EFFECTS OF FLOODING ON SEVEN SPECIES OF TROPICAL PASTURE LEGUMES

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ABSTRACT

Seven tropical pasture legume species were grown in pots inside the glasshouse. At the start of flowering stage, plants were continuously flooded to 5 cm above the soil surface for 10 and 21 days. Dry weights of shoots, roots and nodules of the flooded plants were compared to the corresponding unflooded plants after a recovery period of 7 days. *Macroptilium lathyroides* exhibited superior tolerance to flooding while *Cassia rotundifolia* and *Vigna parkeri* showed very poor tolerance.

Root growth was more affected by flooding than shoot growth. Nodulation was reduced in all species except in *M. lathyroides*. The adaptation of *M. lathyroides, Desmodium heterophyllum, Lotononis bainesii* and *Trifolium semipilosum* to flooding was related to the rapid production of adventitious roots from the immersed stems and branches and to the rapid nodulation of these adventitious roots and the original roots.

High stomatal conductance was maintained in flood-tolerant species with increased duration of flooding while high leaf diffusive resistance was common in species intolerant to flooding.

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KEY WORDS: Pasture legumes. Flooding tolerance. Plant survival. Adventitious roots. Nodulation.

INTRODUCTION

Flooding is a regular occurrence in many humid tropical areas. Due to the highly seasonal distribution of rainfall in these areas, temporary or sometimes prolonged waterlogging often occurs particularly in the lowlands. This, combined with soil of poor internal drainage, may be a major limitation to the growth of plants.

Most agricultural crops require well-drained soil for maximum growth and the gaseous composition of the soil must be similar to that of the atmosphere (Currie, 1962). When the soil is subjected to flooding which creates anaerobic conditions, adverse effects on plant growth are likely to occur. This encourages reductive processes in the soil and consequently alters soil chemistry. Some plants can survive under these conditions, adjusting physiologically to this new environment and maintaining growth. However, most plants cannot survive under flooding and they eventually die.

Assessment of comparative tolerance is valuable for the agronomic selection of species for flooded situations. Francis and Poole (1973) found a wide range of tolerance to flooding in annual *Medicago* species, while the perennial *Medicago sativa* is intolerant to flooding (McKenzie, 1951). McIvor (1976) compared the flooding tolerance of 33 accessions of *Stylosanthes guianensis* and noted that waterlogged plants of the most tolerant accession produced 82% of the control yield while the least tolerant produced only 5%. In this study, the flooding tolerance of some tropical pasture legume species was compared.

MATERIALS AND METHODS

Two experiments were conducted, the first was between April and September, 1981 and the second, between January and June, 1983. In the first experiment, a comparison of flooding tolerance of *Macroptilium lathyroides, Desmodium heterophyllum, Lotononis bainesii* and *Trifolium semi-pilosum* was made while *M. lathyroides* (the standard species), *Calopogonium mucunoides, Cassia rotundifolia* and *Vigna parkeri* species were similarly compared in the second experiment.

Each experiment was laid out in split-split plot arranged in randomized complete block design (RCBD) with 4 replications. Four species, 3 flooding durations (0, 10 and 21 days) and 2 flooding treatments (flooded and unflooded) were assigned as the mainplots, subplots and sub-subplots, respectively.

Plants were grown in 25 cm diameter pots with loamy soil. Scarified seeds were planted and later thinned to 3 plants per pot 7 days after emergence. The plants were inoculated at seedling stage with appropriate ***Rhizobium*** strains (cowpea type). Calcium carbonate ($CaCO_3$) at the rate of 500 kg/ha; superphosphate, 200 kg/ha; and potassium sulphate (K_2SO_4), 50 kg/ha were basally applied. A week after planting, hydrous forms of copper sulphate ($CuSO_4.5H_20$) at 7.0 kg/ha; zinc sulphate ($ZnSO_4.7H_20$) at 7.0 kg/ha; and sodium molybdate ($Na_2Mo0_4.2H_20$) at 0.5 kg/ha were applied.

Flooding treatments were imposed at the onset of the flowering stage of each species so that comparison could be made at the same physiological stage. The potted plants were placed in 20-liter drums filled with water. A water depth of 5 cm above the soil surface was maintained throughout the experimental period. Control (unflooded) pots were watered to field capacity.

Before flooding, the 24 pots planted to each species were divided into groups according to plant height and allocated to the treatments to have uniform plant size in each treatment. The plants in the 4 pots subjected to 0 flooding duration were harvested on the day when flooding was begun in the other 2 durations. To further evaluate the tolerance of a species to flooding, plants in another 4 pots each for flooding treatments of 10 and 21 days were allowed to recover for one week before harvesting. At each harvest, plants in 4 unflooded pots for each flooding duration were simultaneously harvested for comparison.

Using the leaf porometer, the leaf diffusive resistance (s cm^{-1}) was determined twice a week for 3 weeks on the young fully expanded leaves (abaxial surface) between 11:00 a.m. and 12:00 noon. The oven-dry weights (at 65°C for 96 hours) of shoots, roots and nodules were likewise taken at harvest.

RESULTS AND DISCUSSION

Visual Observations

Chlorosis of the older leaves, and wilting and rolling of the younger ones after brief flooding were the early flooding effects observed. All of these were evident in all species except in *M. lathyroides.* Leaf chlorosis caused by flooding resembled that of nitrogen deficiency as described by Kramer (1951).

The wilted appearance of the leaves of the flooded plants such as those observed in *C. rotundifolia* and *V. parkeri,* could be attributed to the inability of the plants to take up water under anaerobic conditions (Wiley, 1970). Excess in carbon and deficiency in oxygen have also some direct and indirect inhibitory effects on water uptake (Slatyer, 1967) and cell permeability (Glinka and Reinholds, 1962). The distinct symptoms of leaf chlorosis and wilting under flooding confirmed the observations of Kramer (1951) in tomato, Heinrichs (1970) in temperate pasture legumes, McIvor (1976) in *Stylosanthes guianensis* and Chudasama (1981) in *Neotonia wightii, Lablab purpureus* and *Macroptiloma axillare.*

With increase in flooding duration, thickening and suberization of the immersed stems became extensive in *M. lathyroides* and *T. semi-pilosum* and less in *L. bainesii, D. heterophyllum* and *C. mucunoides.* Lateral root initiation and development were extensive in *M. lathyroides* (Fig. 1), *T. semi-pilosum* and *D. heterophyllum.* During the final week of flooding, extensive nodulation was observed on the adventitious roots of *M. lathyroides, T. semi-pilosum* and *D. heterophyllum* and lesser nodulation in *L. bainesii.* Although there was extensive adventitious root development in *C. mucunoides,* nodulation was negligible.

M. lathyroides, D. heterophyllum, L. bainesii and *T. semi-pilosum* showed some growth under flooding. This favorable growth was enhanced by the extensive suberization, thickening, and formation of lenticels on the immersed stems and branches which produced adventitious roots that became nodulated when flooding was prolonged

Fig. 1. *Macroptilium lathyroides* submerged stems which developed adventitious roots after 10 days flooding.

Fig. 2. *Trifolium semi-pilosum* immersed stems with developed adventitious roots and nodules after 21 days flooding.

(Whiteman et al., 1981).

Plant Survival (%)

Among the species, *M. lathyroides* was apparently less affected by flooding (Table 1). In contrast, flooded *V. parkeri* plants all died after as early as 10 days. Seventy-five per cent of the flooded *C. rotundifolia* plants survived after 10 days flooding but beyond this period, all plants wilted and died.

An unusual survival pattern under flooding was observed in *C. mucunoides*. Although only 25% of the flooded plants survived after 10 days, survival rose to 82% after 21 days flooding. The growth survival of this species under flooded condition could be attributed to the production of adventitious roots from the immersed stems and branches. The formation of adventitious roots is an important excess-water-stress avoidance strategy (Kramer, 1951). The adventitious roots play a role in water absorption (Jackson, 1955). Just after root initiation from the immersed stems of excess-water-stressed plants, stomates began to open and the plants resumed their growth (Kramer, 1951).

Flooded *D. heterophyllum*, *L. bainesii* and *T. semi-pilosum* plants survived flooding for 10 days with 90, 83 and 78% survival, respectively. When flooding duration was increased to 21 days, per cent survival of *L. bainesii* slightly increased to 87% while those of *D. heterophyllum* and *T. semi-pilosum* slightly decreased to 88 and 68%, respectively (Table 1).

Dry Weight (g/plant)

As flooding duration was lengthened, the species differed in their

Table 1. Per cent survival, total shoot dry weight (a) and dry weight of dead shoot materials (b) of the different tropical pasture legumes as affected by flooding duration.

Species	Flooding Duration (days) 0	10			21		
	%	a	b	%	a	b	%
Experiment 1							
M. lathyroides	100	5.04	–	100	8.47	–	100
T. semi-pilosum	100	10.25	2.21	78	10.53	3.36	68
D. heterophyllum	100	11.70	1.19	90	16.32	1.89	88
L. bainesii	100	20.34	3.36	83	21.83	2.80	87
Experiment 2							
M. lathyroides	100	10.63	–	100	18.40	–	100
C. rotundifolia	100	4.68	1.17	75	4.78	4.78	0
C. mucunoides	100	16.18	12.20	25	20.35	3.75	82
V. parkeri	100	9.95	9.95	0	10.03	10.03	0

growth pattern. *M. lathyroides* showed higher total, shoot, and root dry weights in the flooded treatments than in the control (Table 2). In contrast, the total dry weights of *C. mucunoides, C. rotundifolia* and *V. parkeri* were significantly reduced than that ot the control when flooding lasted until 21 days. *D. heterophyllum* maintained a similar growth in the control and in the flooding treatments. *T. semi-pilosum* and *L. bainesii* had lower total dry weights with increasing duration of flooding.

Nodulation in all species, except in *M. lathyroides,* was adversely affected by flooding (Table 2). In experiments 1 and 2, the nodule dry weights of *M. lathyroides* after 21 days flooding were significantly higher than those of the unflooded. This was due to the extensive nodulation on its adventitious roots. In *C. mucunoides, C. rotundifolia* and *V. parkeri,* the nodules which existed at the time of flooding gradually decayed with the increasing duration of flooding and were reduced to a negligible amount after 21 days. *D. heterophyllum, L. bainesii* and *T. semi-pilosum* (Fig. 2) maintained a similar pattern of nodulation under flooded and unflooded conditions.

Plant dry weight was used as the quantitative means of recording the effects of flooding. Averaged over the 2 experiments, *M. lathyroides* produced 25% more total dry matter under flooding than in the control. The increase in total dry matter was due to the increase in shoot and root dry weights which probably resulted from the improved water status of the plant under flooding. This superior flood tolerance displayed by *M. lathyroides* and the other species such as *D. heterophyllum, L. bainesii* and *T. semi-pilosum* was partially due to the extensive adventitious root development on which the new nodules were formed. Hence, greater nodulation in *M. lathyroides* suggests that this species could maintain a favorable oxygen level within its roots than the rest of the species (Whiteman et al., 1981). The factor most detrimental to the establishment and efficient operation of a legume-*Rhizobium* symbiosis is the lowering of oxygen availability in the nodules (Bergersen, 1971).

Relative Tolerance

The unflooded dry weight ratio is an index of the relative tolerance of a particular species to flooding. *M. lathyroides* showed superior tolerance to flooding as compared with the other species (Table 3). This species also showed relatively higher dry weights of shoots, roots and nodules under flooded conditions than in the control which resulted in high flooded/unflooded dry weight ratios. *D. heterophyllum, L. bainesii* and *C. mucunoides* showed moderate tolerance to flooding (Table 3). *C. rotundifolia* and *V. parkeri* showed poor tolerance as compared with other species.

The flooding tolerances of the different species were compared. *M. lathyroides* was apparently the best species adapted to flooding. This confirms the results of previous studies made by Whiteman et al. (1981) and Chudasama (1981) on the same species. *C. rotundifolia* and *V. parkeri* were the least tolerant. *D. heterophyl-*

Table 2. Dry weight of shoots, roots and nodules (g/plant) of the different tropical pasture legumes as affected by flooding[1].

Species	Shoot Dry Weight		Root Dry Weight		Nodule Dry Weight		Total Dry Weight	
	Unflooded	Flooded[2]	Unflooded	Flooded[2]	Unflooded	Flooded[2]	Unflooded	Flooded[2]
Experiment 1								
M. lathyroides	3.72	5.40	1.62	2.01	0.21	0.30	5.40	7.72
T. semi-pilosum	10.59	8.90	2.18	1.83	0.24	0.17	13.00	10.89
D. heterophyllum	12.84	11.78	1.72	1.84	0.14	0.16	14.70	13.79
L. bainesii	18.12	16.98	5.10	5.18	0.35	0.22	23.53	21.40
LSD .05	1.78		n s		0.07		2.06	
.01	1.85		n s		0.10		2.76	
Experiment 2								
M. lathyroides	9.50	10.75	1.59	2.31	0.31 (0.89)	0.51 (1.00)	11.40	13.56
C. rotundifolia	5.55	3.97	1.33	0.98	0.23 (0.85)	0 (0.71)	7.11	4.80
C. mucunoides	17.28	15.44	4.08	2.32	0.60 (1.04)	0.15 (0.80)	21.92	17.96
V. parkeri	15.14	9.04	2.80	1.25	0.55 (1.01)	0 (0.71)	19.00	10.35
LSD .05	1.23		0.38		0.04		1.51	
.01	1.70		0.52		0.05		2.05	

[1] Average of 3 harvests. Figures inside parentheses are transformed numbers, $\sqrt{X + ½}$, of the nodule dry weight used for analysis.

[2] Average of 2 flooding durations (10 and 21 days).

lum was quite tolerant to flooding and ranked second, followed by *L. bainesii. T. semi-pilosum* and *C. mucunoides* ranked fourth and fifth, respectively (Table 3).

The shoot and root components of those species whose growth was inhibited by flooding were similarly restricted by flooding. Once flooding was begun, root growth and nodule development virtually stopped and these organs rotted with increasing period of flooding while shoot growth continued to a little extent particularly in *C. rotundifolia* and *V. parkeri.* This was accompanied by chlorosis, death and abscission of the leaves. Various mechanisms to explain these changes have been proposed, namely; reduction of water uptake leading to desiccation (Kramer, 1951), accumulation of toxic metabolic substances due to anaerobiosis (McManmon and Crawford, 1971), and accumulation of harmful substances in the waterlogged soil (Jones, 1972). Presumably, all these mechanisms were operating and the relative rank of tolerance of a particular species depended on its adaptation to each particular factor.

Leaf Diffusive Resistance (s cm^{-1})

The stomal responses (abaxial surface) to flooding of the 7 species are presented in Table 4. There were significant differences between the flooded and the unflooded (control) plants.

In both experiments, flooded *M. lathyroides* at any given date of flooding had markedly lower leaf diffusive resistance than the control, indicating that these plants have wide stomatal apertures (Table 4). In contrast, the stomata of flooded *C. rotundifolia* and *V. parkeri* plants suddenly closed after 3 days flooding as indicated by a high leaf diffusive resistance (Table 4) and these remained closed throughout the flooding duration. In these

Table 3. Relative tolerance to flooding and the flooded/unflooded dry weight ratio of the different tropical pasture legumes.

Species	Relative Tolerance[1]	Flooded/Unflooded Dry Weight Ratio		
		Total	Shoot	Root
M. lathyroides (1)	1	1.57	1.61	1.33
M. lathyroides (2)	1	1.21	1.31	1.57
D. heterophyllum	2	0.91	0.87	1.07
L. bainesii	3	0.87	0.92	1.01
T. semi-pilosum	4	0.83	0.85	0.80
C. mucunoides	5	0.77	0.86	0.48
C. rotundifolia	6	0.62	0.67	0.64
V. parkeri	7	0.45	0.52	0.30

[1] Rank 1 represents the highest relative tolerance and rank 7 the lowest.

Table 4. Leaf diffusive resistance of some tropical pasture legumes at different sampling dates as affected by flooding.

Species	**Leaf Diffusive Resistance (s cm^{-1})**						
	Days of Sampling						
	−1	**3**	**7**	**11**	**15**	**19**	**21**
Experiment 1							
M. lathyroides							
unflooded	2.9	3.8	8.4	7.3	4.2	5.8	8.7
flooded	2.8	3.4	6.8	3.3	2.9	4.1	4.9
LSD 5%	ns	ns	1.1	2.6	1.0	1.0	2.9
T. semi-pilosum							
unflooded	1.9	1.6	2.1	1.3	–	0.7	3.3
flooded	2.0	1.4	2.5	2.7	–	2.9	6.4
LSD 5%	ns	ns	ns	0.8	–	0.7	1.2
D. heterophyllum							
unflooded	1.8	1.7	2.1	2.1	2.7	3.3	2.9
flooded	2.0	1.6	3.2	2.7	4.2	4.5	4.4
LSD 5%	ns	ns	0.8	ns	0.5	0.6	0.8
L. bainesii							
unflooded	1.4	1.2	1.1	1.3	2.5	2.4	2.2
flooded	1.6	1.1	2.8	4.2	3.8	6.6	4.8
LSD 5%	ns	ns	1.1	0.8	0.7	1.8	1.1
Experiment 2							
M. lathyroides							
unflooded	3.5	2.4	3.1	0.8	2.1	2.2	2.4
flooded	3.5	2.0	2.3	0.7	1.8	2.1	2.3
LSD 5%	ns	ns	0.6	ns	ns	ns	ns
C. rotundifolia							
unflooded	2.1	2.2	2.4	2.9	4.5	3.2	3.3
flooded	2.3	6.3	10.7	9.5	13.9	10.9	15.0
LSD 5%	ns	1.6	1.9	1.9	1.1	1.7	–
C. mucunoides							
unflooded	2.3	2.8	2.8	1.8	3.1	1.7	2.0
flooded	2.3	2.5	4.1	5.4	14.0	9.8	6.9
LSD 5%	ns	ns	1.0	0.5	1.2	1.5	1.8
V. parkeri							
unflooded	2.7	2.4	3.0	2.6	2.5	3.2	2.8
flooded	3.1	4.3	12.6	14.7	15.0	15.0	15.0
LSD 5%	ns	1.2	1.8	0.5	–	–	–

ns – not significant.

species, probably water uptake was severely disrupted by low oxygen concentration around the roots (Trought and Drew, 1980) and this resulted in the rapid closure of the stomates and later, wilting of the plant leaves (Periera and Kozlowski, 1977).

In flooded *C. mucunoides* plants, high diffusive resistance (closed stomates) was observed after 11 days flooding. However, some flooded plants which produced adventitious roots on their immersed stems and branches resumed their normal stomatal apertures after 19 days flooding (Table 4).

The leaf diffusive resistance of other flooded species showed variable results with increasing duration of flooding. However, the leaf diffusive resistance values of these species ranged from 2.8 to 6.6 s cm^{-1} for *L. bainesii,* 2.7 to 4.5 s cm^{-1} for *D. heterophyllum* and 2.5 to 6.4 s cm^{-1} for *T. semi-pilosum,* indicating slight closure of the stomatal apertures.

Results demonstrate a wide range of adaptation to flooding among species. A similar or wide range of responses between ecotypes within species has been shown (Mc Ivor, 1976). Thus, screening between and within species for flooding tolerance should enable identification of legume cultivars better adapted to many lowland tropical environments.

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