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Photosynthetic response to water stress and changes in metabolites in *Jasminum sambac*

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Abstract

Gas exchange, chlorophyll (Chl) fluorescence, and contents of some metabolites in two genotypes of jasmine (*Jasminum sambac*), single petal (SP) and double petal (DP) one, were analyzed during dehydration and re-hydration. Water stress significantly decreased net photosynthetic rate, stomatal conductance, and maximum photochemical efficiency (F_v/F_m) in both jasmine genotypes, but increased minimum fluorescence (F_0) only in DP-jasmine. Water stress also decreased starch content, while increased contents of total soluble sugars and proline in leaves of both genotypes. SP-jasmine demonstrated higher drought tolerance as evidenced by maintaining higher gas exchange and photochemical efficiency and lower alteration of metabolites than DP-jasmine. Recovery analysis revealed that drought-induced injury in photosynthetic machinery in jasmine plants was reversible. DP-jasmine exhibited a slow recovery of drought-induced impairment in photosynthetic activity and associated metabolites, suggesting that this genotype had lower capacity to adapt to water limited condition. Higher yield stability of SP- than that of DP-jasmine under rain-fed condition finally confirmed higher drought tolerance of SP-jasmine.

Additional key words: chlorophyll fluorescence; gas exchange; proline; starch; total soluble sugars; yield.

Introduction

Drought stress is one of the major stress factors limiting plant growth (Boyer 1982). Plant response to water stress involves changes in carbon assimilation and metabolism (Souza *et al*. 2004, Miyashita *et al*. 2005). Loss of carbon assimilation rate during water stress largely depends on stomatal closure (Flexas and Medrano 2002, Souza *et al*. 2004). Chlorophyll (Chl) fluorescence provides a rapid and non-invasive method to analyze the effect of environmental stress on photosynthetic system (Csintalan *et al*. 1999). Investigations of Chl fluorescence have shown that photosystem 2 (PS2) is resistant to water stress, being either unaffected (Shangguan *et al*. 2000) or affected only under severe drought (Saccardy *et al*. 1998). Drought also affects a group of compounds acting as compatible solutes such as soluble sugars and proline (Šircelj *et al*. 2005). Solute concentrations increase due to direct metabolic injuries in cells, known as osmotic adjustment (Irigoyen *et al*. 1992, Campos *et al*. 1999). Since water stress and precipitation often occur in nature, it is interesting how a plant recovers from a short drought period. Although there are some studies on the recovery of gas exchange, Chl fluorescence, and associated metabolites of water-stressed plants, the mechanisms involved and degree of recovery during re-watering have not been fully clarified (Widodo *et al*. 2003, Souza *et al*. 2004, Miyashita *et al*. 2005).

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Abbreviations: Chl – chlorophyll; F_0 – minimum fluorescence; F_m – maximum fluorescence; F_v – variable fluorescence; F_v/F_m – maximum photochemical efficiency; g_s – stomatal conductance; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PS2 – photosystem 2; Ψ_{pd} – predawn leaf water potential; Ψ_{soil} – soil water potential.
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Jasmine (*Jasminum sambac*) is one of most important cultivated species in China for its medicinal value (Qi and Shi 2003). However, flower yield and quality of two cultivated genotypes such as single petal (SP) and double petal (DP) are largely influenced by the amount and distribution of rainfall (Lai 1995, Qi and Shi 2003). It is therefore important to study physiological changes in response to water stress and recovery for better management of this crop. We selected two genotypes of jasmine that are different in morphology, growth, flower yield, and quality (Lai 1995, Qi and Shi 2003). Generally, flower yield of DP-jasmine is higher than that of SP-jasmine, but the quality of flower in SP-jasmine is higher than that in DP-jasmine (Lai 1995). Recently SP-jasmine has been widely cultivated especially in drought mountainous areas in the south of China. The purpose of our study was to investigate the photosynthetic competence of the two genotypes of jasmine during dehydration and re-hydration as determined by gas exchange, Chl fluorescence, and contents of some associated metabolites. Moreover, we compared yield performance of the genotypes under irrigated and rain-fed conditions.

Materials and methods

Plants and experiment design: Two experiments were carried out to evaluate the changes in physiology and yield of two genotypes of jasmine (viz. SP and DP) in response to water stress. During 2005–2006, yield performance was studied at Hengzhou town (22°41'N, 109°16'E, 56 m altitude), Heng County, Guangxi province, China. The experiment I consisted of three blocks of irrigated and rain-fed grown genotypes of jasmine plots (5 m^2) each containing 46 plants. Rhizogenic cuttings of two genotypes were planted on 15 June in 2001. Plants were protected from bacterial diseases by application of Bordeaux mixture. Weeding and mulching were done as needed. All plants were kept well-irrigated before starting of treatments. Irrigation treatment was carried out when plants were four years old, a stage that was characterized by high flower productivity. Control plants were irrigated on 18 April, 13 May, 15 September, 3 October, and 8 October in 2005, whereas on 22 April, 8 September, 21 September, 28 September, 10 October, and 28 October in 2006. Soil water was saturated in irrigation treatment. Rain-fed plants only received rainfall. Rainfall distribution in 2005 and 2006 is shown in Fig. 1. Soil water potential (Ψ_{soil}) in irrigated and rain-fed plots was recorded at every 10-d interval during the experiment using five granular matrix sensors (*Watermark Mod. Irrometer Co*., Riverside, CA, USA). Yields of fresh flowers were evaluated by picking flowers monthly from May to October every year.

Experiment II was performed to analyze the physiological responses of the two genotypes to water stress and re-hydration at the Institute of Botany of the Chinese Academy of Sciences (IB-CAS, 39°59'N, 116°13'E, 71 m altitude) in 2006. On 8 April 2006, stem cuttings of the two genotypes were rooted in pots containing a mixture of peat moss : perlite (4 : 6 by volume). Two months after sprouting, 160 cuttings per genotype were potted in plastic pots (20 cm inner diameter) filled with a mixture of vermiculite, peat, and field soil (1 : 3 : 6 by volume) in a naturally lit semi-controlled greenhouse in IB-CAS. Plants were grown there until the end of August, then moved to outside at 10 d before initiating stress treatment. On 6 September 2006, water stress was commenced on half of the plants. The control plants were watered at dusk each day. After exposing plants to water stress for 6 d, they were re-watered for another 6 d at dusk. Five plants per treatment were arranged in a completely randomized block design. During the experiment mean air temperature was 20 ºC and relative humidity was 50 %. The maximum daily photosynthetic photon flux density (PPFD) was 1 600 μmol m^{-2} s^{-1}. No rainfall occurred during the experiment.

Leaf and soil water potential: Predawn leaf water potential (Ψ_{pd}) was determined in two fully expanded leaves per plant from the middle portion of the shoot in the Exp. II. Measurements were made using a pressure chamber (*ZLZ-4*, *Lanzhou University*, Gansu Province, China). Ψ_{soil} was recorded for 3 plants per treatment with five granular matrix sensors (*Watermark Mod. Irrometer Co*., Riverside, CA, USA).

Measurements of leaf gas exchange and Chl fluorescence: The most fully expanded leaves from the middle portion of the shoot were sampled for gas exchange measurement in the Exp. II, using a portable photosynthesis system (*LCA*-4, *ADC*, Hoddesdon, Herts, UK). The measurements were made from 10:00 to 12:00, under approximate PPFD of 1 500 μmol m^{-2} s^{-1}, ambient CO_2 concentration of 380 μmol mol^{-1}, and leaf temperature of 30 ºC. Diurnal changes in gas exchange were also determined on 3 d after water stress.

The same leaves that were selected for gas exchange measurement were used for measurement of Chl fluorescence using a portable fluorometer (*FMS2*, *Hansatech*, King's Lynn, Norfolk, UK). Minimum fluorescence (F_0), maximum fluorescence (F_m), and variable fluorescence (F_v) were recorded after 30-min dark adaptation.

Biochemical analysis: The sampled leaves used for gas exchange and fluorescence measurements were harvested for biochemical analysis. The clean samples were blotted dry with paper towels and directly frozen in liquid nitrogen. Leaf samples were pooled and mashed to powder in liquid nitrogen and stored at –80 °C until they were used for biochemical analysis. Quantification of total soluble sugars, starch, and proline was done according to Souza *et al*. (2004).

Statistical analyses were performed using the SPSS statistical package (version *13*, *SPSS*, Chicago, IL, USA). Difference between means of treatments were performed by the Student's *t*-test and considered when $p<0.05$.

Results

Ψ_{soil} in field plots: Irrigated plots maintained higher Ψ_{soil} than rain-fed plots during the study period (Fig. 1). The highest rainfall occurred in June 2005 and July 2006. Ψ_{soil} in rain-fed plots showed similar trend as in rainfall ones during the experiment.

Ψ_{soil} and Ψ_{pd} in potted plants: The lowest Ψ_{soil} and Ψ_{pd} values were observed on 6 d after beginning of water stress for both genotypes (Fig. 2). There was no difference in Ψ_{soil} and Ψ_{pd} between the two genotypes of water-stressed plants. Both genotypes showed rapid recovery in Ψ_{soil} on 2 d after re-watering. Ψ_{pd} in SP- and DP-jasmine reached the control level on 2 and 4 d after re-watering, respectively.

Gas exchange: The highest P_N and g_s were observed at the beginning of water stress, but the lowest values were observed on 6 d after water stress in both jasmine plants (Fig. 3). On 6 d after water stress, P_N and g_s decreased by 96.5 and 99.2 %, respectively, in DP-jasmine, while they decreased by 68.8 and 70.8 %, respectively, in SP-jasmine. SP-jasmine recovered gas exchange to control level on 2 d after re-watering, but DP-jasmine on 4 d after re-watering.

Diurnal trends of P_N and g_s of the two genotypes monitored on 3 d after the beginning of water-stress are shown in Fig. 4. The highest P_N and g_s in both water-stressed and control plants were found in the morning, then declined towards midday. There was significant difference in P_N and g_s between control and water-stressed plants over the daytime. DP-jasmine showed higher relative reduction in P_N and g_s than SP-jasmine.

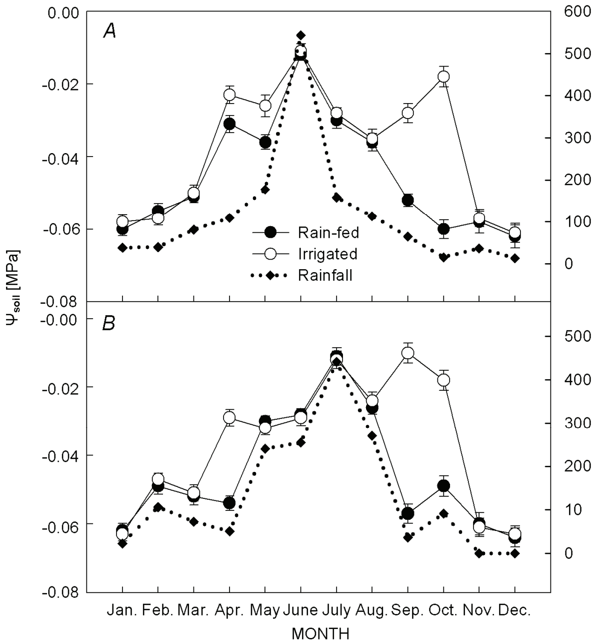

Fig. 1. Soil water potential (Ψ_{soil}) and rainfall of each month in Hengzhou town, Heng County, Guangxi province in 2005 (*A*) and 2006 (*B*). Irrigations in the field were carried out on 18 April, 13 May, 15 September, 3 October, and 8 October in 2005 and on 22 April, 8 September, 21 September, 28 September, 10 October, and 28 October in 2006 (Exp. I). Means±SE (n = 3).

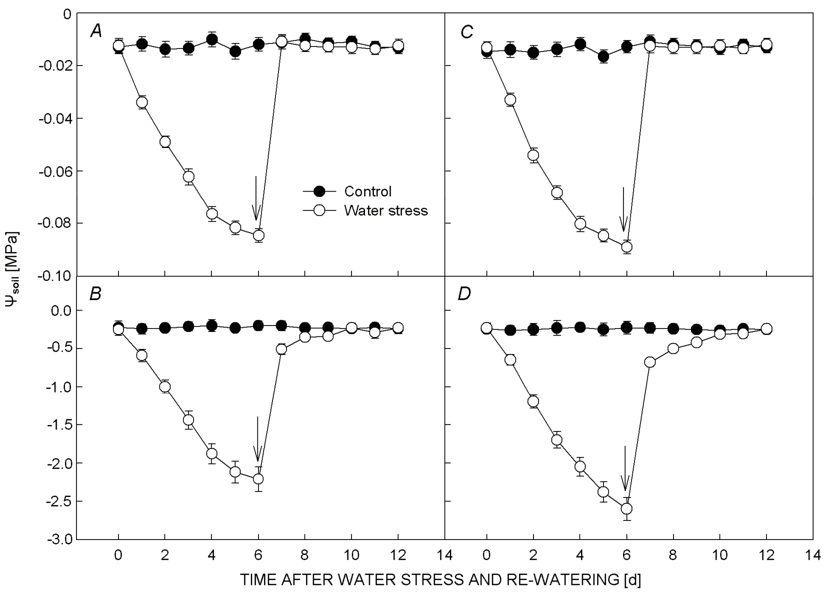

Fig. 2. Soil water potential, Ψ_{soil} (*A* and *C*) and predawn leaf water potential, Ψ_{pd} (*B* and *D*) in response to an imposed water stress period and recovery upon re-watering (*arrow*) in single petal (*A* and *B*) and double petal (*C* and *D*) jasmine (Exp. II). Means±SE (n = 5).

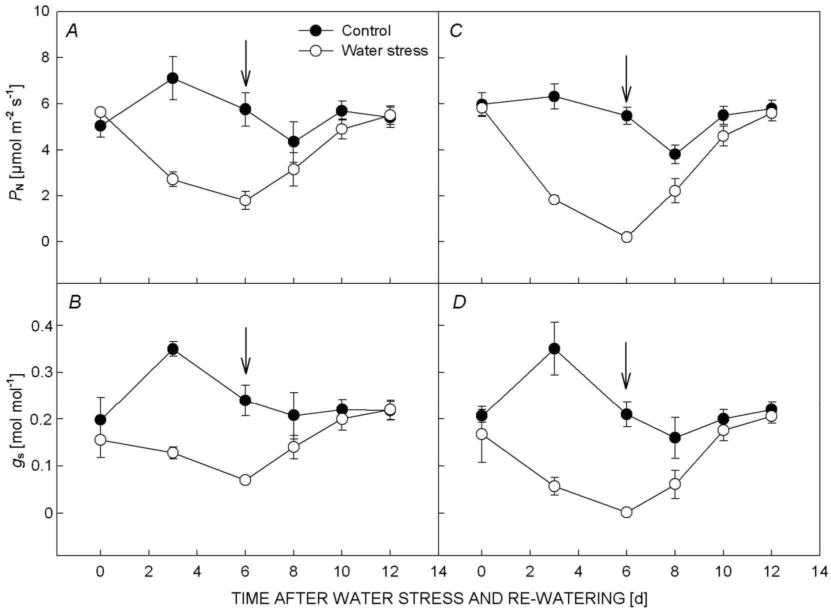

Fig. 3. Net photosynthetic rate, P_N (*A* and *C*) and stomatal conductance, g_s (*B* and *D*) in response to an imposed water stress period and recovery upon re-watering (*arrow*) in single petal (*A* and *B*) and double petal (*C* and *D*) jasmine (Exp. II). Means±SE (*n* = 5).

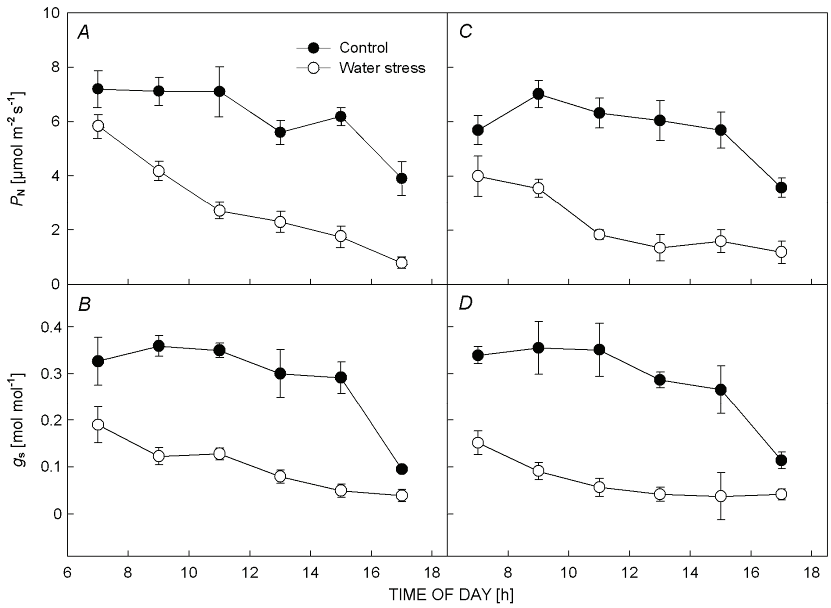

Fig. 4. Diurnal variations of net photosynthetic rate, P_N (*A* and *C*) and stomatal conductance, g_s (*B* and *D*), 3 d after the beginning of imposed water stress in single petal (*A* and *B*) and double petal (*C* and *D*) jasmine (Exp. II). Means±SE (*n* = 5).

Chl fluorescence: Water stress significantly increased F_0, but depressed maximum photochemical efficiency (F_v/F_m; Fig. 5). DP-jasmine exhibited significantly increase in F_0, while SP-jasmine showed non-significant increase in F_0 in response to drought. Water stress decreased F_v/F_m by 21.3 and 36.8 % relative to control in SP- and DP-jasmine, respectively, at maximum stress. Re-watering decreased F_0 and increased F_v/F_m in water-stressed plants. SP-jasmine recovered altered fluorescence signals to control levels on 2 d after re-watering, while DP-jasmine on 4 d after re-watering.

Metabolic changes: Water stress significantly decreased starch content, but increased contents of total soluble sugars and proline in jasmine plants (Fig. 6). At maximum water stress, contents of total soluble sugars and proline increased by 23.3 and 136.4 %, respectively, in SP-jasmine, whereas by 45.0 and 170.7 %, respectively, in DP-jasmine. On 6 d after water stress, starch content in leaves of SP- and DP-jasmine decreased by 40.3 and 52.9 %, respectively. Re-watering increased starch content, but decreased contents of total soluble sugars and proline in water-stressed jasmine plants. SP-jasmine showed no significant difference in metabolites between water-stressed and control plants on 2 d after re-watering, whereas DP-jasmine showed a slow recovery of metabolites and attained control values on 4 d after re-watering.

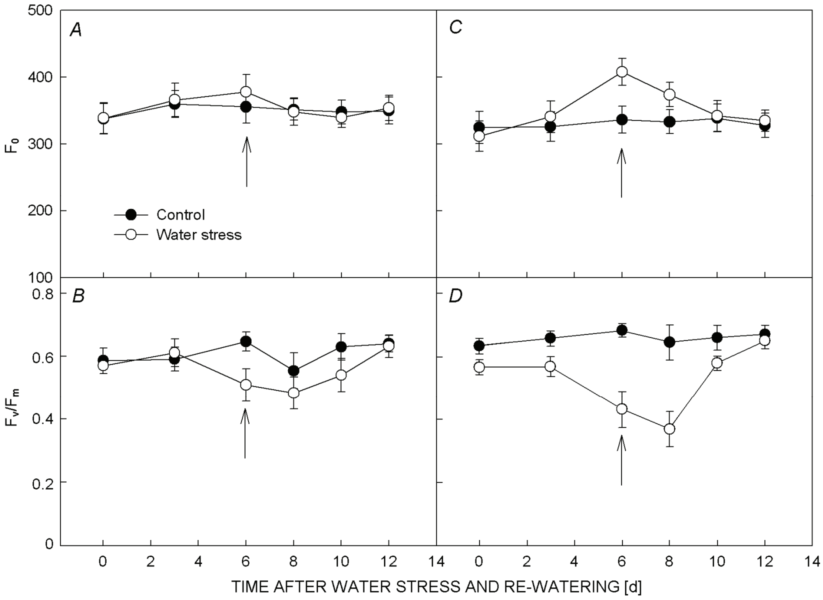

Fig. 5. Minimum fluorescence, F_0 (*A* and *C*) and maximum photochemical efficiency, F_v/F_m (*B* and *D*) in response to an imposed water stress period and recovery upon re-watering (*arrow*) in single petal (*A* and *B*) and double petal (*C* and *D*) jasmine (Exp. II). Means±SE (*n* = 5).

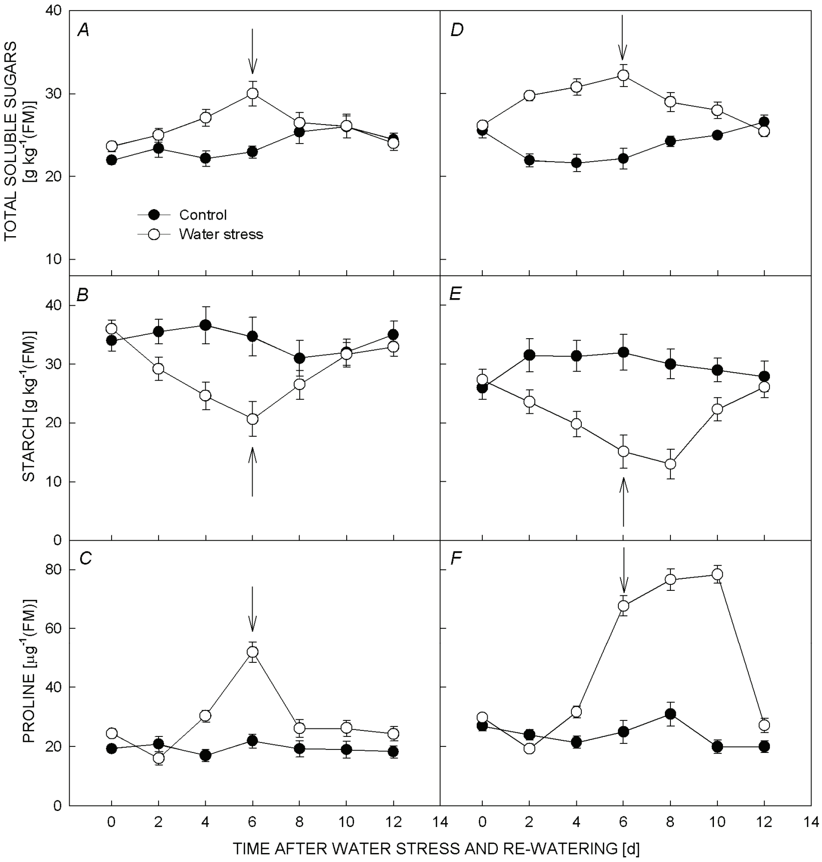

Fig. 6. Leaf contents of total soluble sugars (*A* and *D*), starch (*B* and *E*), and proline (*C* and *F*) in response to an imposed water stress period and recovery upon re-watering (*arrow*) in single petal (*A*, *B*, and *C*) and double petal (*D*, *E*, and *F*) jasmine (Exp. II). Means±SE (*n* = 5).

Fresh flower yield of jasmine was significantly higher in irrigated than in rain-fed condition. In 2005 and 2006, SP-jasmine showed relative reduction in fresh flower yield by 21.5 and 25.0 %, respectively, whereas DP-jasmine showed relative reduction in yield by 33.3 and 37.6 %, respectively (Table 1).

Discussion

Water stress significantly decreased P_N and g_s in jasmine plants. SP-jasmine had higher P_N than DP-jasmine relative to control plants. Since there was no difference in Ψ_{pd} between the two genotypes of water-stressed plants, maintenance of higher P_N in SP-jasmine confirmed the higher stability of photosynthetic apparatus in this genotype compared to DP-jasmine (Schultz 2003). Re-hydration resulted in almost recovery of P_N in droughted jasmine plants, suggesting a reversible inhibition of the photosynthetic apparatus in these two genotypes (Cornic 2000, Souza *et al.* 2004). However, a slower recovery of P_N in water-stressed DP-jasmine upon re-hydration suggested that basic mechanism of photosynthetic biochemistry and photochemistry might be impaired in this genotype due to water stress (Cornic 2000, Souza *et al.* 2004). For example, water stress significantly increased F_0 in DP-jasmine, but not in SP-jasmine. Moreover, F_0 was recovered more slowly in DP- than SP-jasmine during re-hydration. This suggested that water stress caused higher impairment of PS2 in DP- than SP-jasmine (Demmig and Björkman 1987). It can be further explained by maintaining higher F_v/F_m in SP- than DP-jasmine relative to control (Qiu and Lu 2003).

Table 1. Yield of fresh flower and percent decrease in the field under irrigated and rain-fed conditions in single petal and double petal jasmine. Means followed by capital letters indicate significant difference at $p<0.01$ between irrigated and rain-fed treatment. Means±SE ($n = 3$).

	Treatment	Single petal [g per plant]	[g m^{-2}]	Double petal [g per plant]	[g m^{-2}]
2005	Rain-fed	71.6 ± 5.3^B	659.1 ± 48.5^B	97.8 ± 5.1^B	899.6 ± 46.8^B
	Irrigated	91.3 ± 5.8^A	839.6 ± 53.3^A	146.7 ± 7.5^A	1349.3 ± 69.2^A
	Decrease [%]	21.5		33.3	
2006	Rain-fed	61.1 ± 4.2^B	562.2 ± 38.5^B	86.4 ± 6.2^B	794.6 ± 56.8^B
	Irrigated	81.5 ± 4.6^A	749.6 ± 42.8^A	138.5 ± 6.5^A	1274.4 ± 59.4^A
	Decrease [%]	25.0		37.6	

Water stress significantly decreased starch content, but increased contents of total soluble sugars and proline in jasmine plants, similarly as reported for other species in previous studies (Souza *et al.* 2004, Cechin *et al.* 2006). DP-jasmine showed higher relative increase in contents of total soluble sugars and proline than SP-jasmine during water stress and re-watering. Higher accumulation of soluble sugars in DP-jasmine may be a result of higher metabolic impairment affecting sugar composition in the leaf or its translocation, contributing to the inhibition of photosynthetic efficiency during water stress (Campos *et al.* 1999). Increase in proline content possibly due to an excessive protein breakdown during water deficits may be considered as a symptom of injury, despite its known role in osmotic adjustment (Irigoyen *et al.* 1992). This might lead to the conclusion that decreases in P_N result not only from the reduced g_s, but also due to impairment of metabolic activities associated with drought stress (Souza *et al.* 2004).

Inhibition of photosynthesis associated with drought stress often affects plant growth and yield (Hassan 2006). We found that yield of fresh flower significantly decreased under rain-fed condition. However, higher relative yield reduction was observed in DP-jasmine than in SP-jasmine, confirming that SP-jasmine was more resistant to drought stress.

In conclusion, water stress significantly decreased photosynthetic efficiency in the two genotypes of jasmine. Nevertheless, higher relative reduction in P_N was observed in DP- than SP-jasmine subjected to water stress. A slower recovery of P_N in DP- compared to SP-jasmine suggested a higher impairment in photosynthetic physiology in DP-jasmine as evidenced by altered fluorescence and associated metabolites in response to drought. Moreover, SP-jasmine showed higher yield stability than DP-jasmine under drought. Our findings therefore suggest that DP-jasmine is more sensitive to water stress and SP-jasmine can be suitable in the areas with limited irrigation facilities.

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