cm in diameter, and those of

Desmanthus grew to almost 1 cm (forming elongate and lobed or coralloid nodules; (Somasegaran and Hoben 1985). Nodules of *Arachis* and *Stylosanthes* were considerably smaller, with an average diameter of only about 1 to 2 mm, and rarely reaching 3 mm. Again only the accessions of

Centrosema and *Macroptilium* were observed to have healthy reddish or pink nodules (Thomas, 1994), while those of *Desmanthus* were a healthy brown to dark-brown. Reddish or pink coloured nodules are mainly associated with members of the *Fabaceae* (Mahmood and Iqbal 1994). The brown coloured nodules of *Desmanthus* were similar to those of *Myrica rubra*, which has milky-white young nodules, yellow-brown mature nodules, and dark-brown senescent nodules (Wang and Huang 1990). However, Gardiner (1992) found red colouration in various *D. virgatus* accessions. Nodule colour could not be observed in the *Arachis* and *Stylosanthes* genotypes due to their very small size.

Nitrogen-use efficiency

Nitrogen-use efficiency, calculated as mass of herbage yield per unit of nitrogen in the herbage, was not affected by the soil factor or interaction terms, but significant differences were found among the legume genotypes (Table 5).

Table 5. Comparisons of the mean nitrogen use efficiencies (NUE) of the different legumes. Means in a column followed by the same letter are not significantly different.

Legume genotypes	NUE
<i>S. scabra</i> cv. Seca	35.6 d
<i>S. hamata</i> cv. Verano	31.1 e
<i>A. paraguariensis</i>	36.9 d
<i>A. triseminalis</i>	41.4 bc
<i>C. brasilianum</i> cv. Ooloo	38.8 c
<i>C. pascuorum</i>	33.1 de
<i>D. pubescens</i>	54.7 a
<i>D. virgatus</i>	43.3 b
<i>M. bracteatum</i>	38.1 cd
<i>M. martii</i>	44.6 b
s.e.	2.12

The genotypes can be classed into 3 groups of nitrogen-use efficiency in order from the highest to the lowest:

- *D. pubescens*, *M. martii*, *D. virgatus*, *A. triseminalis*, and *C. brasilianum*.
- *M. bracteatum* and *A. paraguariensis*, which had a similar NUE to that of Seca, but significantly higher than that of Verano.
- Only *C. pascuorum* had a NUE similar to that of both stylo cultivars.

The effects of soil type

The soil factor had a significant effect on herbage yields within legume genera for *Arachis* and *Macroptilium*. *Arachis* produced more herbage on the Red Kandosol, while *Macroptilium* performed better on the yellow soil (Table 6).

Table 6. The effect of the different soil types on the herbage yields of *Arachis* and *Macroptilium*. Means in a row followed by different upper case letters are significantly different.

Legume genotypes	Herbage yield (g/plant), on:		s.e.
	Red Kandosol	Yellow Kandosol	
<i>Arachis</i>	8.8 A	5.7 B	1.44
<i>Macroptilium</i>	13.2 B	18.8 A	2.01

The effects of interaction between legume genotype and the soil type

Total herbage yield

The presence of an interaction effect demonstrates the different responses among the legume genotypes to the different soils (Table 7). Only two trends can be identified:

- Most of the genotypes produced a similar amount of herbage on the different soil types.
- Only *M. martii* produced significantly more herbage on the Yellow Kandosol.

C. brasilianum cv. Ooloo generally produced more herbage on both soils than the *Stylosanthes* cultivars, while *M. bracteatum* produced similar yield to the stylos, but on the Yellow Kandosol it yielded more herbage than Seca. The legume genotypes can be classified according to the total herbage yields on both soils as follows:

- High herbage producers are *C. brasilianum* and *M. bracteatum*.
- Medium herbage producers are the *Stylosanthes* cultivars, *C. pascuorum* and *M. martii*.
- Low herbage producers are those with lower yields than the *Stylosanthes* cultivars on both soil types, namely the genotypes of *Arachis* and *Desmanthus*.

Phosphorus-use efficiencies

Unlike nitrogen, phosphorus-use efficiencies (PUE and PUE_N) were significantly influenced by the interaction between genetic and edaphic factors. For most of the legumes there was no significant difference in herbage production in relation to the amount of phosphorus used for plant growth on the different soils (Table 8). *C. brasilianum*, *C. pascuorum* and *M. martii*, however, produced more herbage per unit phosphorus in the herbage when grown on the Yellow Kandosol (Table 8). *C. brasilianum* had the highest PUE on both soils, followed by the *Stylosanthes* cultivars, and *Macroptilium* species.

Table 7. Comparison of means of the total herbage yields produced by pasture legumes grown on different Kandosol soils. Means in a column followed by the same lower case letter are not significantly different. Means in a row followed by different upper case letters are significantly different.

Legume Genotypes	Herbage yield (g/plant), on:	
	Red Kandosol	Yellow Kandosol
<i>S. scabra</i> cv. Seca	16.3 b	16.6 c
<i>S. hamata</i> cv. Verano	17.3 b	20.1 bc
<i>A. paraguariensis</i> CPI 91419	10.5 de	7.7 de
<i>A. triseminalis</i> CPI 91423	7.1 e	3.7 e
<i>C. brasilianum</i> cv. Ooloo	26.0 a	28.9 a
<i>C. pascuorum</i> CPI 55697	14.9 bc	16.7 c
<i>D. pubescens</i>	11.5 cd	9.1 d
<i>D. virgatus</i>	9.3 de	8.1 d
<i>M. bracteatum</i> CPI 55770	17.7 b	20.8 b
<i>M. martii</i> CPI 55783	8.7 deB	16.7 cA
s.e.	1.98	

There are several trends in nitrogen content of the legume herbage per unit phosphorus in the herbage produced (PUE_N) by the different legumes on the Kandosol soils. Most legume genotypes showed no difference between the soils, namely the *Stylosanthes* cultivars, *Arachis* species, *D. virgatus* and *M.*

bracteatum. Both *Centrosema* and *M. martii* species produced more nitrogen per unit phosphorus in their herbage when grown on the Yellow Kandosol. The perennial *C. brasilianum* again produced the highest PUE_N on both soils, followed by the *Stylosanthes* cultivars, *M. bracteatum*, *C. pascuorum* and *A. paraguariensis*.

Table 8. Comparison of means of phosphorus use efficiencies (PUE and PUE_N) of the legume genotypes grown on Kandosol soils (n=8, derived from 2 replicates x 4 harvests). Means in a column followed by the same lower case letter are not significantly different. Means in a row, within the same parameter, followed by different upper case letters are significantly different.

Legume Genotypes	PUE of the plants on	
	Red Kandosol	Yellow Kandosol
<i>S. scabra</i> cv. Seca	650.4 bc	719.7 c
<i>S. hamata</i> cv. Verano	689.0 ab	724.5 bc
<i>A. paraguariensis</i> CPI 91419	576.2 bcd	622.5 cd
<i>A. triseminalis</i> CPI 91423	421.9 d	427.7 e
<i>C. brasilianum</i> cv. Ooloo	837.4 a B	1034.6 a A
<i>C. pascuorum</i> CPI 55697	494.8 cd B	727.5 bc A
<i>D. pubescens</i>	574.3 bcd	461.8 de
<i>D. virgatus</i>	434.3 d	448.0 e
<i>M. bracteatum</i> CPI 55770	644.6 bc	752.8 bc
<i>M. martii</i> CPI 55783	586.1 bcd B	883.0 ab A
s.e.	80.62	
Legume Genotypes	PUE _N of the plants on	
	Red Kandosol	Yellow Kandosol
<i>S. scabra</i> cv. Seca	18.7 ab	20.2 bc
<i>S. hamata</i> cv. Verano	22.3 a	23.0 ab
<i>A. paraguariensis</i> CPI 91419	16.2 bc	17.3 c
<i>A. triseminalis</i> CPI 91423	18.8 d	10.9 de
<i>C. brasilianum</i> cv. Ooloo	22.0 a D	26.5 a C
<i>C. pascuorum</i> CPI 55697	15.0 bc D	21.2 bc C
<i>D. pubescens</i>	12.8 cd C	7.9 e D
<i>D. virgatus</i>	10.4 d	11.2 d
<i>M. bracteatum</i> CPI 55770	17.4 b C	19.2 bc
<i>M. martii</i> CPI 55783	12.5 cd D	21.6 b C
s.e.	2.07	

Hence, the legumes displayed 3 broad levels of phosphorus-use efficiencies.

- The highly efficient genotypes were *C. brasilianum*, Verano, and Seca.
- Moderately efficient genotypes were *A. paraguariensis*, *C. pascuorum* and the 2 *Macroptilium* species.
- The other genotypes are considered as having a low efficiency, namely *A. triseminalis* and the *Desmanthus* genotypes.

Soil nutrient changes

At the beginning of the early study (Amar et al., 2016), the mean soil nitrogen contents were 0.79 g/kg and 0.55 g/kg soil in the Red and Yellow Kandosols, respectively. The mean phosphorus contents of the soils after the addition of 0.43 g single superphosphate per pot were found to be 0.170 g/kg and 0.098 g/kg, in the Red and Yellow Kandosol, respectively. The legume effects on the soil nutrient contents (nitrogen and phosphorus) are compared for each of the soils in Fig. 1 and 2.

All of the legumes significantly increased the nitrogen contents of both soils after 22 months (6 months during the early study, and 16 months for this subsequent Regrowth Performance study) (Fig. 1). The highest contribution to the

soil nitrogen on the Red Kandosol was made by *S. hamata* cv. Verano, followed by *A. paraguariensis*, *C. brasilianum* and *M. martii*. On the Yellow Kandosol, *M. bracteatum* made the highest nitrogen contribution, followed by its annual counterpart, *M. martii*. These species increased the nitrogen concentration of the soil significantly more than did the *Stylosanthes* cultivars. The increase in soil nitrogen was higher on the slightly less fertile Yellow Kandosol.

The legumes also differed in the uptake of phosphorus from the soil during the 22 months of the harvest experiment (Fig. 2). The reductions in phosphorus content of the soils were significant for most of the genotypes, except for *A. triseminalis* and *Centrosema* species on the Red Kandosol, and the *Stylosanthes* cultivars on the Yellow Kandosol (Fig. 2).

The greatest reduction of soil phosphorus on the Red Kandosol resulted from *M. bracteatum*, followed by *M. martii*, *D. virgatus* and *D. pubescens*. The lowest reductions in soil phosphorus were in the pots of *A. triseminalis* and *Centrosema* species. On the Yellow Kandosol, *C. pascuorum*, *D. pubescens*, *M. bracteatum*, *A. paraguariensis* and *C. brasilianum* effected the greatest reduction in soil phosphorus concentration, with the smallest reduction produced by the *Stylosanthes* cultivars.

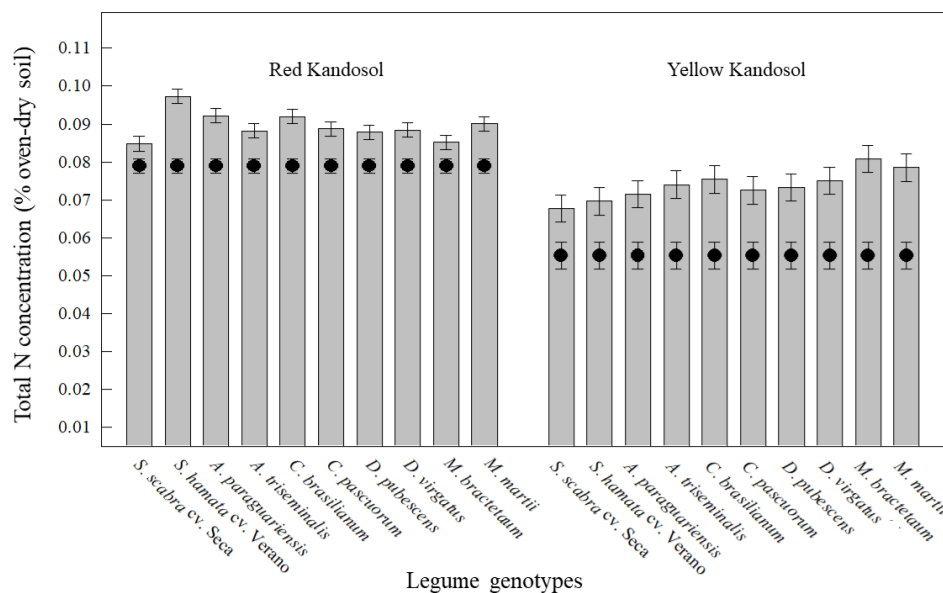


Fig. 1 Nitrogen concentration of the soil in which legume was grown, at planting day (□), and twenty-two months after planting (■). Nitrogen values are means of duplicate soil analyses derived from 4 replicates.

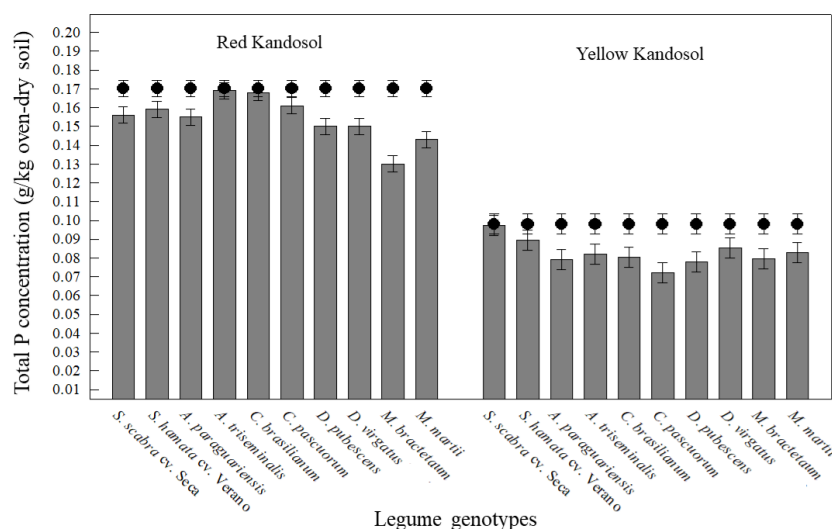


Fig. 2 Phosphorus concentration of the soil in which legume was grown, at planting day (□), and twenty-two months after planting (■). Phosphorus values are means of duplicate soil analyses derived from 4 replicates.

Phosphorus content of the legume herbage

There was a significant interaction effect among the legumes in the phosphorus concentration of their herbage in response to the Kandosol soils (Table 9). On the Red Kandosol, *C. pascuorum* produced herbage with the highest phosphorus

content; and Seca, Verano, *M. bracteatum*, and *C. brasilianum* had the lowest phosphorus concentrations. *A. triseminalis* had the highest phosphorus content on the Yellow Kandosol; while the lowest phosphorus contents were obtained from Seca, Verano, *C. brasilianum*, and the *Macroptilium* species.

Table 9. Mean phosphorus contents of the dry herbage of legumes on different soil types, analysed from 4 different harvests (19 March 1995, 23 July 1995, 24 November 1995, and 29 March 1996) of nine-week harvest intervals (n=16, derived from 4 replicates x 4 harvests). Means in a column followed by the same lower case letter are not significantly different. Means in a row followed by different upper case letters are significantly different.

Legume genotype	Phosphorus content of oven-dry herbage (%)	
	Red Kandosol	Yellow Kandosol
<i>S. scabra</i> cv. Seca	0.16 cd	0.14 c
<i>S. hamata</i> cv. Verano	0.15 cd	0.14 c
<i>A. paraguayensis</i>	0.19 bcd	0.18 bc
<i>A. triseminalis</i>	0.26 ab	0.28 a
<i>C. brasilianum</i> cv. Oolloo	0.13 d	0.11 c
<i>C. pascuorum</i>	0.31 a A	0.17 bc B
<i>D. pubescens</i>	0.19 bcd	0.23 ab
<i>D. virgatus</i>	0.24 abc	0.25 ab
<i>M. bracteatum</i>	0.16 cd	0.14 c
<i>M. martii</i>	0.22 bc A	0.13 c B
s.e.		0.04

The annual species, *C. pascuorum* and *M. martii* produced herbage that contained higher phosphorus contents when grown on the Red Kandosol than on the Yellow Kandosol (Table 9), but the other genotypes did not produce significantly different phosphorus concentrations when grown on either soil.

A. triseminalis and *D. virgatus* were the only genotypes, when grown on both soils, which met the recommended phosphorus

levels for feeding cattle (0.22% to 0.26%; NRC, 1976). *D. pubescens* grown on the Yellow Kandosol, and *M. martii* grown on the Red Kandosol also met the NRC threshold levels. Winks (1990), however, suggested that the NRC recommendation was too high, and that the phosphorus level needed in cattle feed may be as low as 0.12% to 0.16%. All the legumes examined in this study can, therefore, meet the latter minimum dietary phosphorus requirement. Nevertheless, there are many factors which may affect the fulfilment of the

dietary phosphorus requirement, particularly soil fertility. Soils with 3 to 5 ppm plant-available phosphorus are considered too deficient for pasture growth (McCosker and Winks, 1994), and as a result, animals grazed on such a pasture would be deficient in phosphorus, unless phosphorus is applied as fertiliser to the pasture or as a supplement to the animal (Coates, 1994). In the semi-arid tropics of northern Australia, for example, phosphorus applications are known to improve growth, yield and quality of legume-based pastures (Coates et al., 1990; Gilbert et al., 1989).

The edaphic factor had no effect on the number of legume plants able to survive the continuous harvesting regime, but plant genotype had a significant effect on plant survival. *C. brasilianum*, *D. virgatus*, *M. bracteatum*, and both *Stylosanthes* had the highest number of surviving plants, followed by *D. pubescens*. The other genotypes had higher mortality with less than 40% of plants surviving after 22 months. This is particularly true for *M. martii* and *C. pascuorum*, which is expected as they are short-lived plants with an annual habit (Skerman et al., 1988; Correia et al., 1994). In the earlier studies, most of these legumes, however, have ability to produce good quality seeds on the same soils (Amar et al., 2016), and produced extended deep roots on drying-out soil columns (Amar et al., 2022).

The low survivorship of *A. paraguariensis* and *A. triseminalis*, however, was unexpected since both species have a perennial growth habit (Gregory et al., 1980; Krapovickas and Gregory, 1994). On the other hand, the high survival percentage of the annual-biennial *S. hamata* cv. Verano is not surprising due to its indefinite growth pattern allowing it to behave as an annual (Burt et al., 1980; Oram 1990), as a weak biennial (Burt et al., 1980; Gutteridge, 1985), and sometimes as a short-lived perennial.

Most of the legumes did not differ in their total herbage yields on the different soils, except *M. martii*. This species produced more herbage when grown on the Yellow Kandosol. This higher yield is unexpected since the overall chemical properties of the soils used are very similar (Amar et al., 2016). On the other hand, the Red Kandosol has a higher clay content (Cannon and Coventry, 1989). Are there any other chemical attributes of these soils that promote different responses of the species? Is the soil texture controlling the response? These questions should attract attention in further studies.

Regardless of the soil type, *C. brasilianum*, and to a lesser extent *M. bracteatum*, gave a higher herbage production than the *Stylosanthes* cultivars, while the other genotypes produced less or a similar amount of herbage to these standard cultivars. *D. virgatus* produced the second lowest herbage yield, but this might be due to the plant's phenotypic growth as a small decumbent plant. This argument is supported by the genotype having one of the lowest mortalities (more than 90% surviving in the 22-month period after planting), and also producing a

high root biomass which was almost twice that of *D. pubescens*.

Apart from differences in survival percentage and herbage yields, the legumes were very similar in their production trends from one harvest to another. More specifically, all the genotype yields dropped during the cooler period suggesting that their growth is limited by low temperatures. This may reflect their tropical origin since water availability was non-limiting in this experiment. Although the *Stylosanthes* cultivars had the best root nodulation, most of the genotypes showed good root nodulation, except for *D. virgatus* and *A. triseminalis*. However, only *Centrosema*, *Macroptilium* and *Desmanthus* genotypes produced relatively large nodules, some of which showed healthy reddish or pink colours, or brown for the digitate nodules of *Desmanthus*. This suggests effective nitrogen fixation.

The genotypes showed clear differences in nutrient-use efficiency based on biomass production per unit of nutrient in the plant tissue. However, it is difficult to conclude whether the high nutrient-use efficiency species are either really "efficient" in their use of the nutrients, or lack the ability to extract less readily available nutrients from the soil; they may also be poor translocators of nutrients from roots to shoots (Caradus, 1991). In addition, the low nitrogen-use efficiency of some legume genotypes may be due to their greater ability to fix atmospheric nitrogen. Although Caradus (1991) suggested the apparent 'efficiency' of species in using nutrients may be due to their weakness in extracting nutrients from the soil store, the species with a higher nutrient-use efficiency are able to produce a reasonably higher biomass per unit of nutrient than the less "efficient" species. For example, in this study of plant growth with a depleting soil phosphorus supply, the most efficient phosphorus users (both stylo cultivars and *C. brasilianum*) showed a steady increase in herbage yields in the second half of the study period with 9-weekly harvests (Tables 4 and 10). This trend was also evident to a lesser extent for *M. bracteatum*, and the *Desmanthus* genotypes (Tables 4 and 9).

Nitrogen-use efficiency of legumes should be considered together with their root nodulation scores. A species which has a low nitrogen-use efficiency and also poor root nodulation might indicate an inferior ability to fix nitrogen, and an inability to produce a high biomass with low nitrogen uptake (Caradus, 1991). In contrast, a species with a high nitrogen-use efficiency and high herbage yield, and with good root nodulation indicating a good nitrogen contribution to the soil, is probably efficient in using nitrogen. Though not the highest in NUE, nor in nodulation, *C. brasilianum*, and *M. bracteatum* possess such nitrogen-use efficiency characteristics (Tables 6 and 9).

Nutrient-use efficiency was only used as an indicator of the ability of each genotype to use each particular nutrient considered. This may also relate to other factors such as herbage yield, ability to use other plant nutrients, and ability to

overcome detrimental environmental factors such as toxicities, drought and low light. The use of nutrient depletion studies in the soil, such as the changes in phosphorus concentration in this study, is thought to be an effective approach to help to develop better methods for determining real plant nutrient-use efficiency, and ideally should be carried out immediately following any nutrient depletion experiment.

In respect to the latter combined approach, *C. brasilianum*, Seca, and Verano were the most efficient genotypes in using phosphorus. This is indicated by their highest phosphorus-use efficiency (PUE) and high herbage yield, with a non-significant reduction in soil phosphorus concentrations, either on the Red or Yellow Kandosol over the 22 month period of plant growth, although subjected to regular harvests and soil nutrient depletion. It is particularly true for *C. brasilianum* which produced a higher herbage yield than the standard stylo cultivars. The *Macroptilium* species showed a similar phosphorus-use efficiency to the stylo cultivars, but they reduced the phosphorus content of the soil significantly (Fig. 2). *A. triseminalis* did not significantly reduce the soil phosphorus, but it was low in phosphorus-use efficiency and had a low herbage production. Therefore, these observations suggest that the latter two groups are less efficient in using phosphorus. The other genotypes, *A. paraguariensis*, *C. pascuorum*, and both *Desmanthus* genotypes, are clearly inefficient in using soil P, shown by their low phosphorus-use efficiency, a significant reduction in soil phosphorus concentration, and low herbage production throughout the 22 month growth period.

The two *Stylosanthes* cultivars have previously shown their strong adaptation to both the Red and Yellow Kandosols as is evident from their well known abilities to establish, grow and persist on infertile soils and their widespread use in a wide range of climates (Edye 1987; Partridge et al., 1996). In the present study, they performed similarly on each soil type and soil habitat. This was shown by their similar low plant mortalities, similar root biomass and high root nodulation scores, and they had similar trends of production changes throughout the experimental period.

All the legume genotypes demonstrated their tropical origin and adaptation with a higher herbage yield during warmer periods, and a decrease in production during the cooler period of the year. Most of the legumes showed promise for use in tropical soils of low fertility, particularly *C. brasilianum* and *M. bracteatum* which performed better than the *Stylosanthes* cultivars, Seca and Verano. However, *M. bracteatum* showed a higher phosphorus requirement for its production. Regardless of the soil factor, most of the other genotypes gave better phosphorus-use efficiencies, and similar or better nitrogen-use efficiencies and phosphorus concentrations in their herbage than the *Stylosanthes* cultivars.

Dry herbage produced per unit of nutrient is an indicator of plant nutrient-use efficiency, which means that efficient genotypes use a small amount of soil nutrient to produce more

herbage than do the inefficient genotypes. As a consequence of this, the efficient genotypes, however, have lower nutrient concentrations. On the other hand, higher nutrient content in the herbage provides better nutritive values for animal feed. As long as herbage produced meets the minimum of dietary requirement, plants yielding a greater amount of herbage with a high level of nutrient-use efficiency are desired. In this study, both *Stylosanthes* cultivars, *M. bracteatum* and *C. brasilianum* met the criterion. A low production genotype that shows a high nutrient-use efficiency may not be preferred for herbage production, but it might be important for soil nutrient conservation, particularly in soils low in phosphorus, where persistence in the field is required. *A. triseminalis* is a possible candidate from this experiment.

Nitrogen-use efficiency level, with respect to the amount of herbage produced per unit of nitrogen, seems not to be as important as phosphorus-use efficiency, since legumes can fix nitrogen from the atmosphere. Therefore, an important characteristic is the ability of a legume to produce a greater amount of herbage with a high nitrogen concentration, while making a high contribution to the nitrogen pool of the soil. In this respect, root nodulation plays an important role. This regrowth study indicated that most of the genotypes studied met this criterion, but Verano, *C. brasilianum* and both *Macroptilium* species are probably better than the others.

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Conflict of Interest

The author hereby declares no conflict of interest.

Consent for publication

The author declares that the work has consent for publication.

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