PHOTOSYNTHETICA 35 (2): 279-283, 1998

BRIEF COMMUNICATION

Effect of water stress on photosynthesis in two mulberry genotypes with different drought tolerance

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Abstract

Three-month-old mulberry (*Morus alba* L.) cultivars (drought tolerant S13 and drought sensitive S54) were subjected to water stress for 15 d. Water stress decreased the leaf water potential, net photosynthetic rate (P_N), and stomatal conductance (g_s) in both the cultivars. However, the magnitude of decline was comparatively greater in the sensitive cultivar (S54). Intercellular CO_2 concentration (C_i) was unaltered during mild stress, but significantly increased at severe stress in both cultivars. The photosystem 2 activity significantly declined only at a severe stress in both cultivars. The C_i/g_s ratio representing the mesophyll efficiency was greater in the tolerant cultivar S13. Involvement of stomatal and/or non-stomatal components in declining P_N depended on the severity and duration of stress. However, the degree of non-stomatal limitations was relatively less in the drought tolerant cultivar.

Additional key words: C_i/g_s ratio; cultivar differences; intercellular CO_2 concentration; *Morus alba;* net photosynthetic rate; photosystem 2, stomatal conductance.

Drought can severely reduce photosynthesis. The nature and extent of water stress effects are a function of the intensity and duration of the stress, as well as the genetically determined capacity of species to cope with the environment. Breeding for tolerance to drought relies primarily in the identification of proper traits among genotypes and their inheritance (Blum 1988). The inhibition in P_N under moderate water stress was demonstrated by Kaiser (1987), Chaves (1991), and Ramanjulu and Sudhakar (1998). The initial limitation on photosynthesis during water stress is

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Received 1 August 1997, *accepted* 5 November 1997.

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Abbreviations: C_i - intercellular CO_2 concentration; g_s - stomatal conductance; P_N - net photosynthetic rate; PS2 - photosystem 2; Ψ_w - water potential.

Acknowledgements: S.R. is grateful to the Council of Scientific and Industrial Research, New Delhi for awarding Research Associateship. We thank Dr. G. Rajendrudu, Department of Botany, S.V. University, Tirupati for extending IRGA facility.

believed to be stomatal restriction of CO_2 availability (Chaves 1991, Cornic *et al.* 1992). However, as leaf water potential (Ψ_w) decreases further, non-stomatal limitations occur (Renou *et al.* 1990), the extent of which is varied with stress severity and genotype's ability (Weng 1993, Gunasekera *et al.* 1994). Stomatal restriction of CO_2 uptake may not be the only determinant of reduced photosynthetic activity during the initial stages of drought. A recent analysis revealed that stomatal control of photosynthesis accounted for less than 50 % of changes in carbon fixation under water stress (Ni and Pallardy 1992). In the present study we try to assess the tolerance potentials based on photosynthetic rate and its associated parameters in two mulberry cultivars differing in sensitivity to water stress.

The mulberry *(Morus alba* L.) cultivars were classified as drought tolerant (S13) and drought sensitive (S54). Cuttings 12 to 15 cm long, of 8 to 10 mm diameter with 3 to 4 active buds were planted in earthen pots containing 5 kg of air-dried red soil and farm yard manure in 3 : 1 proportion. Pots were watered daily for 3 months under natural photoperiod in the botanical garden. Pots of each cultivar were then divided into 4 sets and arranged in complete randomized block design. One set of pots received water daily to field capacity and served as control. Water stress induced by adding water daily to 75, 50, and 25 % of field capacity was characterized as mild, moderate, and severe, respectively. Experimental values were collected on days 5, 10, and 15 after stress induction.

The leaf Ψ_w was measured by a *PR55* psychrometer (*Wescor*, Logan, USA). P_N, g_s, and C_i were measured between 08:00 and 10:00 h by a portable photosynthesis system, *LCA-3* (*ADC*, UK) using the *Parkinson* leaf chamber (6.2 cm^2), under irradiance of 1100 ± 100 $\mu mol\ m^{-2}\ s^{-1}$ and temperature of 32 ± 2 °C. The 3rd fully expanded leaf (from top) was measured as this leaf possesses maximum P_N (Lakshmi *et al.* 1996, Ramanjulu and Sudhakar 1998). The 1,6-dichlorophenol indophenol (DCPIP) reduction in isolated chloroplasts was estimated according to Sudhasundari and Raghavendra (1990).

Water stress caused a decline in P_N in both the cultivars (Table 1). P_N decreased linearly with increasing severity and duration of stress (mild stress did not cause an appreciable inhibition in P_N of both cultivars). The P_N was reduced by 68 and 86 % on the 15th day of exposure in cultivars S13 and S54, respectively, at severe stress treatment. Genotypic variations in P_N of several stressed-crop plants were evident from the studies of Weng (1993), Gunasekera *et al.* (1994), and Kicheva *et al.* (1994). The drought tolerance in cultivars studied was well correlated with their capacity to maintain relatively high P_N under drought stress.

Moderate and severe stress treatments significantly decreased the g_s in both cultivars (Table 1) (mild stress did not). However, the g_s was reduced more in S54 than in S13. Genotypic variation in stomatal response to water deficits has been demonstrated by Quarrie (1982), who connected it with genetic difference in the capacity to produce abscisic acid. A strong correlation between g_s and P_N represents an adjustment of g_s to match the genotype intrinsic photosynthetic capacity under stress.

The C_i values were almost unaltered under mild stress and only slightly increased under moderate stress (Table 1). However, they were significantly increased under severe stress in both cultivars. Nevertheless, the increase was greater in S54 compared to S13. Kicheva *et al.* (1994) take the occurrence of high C_i values at reduced g_s under water stress as an indication of non-stomatal limitation to photosynthesis. Partial stomatal closure at moderate water stress did not cause a decline in C_i in both cultivars, which suggested that at this level of drought stress, stomatal constraints prevailed over the non-stomatal effects. Severe stress treatment resulted in increased C_i in both cultivars; this may indicate a decreased carboxylation efficiency (non-stomatal limitations prevailed under severe water stress).

The reduced P_N during water deficits can also be attributed to impairment of the primary photosynthetic machinery. According to He *et al.* (1995), water stress affects directly the photochemical events largely by affecting photosystem 2 (PS2) activity both by degradation of D1 and D2 proteins of PS2 reaction centre and retarded synthesis of these proteins, which leads to lowered electron transport. However, some investigations confirm the drought-tolerant nature of PS2 (Kaiser 1987, Chaves 1991, Kicheva *et al.* 1994, Fedina and Popova 1996). In the present study, PS2 activity was significantly inhibited only under severe stress (Table 1), and a greater magnitude of inhibition of PS2 activity was noticed in S54 than S13.

Table 1. Time-modified effects of water stress on leaf water potential, Ψ_w [-MPa], net photosynthetic rate, P_N [μmol m^{-2} s^{-1}], stomatal conductance, g_s [mmol m^{-2} s^{-1}], intercellular CO$_2$ concentration, C_i [μmol mol^{-1}], photosystem 2 (PS2) activity [mmol kg^{-1}(Chl) s^{-1}], and C_i/g_s ratio in mulberry genotypes S54 and S13. The mean values ($n = 6$) in a row followed by a different letter for each cultivar are significantly different ($p \leq 0.05$) according to Duncan's multiple range (DMR) test.

	Day	S54				S13			
		control	mild	moderate	severe	control	mild	moderate	severe
Ψ_w	5	0.72a	0.79b	1.08c	1.31d	0.83a	0.88a	1.08b	1.27c
	10	0.74a	0.90b	1.82c	2.41	0.85a	0.96b	1.57c	2.04d
	15	0.72a	0.96b	2.58c	3.14d	0.86a	0.98b	2.15c	2.81d
P_N	5	11.40c	11.20c	8.20b	3.80a	11.20c	11.20c	9.30b	6.10a
	10	11.40c	11.00c	6.80b	2.30a	11.40c	11.40c	8.60b	4.60a
	15	11.20c	11.00c	5.40b	1.50a	11.40c	11.40c	8.20b	3.60a
g_s	5	0.62c	0.59c	0.40b	0.31a	0.59c	0.59c	0.44b	0.37a
	10	0.70c	0.66c	0.33b	0.28a	0.62c	0.62c	0.41b	0.33a
	15	0.75c	0.72c	0.30b	0.18a	0.66c	0.66c	0.40b	0.20a
C_i	5	233a	233a	242a	269b	230a	230a	238a	253b
	10	236a	236a	251a	295b	232a	232a	242a	269b
	15	236a	236a	267b	318c	234a	234a	244a	280b
PS2	5	70.20b	69.49b	68.70b	40.71a	69.40b	69.40b	68.70b	55.52a
	10	70.60b	69.89b	67.77b	31.06a	68.80b	68.80b	68.11b	47.77a
	15	68.70b	68.70b	64.60b	17.68a	66.50b	66.50b	65.83b	31.92a
C_i/g_s	5	3.75	3.96	6.05	8.67	3.89	3.89	5.40	6.83
	10	3.37	3.57	7.60	10.53	3.74	3.93	5.90	8.15
	15	3.14	3.27	8.90	17.66	3.54	3.71	6.10	14.00

P_N is under the control of both stomatal and mesophyll factors. The stomatal factors can be directly measured, and the estimation of mesophyll factors can be determined by the P_N/C_i curve. In this context, Seshashayee *et al.* (1996) and Ramanjulu and Sudhakar (1997) have suggested the ratio of C_i/g_s as a parameter to determine the non-stomatal limitations to photosynthesis. Increase in this ratio reflects the decreased mesophyll efficiency. The C_i/g_s ratio increased particularly under moderate and severe stresses in both genotypes (Table 1). Changes in this ratio further support the drought tolerance of S13.

The drought tolerance of S13 could be ascertained from the present study, based on relatively smaller decrease in P_N and g_s coupled with smaller increase in C_i. The PS2 activity and the C_i/g_s ratio also supported the tolerant nature of S13. The better performance of S13 during drought stress may also be related to the better osmotic adjustment as reported by Weng (1993) and Gunasekera *et al.* (1994). The degree of accumulation of osmolytes contributing to osmotic adjustment was varied among these mulberry genotypes, and S13 accumulated during water stress relatively greater amounts of organic osmolytes than S54 (Ramanjulu 1996, Ramanjulu and Sudhakar 1997). The involvement of non-stomatal factors in limiting P_N varied among the two genotypes of mulberry, wherein the degree of non-stomatal limitations was comparatively less in S13 than S54.

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