

Drought induced changes in growth, leaf gas exchange and biomass production in *Albizia lebbbeck* and *Cassia siamea* seedlings

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Abstract

Diurnal trends in net photosynthesis rate (P_N), stomatal conductance (g_s), water use efficiency (WUE) and biomass were compared in six-month-old seedlings of *Albizia lebbbeck* and *Cassia siamea*, under different levels of drought stress. The potted plants were subjected to four varying drought treatment by withholding watering for 7 (D1), 14 (D2) and 25 (D3) days. The fourth group (C) was watered daily and treated as unstressed (control). Species differed significantly ($p < 0.001$) in their physiological performance under varying stress conditions. Higher P_N of 11.6 ± 0.05 in control followed by 4.35 ± 0.4 in D1 and $2.83 \pm 0.18 \mu\text{mol m}^{-2} \text{s}^{-1}$ in D2 was observed in *A. lebbbeck*. A significant ($p < 0.001$) reduction in P_N was observed in *C. siamea* ($7.65 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, D1, $2.56 \pm 0.33 \mu\text{mol m}^{-2} \text{s}^{-1}$ and D2, $1.4 \pm 0.01 \mu\text{mol m}^{-2} \text{s}^{-1}$) at 9 hr. A positive correlation was seen between P_N and g_s (*A. lebbbeck*, $r^2 = 0.84$; *C. siamea*, $r^2 = 0.82$). Higher WUE was observed in *C. siamea* (D2, $7.1 \pm 0.18 \mu\text{mol m}^{-2} \text{s}^{-1}$; D3, $8.39 \pm 0.11 \mu\text{mol m}^{-2} \text{s}^{-1}$) than *A. lebbbeck*, (control, $7.58 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ and D3, $8.12 \pm 0.15 \mu\text{mol m}^{-2} \text{s}^{-1}$). The chlorophyll and relative water content (RWC) was more in *A. lebbbeck* than *C. siamea*. Maximum biomass was produced by *A. lebbbeck* than *C. siamea*. From the study, one could conclude that *A. lebbbeck* is better than *C. siamea* in adopting suitable resource management strategy and be best suited for the plantation programs in the semi-arid dry lands.

Key words

Albizia lebbbeck, *Cassia siamea*, Leaf gas exchange, Photosynthesis rate, Stomatal conductance, Water use efficiency, Biomass, Drought stress

Introduction

In the natural habitat, plants are often subjected to drought stress during their life cycle. The frequency of such conditions is likely to be in many folds in the future especially with reference to arid and semi-arid regions (Chaves *et al.*, 2002). Drought stress affects many aspects of physiology in plants, such as gas exchange, water use efficiency and biomass production (Chalapathi Rao and Reddy, 2008). Water availability has the potential to regulate the productivity through gas exchange, carbon assimilation and stomatal control in response to irradiance (Castillo *et al.*, 2002). Decreased rates of net photosynthesis and transpiration were observed under high irradiance / temperature in our previous studies (Saraswathi and Paliwal, 2008). *Albizia lebbbeck* and *Cassia siamea* are two important multipurpose tree species. Multipurpose tree (MPT) is a tree that clearly constitutes an essential component of an agro-forestry system significantly contributing for ecological stability. Large-scale plantation of fast growing tree genera such as *A. lebbbeck* and *C. siamea* holds a great potential in tackling the problem of fuelwood

scarcity, improving soil fertility and controlling land degradation on one hand and in meeting the demand for food, fiber, fodder, fuelwood, timber *etc.*, on the other (Saraswathi and Paliwal, 2008). Incorporation of multipurpose tree species, which are introduced in the small farms of India in a well-organized manner, can be expected to have better yields through sustainable management of land resources on long-term basis (Bhan, 2007). Despite the considerable economic and ecological importance of the multipurpose tree species, the presently available eco-physiological data describing photosynthesis of these multipurpose tree species growing in semi-arid eco-climatic region of Madurai are limited. Therefore, it was planned to study, the growth and diurnal leaf gas exchange under drought stress conditions and to establish relationship between photosynthetic parameters and the biomass production of these two species.

Materials and Methods

Seed collection, treatment and germination: The seeds of *A. lebbbeck* and *C. siamea* were obtained from Palani Hills Conservation

Council, Odukkam Seed Centre, Dindigul, Tamil Nadu. The seeds were soaked in hot water. After 24 hr, the seeds were sown in seed bed raised in the Botanical Garden of Madurai Kamaraj University, Madurai. The seed bed was irrigated depending upon the moisture in seed bed to avoid any fungal infection due to excessive moisture. The germination was observed during the third week from the date of sowing. The germinated seedlings were transferred to polythene bags with an outside dimension of 10x20 cm containing garden soil, sand and farmyard manure at 2:1:1 ratio by volume. Watering was done regularly. The seedlings were kept under the shade in the nursery for around 3 months. Then, they were transferred to earthen pots. Four-month-old seedlings of *A. lebbeck* and *C. siamea* were used for the experiment.

Drought treatment: The planted pots were distributed into four groups to maintain them at four varying drought treatment among which three were subjected to different drought stress levels developed by withholding watering for 7th (D1), 14th (D2) and 25th (D3) days. The fourth group was watered daily and treated as unstressed or control (C).

Leaf gas exchange: Photosynthetic parameters were measured in the leaf on 7th (D1), 14th (D2) and 25th (D3) day, using an open gas exchange portable photosynthesis system (Li-6400, LI-COR, Lincoln, NE, USA) with independent control, using 6 cm² clamp-on leaf cuvette, under the natural environmental conditions. For all the measurements, healthy and fully expanded leaves of the third or fourth pair from the apex were used. The measurements were taken diurnally from 7 am to 5 pm.

Relative water content (RWC): RWC of the leaves was measured in the leaf on 7th (D1), 14th (D2) and 25th (D3) day, by saturated weighing method (Lin and Ehleringer 1982).

$$\text{Relative water content (RWC)} = \frac{(\text{Fresh weight} - \text{Dry weight})}{(\text{Turgid weight} - \text{Dry weight})} \times 100$$

The turgid leaf weight was determined after keeping the leaf in distilled water in darkness at 4°C to minimize respiration losses, until it reached a constant weight (full turgid, typically after 12 hr). Leaf dry weight was obtained after keeping the turgid leaf at 30°C in an oven for 24 hr. Five replicates were kept for each treatment.

Chlorophyll content: Determination of chlorophyll (*Chl*) content was carried out in the leaf on 7th (D1), 14th (D2) and 25th (D3) day, following the method of Arnon (1949). Absorbance of extracts was measured at 645 nm for *Chl a* and 663 nm for *Chl b* content using a spectrophotometer U-2000 (Hitachi instruments, Tokyo, Japan). Estimation of *Chl* content was done grinding 0.1 g of leaf material in 80% acetone. The extraction was centrifuged at 3000 rpm for 5 min. The supernatant was collected and the process was repeated until the pellet became white or yellow in color. The supernatants were pooled and the optical density was noted for the chlorophyll content estimation.

Biomass: The productivity of the two species, *A. lebbeck* and *C. siamea* under drought stress was estimated by harvest method (Flombaum and Sala, 2007). Five individual plants from each treatment were harvested on 7th (D1), 14th (D2) and 25th (D3) day and roots excavated carefully through putting the pot upside down at the time of experiment termination. Leaf, stem and root were separated and the fresh mass was recorded. These samples were dried in the oven at 80°C and the dry weight was recorded.

Statistical analysis: This study was conducted in a completely randomized experimental design with five treatment levels in four replications. All leaf gas exchange parameters were subjected to one-way-analysis ($p < 0.001$) and compared using Tukey's test, 5% of probability (Sheskin, 2004).

Results and Discussion

Diurnal trends in leaf gas exchange: The net photosynthesis rate (P_N) and stomatal conductance (g_s) were maximum in the watered (control) plants where as, they decreased in the plants under drought conditions. In general, P_N gradually increased from 7 hr, reached its maximum at 9 hr, and then decreased during 11 hr. Slight recovery in P_N and g_s was observed at 13 hr through 15 hr in control and D1. Similar trend was observed in D2. However, the recovery was minimum with decreased rates at 15 hr.

There is statistically significant difference observed between control and plants under drought conditions ($p < 0.001$) in leaf gas exchange parameters. *A. lebbeck* showed the maximum P_N in control ($11.6 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) at 9 hr. The decreased P_N during mid morning ($6.42 \pm 0.16 \mu\text{mol m}^{-2} \text{s}^{-1}$), recovered at 13 hr ($9.07 \pm 0.19 \mu\text{mol m}^{-2} \text{s}^{-1}$) and continued till 15 hr ($8.9 \pm 0.7 \mu\text{mol m}^{-2} \text{s}^{-1}$) and again it decreased at 17 hr ($2.86 \pm 1.01 \mu\text{mol m}^{-2} \text{s}^{-1}$). The maximum P_N was observed at 9 hr both in D1 ($4.35 \pm 0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) and D2 ($2.83 \pm 0.18 \mu\text{mol m}^{-2} \text{s}^{-1}$) showing midday depression ($3.17 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$, $1.08 \pm 0.07 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively). A slight recovery was observed at 15 hr in D1 plants ($3.12 \pm 0.17 \mu\text{mol m}^{-2} \text{s}^{-1}$), where as, the recovery in D2 ($1.51 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$) plants at 13 hr is negligible. There was no carbon assimilation in D3 plants. It does only respiration under severe drought condition (Fig. 1). Similar trend was observed in stomatal conductance in the control and stressed plants (Fig. 2).

Water use efficiency increased from 7 hr and found maximum at around 9 hr both in *A. lebbeck* and *C. siamea*. Decreased water use efficiency was observed after 9 hr until 17 hr. In *A. lebbeck*, the maximum water use efficiency ($8.12 \pm 0.15 \text{mmol m}^{-2} \text{s}^{-1}$) was observed in D3 at 9 hr followed by control ($7.58 \pm 0.3 \text{mmol m}^{-2} \text{s}^{-1}$), D1 ($5.69 \pm 0.26 \text{mmol m}^{-2} \text{s}^{-1}$) and D2 ($5.29 \pm 0.017 \text{mmol m}^{-2} \text{s}^{-1}$). *C. siamea* showed slightly different pattern in that, maximum water use efficiency was observed in D3 ($8.39 \pm 0.11 \text{mmol m}^{-2} \text{s}^{-1}$) at 9 hr, followed by D2 ($7.1 \pm 0.18 \text{mmol m}^{-2} \text{s}^{-1}$), D1 ($5.68 \pm 0.4 \text{mmol m}^{-2} \text{s}^{-1}$) and control ($5.13 \pm 0.3 \text{mmol m}^{-2} \text{s}^{-1}$) (Fig. 3).

Table - 1: Mean relative water content (g leaf⁻¹) of *A. lebbbeck* and *C. siamea* seedlings under drought stress

Treatment	<i>Albizia lebbbeck</i>				<i>Cassia siamea</i>			
	Fresh wt. (in g)	Turgid wt. (in g)	Dry wt. (in g)	RWC (%)	Fresh wt. (in g)	Turgid wt. (in g)	Dry wt. (in g)	RWC (%)
Control	0.42 ± 0.02	0.43 ± 0.01	0.14 ± 0.01	51.2	0.38 ± 0.05	0.42 ± 0.02	0.12 ± 0.03	49.9
D1	0.23 ± 0.01	0.32 ± 0.07	0.08 ± 0.01	38.9	0.21 ± 0.01	0.35 ± 0.02	0.10 ± 0.03	21.4
D2	0.15 ± 0.05	0.31 ± 0.04	0.06 ± 0.01	23.0	0.12 ± 0.03	0.33 ± 0.04	0.05 ± 0.00	16.2
D3	0.06 ± 0.01	0.27 ± 0.03	0.04 ± 0.01	3.4	0.06 ± 0.01	0.27 ± 0.01	0.03 ± 0.01	8.11

RWC = Relative water content, Values are mean ± SE of 7th (D1), 14th (D2) and 25th (D3) day estimations (p<0.001)

Table - 2: Effect of drought stress on total chlorophyll content (mg g⁻¹ of leaves) of *A. lebbbeck* and *C. siamea*

Treatment	Total chlorophyll content (mg g ⁻¹ of leaves)	
	<i>A. lebbbeck</i>	<i>C. siamea</i>
Control	7.025 ± 0.07 ^d	5.23 ± 0.04 ^d
D1	5.85 ± 0.07 ^c	3.89 ± 0.04 ^c
D2	4.36 ± 0.07 ^b	2.16 ± 0.04 ^b
D3	2.66 ± 0.07 ^a	0.98 ± 0.04 ^a

Means followed by the same letters (a,b,c,d) are not statistically different at p=0.05 level according to the Least Significant Difference (LSD) test

There is a good correlation between photosynthesis and stomatal conductance both in control and drought plants (r² = 0.88) (Fig 4).

Biomass production: Control and drought plants showed significant difference (p<0.001) in fresh and dry matter production in both the species. However, species did not differ much in the dry matter production. In *A. lebbbeck*, the fresh (14.45 ± 0.04 g pt⁻¹) and dry matter production (6.2 ± 0.01 g pt⁻¹) was more in control plants than in drought plants followed by D1 (Fresh wt, 9.68 ± 0.01; Dry wt, 4.27 g pt⁻¹), D2 (Fresh wt, 7.49 ± 0.01 g pt⁻¹; Dry wt, 4.19 g pt⁻¹) and D3 (Fresh wt, 1.83 ± 0.05; Dry wt, 1.27 ± 0.03 g pt⁻¹). The fresh and dry matter production in *C. siamea* did not differ much from that of *A. lebbbeck*. In *C. siamea*, maximum fresh wt of 12.24 ± 0.01 g pt⁻¹ and dry wt of 4.35 ± 0.03 g pt⁻¹ was observed in control followed by D1 (Fresh wt, 7.45 ± 0.02 g pt⁻¹; dry wt, 3.47 ± 0.01 g pt⁻¹) and D2 (Fresh wt, 5.67 ± 0.03 g pt⁻¹; dry wt, 2.34 ± 0.02 g pt⁻¹). Minimum fresh weight of 0.89 ± 0.001 g pt⁻¹ and dry wt, 0.42 ± 0.004 g pt⁻¹ was observed in D3 (Fig. 5).

Relative water content (RWC): The RWC content was more in control (51.16%) than the stressed plants (D1, 38.87; D2, 23.03 and D3, 3.40%) in *A. lebbbeck*. Similarly, in *C. siamea* more RWC was observed in control (49.9%) followed by D1 (21.42), D2 (16.21) and D3 (8.11%). Drought stress treatment significantly (p<0.001) decreased the RWC (Table 1).

Chlorophyll content: The total chlorophyll content (in mg g⁻¹ of leaves) was more in well-watered plants in both the species. The total Chl content decreased as the drought treatment increased. *A. lebbbeck* showed more total Chl content in control (7.025 ± 0.07 mg g⁻¹) followed by D1 (5.85 ± 0.07 mg g⁻¹), D2 (4.36 ± 0.07 mg g⁻¹) and D3 (2.66 ± 0.07 mg g⁻¹). Similar trend

was exhibited in *C. siamea* in which, more Chl content was observed in control (5.23 mg g⁻¹) followed by D1 (3.89 ± 0.04 mg g⁻¹), D2 (2.16 ± 0.04 mg g⁻¹) and D3 (0.98 ± 0.04 mg g⁻¹) (Table 2).

Drought stress impaired physiological functions and biomass production. Significant reductions in the net photosynthesis rate, stomatal conductance, water use efficiency, relative water content, chlorophyll content and decreased total biomass production are due to a decreased leaf size and leaf area affecting carbon assimilation. Our results are in agreement with Singh and Singh (2003) in that, highest P_N and g_s for the seedlings in control might be related with high soil water content. Increased g_s probably increased CO₂ diffusion into mesophyll resulting in high CO₂ fixation and biomass when compared to the seedlings of other treatments (Singh and Singh, 2003). Maximum P_N at 9 hr may be attributed to optimum environmental factors such as photosynthetic photon flux density (PPFD) and vapor pressure deficit (VPD). The midday depression in control and D1 suggests that the plants are able to manage the adverse environmental conditions such as high temperature, high VPD and high PPFD by closing the stomata, thereby, reducing the net photosynthesis rate. The recovery of photosynthesis after 13 hr in control and D1 clearly proves that the plants are capable to use the resources available thereby, providing as evidence for suitable resource management strategy to increase the growth and productivity even in the slightest conditions favoring their physiological activities. Furthermore, in agreement with the more drought avoiding strategy of species (Llorens *et al.*, 2003b), these two species were more sensitive to soil drying, experiencing higher reductions in their leaf gas exchange rates to avoid dehydration. Higher photorespiration rates in plants under severe drought of both the species were probably one of the main drivers accounting for the maintenance of its electron flow, since C₃ plants, in PSII activity is mainly partitioned between photosynthesis and photorespiration (Krall and Edwards, 1992).

The plant species studied were efficient in restricting water loss through stomatal closure that resulted in low water use efficiency. This is evident from the values at 13, 15 and 17 hr. This may be attributed to an increase in leaf temperature due to increase in temperature in the atmosphere that in turn increased the vapor pressure gradient and water loss (Khairi and Hall, 1976). This view may further be extended that non-stomatal factor may play a

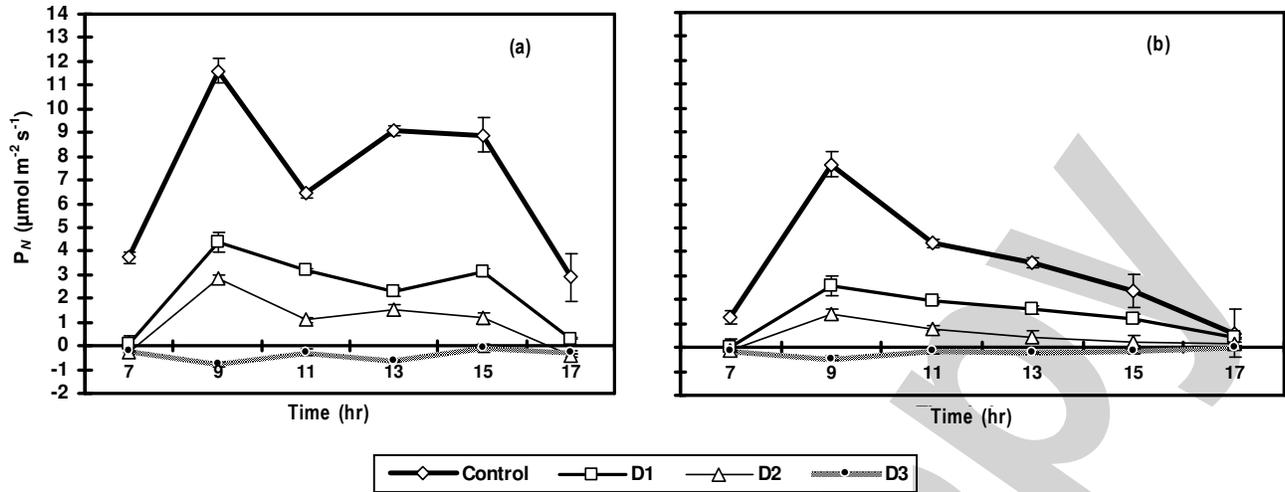


Fig. 1: Effect of drought stress on net photosynthesis rate (P_N) in the seedlings of *Albizzia lebbbeck* (a) and *Cassia siamea* (b)

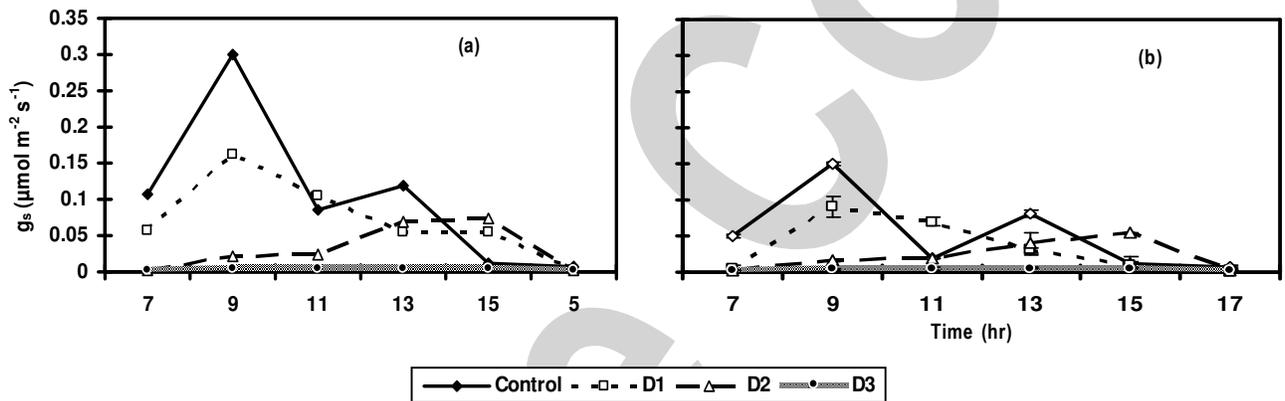


Fig. 2: Effect of drought stress on stomatal conductance (g_s) in the seedlings of *A. lebbbeck* (a) and *C. siamea* (b)

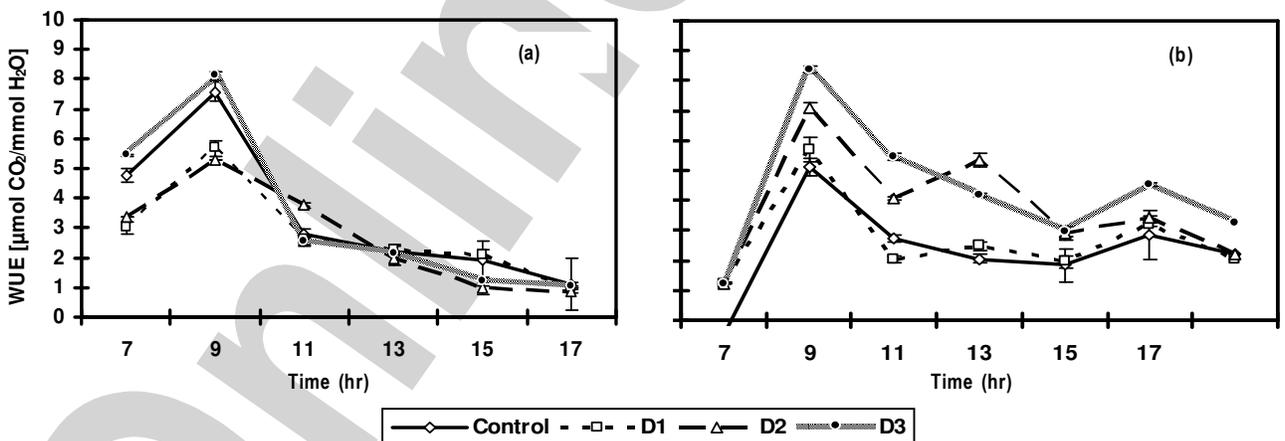


Fig. 3: Effect of drought stress on water use efficiency (WUE) in the seedlings of *A. lebbbeck* (a) and *C. siamea* (b)

major role in regulating the net photosynthesis rate at high temperature. Increased water use efficiency for the seedlings in D2 and D3 might be due to increase in net photosynthesis rate through the utilization of intercellular CO_2 by mesophyll cells which was more directly related to photosynthesis than to stomatal aperture (Singh and Singh, 2003). High water use efficiency at D2 and D3

9 hr and subsequent significant decline at later hours support the drought tolerance of the species (Abril and Hanano, 1998). Although in many experimental and field studies, drought has been shown to studies, increase the instantaneous and / or the integrated water-use efficiency of woody plants (Meinzer *et al.*, 1992; Saraswathi and Paliwal, 2008), proportional decreases of leaf net photosynthesis

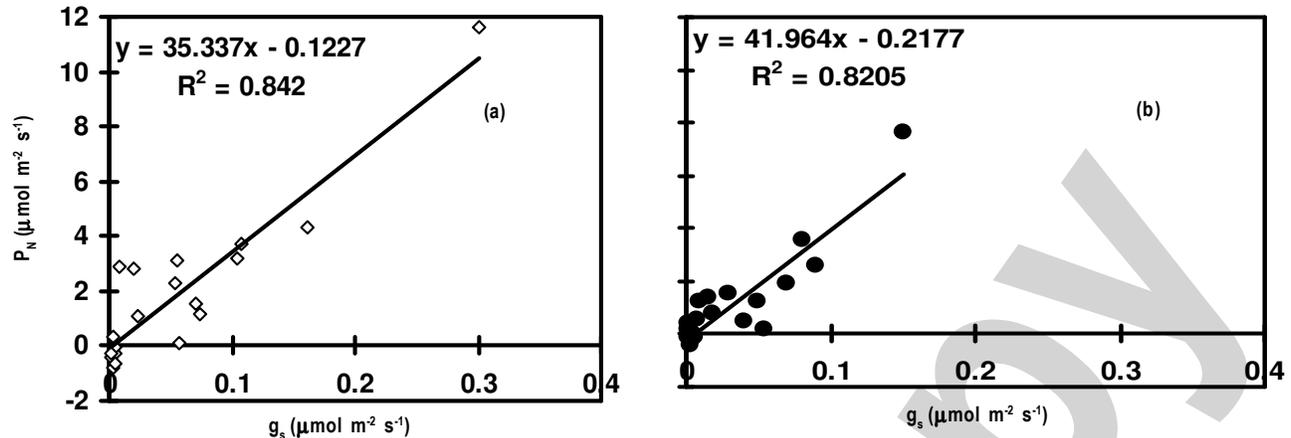


Fig. 4: The relationship between stomatal conductance (g_s) and photosynthesis (P_N) in *A. lebbbeck* (a) and *C. siamea* (b) seedlings under drought stress

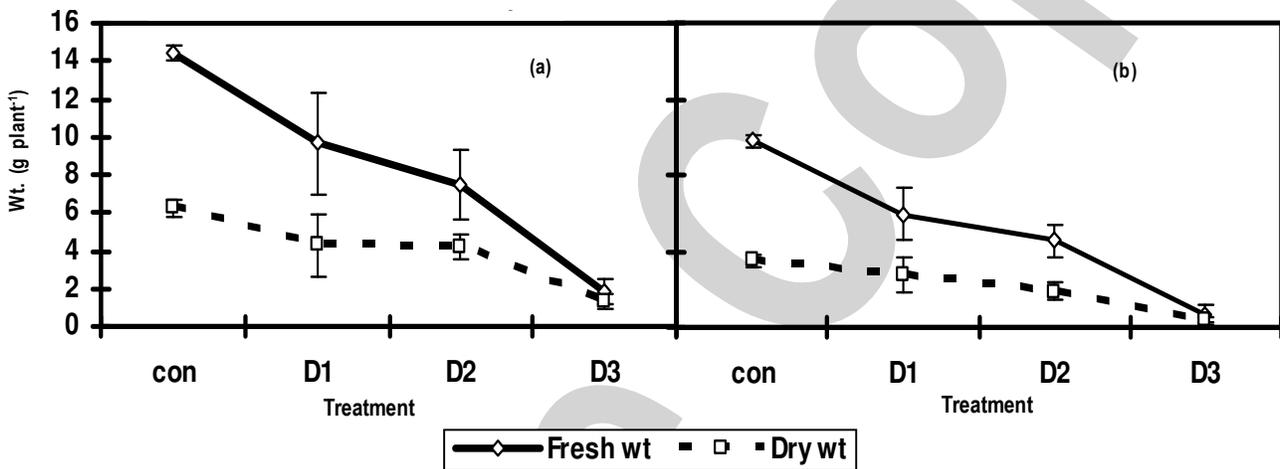


Fig. 5: The fresh and dry matter production of the seedlings of *A. lebbbeck* (a) and *C. siamea*. (b) Bars indicate standard error ($n=5$) ($p<0.001$), D1 = 7th day, D2 = parenthesis] D3 = 25th day

and stomatal conductance have also been frequently reported (Llorens *et al.*, 2003).

The fresh and dry weight markedly decreased in stressed plants when compared to control. The marked reduction is due to reduction in leaf thickness and size. Decreased dry matter production is due to stress, which may be attributed to the altered carbon and nitrogen and due to both senescence and death of leaves, which was considered as an avoidance mechanism that allows minimizing water losses. This is in agreement with a mechanism minimizing water losses and irreversible damages like to xylem cavitations (sap column breaking) when the air evaporating demand is high during water stress by limiting the produced transpiring leaf area (Ruiz-Sanchez *et al.*, 2000).

The results obtained for the Chl content in control and drought conditions are in agreement with earlier report (Bertamini *et al.*, 2006). Such water deficit conditions induced reduction in Chl content has been ascribed to loss of chloroplast membranes, excessive swelling, and distortion of the lamellae

vesiculation and the appearance of lipid droplets (Kaiser *et al.*, 1981). Our results are contradictory with Ashraf *et al.* (2002) in that, they found drought stress did not cause any significant effect on Chl content. The symptom of drought was apparent by wilting of the plants and gradually diminution in total chlorophyll content. The marked reduction of total chlorophyll content in drought stressed plants was due to the decrease in both Chl *a* and Chl *b* contents. Chl *a* was degraded more than Chl *b* under water deficit conditions. Such water deficit induced reduction in Chl content has been ascribed to loss of chloroplast membranes. The chlorophyll content decreased significantly ($p<0.001$) as the drought treatment increased. Similar trend was exhibited in carotenoid contents in which control plants have more carotenoids than the plants under drought condition.

RWC is considered as a measure of plant water status reflecting the metabolic activity in tissues and used as a most meaningful index for identifying legumes with contrasting differences in dehydration tolerance (Sinclair and Ludlow, 1986). In the present study, water deficit treatment significantly ($p<0.001$) decreased RWC. RWC of several stressed crop plants were evident from the studies of El Hafid *et al.* (1998). Our results are consistent with the

observations made by Medrano *et al.* (2002) in that, proportional decreases of g_s and RWC was observed in response to soil drying especially as in both the plant species. Relative water content of the leaves of *A. lebbbeck* and *C. siamea* declined at the beginning of drought stress in D1 and decreases further with severe drought stress conditions. It was expressed that these two species have certain adaptability and adjusting capacity on drought stress, which is similar with the results observed by Yuyan *et al.* (2007).

Our study clearly shows that *A. lebbbeck* indicated a significant adaptation changes to varying water stress when compared to *C. siamea* therefore, it can be considered as a better candidate suitable for plantation programmes in semi-arid tropics. However, the response of *C. siamea* was significant in biomass production, which is similar to that of *A. lebbbeck* at severe drought conditions. Even though the results of our study predicted that the future drier conditions might decrease the biomass productivity, the magnitude of such decrease will be species-specific.

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