

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

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Abstract

Biomass, leaf water potential (Ψ_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 (Ψ_{pd}) and midday (Ψ_{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; Ψ_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⁻¹, 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⁻¹), phosphorus (10.01 mg kg⁻¹ P₂O₅), and potash (106 mg kg⁻¹ 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 (W₁ 20 mm), -0.10 to -0.50 MPa (W₂ 14 mm), -0.50 to -1.00 MPa (W₃ 10 mm), and -1.00 to -1.50 MPa (W₄ 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 (W₅). The experiment was terminated in the first week of May 1999 when the seedlings of W₅ 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 W₁, 5.6 % in W₂, 4.3 % in W₃, and 3.2 % in W₄ treatment. Leaf water potential (Ψ_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 (Ψ_{pd}) between 05:00 to 07:00 and midday (Ψ_{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 CO₂ gas analyser, model CI-301 (CT-301 PSO; 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 W₃, W₄, and W₅ treatments, the leaves of which were comparatively smaller than those in W₁ and W₂ treatments. Leaf to air temperature difference (T_{diff})

was calculated using a difference between T_1 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⁻¹ in December to 8.54 mm d⁻¹ 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 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in January to 1 933 $\mu\text{mol m}^{-2} \text{s}^{-1}$

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 Ψ_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 sever 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

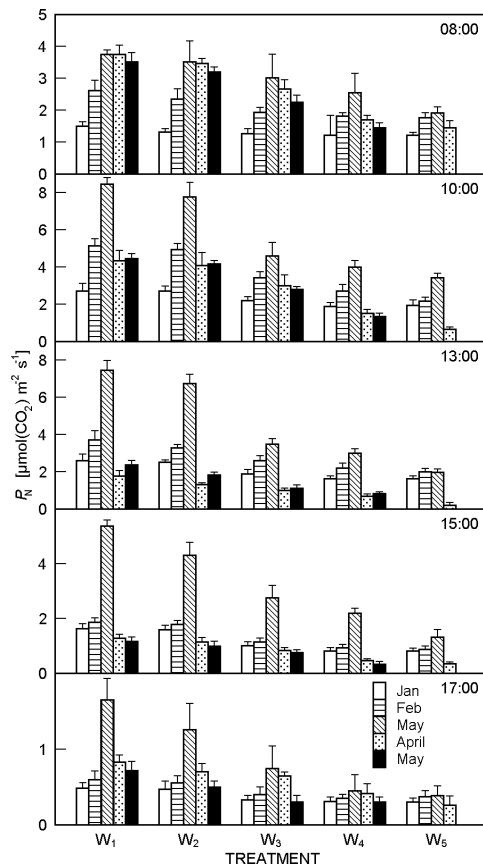
Water relations: Ψ_l decreased due to low irrigation and high VPD during April and May 1999. Seedling of W_1 maintained the highest Ψ_l . With increasing soil water stress from W_1 to W_2 , the drops in Ψ_{pd} and Ψ_{mid} were not appreciable ($p > 0.05$) but they decreased by 14 and 27 % at W_3 and 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 Ψ_{mid} was comparable to Ψ_{pd} ($p > 0.05$). The Ψ_{pd} was higher than Ψ_{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 Ψ_{pd} and Ψ_{mid} , respectively.

The initial difference of 0.13 MPa between Ψ_{pd} and Ψ_{mid} increased to 1.24 MPa in April ($\Psi_s < -1.96$ MPa) for the seedlings of W_5 treatment. The reduction in both Ψ_{pd} and Ψ_{mid} was high after March (Table 2). The drastically low Ψ_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 (Ψ_{pd}) and midday leaf water potential (Ψ_{mid}) of *Dalbergia sissoo* seedlings. Means \pm SE of three replications of each month for each treatment.

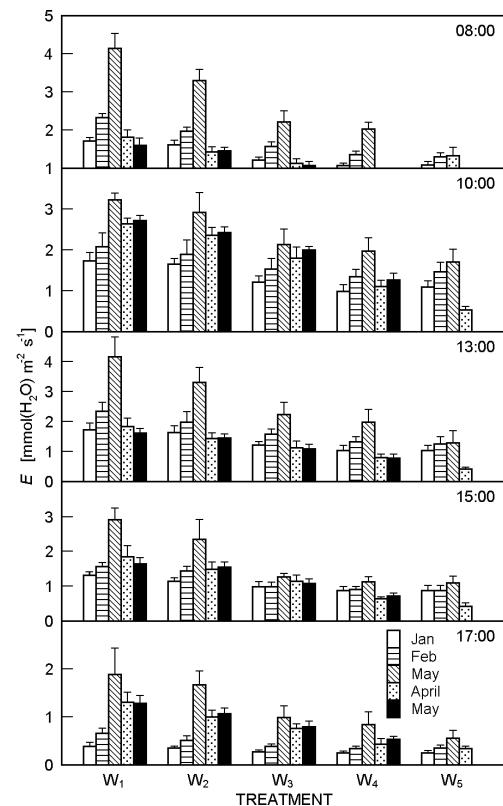
	Treatment	January	February	March	April	May
Ψ_{pd} [-MPa]	W ₁	1.29 \pm 0.10	1.56 \pm 0.04	1.96 \pm 0.07	2.13 \pm 0.07	2.40 \pm 0.07
	W ₂	1.36 \pm 0.11	1.73 \pm 0.07	2.25 \pm 0.15	2.31 \pm 0.21	2.84 \pm 0.04
	W ₃	1.47 \pm 0.07	1.96 \pm 0.04	2.42 \pm 0.11	2.78 \pm 0.11	3.33 \pm 0.07
	W ₄	1.56 \pm 0.04	2.13 \pm 0.07	2.68 \pm 0.17	2.98 \pm 0.17	3.42 \pm 0.04
	W ₅	1.69 \pm 0.08	2.36 \pm 0.04	3.29 \pm 0.08	5.42 \pm 0.94	Dry
Ψ_{mid} [-MPa]	W ₁	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 ₂	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 ₃	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 ₄	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 ₅	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 W₁ treatment. Compared to that in W₁, the reduction in P_N was significant ($p<0.05$) for the seedlings at W₃, W₄, and W₅ 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 W₄ and W₅ 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 W₁ 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 W₅ compared to W₁ in April. E of seedlings at W₁, W₂, W₃,

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.

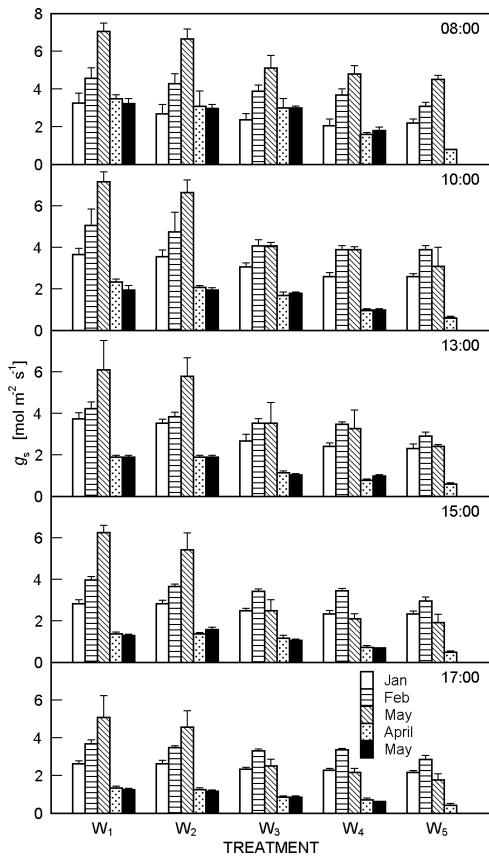


Fig. 3. Monthly changes in stomatal conductance (g_s) in the seedlings of *D. sissoo* irrigated at different levels of water and measured at 08:00, 10:00, 13:00, 15:00, and 17:00. Error bars are \pm SE.

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.

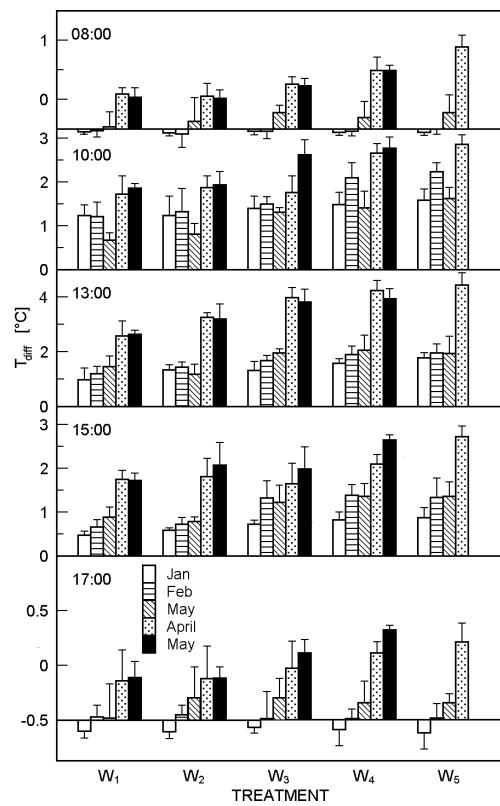


Fig. 4. Monthly changes in leaf to air temperature differences (T_{diff}) in the seedlings of *D. sissoo* irrigated at different levels of water and measured at 08:00, 10:00, 13:00, 15:00, and 17:00. Error bars are \pm SE.

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_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 (Ψ_{pd}), soil water content (SWC), and vapour pressure deficit (VPD) had the following equations:

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

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

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

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

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 Ψ_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 Ψ_{pd} and Ψ_{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 Ψ_{pd} and Ψ_{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 Ψ_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 Ψ_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 , Ψ_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

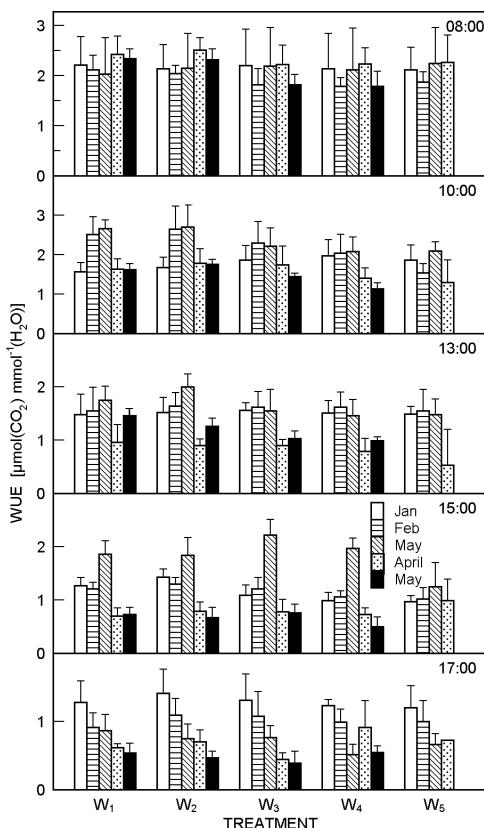


Fig. 5. Monthly changes in instantaneous water use efficiency (WUE) in the seedlings of *D. sissoo* irrigated at different levels of water and measured at 08:00, 10:00, 13:00, 15:00, and 17:00. Error bars are \pm SE.

W_2 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 Ψ_l .

Increased WUE for the seedlings of W_2 might be due to increase in P_N through utilisation of intercellular CO_2 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_2 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_4 and W_5 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 take water from the deeper layer. Higher P_N , E , and g_s in seedlings of W_1 and W_2 than in the seedlings of W_3 , W_4 , and W_5 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 Ψ_l , P_N , E , and g_s for the seedlings of W_3 , W_4 , and W_5 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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