

## Biomass partitioning and gas exchange in *Dalbergia sissoo* seedlings under water stress

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### Abstract

Biomass, leaf water potential ( $\Psi_l$ ), net photosynthetic rate ( $P_N$ ), transpiration rate ( $E$ ), stomatal conductance ( $g_s$ ), leaf to air temperature difference ( $T_{diff}$ ), and instantaneous water use efficiency (WUE) were measured in the seedlings of *Dalbergia sissoo* Roxb. grown under irrigation of 20 ( $W_1$ ), 14 ( $W_2$ ), 10 ( $W_3$ ), and 8 ( $W_4$ ) mm. Treatments were maintained by re-irrigation when water content of the soil reached 7.4 % in  $W_1$ , 5.6 % in  $W_2$ , 4.3 % in  $W_3$ , and 3.2 % in  $W_4$ . Seedlings in a control ( $W_5$ ) were left without irrigation after maintaining the soil field capacity (10.7 %). Seedlings of  $W_1$  had highest biomass that was one tenth in  $W_5$ . Biomass allocation was highest in leaf in  $W_2$  and in root in  $W_4$  and  $W_5$  treatments. Difference between predawn leaf water potential ( $\Psi_{pd}$ ) and midday ( $\Psi_{mid}$ ) increased with soil water stress and with vapour pressure deficit (VPD) in April and May slowing down the recovery in plant leaf water status after transpiration loss.  $P_N$ ,  $E$ , and  $g_s$  declined and  $T_{diff}$  increased from  $W_1$  to  $W_5$ . Their values were highly significant in April and May for the severely stressed seedlings of  $W_4$  and  $W_5$ .  $P_N$  increased from 08:00 to 10:00 and  $E$  increased until 13:00 within the day for most of the seedlings whereas  $g_s$  decreased throughout the day from 08:00 to 17:00.  $P_N$  and  $E$  were highest in March but their values were low in January, February, April, and May. Large variations in physiological variables to air temperature, photosynthetically active radiation, and vapour pressure deficit (VPD) indicated greater sensitivity of the species to environmental factors. WUE increased from  $W_1$  to  $W_2$  but decreased drastically at high water stress particularly during hot summer showing a kind of adaptation in *D. sissoo* to water stress. However, low biomass and reduced physiological functions at <50 % of soil field capacity suggest that this species does not produce significant biomass at severe soil water stress or drought of a prolonged period.

*Additional key words:* arid areas; leaf water potential; net photosynthetic rate; soil water availability; stomatal conductance; transpiration rate; water use efficiency.

### Introduction

Physiological and structural adaptations in desert plants compensate the effects of reduced water availability (Tuomela 1997) and provide substantial advantage against the arid environment (Ni and Pallardy 1991). Water availability regulates productivity in arid ecosystem through gas exchange and carbon assimilation (Manes *et al.* 1998) and stomatal control in response to increasing irradiance (Castillo *et al.* 2002). Recurring drought and prolonged periods of high irradiance in dry region reduce leaf water potential and stomatal conductance ( $g_s$ ) in plants (Cutini and Nocentini 1998). Drops in net photosynthetic rate ( $P_N$ ) and transpiration rate ( $E$ ) are

observed under high irradiance/temperature (Sandford and Jarvis 1986, Teskey *et al.* 1986, Vann *et al.* 1994). There is need to adopt suitable resource management strategy to increase growth and productivity in the dry areas. Increased availability of water and selection of comparatively fast growing species of local importance will be the better option.

*Dalbergia sissoo* Roxb. ex D.C. Prodr, an important species of Indian subcontinent and other tropical countries, was introduced in canal command area to grow it on the irrigated canal banks. The excellent performing *D. sissoo* plantation raised under irrigation during first

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*Abbreviations:* DM = dry mass;  $E$  = transpiration rate;  $g_s$  = stomatal conductance;  $P_N$  = net photosynthetic rate; PAR = photosynthetically active radiation; SWC = soil water content;  $T_a$  = air temperature;  $T_{diff}$  = leaf to air temperature difference;  $T_l$  = leaf temperature, VPD = vapour pressure deficit; WUE = instantaneous water use efficiency;  $\Psi_l$  = leaf water potential.

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five years started drying after discontinuing the irrigation resulted in large-scale mortality in the plantation. The mortality, after discontinuity of the irrigation, was probably the result of decreased soil water availability that affected plant water balance and physiological functions of the trees. Therefore, it is needed to quantify the tolerance levels of this species to water stress in the prevailing set of climatic variables, namely high irradiance, soil water deficit, and high vapour pressure deficit, for better management and improved growth of this species. The works available on this species in dry areas use *D. sissoo* in an afforestation programme (Bhimaya 1963),

## Materials and methods

**Study site:** Experiment was carried out at the experimental farm of Arid Forest Research Institute (AFRI), Jodhpur (26°45'N, 72°03'E). Among the three prominent seasons, summer is the most dominant being characterised by high temperature spanning from March to mid July. The period from mid July to September is the monsoon, when most of the rainfall is received. The winter season spreads from November to February. Mean monthly minimum and maximum temperatures were 10.0 and 41.3 °C, respectively. Soil used in the experiment was loamy sand having pH 8.32, EC 0.52 dS m<sup>-1</sup>, and water holding capacity of 10.67 % (m/m) at -0.03 MPa and 3.23 % at -1.50 MPa. Soil was deficient in available nitrogen (12.56 mg kg<sup>-1</sup>), phosphorus (10.01 mg kg<sup>-1</sup> P<sub>2</sub>O<sub>5</sub>), and potash (106 mg kg<sup>-1</sup> K).

**Plantation and experimental design:** Four-month-old single clone seedlings of *D. sissoo* from the experimental nursery of AFRI were used. Seedlings were planted in galvanised iron containers of 45 cm diameter and 55 cm depth filled with 120 kg of loamy sand soil up to 52 cm. A drainage hole was provided in the container. At the time of planting in August 1998, seedlings had mean height of 47.0±1.4 cm (mean±SE) and collar diameter of 0.40±0.09 cm. The planted containers were distributed into five groups to maintain them at five varying irrigation treatments. Each treatment was taken in eight replications and experiment was laid in Randomised Complete Block Design.

Treatment was initiated by saturating the soil of all the containers through addition of 82 mm of water in the first week of October 1998 after proper establishment of the seedlings. Drainage of excess water was allowed till the soil water ceased to drain down. Soil water content was continuously monitored gravimetrically after oven drying of soil samples at 110 °C to a constant mass. Irrigations were based on the percent soil water content (m/m) at the pressures of -0.03 MPa (10.7 %), -0.05 MPa (9.9 %), -0.10 MPa (7.4 %), -0.50 MPa (5.6 %), -1.00 MPa (4.3 %), and -1.50 MPa (3.2 %). The seedlings were re-irrigated by addition of differences in soil

water use and biomass production (Chaturvedi *et al.* 1988), and wastewater utilisation (Singh and Bhati 2003). But there is no work related to varying soil water stress in which sufficient availability of soil water (field capacity) occurs for a very short time. Such situation is often observed in drought prone arid region.

The objective of the present study was to monitor biomass production, its partitioning and adaptation changes in leaf water status, gas exchange, and water use efficiency (WUE) in *D. sissoo* seedlings at different soil water contents.

water content between -0.05 to -0.10 MPa (W<sub>1</sub> 20 mm), -0.10 to -0.50 MPa (W<sub>2</sub> 14 mm), -0.50 to -1.00 MPa (W<sub>3</sub> 10 mm), and -1.00 to -1.50 MPa (W<sub>4</sub> 8 mm) when the soil water content reached 7.4, 5.6, 4.3, and 3.2 % in the respective treatments. No irrigation was done in control (W<sub>5</sub>). The experiment was terminated in the first week of May 1999 when the seedlings of W<sub>5</sub> treatments suffered permanent wilting (4.2 mm, 0.56 % of the soil mass). At the time of treatment application, average seedling height and collar diameter were 52.00±1.80 and 0.40±0.08 cm, respectively.

**Growth:** The seedlings were harvested and roots were excavated carefully through putting the pot upside down at the time of experiment termination. Leaf, stem, and root were separated and fresh mass determined. These parts were dried at 80 °C.

**Physiological variables** were recorded when water content of the soil approached 7.4 % in W<sub>1</sub>, 5.6 % in W<sub>2</sub>, 4.3 % in W<sub>3</sub>, and 3.2 % in W<sub>4</sub> treatment. Leaf water potential ( $\Psi_l$ ) was recorded in triplicate at one month interval for each treatment using HR 33 T Dew Point micro-voltmeter (Logan, UT, USA). Observations were recorded during predawn ( $\Psi_{pd}$ ) between 05:00 to 07:00 and midday ( $\Psi_{mid}$ ) between 14:00 to 16:00 from January 1999 to May 1999.

$P_N$ ,  $E$ ,  $g_s$ , air temperature ( $T_a$ ), and leaf temperature ( $T_l$ ) were recorded in open system with portable CO<sub>2</sub> gas analyser, model CI-301 (CT-301 PS0; CID, Vancouver, USA).  $g_s$  was calculated as 1/stomatal resistance. The diurnal physiological observations were recorded in triplicate quarterly at 08:00, 10:00, 13:00, 15:00, and 17:00 and subsequently averaged to provide a mean value for each solar time in a month. All these observations were recorded on leaves of middle canopy of the seedlings. Self shading within the cuvette was minimised by ensuring that the leaves did not overlap, particularly in the seedlings of W<sub>3</sub>, W<sub>4</sub>, and W<sub>5</sub> treatments, the leaves of which were comparatively smaller than those in W<sub>1</sub> and W<sub>2</sub> treatments. Leaf to air temperature difference ( $T_{diff}$ )

was calculated using a difference between  $T_l$  and  $T_a$  at a particular time. Instantaneous WUE was calculated as  $P_N/E$ .

**Statistical analysis:** Physiological variables under different irrigation levels were analysed using a two-way analysis of variance. Irrigation level and solar time were the fixed effect and within treatment variations was the error term. Since the data were collected for five months, the data were also analysed by repeated measure using

## Results

**Environmental variables:** Rainfall was 237 mm and total pan evaporation was 2 109 mm during August 1998 to May 1999 showing high water deficit at the experimental site. Environmental variables varied within day and months. Mean monthly minimum and maximum air temperatures were 10.0 and 25.0 °C in January and increased gradually to 27.9 and 40.7 °C, respectively, in May. They increased from the lowest at 08:00 to 13:00 and decreased in the evening (17:00). Vapour pressure deficit (VPD) increased from 1 286 Pa (389 in morning to 2 183 Pa at midday) in January to 5 115 Pa (2 943 in morning to 7 753 Pa at midday) in May. Potential evapotranspiration fluctuated between 2.47 mm d<sup>-1</sup> in December to 8.54 mm d<sup>-1</sup> in May (Rao *et al.* 1971). Photosynthetically active radiation (PAR) increased from the lowest at 08:00 to midday (13:00) and decreased during the post dawn period. Maximum PAR oscillated between 1 060 µmol m<sup>-2</sup> s<sup>-1</sup> in January to 1 933 µmol m<sup>-2</sup> s<sup>-1</sup>

different physiological parameters as the dependent variable. Months were the between subject effect and the treatments and solar times were the within subject effect. Variations were the error term. Protected LSD was used as comparisons at a threshold  $p = 0.05$  to test for differences among treatments and solar times. Multiple regression technique was used to study relationships of  $\Psi_l$ ,  $P_N$ , and  $E$  with soil water availability and environmental variables.

in May.

**Biomass partitioning:** Irrigation levels affected total dry mass (DM) of seedlings (Table 1). The seedlings of  $W_1$  produced greater ( $p < 0.001$ ) biomass (100.5 g per seedling) than seedlings of other treatments. The  $W_3$  treatment caused 66 % reduction in DM when compared with the seedlings of  $W_1$ . Seedlings of  $W_5$  produced one tenth of total DM than those in  $W_1$  treatment. LSD indicated significantly ( $p < 0.05$ ) low DM in leaves for the seedlings of  $W_4$  and  $W_5$  treatments. Percent DM allocation to root was highest ( $p < 0.01$ ) in the seedlings of  $W_4$  and  $W_5$  treatments than in the remaining treatments. The allocation was high in leaf and stem for the seedling of  $W_2$ , in which allocation to root was the lowest. The stress became abruptly severe in the seedlings of  $W_5$  resulting in plant drying and leaf fall that affected leaf biomass.

Table 1. Effect of water stress on biomass production [g per seedling] of 215-d-old *Dalbergia sissoo* seedlings. Means±SE.  $W_1$ ,  $W_2$ ,  $W_3$ , and  $W_4$  are 20, 14, 10, or 8 mm irrigation levels and  $W_5$  is control (from 82.0 to 4.2 mm).  $p$  was always 0.001.

Parameter	$W_1$	$W_2$	$W_3$	$W_4$	$W_5$	F
Leaf	33.72±0.99	27.36±1.00	9.16±0.86	4.47±0.80	1.43±0.05	314.22
Stem	40.35±1.26	29.66±1.19	14.32±0.48	9.28±0.82	3.68±0.22	475.48
Root	26.52±0.94	18.78±0.68	11.83±0.50	12.48±1.00	5.00±0.31	121.85
Total	100.50±2.95	83.10±2.58	33.99±1.14	26.25±2.05	10.20±0.59	331.05

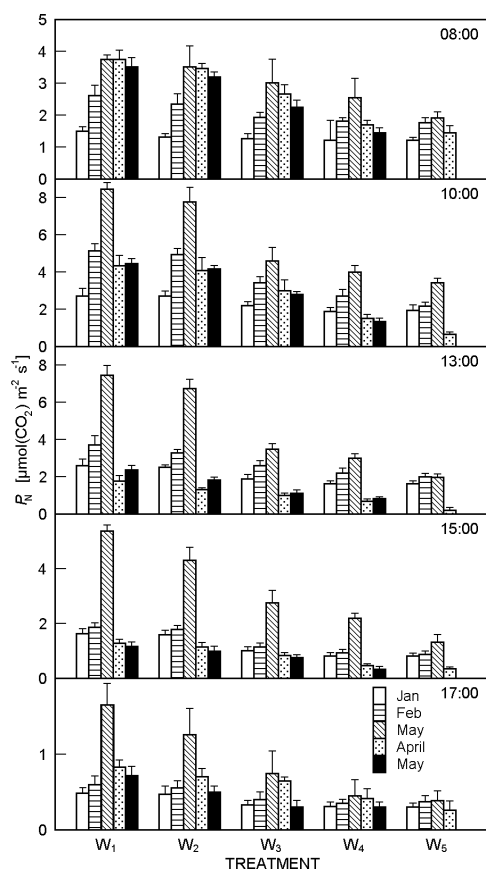
**Water relations:**  $\Psi_l$  decreased due to low irrigation and high VPD during April and May 1999. Seedling of  $W_1$  maintained the highest  $\Psi_l$ . With increasing soil water stress from  $W_1$  to  $W_2$ , the drops in  $\Psi_{pd}$  and  $\Psi_{mid}$  were not appreciable ( $p > 0.05$ ) but they decreased by 14 and 27 % at  $W_3$  and 21 and 34 % in  $W_4$  in January. However, they declined by 39 and 50 % in  $W_3$  and by 43 and 61 % in  $W_4$  during April. For the seedlings of the  $W_5$  treatment, the decline in  $\Psi_{mid}$  was comparable to  $\Psi_{pd}$  ( $p > 0.05$ ). The  $\Psi_{pd}$  was higher than  $\Psi_{mid}$  and the difference between these two increased from 0.04 MPa in January to 0.67 MPa in May for the seedling of  $W_1$ , whereas it was 0.22 MPa in January to 1.52 MPa in May in  $W_4$  treatment (Table 2).

The differences between the seedlings of  $W_1$  and  $W_5$  treatments were 0.40 and 0.49 MPa in January and 1.33 and 1.55 MPa in March for the  $\Psi_{pd}$  and  $\Psi_{mid}$ , respectively.

The initial difference of 0.13 MPa between  $\Psi_{pd}$  and  $\Psi_{mid}$  increased to 1.24 MPa in April ( $\Psi_s < -1.96$  MPa) for the seedlings of  $W_5$  treatment. The reduction in both  $\Psi_{pd}$  and  $\Psi_{mid}$  was high after March (Table 2). The drastically low  $\Psi_l$  in  $W_5$  (soil water potential of  $< -1.96$  MPa) resulted in permanent wilting and defoliation of newly formed leaf, which dried and abscised in May (soil water potential of  $-2.02$  MPa).

Table 2. Effect of soil water stress on predawn leaf water potential ( $\Psi_{pd}$ ) and midday leaf water potential ( $\Psi_{mid}$ ) of *Dalbergia sissoo* seedlings. Means $\pm$ SE of three replications of each month for each treatment.

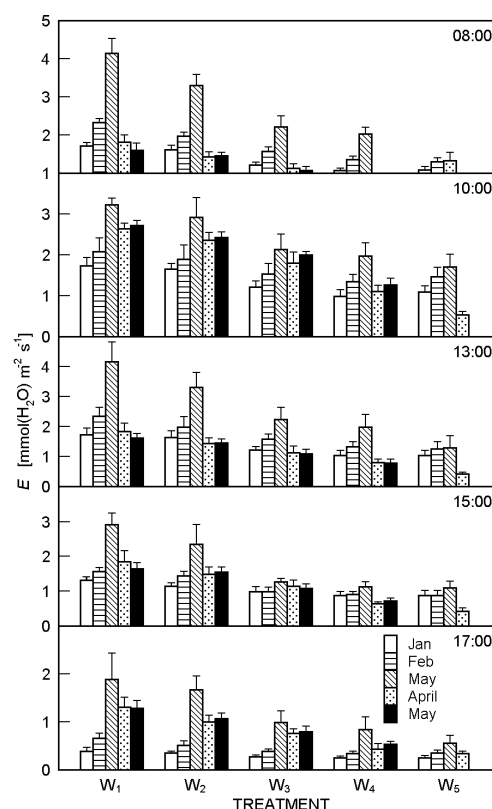
	Treatment	January	February	March	April	May
$\Psi_{pd}$ [-MPa]	W <sub>1</sub>	1.29 $\pm$ 0.10	1.56 $\pm$ 0.04	1.96 $\pm$ 0.07	2.13 $\pm$ 0.07	2.40 $\pm$ 0.07
	W <sub>2</sub>	1.36 $\pm$ 0.11	1.73 $\pm$ 0.07	2.25 $\pm$ 0.15	2.31 $\pm$ 0.21	2.84 $\pm$ 0.04
	W <sub>3</sub>	1.47 $\pm$ 0.07	1.96 $\pm$ 0.04	2.42 $\pm$ 0.11	2.78 $\pm$ 0.11	3.33 $\pm$ 0.07
	W <sub>4</sub>	1.56 $\pm$ 0.04	2.13 $\pm$ 0.07	2.68 $\pm$ 0.17	2.98 $\pm$ 0.17	3.42 $\pm$ 0.04
	W <sub>5</sub>	1.69 $\pm$ 0.08	2.36 $\pm$ 0.04	3.29 $\pm$ 0.08	5.42 $\pm$ 0.94	Dry
$\Psi_{mid}$ [-MPa]	W <sub>1</sub>	1.33 $\pm$ 0.07	1.64 $\pm$ 0.04	2.14 $\pm$ 0.15	2.68 $\pm$ 0.13	3.07 $\pm$ 0.14
	W <sub>2</sub>	1.51 $\pm$ 0.10	1.87 $\pm$ 0.07	2.46 $\pm$ 0.15	2.71 $\pm$ 0.10	3.60 $\pm$ 0.07
	W <sub>3</sub>	1.69 $\pm$ 0.10	2.18 $\pm$ 0.08	2.68 $\pm$ 0.04	3.37 $\pm$ 0.19	4.62 $\pm$ 0.17
	W <sub>4</sub>	1.78 $\pm$ 0.08	2.40 $\pm$ 0.07	3.20 $\pm$ 0.38	3.73 $\pm$ 0.28	4.93 $\pm$ 0.19
	W <sub>5</sub>	1.82 $\pm$ 0.10	2.67 $\pm$ 0.07	3.69 $\pm$ 0.39	6.66 $\pm$ 1.89	Dry

Fig. 1. Monthly changes in net photosynthetic rate ( $P_N$ ) in seedlings of *D. sissoo* irrigated at different levels of water and measured at 08:00, 10:00, 13:00, 15:00, and 17:00. Error bars are  $\pm$  SE.

**Gas exchange:**  $P_N$  was highest for the W<sub>1</sub> treatment. Compared to that in W<sub>1</sub>, the reduction in  $P_N$  was significant ( $p < 0.05$ ) for the seedlings at W<sub>3</sub>, W<sub>4</sub>, and W<sub>5</sub> treatments. It increased from January to March and decreased thereafter (Fig. 1) showing lowest value in May.  $P_N$  was highest at 10:00 except for the seedlings of W<sub>4</sub> and W<sub>5</sub> during April and May when it was highest at 08:00. However, the value of  $P_N$  was higher at 13:00 than

at the other solar times from January to March and at 08:00 from April to May except at 10:00. Lowest  $P_N$  was found at 17:00.

$E$  was high for the seedlings of W<sub>1</sub> treatment and decreased with decreasing irrigation (Fig. 2). The reduction in  $E$  ranged from non-significant ( $p > 0.05$ ) in January to highly significant ( $p < 0.01$ ) in May (particularly at 17:00).  $E$  increased up to March and decreased in April and May.  $E$  was reduced to  $< 10\%$  in the seedlings of W<sub>5</sub> compared to W<sub>1</sub> in April.  $E$  of seedlings at W<sub>1</sub>, W<sub>2</sub>, W<sub>3</sub>,

Fig. 2. Monthly changes in transpiration rate ( $E$ ) in the seedlings of *D. sissoo* irrigated at different levels of water and measured at 08:00, 10:00, 13:00, 15:00, and 17:00. Error bars are  $\pm$  SE.

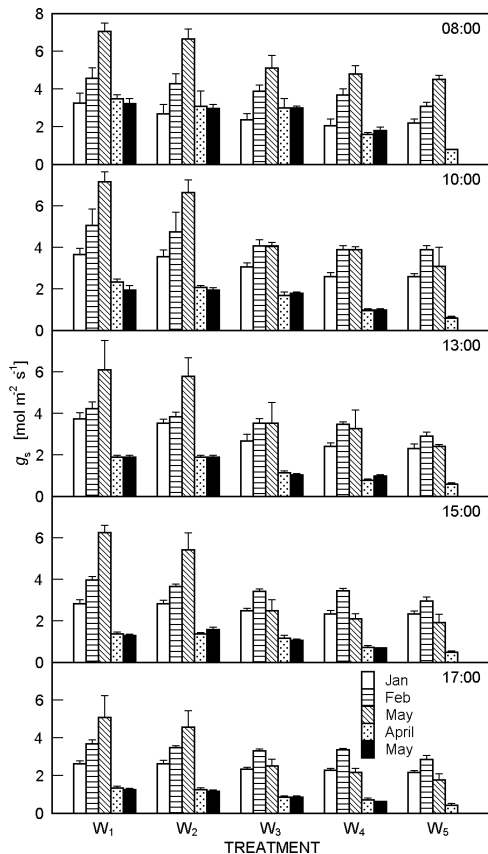


Fig. 3. Monthly changes in stomatal conductance ( $g_s$ ) in the seedlings of *D. sissoo* irrigated at different levels of water and measured at 08:00, 10:00, 13:00, 15:00, and 17:00. Error bars are  $\pm$  SE.

and  $W_4$  was highest at 13:00 until March whereas at 10:00 in April and May. For the seedlings of  $W_5$ ,  $E$  was the highest at 10:00 in all months except January (13:00).  $E$  decreased to the lowest value at 17:00.

$g_s$  followed similar trend like  $P_N$  and  $E$  (Fig. 3). It increased to maximum in March and decreased thereafter. Within the day, it was highest at 10:00 for the seedlings of  $W_1$ ,  $W_2$ ,  $W_3$ , and  $W_4$ , and at 08:00 for the seedlings of  $W_5$ . In April and May,  $g_s$  was highest at 08:00 for all the seedlings. In January, it was higher at 13:00 than at 08:00.  $g_s$  was the lowest at 17:00 but it did not differ significantly ( $p>0.05$ ) at 13:00 and 15:00.

**Leaf to air temperature differences** ( $T_{diff}$ ) increased both due to soil water stress from  $W_1$  to  $W_5$  and increasing  $T_a$  from January to May (Fig. 4). They were negative at 08:00 in January and February in the seedlings of all the treatments, i.e.  $T_l$  was lower than  $T_a$ . Negative  $T_{diff}$  was also observed at 17:00, but only in January. In all the other observations it was positive. The highest  $T_{diff}$  was in April and May. It was the highest at 13:00 except for  $W_1$  in January and  $W_4$  and  $W_5$  in February.

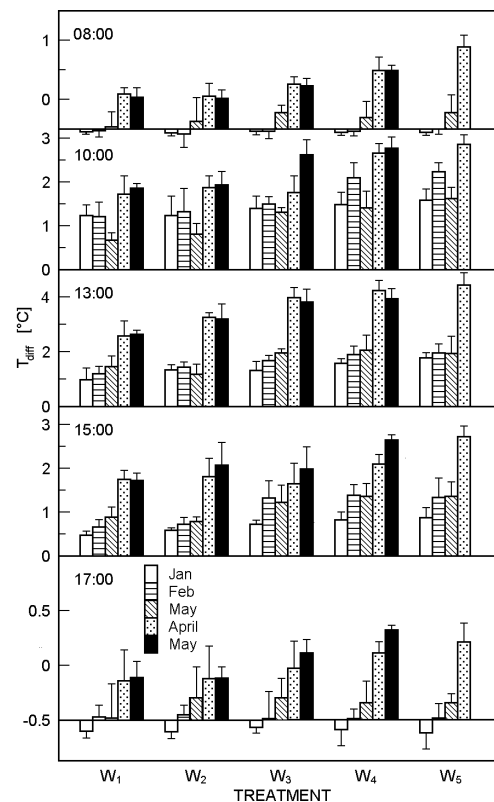


Fig. 4. Monthly changes in leaf to air temperature differences ( $T_{diff}$ ) in the seedlings of *D. sissoo* irrigated at different levels of water and measured at 08:00, 10:00, 13:00, 15:00, and 17:00. Error bars are  $\pm$  SE.

**Instantaneous WUE** did not differ ( $p>0.05$ ) due to different water stress (Fig. 5). WUE increased with soil water stress in January at 08:00, 10:00, and 17:00 and showed decreasing trend at 13:00 and 15:00. However, in the seedlings of  $W_5$  WUE continuously decreased. WUE was higher in  $W_2$  than in  $W_1$  but further increase in soil water stress led to decrease in WUE particularly in April and May when the vapour pressure deficit was high. Highest WUE was found at 08:00 except for the seedlings of  $W_1$ ,  $W_2$ , and  $W_3$  that had high WUE at 10:00 during February and March. The lowest WUE was at 17:00 for all the seedlings.

**Models:** Linear multiple regressions among predawn leaf water potential ( $\Psi_{pd}$ ), soil water content (SWC), and vapour pressure deficit (VPD) had the following equations:

$$\Psi_{pd} = -1.799 + 0.250 \text{ SWC} - 0.054 \text{ VPD} \quad (r^2 = 0.69, F = 165.67, \text{SEE} = 0.75)$$

The best equations for  $P_N$  and  $E$  at 10:00 are:

$$P_N = -3.304 + 0.399 \text{ SWC} - 0.212 \text{ VPD} + 0.008 \text{ PAR} \quad (r^2 = 0.51, F = 49.99, \text{SEE} = 1.37)$$

$$E = -0.268 + 0.170 \text{ SWC} - 0.031 \text{ VPD} + 0.002 \text{ PAR} \quad (r^2 = 0.55, F = 59.42, \text{SEE} = 0.50)$$

## Discussion

Soil water stress impaired physiological functions and biomass production. Significant reductions in total DM for the seedlings of  $W_3$  and onwards than those in  $W_1$  and  $W_2$  were due to decreased total production as a function of decreased leaf size and leaf area affecting carbon assimilation. Higher biomass in root than in leaf and stem in the seedlings of  $W_3$ ,  $W_4$ , and  $W_5$  treatments was probably because of higher allocation of assimilates to root with increasing soil water stress (Pallardy and Rhoads 1993). Bongarten and Teskey (1987) observed an increase in root biomass at the expense of stem biomass when the seedlings were exposed to repeated drought cycles. But in the present study, the percent increase in root biomass was at the expense of leaf biomass in  $W_1$  and at the expense of stem biomass in  $W_3$  seedlings. Lower percent root biomass in the seedlings of  $W_2$  than in the seedlings of other treatments may be due to photosynthates allocation in maximising leaf biomass at mild water stress (Table 1). However, at severe water stress, percent DM allocation to root increased with simultaneous decrease in biomass of leaf, which was more sensitive to water stress than the root. Higher total root DM

in  $W_1$  might be due to larger number of secondary and tertiary roots for absorption of sufficient water available in the system compared to that in the other treatments.

Decreased  $\Psi_l$  in *D. sissoo* seedlings with water stress increasing from  $W_1$  to  $W_5$  treatment was similar to observations in *Quercus pubescens* Willd growing in Mediterranean climate and showing strong relations with soil water availability (Tognetti *et al.* 1999). A difference of 0.04 to 0.22 MPa in  $\Psi_{pd}$  and  $\Psi_{mid}$  during January indicated low water loss (suppressed transpiration) but these differences increased to 0.50 MPa in  $W_1$  and >1.50 MPa in  $W_4$  and  $W_5$  seedlings suggesting that transpiration exceeds absorption. Such difference might be due to decrease in hydraulic conductance of soil-leaf continuum (increase in resistance in water flow in soil-plant-atmosphere continuum) because of decreased cell turgor (Ni and Pallardy 1990, Stiller *et al.* 2003). Gradual decline in  $\Psi_{pd}$  and  $\Psi_{mid}$  for the seedlings of  $W_1$  and  $W_2$  treatments with increasing PAR and VPD from January to May indicated significant relations of these environmental factors with the seedling water status. The large daily and monthly variations in  $\Psi_l$  suggest that *D. sissoo* is very sensible to changes in soil water content thereby showing moderate drought tolerance. It could be due to a relative inability of the stomata to restrict water loss at low soil water availability (Miller *et al.* 1993) like in *Q. robur* (Fort *et al.* 1997) and *Q. frainetto* (Fotelli *et al.* 2000).

Highest  $P_N$  and  $E$  for the seedlings of  $W_1$  and  $W_2$  treatment might be related with high  $\Psi_l$ ,  $g_s$ , and soil water content (SWC). Increased  $g_s$  probably enhanced  $CO_2$  diffusion into mesophyll cells resulting in high  $CO_2$  fixation and biomass compared to the seedlings of other treatments (Ni and Pallardy 1991). Negative relations of  $P_N$ ,  $\Psi_l$ , and  $E$  with soil water stress may be an indicator of drought tolerance behaviour in *D. sissoo* seedlings (Allen *et al.* 1999). Highest  $P_N$  at 10:00 was probably due to optimum environmental factors such as PAR and VPD. However, higher  $P_N$  at 13:00 during January and February and at 08:00 during April and May compared to the other times (except 10:00) suggest the negative effect of PAR that was high at 13:00 in April and May. Larger variations in  $P_N$  compared to  $E$  within the day and the months indicated that  $P_N$  was more sensitive to environment. Lower  $P_N$  than  $E$  at 15:00 and 17:00 suggested that *D. sissoo* seedling failed to restrict water loss through stomata that resulted in low WUE. This is supported by similar values of  $g_s$  at 13:00, 15:00, and 17:00. It might be due to an increase in  $T_l$  relative to  $T_a$  that increased vapour pressure gradient and water loss (Khairi and Hall 1976). It further suggests that non-stomatal factors played a major role in regulation of  $P_N$  and  $E$  during irradiation and high temperature. Low SWC for the  $W_3$  to  $W_5$  treatments might limit evaporative leaf cooling resulting in a high  $T_l$  and in higher  $T_{diff}$  than in the seedlings of  $W_1$  and

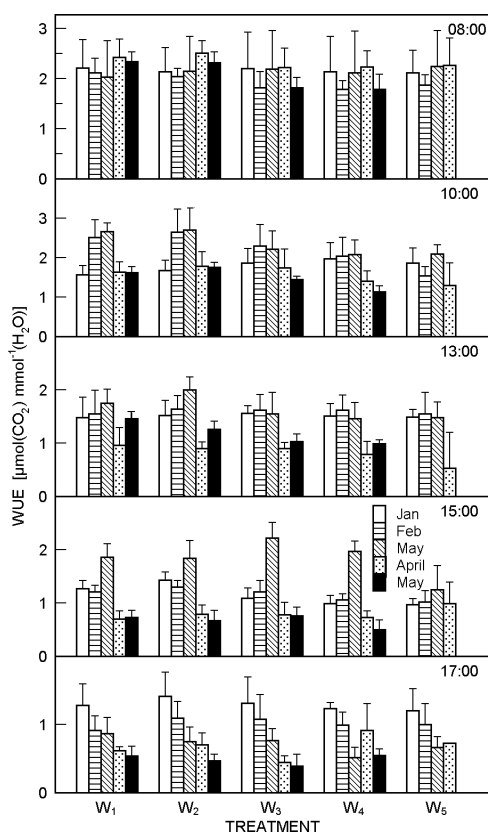


Fig. 5. Monthly changes in instantaneous water use efficiency (WUE) in the seedlings of *D. sissoo* irrigated at different levels of water and measured at 08:00, 10:00, 13:00, 15:00, and 17:00. Error bars are  $\pm$  SE.

W<sub>2</sub> treatments (Fig. 4). However, negative  $T_{diff}$  during January and February at 08:00 and 17:00 indicated higher uptake of soil water than the loss through transpiration as inferred by high  $\Psi_l$ .

Increased WUE for the seedlings of W<sub>2</sub> might be due to increase in  $P_N$  through utilisation of intercellular CO<sub>2</sub> by mesophyll cells which was more directly related to photosynthesis than to stomatal aperture (Teskey *et al.* 1986). These authors found an increase in gas phase limitation to photosynthesis in *Pinus taeda* L. when xylem pressure potential declined from -0.70 to -1.60 MPa. This was due to decrease in concentration of intercellular CO<sub>2</sub> and led in turn to increased WUE at mild water stress (Ni and Pallardy 1991). Increase in instantaneous WUE at mild water stress and significant decline at severe water stress support moderate drought tolerance of the species (Abril and Hanano 1998). However, decrease in WUE in severely soil water stressed seedlings of W<sub>4</sub> and W<sub>5</sub> particularly during April and May was due to increased air temperature, PAR, and VPD that induced water loss through transpiration (Miller *et al.* 1993) that limited biomass production. Low WUE in *Azadirachta indica* at low SWC might be due to increase in mesophyll resistance rather than by  $g_s$  (Pandey 1999). Midday depression in photosynthesis was also observed in other

species (Jifon and Syvertsen 2003) but transpiration either did not decrease or dropped much less under both low and high soil moisture. A weak negative relation of VPD with  $P_N$  and  $E$  was probably due to decreased  $P_N$  and  $E$  in April and May (Figs. 1 and 2). However, the observations are consistent with the results of Teskey *et al.* (1987) in which  $P_N$  increased initially with absolute humidity deficit (AHD) and decreased at high AHD.

Conclusively, *D. sissoo* seedlings are sensitive to both soil and environmental stresses and adapted to growing conditions. Biomass partitioning was higher in leaf at mild water stress and to root at severe water stress to tape water from the deeper layer. Higher  $P_N$ ,  $E$ , and  $g_s$  in seedlings of W<sub>1</sub> and W<sub>2</sub> than in the seedlings of W<sub>3</sub>, W<sub>4</sub>, and W<sub>5</sub> suggests that this species could be grown under sufficient to moderate irrigation (>50 % of field capacity) for high biomass production in arid areas. Significantly low  $\Psi_l$ ,  $P_N$ ,  $E$ , and  $g_s$  for the seedlings of W<sub>3</sub>, W<sub>4</sub>, and W<sub>5</sub> treatment is the indicator of low production and the strategy for survival. Our study shows that *D. sissoo* indicated significant adaptation changes to varying water stress. However, the response of this species was not significant in biomass production at severe soil water stress or during prolonged drought.

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