



[Science Archives \(ISSN:2582-6697\)](https://doi.org/10.47587/SA.2022.3303)

Journal homepage: www.sciencearchives.org



<https://doi.org/10.47587/SA.2022.3303>



Research Article


Responses of selected tropical forage legumes to imposed drought

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Received: June 30, 2022 / Revised: Aug 1, 2022/ Accepted: Aug 2, 2022

Abstract

Drought tolerance is an important attribute for the establishment of forage legumes in the rangelands of the seasonal semi-arid tropics. This experiment examined the seedling rooting depth, plant biomass, and other growth parameters of 5 perennial tropical legumes in response to different watering and drying regimes. *Centrosema brasilianum* cv. Ooloo and *Macroptilium bracteatum* (CPI 55770) produced deeper roots, greater root biomass, and more root nodules than *Stylosanthes scabra* cv. Seca and *Desmanthus virgatus* (CPI 79653), however only *D. virgatus* produced deeper roots and increased biomass in response to the drought treatment. *Arachis triseminalis* (CPI 91423), *C. brasilianum* and *M. bracteatum* flowered during the 9-week course of the experiment, with the latter two species producing pods. Seca, *A. triseminalis* and *D. virgatus* show adaptations of drought-tolerance, whilst *C. brasilianum* and *M. bracteatum* are adapted to drought avoidance.

Keywords Savanna, Pasture Legumes, Water Stress

Introduction

One of the major causes of mortality in seedlings is lack of soil moisture (Mack, 1976; Miles, 1972), and the most sensitive period is shortly after germination when seedlings switch from internal reserves to external sources of support (Harper, 1977). Several studies have suggested that morphological plasticity of the plant genotype may facilitate growth in a range of environments (Campbell and Grime 1989; Campbell et al. 1991; Slade and Hutching 1987a; Slade and Hutching 1987b). Studies have explored this plasticity with respect to maize (Sharp and Davies 1985), 15 species of British plants (Evans and Etherington 1991), and some temperate species that are either “seed-regenerators” (growing from seed) or “dual-regenerators” (growing from both seed and vegetatively) (Reader et al., 1992). The latter found that some plant species produce deeper rooting systems in a drying soil compared to plants under a controlled watering regime. No studies, however, have examined this aspect in tropical pasture legumes.

Plasticity in rooting depth and the ability to grow over a gradient of resources are important characteristics for plant establishment and persistence, particularly for colonizing species. This is particularly so where variable moisture availability can limit seedling establishment, such as in the seasonal semi-arid tropics. For instance, deep root systems in *Centrosema brasilianum* (Cook, et al., 2020) and the suitability of *Desmanthus virgatus* cv. Marc for use in mixes with digit grass during drought conditions (Boschma, et al., 2021). In addition, Mwangi, et al. (2022) have suggested that desmanthus alone or in combination with other high-quality legume forages can be used to supplement grass-based diets of beef cattle. In general, Schultze-Kraft, et al. (2018) maintained that legumes have the potential to contribute significantly to sustainable intensification of livestock production in the tropics.

This paper describes the results of an experiment designed to compare seedling rooting depth, plant biomass, and other growth parameters of 5 perennial tropical pasture legumes in response to various watering and drying regimes. This information should be

a useful indicator of plant plasticity to sustain growth as the soil dries from the surface downwards after rain or during extended dry periods.

Materials and Methods

Plant genotypes and soils used

Five legume genotypes were perennials, which eliminates any possible confounding effects due to differences in annual or perennial habits. All the chosen genotypes were selected using information on plant survival results from an earlier study (Amar and Gardiner 1999) and some other publications are considered. The selected legumes for this study were.

- i. *Stylosanthes scabra* cv. Seca: selected for comparison due to its strong tolerance of dry conditions and its deep rooting characteristics (Cameron, 1988; Mpanza et al., 2020).
- ii. *Centrosema brasilianum* cv Ooloo: with the exception of Seca, this genotype had the highest number of surviving plants in an earlier study, and its adaptation to drought **is attributed to its deep rooting system** (Cook et al., 2020).
- iii. *Desmanthus virgatus* CPI 79653: which had a higher seedling survivorship percentage than another *Desmanthus* genotype (*D. pubescens*) in a previous drought field study; and *D. virgatus* CPI 79653 and *M. bracteatum* produced the highest percentages of readily germinable seeds from plants grown on low fertility soils (Amar et al., 2016).
- iv. *Macroptilium bracteatum* CPI 55770: a perennial species, to represent the genus *Macroptilium*; found to be the most outstanding perennial species for use in ley pastures in central Queensland – two very similar accessions have been released as cultivars cv Cadarga (CPI 55769) and cv Juanita (CPI 68892) (Pengelly, et al., 1998); and presents endogenous root buds from one-year-old roots with secondary growth (Martin Montiel et al., 2012).
- v. *Arachis triseminalis* CPI 91423: a survivor in north Queensland's rangelands (Amar and Gardiner, 1999). *A. triseminalis* had a higher percentage survival than the other *Arachis* species, *A. paraquariensis*.

For this experiment, the soil needed to be very freely draining with a low water holding capacity. Therefore, the soil used was a commercial 'topsoil' of sandy clay loam texture. This soil texture was selected to avoid a very quick loss of water from a soil of lighter texture and possible water logging in heavier textured soil.

Experimental design

This study was carried out in a glasshouse, with daily maximum and minimum temperatures during the nine-week study period (February to April) ranging from 30.5°C to 37.0°C, and from 22.0°C to 25.0°C, respectively. The experimental treatments involved 2 factors, the 5 legume genotypes, and the drought treatment, which consisted of three different watering regimes:

- 1) 'a **non-drought**' treatment is watered daily throughout the 9-week study period;

- 2) 'a **5-week drought**' treatment is watered daily for the first four weeks to fully establish seedlings with no subsequent watering; and
- 3) 'a **7-week drought**' treatment is watered daily for the first two weeks to establish seedlings, and no subsequent watering.

The study consisted of 60 soil columns (5 legumes x 3 watering regimes x four replicates). Four replicates of three soil columns without any plants were included in each watering regime and were considered as 'controls' to determine water loss due to evaporation, so water reduction by plants through uptake and transpiration could be estimated. The columns made up 72 experimental units which were placed in a randomised block design (Steel, et al., 1981). The data obtained 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, $P < 0.05$).

Experimental procedure

The soil was passed through a 2 mm sieve to reduce variability in the growing medium, and to facilitate plant root extractions by washing the soil through the same sieve at the end of the experiment. Instead of using conventional pots, soil columns of 105 cm length x 14.5 cm diameter were made from polyethyl plumber's fluming with holes at the bottom to facilitate water drainage. The long soil columns allowed a deep moist soil profile to develop in the early part of the experiment, and provided a good soil profile water store for roots to exploit after watering ceased. Each of the columns was filled with approximately 25 litres of air-dry soil. The columns were then saturated with water to determine the extent of post-watering compaction and to obtain soil profiles of 100 cm depth for the experiment. The soil depth in each of the columns was measured. There were no differences in soil depth among the columns for the different watering treatments nor for the different species ($P > 0.05$).

The soil columns were watered for 2 weeks before the experiment started to determine the appropriate amounts of water to be added daily to re-wet the soils with minimal excess water draining from the growing medium. Profile saturation was recognized by the appearance of water draining from the bottom of each soil column during the day of irrigation. It was decided to water with 100 mL/column/day during the early seedling growth period, followed by an increased amount of water as the plants grew and transpiration increased. The amount of water added was gradually increased by 50 mL/column when necessary. The need for an increment was recognized when there was no sign of excess water at the bottom of a soil column by the following day. Single superphosphate was applied on the soil surface as a basal phosphorus dressing equivalent to 20 kg P/ha.

Seeds of the genotypes were treated with hot water for seed scarification and then germinated in petri-dishes lined with three layers of filter paper moistened with distilled water. The germinated seeds were transferred to the soil columns (3 plants/column) when the radicles had grown to 3-5 mm long, defining the starting time of the experiment. From this day, the 3

different watering treatments were applied. Two weeks after planting, the seedlings were thinned to one plant per soil column by cutting the least and the most vigorous seedlings at the soil surface.

At the end of the 9-week study period, the plant tops were harvested by cutting at the soil surface and the shoot yield was determined after drying in a forced-draught oven at 70°C. No water was added on the harvesting day and soil samples were collected to determine soil moisture contents. Soil samples were collected by inserting a small, sharpened polyvinyl chloride pipe (1.5 cm diameter), horizontally through the polythene fluming and 4 cm into the soil columns at 10, 30, 50, 70, and 90 cm depths. Each soil sample was put directly into a labelled glass bottle and moisture content was determined after drying in a forced-draught oven at 105°C. The mean total moisture of each soil column was calculated from the 5 values.

Each soil column was then cut into 20 cm sections. Rooting depths were determined by the method of Reader et al. (1992), using the following modified formula:

$$RD = (20N) + RP_{max}$$

where,

RD = rooting depth

N = number of 20 cm sections cut from the soil columns with roots reaching to the bottom of each section, and

RP_{max} = the length of the root in the last section with the furthest maximum root penetration.

The roots were gently washed from each section of the soil and collected on a 2 mm sieve. Due to their long roots (>100 cm), most of the plants had coiled roots in the bottom of the columns, which were untangled by shaking in a bucket of water, and their lengths measured.

The extent of root nodulation was scored in each 20 cm section, and ranked based on the number of nodules as follows:

0 = nil (no nodules evident)

1 = 1-10 nodules

2 = 11-20 nodules

3 = 21-30 nodules

4 = 31-40 nodules

5 = more than 40 nodules

A root nodulation score was obtained for each plant by summing the scores for roots collected from each of the five soil sections. Roots from each section of the soil column were dried (70°C in a forced-draught oven) and weighed separately. The “total root biomass/plant” was obtained by summing the individual root biomasses from each section of each soil column. The masses of

the dried shoots and roots were added to determine “the total plant biomass”.

Results and Discussion

Results

Except for the shoot: root ratio, all of the legume responses were significantly influenced by either the genetic factor or drought treatment, or an interaction among these factors. The shoot:root ratios of the legumes were 2.9, 2.8, 3.4, 2.5, and 2.6 for *S. scabra* cv. Seca, *A. triseminalis*, *C. brasilianum*, *Desmanthus virgatus* and *M. bracteatum*, respectively. The moisture contents were significantly influenced by the watering treatments, legume genotypes, and sampling depths (Table 1). The root biomass within genotypes differed among the 20 cm sections down to the bottom of the column, generally with the highest root biomasses in the top soil section.

The effects of plant genotype

Plant genotype affected all the plant parameters observed except the shoot:root ratio. Where there were no genotype x drought interactions, *S. scabra* cv. Seca produced the shortest roots but did not differ significantly from *D. virgatus* and *A. triseminalis* (Table 2). *C. brasilianum* and *M. bracteatum* produced longer roots than the first two genotypes, but they were not significantly different to *A. triseminalis*. Similarly, the deepest rooting genotypes, *C. brasilianum* and *M. bracteatum*, nodulated better than the other three legumes (Table 2).

The effects of drought treatment

The drought treatments also affected most of the plant parameters observed, except the plant shoot: root ratio. Where there were no interaction effects, plants grown under the imposed drought treatments developed longer roots than those with no drought imposed (Table 3), which indicates that the legumes have to root depth plasticity in response to drought conditions. On the other hand, the control plants showed better root nodulation than those with drought treatments. Generally, the largest numbers of root nodules appeared in the first 20 cm section of the soil columns (at the top of the 10 cm soil profiles).

The effects of interaction between legume genotype and drought treatment

The mean shoot, root, and total plant biomasses were significantly influenced by the legume genotype, drought treatment, and genotype x drought interactions (Table 4).

Table 1. Imposed Drought Experiment: mean moisture content of the soil, and plant root biomass for the different legumes, drought treatments and sampling depths after 9 weeks of growth (n=4).

Legume genotype	Depth (cm)	A. Soil moisture (%) in each drought treatment				B. Root biomass (g) in each drought treatment			
		0 week	5 week	7 week	s.e.	0 week	5 week	7 week	s.e.
Control (No plant)	10	21.0 bA	16.1 cB	16.7 bB	1.28	-	-	-	-
	30	22.1 bA	18.5 bcB	18.0 bB					
	50	21.5 bA	19.3 bAB	18.2 bB					
	70	23.4 abA	19.5 bB	20.0 abB					
	90	25.3 a	23.5 a	22.8 a					
<i>S. scabra</i>	10	19.2 bA	10.0 cB	10.3 bB	1.83	0.40 a	0.44 a	0.35 a	0.06
	30	19.4 abA	14.0 bB	12.4 bB		0.20 b	0.21 b	0.19 b	
	50	19.6 abA	16.6 aAB	13.3 abB		0.20 b	0.19 b	0.19 b	
	70	20.2 abA	17.1 aAB	13.9 abB		0.16 b	0.21 b	0.20 b	
	90	23.0 aA	19.2 aB	15.1 aC		0.12 bE	0.24 bDE	0.25 abD	
<i>A. triseminalis</i>	10	21.2 aA	9.1 aB	7.6 bB	1.87	0.54 a	0.61 a	0.54 a	0.10
	30	19.3 aA	10.9 aB	13.1 aB		0.23 b	0.32 b	0.28 b	
	50	19.5 aA	11.5 aB	11.1 abB		0.22 b	0.28 b	0.24 b	
	70	20.0 aA	11.7 aB	11.9 aB		0.22 b	0.27 b	0.21 b	
	90	23.0 aA	12.1 aB	12.6 aB		0.32 b	0.48 ab	0.39 ab	
<i>C. brasilianum</i>	10	11.6 aA	5.0 aB	5.1 aB	1.43	2.32 aD	0.99 aE	1.03 aE	0.13
	30	9.5 abA	6.1 aB	5.3 aB		0.83 c	0.62 b	0.62 b	
	50	7.2 bA	5.6 aA	5.2 aB		0.58 cd	0.61 b	0.55 b	
	70	6.9 bA	6.0 aA	5.1 aB		0.56 d	0.53 b	0.56 b	
	90	8.5 bA	5.9 aAB	5.1 aB		1.05 b	0.58 b	0.97 a	
<i>D. virgatus</i>	10	19.0 aA	13.2 bB	9.1 aC	1.99	0.31 aF	0.52 aE	0.93 aD	0.07
	30	16.2 bA	15.9 abA	9.5 aB		0.12 bE	0.41 bD	0.41 bD	
	50	18.6 aA	14.6 bB	11.0 aC		0.14 bE	0.25 bE	0.31 bD	
	70	19.1 aA	13.9 bB	11.6 aB		0.11 bE	bE	0.31 bD	
	90	21.7 aA	19.3 aA	12.4 aB		0.13 bE	0.19 bDE	0.38 bD	
<i>M. bracteatum</i>	10	8.5 aA	5.3 aB	4.6 bB	0.45	4.51 aD	2.29 aE	1.75 aF	0.17
	30	6.3 bA	5.4 aAB	5.3 abB		1.37 bD	0.55 bE	0.55 bE	
	50	6.5 bA	5.5 aB	5.2 abB		0.88 cD	0.88 bDE	0.43 bE	
	70	6.1 bA	5.4 aAB	5.1 abB		0.63 c	bDE	0.36 b	
	90	6.5 b	5.6 a	5.8 a		0.73 c	0.60 bcDE	0.46 b	
						0.45 c	0.51 c		

Means in a column followed by the same lower case letter do not differ significantly (P<0.05). Means followed by different upper case letters in a row, within soil moisture and root biomass, are significantly different.

Table 2. Rooting depth and root nodulation of five tropical pasture legumes in response to imposed drought (n=12, derived from 4 replicates x 3 drought treatments)

Legume genotypes	Root length (cm)	Nodulation score
<i>S. scabra</i> cv. Seca	99.8 b	3.4 b
<i>A. triseminalis</i> CPI 911423	106.5 ab	2.3 b
<i>C. brasilianum</i> CPI 55698	114.5 a	10.1 a
<i>D. virgatus</i> CPI 79653	105.2 b	1.8 b
<i>M. bracteatum</i> CPI 55770	114.4 a	9.6 a
s.e.	4.23	0.95

Means in a column followed by the same lower case letter are not significantly different.

The effects of drought treatment

The drought treatments also affected most of the plant parameters observed, except the plant shoot: root ratio. Where there were no interaction effects, plants grown under the imposed drought treatments developed longer roots than those with no drought imposed (Table 3), which indicates that the legumes have root depth plasticity in response to drought conditions. On the other

hand, the control plants showed better root nodulation than those with drought treatments. Generally, the largest numbers of root nodules appeared in the first 20 cm section of the soil columns (at the top of the 10 cm soil profiles).

The effects of interaction between legume genotype and drought treatment

The mean shoot, root, and total plant biomasses were significantly influenced by the legume genotype, drought treatment, and genotype x drought interactions (Table 4).

Table 3. Effect of the drought treatments on root biomass and root nodulation of five tropical pasture legumes (n=20, derived from 4 replicates x 5 genotypes).

Drought treatments	Root length (cm)	Nodulation score
Control (0 drought)	100.5 b	7.3 a
5-week drought	110.2 a	4.7 b
7-week drought	113.6 a	4.4 b
s.e.	3.27	0.74

Means in a column followed by the same lower case letter are not significantly different.

Table 4. Comparison of shoot, root and total plant biomass produced five tropical pasture legumes after different drought periods

Legume Genotypes	Shoot biomass (g/plant)			Root biomass (g/plant)			Total plant biomass (g/plant)		
	0 drought	5-week	7-week	0 drought	5-week	7-week	0 drought	5-week	7-week
<i>S. scabra</i> cv. Seca	4.49 c	2.92 b	2.62 d	1.08 c	1.28 c	1.17 c	5.57 c	4.20 b	3.79 d
<i>A. triseminalis</i>	3.70 c	5.49 b	5.28 cd	1.53 c	2.00 c	1.17 c	5.23 c	7.49 b	6.45 cd
<i>C. brasilianum</i>	19.73 bA	12.15 aB	11.28 aB	5.33 bD	3.61 bE	3.77 aE	25.06 bG	15.76 aH	15.04 aH
<i>D. virgatus</i>	1.70 cB	3.54 bB	6.66 bcA	0.81 cE	1.32 cE	2.35 bD	2.51 cH	4.86 bH	9.01 bcG
<i>M. bracteatum</i>	24.45 aA	10.06 aB	9.37 abB	8.11 aD	4.72 aE	3.54 aF	32.56 aG	14.78 aH	12.91 abH
s.e.		1.37			0.44			1.62	

0 drought, 5-week, and 7-week are the drought treatments, i.e. no-drought, 5 weeks, and 7-week periods of drought, respectively.

Means in a column followed by the same lower case letter are not significantly different. Means in a row, within the same plant attribute, followed by different upper case letters are significantly different.

Three responses were shown by the legumes. Seca and *A. triseminalis* responded similarly, in that they did not show a significant change in the shoot, root, and total biomass produced due to the treatments. Secondly, *D. virgatus* produced significantly more shoot, root, and total biomass in the longest drought treatment than in the non-drought and 5-week drought treatments, with the latter two treatments showing no significant differences (Table 4). In contrast to *Desmanthus*, the shoot and root biomass of *C. brasilianum* and *M. bracteatum* decreased with increased drought period (Table 4). Plants in the 5-week and 7-week drought treatments produced significantly less biomass

than those in the non-drought treatment, and the root biomass of *M. bracteatum* in the 7-week drought treatment was also significantly lower than for the 5-week drought. Figure 1 shows the total plant biomass produced by the different genotypes related to the soil moisture contents at the end of the study period. The soils of the high production genotypes, *C. brasilianum* and *M. bracteatum*, had a lower moisture content than those of the other genotypes. After the study, *C. brasilianum* and *M. bracteatum* had total biomass yields ranging from 13 to 33 g per plant with soil moisture contents of 5 to 9%. The other genotypes produced total biomasses in the range of 2.5 to 9.0 g per plant

with soil moisture contents of 11 to 21% at the end of 9 weeks of plant growth (Fig. 1).

Most soil moisture contents tended to be higher with the shorter periods of drought treatment, and from the top layer down to the bottom of the soil columns (see, for example, ‘control’ row of Table 1). The most vigorously growing genotypes, *M. bracteatum* and *C. brasilianum* had the greatest root biomass and used (i.e. depleted) the soil moisture (Table 1). The moisture contents of the soils in which either *C. brasilianum* or *M. bracteatum* were grown tended to vary little and were low from the top to the bottom of the column profile, except at the top of the columns with nine weeks of watering (the ‘0-week drought’ treatment; Table 1).

Seca, which is known to be well adapted to dry conditions (Cameron, 1988), showed a low productivity and low use of the soil water store. Similar patterns were shown by *A. triseminalis* and *D. virgatus* in this study (Table 4 and Fig. 1). This suggests that these species might be adapted to dry conditions with low growth rates, and make minimal use of the soil moisture, even when moisture availability is not limiting.

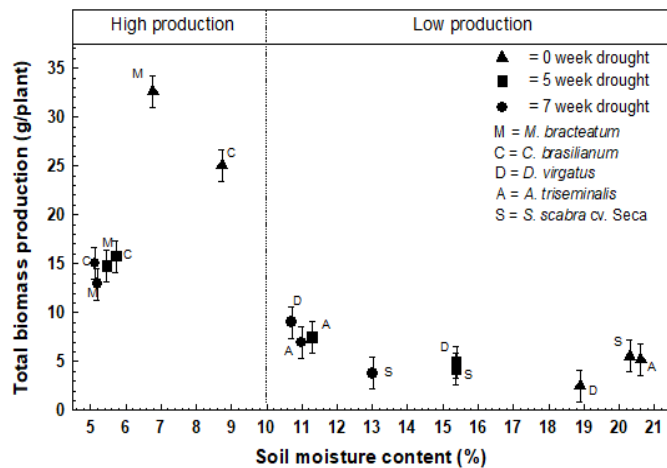


Fig. 1 Soil moisture content (mean % per soil column) and total plant biomass production at the end of the 9-week experimental period for legumes grown for different drought periods (n = 4). Error bars are s.e.

D. virgatus, however, produced significantly higher shoot, root, and total biomass during the extended drought period than under continuous watering (the ‘0 week drought’ treatment; Table 4). Growth of this genotype appeared to be inhibited by frequent water additions. This suggests that the low soil moisture, or the most severe drought treatment imposed, was the best growing condition for *D. virgatus* during the early establishment period, even though the soils in the experimental pots were never waterlogged.

Reproductive attributes

The availability of data on plant reproductive characteristics (time to flowering, time to produce first emerged pod, and pod ripening) varied greatly among the genotypes under the different drought treatments, and restricted statistical analysis (Table 5). Seca did not flower during the 9-week experimental period, and *D. virgatus* flowered over the same time period in only the non-drought and 7-week drought treatments. These 2 genotypes, therefore, were not included in the statistical analysis.

A. triseminalis was the earliest to flower but did not produce seed (Table 6). *M. bracteatum* also flowered and produced its first pods earlier than *C. brasilianum*, but *M. bracteatum* in the longest drought treatment was the only genotype (in 3 out of 4 replicates) that produced ripe pods in the last few days of the study period (Table 5). These 3 genotypes were all found to flower earlier in the longest drought treatment than when they were grown in the other drought treatments (Table 7). Similarly, the first pods emerged earlier in the 7-week drought treatment than under the other treatments for the group of 2 genotypes (*C. brasilianum*, and *M. bracteatum*: Table 7).

Discussion

Although *S. scabra* cv. Seca is known to have a deep rooting system that serves for drought adaptation (Cameron 1988), this study showed that the stylo genotype and *D. virgatus* produced significantly shorter roots than *C. brasilianum* and *M. bracteatum*. Nevertheless, all 5 genotypes had deep, branching root systems which might relate to their perennial growth habit and serve as drought tolerance mechanisms for improved plant survival (Jones et al., 1981). A deep, wide-spreading, and much-branched root system is one of the most effective safeguards for a plant in drought conditions (Jones et al., 1981; Kramer, 1983; Qian et al., 1997). For example, Cook et al. (2020) maintained that drought tolerance of *C. brasilianum* is facilitated by its deep rooting system.

This study suggests that the 5 legumes are adapted to dry conditions, partly as a result of their deep root system, and partly through their rooting plasticity in being able to produce deeper root systems under drier conditions. This agrees with the findings of Reader et al. (1992), who found that some plants extend their rooting depth in response to dry conditions. They found that genotypes with the greatest rooting plasticity also had the greatest ability to promote shoot growth under dry conditions. In the present study, rooting plasticity is indicated by a significant increase in rooting depth as a response to drier conditions. *D. virgatus* was the only genotype that gave an increase in shoot production with the increased drought period. The *D. virgatus* growth might be in response to a reduction of excess water in the soil profile, or perhaps to better soil aeration.

Table 5. The time to flowering, first pod emergence, and pod ripening of 5 tropical pasture legumes under drought treatments were presented as the range of days after planting during the 63-day experiment (n=4).

Legume genotype	Drought Treatment	Days after planting germinated seeds		
		1st flower	1st pod	Pod ripe
<i>S. scabra</i> cv. Seca	0 week	-	-	-
	5 weeks	-	-	-
	7 weeks	-	-	-
<i>A. triseminalis</i>	0 week	33-35 (4)	-	-
	5 weeks	28-36 (4)	-	-
	7 weeks	27-33 (4)	-	-
<i>C. brasilianum</i>	0 week	57-58 (2)	60-62 (2)	-
	5 weeks	57-58 (2)	60-62 (2)	-
	7 weeks	54-55 (3)	56-57 (3)	-
<i>D. virgatus</i>	0 week	54-57 (2)	57-60 (2)	-
	5 weeks	-	-	-
	7 weeks	54-57(3)	57-60 (2)	-
<i>M. bracteatum</i>	0 week	54-57 (4)	56-59 (4)	-
	5 weeks	54-56 (4)	56-57 (4)	-
	7 weeks	46-53 (4)	58-55 (4)	60-62 (3)

‘-’ indicates no flowers, pods, or ripe pods produced in the 9 weeks. Values in brackets indicate the number of replicates which possessed the recorded characteristic. *A. triseminalis* produces underground seeds, which could not be recorded before the roots were collected by washing when it was found that none of these plants produced pods

Table 6. Pairwise comparisons of mean time to flowering between 3 genotypes (*A. triseminalis*, *C. brasilianum*, and *M. bracteatum*), and first pod emergence between 2 genotypes (*C. brasilianum* and *M. bracteatum*) of legumes across different drought periods.

Legume genotype	Time (days after planting germinated seeds)	
	To flowering	To pod emergence
<i>A. triseminalis</i>	32.3 c	-
<i>C. brasilianum</i>	56.4 a	59.6 a
<i>M. bracteatum</i>	53.4 b	55.5 b
s.e.	0.88	0.73

Means in a column followed by the same lower case letter do not differ significantly. ‘-’ = did not produce pod, and excluded from the analysis.

Table 7. Pairwise comparisons of mean time to flowering within 3 genotypes (*A. triseminalis*, *C. brasilianum*, and *M. bracteatum*), and first pod emergence within genotypes (*C. brasilianum* and *M. bracteatum*) of legumes under the different drought treatments.

Drought treatments	Time (days after planting germinated seeds)	
	To flowering	To pod emergence
0 drought	49.2 a	59.7 a
5 week drought	48.6 a	59.0 a
7 week drought	44.3 b	54.0 b
s.e.	0.88	0.73

Means in a column followed by the same lower case letter do not differ significantly.

C. brasilianum and *M. bracteatum* produced a significantly higher root nodule score than the other 3 genotypes under the drought treatments, which appears to be related to their better overall growth performance throughout the experiment. Root nodulation was inversely related to rooting depth, with the legumes showing better root nodulation on the control plants subjected to no drought than those under the drought treatments (Table 3). This suggests that these legumes are better able to fix nitrogen where higher soil moisture prevails. This agrees with the results of Budelman (1989) who found that, in the tropics, nitrogen fixation increased with lower temperatures and higher moisture in the top of the soil profile.

Fast-growing and deep rooting plants with high rates of transpiration impose a strong demand on soil water and can dry out the soil to a considerable extent (Christinck et al., 1997), such as was found here for *C. brasilianum* and *M. bracteatum*. This is similar to the results of Sharp and Davies (1985) who found, for maize, that depletion of the soil water store corresponded with increased root densities. However, the results from the present study disagree with the theory that plants increase their root biomass in drier conditions (Fitter and Hay, 1981). The legumes of the present study, except for *Desmanthus*, produced greater root biomass under wetter conditions. It is possible, however, that the drought treatments in this study may not have been severe enough to fully explore the rooting plasticity of the legumes. The legumes clearly have different growth patterns in their early development, which was reflected in their biomass production and root length, and these have impacted the moisture levels of the soils in which they were grown (Table 2 and Fig. 1). The imposed drought treatments also affected the soil moisture levels and plant biomass, with higher soil moisture contents and plant biomass production resulting from the extended watering treatment (0 weeks of imposed drought), but the time to flowering was longer. This indicates a drought escape or drought avoidance mechanism in that the plants tend to complete their life cycle before a serious water deficit develops and injures the plants (Jones et al., 1981; Kramer, 1983). This is particularly true in the case of *M. bracteatum*, the only genotype to produce ripe pods by the end of the experiment.

The plant genotypes showed 3 different trends in biomass production in response to the imposed drought treatments (Table 4, Fig. 1).

- 1) *Seca* and *A. triseminalis* tended to have similar, low biomasses in response to all the drought treatments. This suggests that *Seca* is adapted to dry conditions not only because the plant is a dehydration tolerator (Fisher and Ludlow, 1984), and has deep rooting systems (Cameron 1988), but also because its low growth rates make a low demand on the available soil water. For similar reasons, *A. triseminalis* would appear to be well adapted to drought conditions (Amar and Gardiner 1999).
- 2) *C. brasilianum* and *M. bracteatum* produced much higher biomasses (1.5-2 times) under the fully watered, non-

drought condition than in any of the imposed drought treatments.

- 3) *D. virgatus* produced more biomass as the drought period was extended. This may indicate that the growth of this legume is inhibited by high soil moisture.

The high biomass producers, *C. brasilianum* and *M. bracteatum*, produced the deepest root systems followed by the *Arachis* species, but the latter response was not significantly different from that of the *Desmanthus* and *Stylosanthes* genotypes (Table 2). Regardless of plant genotype, the legumes show rooting depth plasticity by extending their roots more deeply under the drier conditions (Table 4). However, it should be noted that even though the columns were 1m deep, coiling at the base of the column might have altered the nature of the root growth which may have impacted their rooting plasticity. Hence, further studies of rooting plasticity should be carried out using a shorter experimental period, or deeper soil columns.

Differences were also found between the legumes in the time taken to produce the first flowers and pods (Tables 5 and 6), and there were some indications that the imposed drought treatments affected these parameters (Table 7). *M. bracteatum* was the only species which produced ripe pods during the study, and only under the longest drought treatment, suggesting a drought avoidance mechanism. This is not to say that the other genotypes failed in this regard since *C. brasilianum* and *D. virgatus* also produced pods over the short experimental period. *C. brasilianum* and the *Seca* have previously been found to have a high tolerance to water deficit conditions (Fisher and Ludlow 1984; Ludlow et al., 1983), to be dehydration tolerators and insensitive to desiccation (Fisher and Ludlow 1984; Ludlow 1980; Ludlow et al., 1983; Wilson et al., 1989).

Though perennial species may persist for longer growth periods than annuals, seed production still plays an important role in regeneration of the plant. This is particularly important in difficult environments where, for example during an extended drought period, a plant may not survive. In this case, the ability of a species to produce seed is very important for regeneration when favorable conditions re-occur. This is known as a 'drought escape' strategy and is a strategy that allows the plant to complete its life cycle before being severely affected by a serious water deficit. Such strategies are normally possessed by annual species (Fisher and Ludlow 1984; Fitter and Hay 1981).

However, more studies are required to examine the effect of drought on further growth, the persistence of the accessions, and their offspring. Chen, et al. (2022) have suggested that drought-selection caused a significant difference (relative to ambient-selection) in biodiversity effects on productivity only after a subsequent drought event in the glasshouse. They maintained further that, exposure to extreme climatic events during previous generations could improve the responses of offspring generations to future events in mixed species grassland communities.

Conclusions

Some general conclusions can be drawn from this experiment:

- 1) All the accessions showed different responses to drought treatments and in the way that they depleted the soil water stores. These responses were highly correlated with biomass production.
- 2) Drying conditions altered the growth patterns of the genotypes differently, decreasing plant biomass in *C. brasilianum* and *M. bracteatum*, and increasing biomass in *D. virgatus*.
- 3) The legumes showed a trend of rooting depth plasticity by extending their root length in the drought treatments.
- 4) Greater water use was shown by the high biomass producers, namely *C. brasilianum* and *M. bracteatum*, which also had greater root biomasses and deeper roots than *Seca* and *Desmanthus*.
- 5) *M. bracteatum* was able to produce ripe pods, hence mature seeds, in the driest treatment. It can therefore be concluded that *M. bracteatum* has a double strategy to persist, namely a perennial habit and the ability to produce seeds quickly as drought becomes established

Acknowledgments

The authors are grateful to the Australian Agency for International Development (*AusAID*) for financial assistance. We wish to express our appreciation to Dr. Robert L. Burt for his advice at the initiation of this study.

Conflict of Interest

The author hereby declares no conflict of interest.

Consent for publication

The author declares that the work has consent for publication

Funding support

The author declares that they have no funding support for this study

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How to cite this article

Andi L. Amar, A. L., Robert, A., Congdon, R. A., Coventry, R. J. and Gardiner, C. P. (2022). Responses of selected tropical forage legumes to imposed drought. *Science Archives*, Vol. 3 (3), 158-167. <https://doi.org/10.47587/SA.2022.3303>

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