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BRIEF COMMUNICATION

Growth and leaf gas exchange characteristics in *Dalbergia sissoo* Roxb. and *D. latifolia* Roxb. under water deficit

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Abstract

Forty two-month-old plants of *Dalbergia sissoo* and *D. latifolia* were subjected for 56 d to water deficit induced by withholding water. Drought stress caused a significant reduction in plant height, stem diameter, net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) in both species, but the reduction was greater in *D. sissoo* than in *D. latifolia*. Water use efficiency (P_N/E) was adversely affected due to water stress only in *D. latifolia*, and intrinsic water use efficiency (P_N/g_s) was increased in both species. There was a slight effect of water stress on variable to maximum fluorescence (F_v/F_m) (quantum yield of photosystem 2) in both species, but the species did not differ significantly in this attribute.

Additional key words: net photosynthetic rate; stomatal conductance; transpiration; water use efficiency.

Dalbergia sissoo is a large deciduous tree with very hard wood. It grows to a fairly large size reaching a height of 24 m or more and in girth much over 1.9 m. The wood of the tree is very useful because it is very durable, seasons well, and does not wrap or split. Because of these properties the *Dalbergia* wood is extensively used for boat building, carts, carriages, agricultural implements, and furniture. Another similar tree *Dalbergia latifolia* has gained ground on account of its high quality wood like that of *D. sissoo*. However, unlike *D. sissoo* it grows tall and straight and reaches a height of 30 m (Prasad and Shilalingadaradhya 1988). The main use of its wood is for furniture. Despite considerable importance of these two trees the information on their comparative drought tolerance is not available in the literature. Thus the primary objective of the present study was to assess the comparative drought tolerance of the two tree species. An attempt was made to establish whether or not the growth responses of the two trees under drought were attributable to their high photosynthetic capacity and water use efficiency (WUE). Photosynthetic capacity in plants is the major component of dry matter productivity. The final biological or economical yield can be enhanced either by increasing photosynthetic rate, by minimizing wasteful respiration, or by optimizing assimilate partitioning (Lawlor 1995).

Drought is the most important abiotic stress, which limits photosynthesis thereby limiting plant productivity (*e.g.* Lawlor and Cornic 2002, Tezara *et al.* 2002). A general decline in net photosynthetic rate (P_N) is due to closure of stomata and/or inhibition in the activity of appropriate enzymes involved in photosynthesis. Thus in the present study relationships were drawn between growth of the two trees and their P_N and other gas exchange attributes such as stomatal conductance (g_s), transpiration rate (E), and WUE under water deficit.

The experimental 42-month-old plants of *Dalbergia sissoo* Roxb. and *D. latifolia* Roxb. were raised from seeds in February 1999 in two separate fields adjacent to each other at the Punjab Forestry Research Institute Faisalabad, Pakistan (latitude 31°30'N, longitude 73°10'E, and altitude 213 m). Agronomic practices and irrigations were the same for both species. The soil was clay loam with pH = 7.76 and electrical conductivity of the saturation paste = 1.40 dS m^{-1}.

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In August 2002, 15 plants of each species were well watered (control), whereas another set of 15 plants were drought treated by withholding water for 8 weeks.

Plant height, stem diameter, and physiological parameters of both well-watered and drought-treated plants of both species were measured 8 weeks after the start of drought treatment.

Determination of chlorophyll (Chl) content was carried out following the method of Arnon (1949). Absorbance of the extracts was measured at 652 and 663 nm using a spectrophotometer U-2000 (*Hitachi Instruments*, Tokyo, Japan). Instantaneous measurements of P_N, E, and g_s were made on two fully expanded youngest attached leaves of each plant using an open system portable infrared gas analyzer LCA-4 (*Analytical Development Company*, Hoddesdon, England). Measurements were performed from 10:00 to 11:30 with the following conditions: molar flow of air per unit leaf area 407.8 mmol m^{-2} s^{-1}, atmospheric pressure 98.4 kPa, water vapour pressure inside chamber 1 120–1 220 Pa, photosymthetic photon flux density (PPFD) at leaf surface was maximum up to 1 280 μmol m^{-2} s^{-1}, temperature of leaf was maximum up to 40.4 °C, ambient temperature ranged between 37.3–39.8 °C, ambient CO_2 concentration was 351.8 μmol mol^{-1}. Non-variable fluorescence (F_0), variable fluorescence (F_v), maximal fluorescence (F_m), and photochemical efficiency of photosystem 2 (PS2) (F_v/F_m) were measured using a portable Plant Efficiency Analyzer (*Hansatech Instruments*, Kings Lynn, England). The same attached leaves as used for the measurement of gas exchange attributes were used for measuring all the fluorescence parameters. A measuring radiation of 30 % was set in the instrument.

Analysis of variance of data for all the parameters was computed using *COSTAT* computer package (*CoHort Software*, Berkeley, USA). The least significant differences between the mean values were calculated following Snedecor and Cochran (1980).

Water deficit conditions imposed for 56 d to 42-month-old plants of two *Dalbergia* species had a significant inhibitory effect ($p < 0.001$) on increase in plant height and stem diameter (Table 1). Species differed significantly for these two variables. Increase in plant height and stem diameter was larger in *D. latifolia* than in *D. issoo* under water deficit (Table 1).

Drought had a significant adverse effect on P_N, g_s, and E of both *Dalbergia* species (Table 1). The species differed significantly in these gas exchange attributes. *D. latifolia* had significantly higher P_N, g_s, and E than *D. issoo* under water deficit. WUE, estimated as P_N/E, was not affected in *D. sissoo*, but there was a marked reduction in this attribute in *D. latifolia* (Table 1). Water stress caused a significant increase in intrinsic WUE (P_N/g_s) in both species, but this increase was more marked in *D. sissoo* than in *D. latifolia* (Table 1). Although there was a slight decrease in sub-stomatal CO_2/ambient CO_2 ratio (C_i/C_a) in both species, the species did not differ significantly in this attribute (Table 1).

Drought stress did not cause any significant effect on Chl *a* and Chl *b* contents, and Chl *a*/*b* ratio, and the species did not differ significantly in these pigments (Table 1). Water stress imposed caused significant changes in different fluorescence parameters in both species (Table 1). F_0 was slightly higher in both species under drought treatment than in the control. F_v remained unaffected in *D. sissoo* under drought stress, whereas that in *D. latifolia* decreased significantly (Table 1). In contrast, F_m was significantly lower in *D. latifolia* than that in *D. sissoo* under water stress. There was a slight decrease of F_v/F_m, and the species did not differ significantly in this attribute (Table 1).

The results for different growth parameters revealed that *D. latifolia* was superior to *D. sissoo* in tolerating drought stress. The relatively more drought tolerant *D. latifolia* had also higher P_N than the drought sensitive *D. sissoo* under water deficit. The strong positive association between growth and P_N observed here is parallel to what has earlier been observed in different crop species, *e.g.* in spinach (Robinson *et al.* 1983), *Phaseolus vulgaris* (Seemann and Critchley 1985), *Vigna mungo* (Chandra Babu *et al.* 1985), *Zea mays* (Crosbie and Pearce 1982), *Gossypium hirsutum* (Pettigrew and Meredith 1994), *Gossypium barbadense* (Cornish *et al.* 1991), and asparagus (Faville *et al.* 1999).

Stomatal closure is one of the earliest responses of plants to water stress, and it is the main cause for drought-induced suppression in photosynthesis, because stomatal closure in plants decreases CO_2 diffusion into leaf thereby perturbing photosynthesis (Cornic and Massacci 1996, Flexas *et al.* 1999). In a study with grapevine, Flexas *et al.* (2002) reported that stomatal regulation was the major factor limiting photosynthesis under drought stress. Similarly, a positive relationship between g_s and P_N was earlier observed in fig and peach trees (Clifford *et al.* 1997). Our results for P_N and g_s for two *Dalbergia* species showed a positive relationship because both characteristics were higher in drought tolerant *D. latifolia* than in drought sensitive *D. sissoo* under drought stress, although these two attributes declined markedly under water deficit conditions.

E declined markedly in both the tree species under water limiting conditions, but the reduction was greater in *D. sissoo* than in *D. latifolia*, although the reverse was true in intrinsic WUE (P_N/g_s). The higher *E* in *D. latifolia* was responsible for lowering its WUE (P_N/E). Thus WUE and P_N were not positively correlated in the two *Dalbergia* species. This is in contrast to what has already been found in the C_4 dicot *Amaranthus retroflexus* (Sage and Pearcy 1987) and sugarcane (Ranjith and Meinzer 1997).

Drought stress perturbs photosynthesis due to either reduced g_s or inhibition of appropriate metabolic phenomena or combination of both (Lawlor 1995, Flexas *et al.* 1999, Ashraf 2001). But the data for C_i/C_a showed

Table 1. Different growth and photosynthesis related attributes of *Dalbergia sissoo* and *D. latifolia* when 42 month-old plants were subjected for 56 d to water deficit. Means ± SE. Means with the same letters in each column (a and b) did not differ significantly at the 5 % level. Only values for *E* in *D. latifolia* and P_N/E and F_v and F_m for *D. sissoo* did not differ significantly under well watered and stressed conditions. LSD values at 5 % significance are given for species × treatments. NS = non-significant.

Attribute	Species	Well watered (control)	Water deficit
Increase in plant height [cm]	*D. sissoo*	25.41 ± 4.11a	12.63 ± 1.68a
	D. latifolia	23.52 ± 3.83a	17.54 ± 2.74b
		LSD = 3.52	
Increase in stem diameter [cm]	*D. sissoo*	1.12 ± 0.18 a	0.84 ± 0.041 a
	D. latifolia	1.20 ± 0.11 b	0.96 ± 0.062 b
		LSD = 0.07	
Chlorophyll *a* [g kg^{-1}(f.m.)]	*D. sissoo*	0.504 ± 0.091	0.499 ± 0.062
	D. latifolia	0.487 ± 0.070	0.492 ± 0.084
		LSD = NS	
Chlorophyll *b* [g kg^{-1} (f.m.)]	*D. sissoo*	0.293 ± 0.031	0.294 ± 0.036
	D. latifolia	0.297 ± 0.023	0.288 ± 0.046
		LSD = NS	
Chlorophyll *a/b*	*D. sissoo*	1.72 ± 0.24	1.70 ± 0.23
	D. latifolia	1.64 ± 0.19	1.71 ± 0.18
		LSD = NS	
Net photosynthetic rate (P_N) [µmol(CO_2) m^{-2} s^{-1}]	*D. sissoo*	11.29 ± 1.12a	1.54 ± 0.15a
	D. latifolia	9.48 ± 0.98a	3.65 ± 0.31b
		LSD = 1.86	
Transpiration (E) [mmol(H_2O) m^{-2} s^{-1}]	*D. sissoo*	2.05 ± 0.12 a	0.27 ± 0.02 a
	D. latifolia	2.08 ± 0.15 a	1.17 ± 0.03 b
		LSD = 0.58	
Stomatal conductance (g_s) [mmol m^{-2} s^{-1}]	*D. sissoo*	588.0 ± 48.4a	27.2 ± 3.01a
	D. latifolia	449.0 ± 32.8b	115.0 ± 8.90b
		LSD = 72.6	
Water-use efficiency (P_N/E) [µmol(CO_2) mmol^{-1}(H_2O)]	*D. sissoo*	5.51 ± 0.32a	5.70 ± 0.51a
	D. latifolia	4.56 ± 0.41a	3.12 ± 0.28b
		LSD = 1.08	
Intrinsic water-use efficiency (P_N/g_s) [µmol mmol^{-1}]	*D. sissoo*	0.019 ± 0.001a	0.057 ± 0.005a
	D. latifolia	0.021 ± 0.002a	0.032 ± 0.004b
		LSD = 0.008	
Substomatal CO_2/ambient CO_2 ratio (c_i/c_a)	*D. sissoo*	0.68 ± 0.092	0.61 ± 0.11
	D. latifolia	0.80 ± 0.094	0.71 ± 0.13
		LSD = NS	
F_0	*D. sissoo*	368.0 ± 29.3a	423.7 ± 40.8a
	D. latifolia	319.4 ± 33.4b	410.0 ± 38.3a
		LSD = 41.3	
F_v	*D. sissoo*	1245.2 ± 101.6a	1289.3 ± 131.8a
	D. latifolia	1261.6 ± 122.7a	1038.1 ± 104.7b
		LSD = 98.7	
F_m	*D. sissoo*	1607.2 ± 98.6a	1717.7 ± 141.9a
	D. latifolia	1561.0 ± 105.7a	1382.8 ± 112.4b
		LSD = 167.4	
F_v/F_m	*D. sissoo*	0.771 ± 0.052a	0.656 ± 0.034a
	D. latifolia	0.774 ± 0.041a	0.705 ± 0.026a
		LSD = 58.6	

that the sub-stomatal concentration decreased uniformly in both *Dalbergia* species under drought stress. This suggests that the decline in photosynthesis in both species to some extent occurred through stomatal closure.

Similarly, Flexas *et al.* (2002) have also reported a reduction in sub-stomatal CO_2 concentration in grapevine due to water stress.

Drought stress causes drastic changes in Chl fluorescence in many plant species. The thylakoid related photochemical activities decline under water deficit with PS2 being more drought sensitive than photosystem 1 (Dubey 1997). The decline in PS2 activity under water stress might not be due to the direct effect of stress on photochemical activity but due to photoinhibition. Flexas *et al.* (1999) found that water stress did not cause photoinhibition in grapevine. In contrast, in our study F_v declined considerably in *D. latifolia* due to water stress, but F_v/F_m (photochemical efficiency of PS2) values declined uniformly in both *Dalbergia* species reflecting that photoinhibition occurred in both species. This may have been one of the major factors for decline in overall rate of photosynthesis in both tree species.

Chl *a* and *b* contents and Chl *a*/*b* ratio remained unaffected in both species due to water stress. This is in contrast to some earlier studies reflecting that Chl *a/b* under water deficit increases in most crop species (García *et al.* 1987, Estill *et al.* 1991).

In conclusion, *D. latifolia* maintained higher growth as compared to *D. sissoo* under water deficit. The differential growth of two *Dalbergia* species was strongly associated with their different P_N, E, and g_s, but not with P_N/E under drought stress. Decline in P_N in both species under drought stress was due to both stomatal and non-stomatal limitations, although photoinhibition in PS2 also seemed to have played some role in this decline.

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