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Architectural plasticity, photosynthesis and growth responses of velvetleaf (*Abutilon theophrasti* Medicus) plants to water stress in a semi-arid environment

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Abstract

Plasticity of the phenotypic architecture, growth and photosynthesis of velvetleaf (*Abutilon theophrasti* Medicus) was studied in response to water stress. A two-year experiment with three irrigation regimes was carried out in a completely randomized design with four replications. Plants were subjected to three moisture levels: water stress, slight water stress and well-watered. Water stress reduced dry weight of velvetleaf plants. However, root growth was not affected by water stress. Physiological characteristics were significantly influenced by water stress. The highest water-use efficiency, stomatal conductance and photosynthetic rates were found in well-watered plants. Velvetleaf plants flowered early under water stress conditions, whereas plants under well-watered conditions delayed flowering to allocate more biomass to vegetative growth. Finally, our results demonstrate that the leaf angle in velvetleaf is plastic and sensitive to unstable availability of water. This mechanism enables velvetleaf plants to keep leaf temperature at logical levels.

Keywords*:* Dry weight, photosynthetic rate, plasticity, stomatal conductance, velvetleaf, water stress, water use efficiency.
Abbreviations: DAS-days after sowing; E-transpiration rate; S-stomatal conductance; T-temperature; WUE-water use efficiency.

Introduction

Drought stress is one of the most frequent abiotic stresses in agriculture worldwide (Mafakheri et al., 2010). The effects of water stress on plant growth vary between species. The morphological mechanisms which enable plants to adapt to water stress include reductions in leaf size and aboveground biomass (Pedrol et al., 2000). In addition, physiological mechanisms exist which enable plants to adapt to water stress, including seed priming, stomatal control of water loss, osmotic adjustment, and cellular tolerance of dehydration (Turner and Begg, 1981). Moussa and Abdel-Aziz (2008) reported that drought stress was the result of accumulation of glycine betaine and free proline in maize. Such low-molecular-weight osmolytes, and other amino acids, organic acids and polyols, are crucial to sustain cellular functions under drought (Farooq et al., 2009). Shoot growth is affected by moisture stress more than root growth because roots are more able to compensate for moisture stress (Sharp, 2002). Low water availability can also cause physical limitations in plants. The stomata control movement of water, carbon dioxide and oxygen into and out of the plant. During moisture stress, stomata close to conserve water (Zhang and Outlaw, 2001). This also closes the pathway for the exchange of water, carbon dioxide and oxygen, resulting in decreases in photosynthetic rate. Drought conditions also have the potential to alter the competition of weeds. Some weed species that show a reduction in competitiveness when subjected to water stress include *Galium aparine* L. (Inavy et al., 1993), *Avena fatua* L. (Akey and Morrison, 1984), *Avena sterilis* L. (Gonzales-Ponce and Santin, 2001), *Echinochloa crus-galli* L. and *Xanthium pensylvanicum* Wallr. (Weise and Vandiner, 1970). During conditions of limited water supply, higher benefits for weed control may be achieved by adopting suitable irrigation and planting techniques (Karkanis et al., 2007). Effective weed management is dependent upon farmers gaining knowledge of the characteristics of the weeds they manage (Efthimiadou et al., 2009). *Abutilon theophrasti* Medicus is an annual broad-leaved weed of the Malvaceae family, which infests spring-sown crops in the Mediterranean area, as well as in many other parts of the world. It is a vigorous plant that can reach a height of 1-2 m. The plant is covered with short, fine hairs and is commonly called ‘velvetleaf’. Velvetleaf grows in cultivated fields, roadsides, ditches and field margins. Water stress is the main factor strongly affecting the growth, photosynthesis and survival of weeds. Patterson and Highsmith (1989) found that water stress reduced plant height, dry weight and leaf area of velvetleaf. Leaf water potential declined 0.02 and 0.08 MPa day^{-1} for velvetleaf subjected to −0.03 and −0.4 MPa soil water potential, respectively (Hinz and Owen, 1994). Plants can use a variety of strategies to respond to the same environmental stresses. Schmidt et al. (2011) reported that velvetleaf responded to drought by senescing its oldest leaves, whereas maize maintained its leaf area but with rolled leaves during peak drought stress. Moreover, Hatterman-Valenti et al. (2011) reported that velvetleaf plants grown under drought stress had greater leaf epicuticular wax deposition compared to plants grown in soil with moisture at field capacity. This study investigated the effect of water stress on vegetative growth and on important photosynthetic characteristics (stomatal conductance and photosynthetic rate) of velvetleaf.

Table 1. Influence of irrigation treatments on aboveground biomass (g plant^{-1}), dry weight of roots (g plant^{-1}), aboveground biomass/root biomass ratio, leaf area (cm^2 plant^{-1}), days to flowering, number of bolls (no. plant^{-1}) of velvetleaf.

Treatment	Aboveground biomass		Dry weight of roots		Aboveground biomass/root biomass	
	2005	2006	2005	2006	2005	2006
Water stress	2.13a	1.76a	4.31a	4.64a	0.49a	0.37a
Slight water stress	3.75b	2.75b	3.96a	4.70a	0.94b	0.58a
Well-watered	4.19c	3.61c	4.74a	4.36a	0.88b	0.82b
LSD *(p=0.05)*	0.95	0.57	1.09	0.81	0.31	0.22
Treatment	Days to flowering		Number of bolls		Leaf area	
	2005	2006	2005	2006	2005	2006
Water stress	45a	44a	463a	387a	463a	387a
Slight water stress	46a	47a	678b	543b	678b	543b
Well-watered	53b	55b	812c	890c	812c	890c
LSD *(p=0.05)*	6.32	7.32	78.31	102.12	78.31	102.12

Means in each column followed by the same letter are not significantly different according to LSD (p=0.05) test.

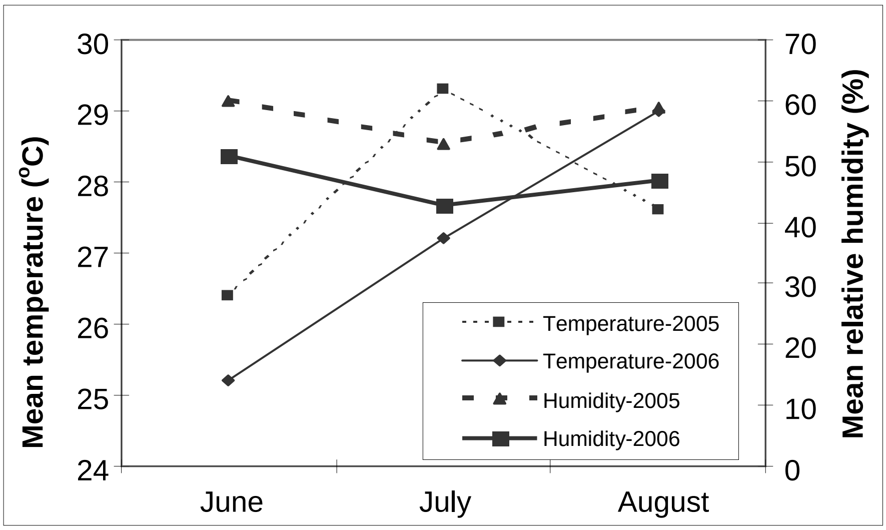

Fig 1. Meteorological data for the experimental site during the experimental periods (June-August, 2005 and 2006).

Materials and methods

Plant material and growing conditions

The seeds of velvetleaf (*Abutilon theophrasti* Medicus) were obtained in the autumn of 2004 from the experimental fields at Agricultural University of Athens. The experiment was conducted in the experimental field (outdoors) of the Agricultural University of Athens (23.43E, 34.58N), Greece, from June to September in 2005 and 2006. The site is characterized by dry and hot summers. Some meteorological data of the experimental site are presented in Figure 1. The precipitation during the growing season in 2005 (44.2 mm) was higher than that in 2006 (13.6 mm). Velvetleaf seeds were sown (10 seeds/pot) in cylindrical pots (height/diameter 24 cm), in clay-loam soil (29.8% clay, 34.3% silt, 35.9% sand, pH 7.24, 1.17% organic matter and EC of 0.54 mS cm^{-1}) taken from the topsoil of the experimental field.

Treatments

The irrigation treatments were: water stress (500 ml H_2O pot^{-1}), slight water stress: (750 ml H_2O pot^{-1}) and well-watered (1000 ml H_2O pot^{-1}). The amount of water added to return the soil moisture to field capacity was 1000 ml H_2O pot^{-1}. Pots were arranged in rows (4 rows, 4 pots row^{-1}). Velvetleaf was sown on the same dates in both years (15/6/2005 and 15/6/2006). After plant emergence, seedlings were thinned to 4 seedlings pot^{-1}. During growth, plants were not fertilized. Irrigation took place at intervals of 2-3 days.

Samplings, measurements and methods

Agronomic characteristics: Dry weight of plants and roots, number of bolls, leaf area, angle of leaves, water use efficiency (WUE) and days to flowering were recorded. Plants were harvested on the 30th of August (in 2005 and 2006). Dry weight was determined by measurement of 4 plants per pot. Each sample (1 pot) was separated from soil after standing for 24 h in water + $(NaPO_3)_6$ + Na_2CO_3. The dry weights of all plant parts were determined after drying for 48 h at 70ºC. Leaf area was measured using an automatic leaf area meter (Delta-T Devices Ltd). For computation of WUE the aboveground biomass/pot was divided by amount of water applied. *Physiological characteristics:* Stomatal conductance (mo lm^{-2} s^{-1}), photosynthetic rate (μmol CO_2 m^{-2} s^{-1}), transpiration rate (mmol m^{-2} s^{-1}) and leaf temperature (ºC) were recorded. Measurements of physiological traits were undertaken between the hours of 10.30 and 14.30, on

Table 2. Influence of irrigation treatments on water use efficiency (WUE: dry weight of plants/amount of water applied, g l^{-1} H_2O) and leaf angle (º) of velvetleaf.

Treatments	WUE		Leaf angle	
	2005	2006	2005	2006
Water stress	0.86a	0.61a	4.5a	3.5a
Slight water stress	1.08b	0.71b	55b	51b
Well-watered	0.94c	0.71b	79.5c	77c
LSD *(p=0.05)*	0.07	0.06	22.54	17.89

Means in each column followed by the same letter are not significantly different according to LSD (p=0.05) test.

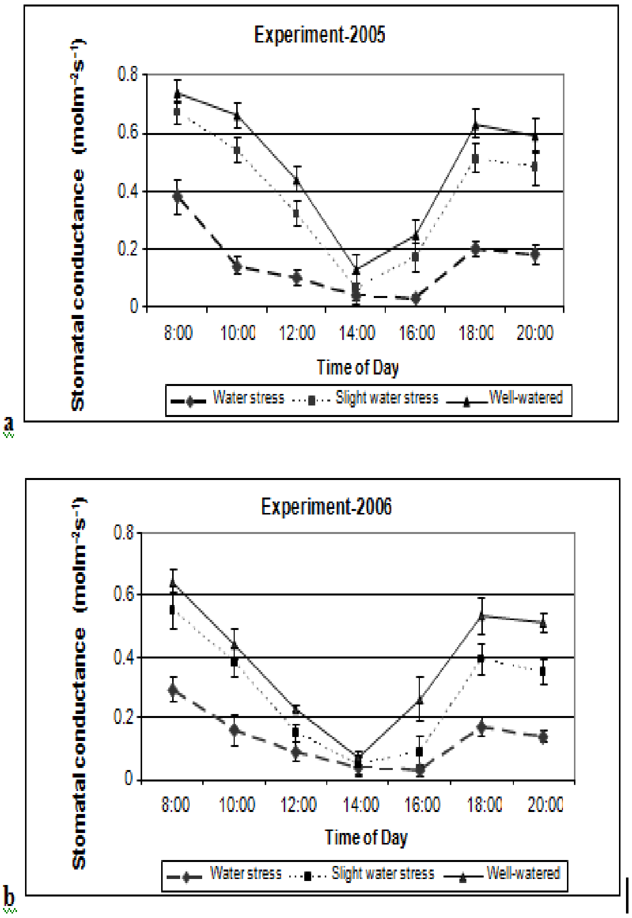

Fig 2. Diurnal changes in stomatal conductance on irrigation treatments a) in 2005 and b) in 2006, 55 days after sowing (DAS).

fully expanded leaves at 34, 48 and 63 days after sowing (DAS). Measurements were made using an LCi Leaf Chamber Analysis System (ADC, Bioscientific, Hoddesdon, UK). Finally, the temperature of leaves was determined using an infrared thermometer (Model 42529, Extech Instruments).

Statistical analysis

The experimental design was a completely randomized design with four replications and three irrigation treatments. For statistical analysis of variance and mean comparisons, the software Statsoft (1996) was used. If the ANOVA results were significant (*P*<0.05), differences among the means were compared using Least Significant Difference test (LSD). Regression and correlation analyses were used to describe the relationships between the transpiration rate, temperature, stomatal conductance, photosynthetic rate and aboveground biomass.

Results

Aboveground biomass, dry weight of roots and aboveground/root ratio

The lowest dry weight (2.13 and 1.76 g plant^{-1}, in 2006 and 2005, respectively) of velvetleaf was found under the water stress treatment. There were significant differences between the slight water stress and well-watered treatments for dry weight (Table 1). Concerning the root biomass of velvetleaf, there were no significant differences between the water stress and well-watered treatments. Moreover, the lowest aboveground/root ratio was found under the water stress treatment.

Days to flowering, number of bolls and leaf area

Plants flowered early under conditions of water stress, whereas plants under favorable conditions delayed flowering to allocate more biomass to vegetative growth. There were no significant differences between the slight water stress and water stress treatments for the number of days to flowering (Table 1). Concerning the number of bolls, there were no significant differences between the water stress and slight water stress treatments. Moreover, the lowest leaf area (387 and 463 cm^2 plant^{-1}, in 2006 and 2005, respectively) was found under the water stress treatment.

Water use efficiency and leaf angle

Water stress reduced the WUE of velvetleaf by 8-20% (Table 2). In 2006, there were no significant differences between the slight water stress and well-watered treatments. The lowest leaf angle (4.5° and 3.5°, in 2006 and 2005, respectively) was found under the water stress treatment. In addition, there were significant differences between slight water stress and well-watered treatments.

Leaf temperature and stomatal conductance

Water stress increased the leaf temperature of velvetleaf (Table 3). The leaf temperature ranged between 27 to 35.5 ºC under the water stress treatment, 27-35 ºC under slight water stress treatment and 27-32 ºC under the well-watered treatment. Water stress reduced stomatal conductance by 37-89% (Table 3). The stomatal conductance of velvetleaf ranged between 0.03 to 0.12 mol m^{-2}s^{-1} under water stress treatment and 0.19-0.39 mol m^{-2}s^{-1} under well-watered treatment. Concerning the diurnal measurements of stomatal conductance, there were significant differences between the irrigation treatments (Figure 2). The weather on both days of measurement was clear and there was a similar diurnal stomatal conductance pattern.

Photosynthetic rate and transpiration rate

Water stress reduced velvetleaf photosynthetic rate by 74-88% (Table 4). The photosynthetic rate of weed velvetleaf ranged between 1.42 and 9.70 µmol CO_2 m^{-2}s^{-1} under water stress treatment, 4.42-11.89 µmol CO_2 m^{-2}s^{-1} under slight water stress treatment and 5.32-15.81 µmol CO_2 m^{-2}s^{-1} under

Table 3. Influence of irrigation treatments on temperature of leaves (ºC) and stomatal conductance (mol m^{-2}s^{-1}) of velvetleaf, 34, 48 and 83 days after sowing (DAS).

Temperature of leaves						
Treatment	34 DAS		48 DAS		63 DAS	
	2005	2006	2005	2006	2005	2006
Water stress	34.75a	31.75a	35.5a	34.75a	27a	34.5a
Slight water stress	35a	31.2a	32.25b	31.75b	27a	31.75b
Well-watered	31.5b	32a	32b	29.75c	27a	31.75b
LSD *(p=0.05)*	1.48	1.80	1.58	1.86	1.48	0.84
Stomatal conductance						
Treatment	34 DAS		48 DAS		63 DAS	
	2005	2006	2005	2006	2005	2006
Water stress	0.05a	0.08a	0.10a	0.12a	0.03a	0.05a
Slight water stress	0.08a	0.20b	0.32b	0.15a	0.06a	0.10a
Well-watered	0.39b	0.21b	0.24c	0.20b	0.19b	0.19b
LSD *(p=0.05)*	0.08	0.04	0.03	0.03	0.03	0.05

Means in each column followed by the same letter are not significantly different according to LSD (p=0.05) test.

Table 4. Influence of irrigation treatments on transpiration rate (mmol m^{-2} s^{-1}) and photosynthetic rate (µmol CO$_2$ m^{-2}s^{-1}) of velvetleaf, 34, 48 and 83 days after sowing (DAS).

Transpiration rate						
Treatment	34 DAS		48 DAS		63 DAS	
	2005	2006	2005	2006	2005	2006
Water stress	2.59a	3.36a	4.87b	3.78a	0.83a	1.51a
Slight water stress	3.29a	4.99b	7.80a	4.04a	2.50b	4.43b
Well-watered	8.01b	5.18b	6.44ab	5.02b	5.06c	4.79b
LSD (*p=0.05*)	1.45	0.82	1.62	0.42	1.29	0.70
Photosynthetic rate						
Treatment	34 DAS		48 DAS		63 DAS	
	2005	2006	2005	2006	2005	2006
Water stress	4.04a	6.16a	6.41a	9.70a	1.42a	2.70a
Slight water stress	6.60b	10.5b	11.89b	9.50a	4.42b	5.09b
Well-watered	15.81c	13.29c	11.13b	12.19b	7.42c	5.32b
LSD *(p=0.05)*	1.25	0.98	1.13	0.96	2.54	0.70

Means in each column followed by the same letter are not significantly different according to LSD (p=0.05) test.

well-watered treatment. Moreover, the lowest transpiration rate (0.83 to 4.87 mmol m^{-2}s^{-1}) was obtained under water stress treatment and the highest under well-watered treatment (4.79-8.01 mmol m^{-2}s^{-1}).

Discussion

Velvetleaf growth-plasticity

Water stress affected velvetleaf growth. The lowest velvetleaf aboveground biomass was found under the water stress treatment. High correlation between the photosynthetic rate and dry weight of weed plants was observed (Table 5). However, there were no differences in root biomass measurements between irrigation treatments. Sharp (2002) reported that shoot and root growth are differentially sensitive to water stress. Interest in the involvement of hormones in regulating these responses has focused on abscisic acid (ABA) because it accumulates in shoot and root tissues under water-limited conditions, and because it usually inhibits growth when applied to well-watered plants. Drought triggers the production of ABA in roots which is transported to the shoots, causing stomatal closure. Water stress reduced the leaf area and the number of bolls of velvetleaf (Table 1). Patterson and Highsmith (1989) also found that water stress reduced plant height, dry weight and leaf area of spurred anoda (*Anoda cristata* L.) and velvetleaf. Reductions in leaf area were of greater magnitude in comparison to reductions in biomass, suggesting a higher effect of drought on leaf area. Water stress lowered the leaf angle of velvetleaf plants (Table 2). Leaf angle specifies the orientation of leaves to incoming radiation and therefore, strongly affects light capture. This mechanism enables velvetleaf plants to keep leaf temperature at logical levels. Ward et al. (1999) found that in response to drought, C3 plants (*Abutilon theophrasti*) shed many leaves and maintained relatively high leaf water potential in remaining leaves, whereas C4 (*Amaranthus retroflexus* L.) plants retained a greater leaf area, but at a lower leaf water potential. *Ctenanthe setosa* (Rosc) also showed a leaf rolling response to drought (Ayaz et al. 2001). Velvetleaf plants flower early under water stress conditions, whereas plants under favorable conditions delay flowering to allocate more biomass to vegetative growth. These contrasting reproductive patterns reflect different fitness priorities under the two types of environment: under water stress conditions, plants have less biomass and maximizing flower production is advantageous; under favorable conditions, where plants live longer, greater allocation to vegetative growth followed by later flowering maximizes fitness. Plastic reproductive timing and allocation have been documented by Sultan (2000). Volis et al. (2004) have also reported earlier onset of reproduction for wild barley (*Hordeum spontaneum* Koch) under water stress.

Table 5. Correlation coefficients[1] between plant parameters of velvetleaf.

Parameters	2005	2006
Stomatal conductance × photosynthetic rate	0.97***	0.77**
Stomatal conductance × dry weight of plants	0.74**	0.68**
Photosynthetic rate × dry weight of plants	0.83***	0.66 **
Photosynthetic rate × transpiration rate	0.96***	0.70*
Stomatal conductance × transpiration rate	0.95***	0.89*

[1] r was calculated using the linear equation. Significant at *p=0.05, **p=0.01, *** p=0.001; ns: not significant.

Table 6. Multiple regression analysis between transpiration rate (E), temperature of leaves (T) and stomatal conductance (S).

	Experiment 2005			
Equation 1	$E = 18.18 \times S + 0.145 \times T - 2.87$			$R - squared(adjust) = 90.04\%$
St. Error	1.05	0.04	1.21	
p-level	0.001	0.0007	0.02	
	Experiment 2006			
Equation 2	$E = 10.33 + 10.46 \times S - 0.24 \times T$			$R - squared(adjust) = 53.65\%$
St. Error	2.98	2.52	0.08	
p-level	0.001	0.0002	0.01	

Velvetleaf physiology-plasticity

Plants possess a variety of physiological mechanisms (*e.g.* stomatal closure) which enable them to adapt to water stress. Water stress resulted in lower stomatal conductance (during moisture stress stomata close to conserve water) of velvetleaf (Table 3). Xu et al. (2006) also found that during the process of soil drying, stomatal conductance of foxtail millet (*Setaria italica* L.) declined linearly, whereas that of switch grass *(Panicum virgatum* L.) declined paradoxically. The diurnal estimates of stomatal conductance of velvetleaf showed an apparent decline under high evaporative demand (at midday) under all moisture regimes (Figure 2). Such midday declines in stomatal conductance were also observed in field-grown wheat in Syria (Sato et al. 2006). Water stress caused a decrease in transpiration rate of velvetleaf (Table 4). The multiple regression analysis (Table 6) indicates that there is a statistically significant relationship between transpiration rate (E), temperature of leaves (T) and stomatal conductance (S) (equation 1 and 2). The R-squared statistic indicates that the two models (Equation 1 and Equation 2) explain the variability in transpiration rate in 2005 and 2006 by 90% and 53%, respectively. Water stress reduced the WUE of velvetleaf. Al-Tabbal and Jama (2007) observed that water stress reduced the WUE of two wheat varieties. Moreover, Xu et al. (2006) found that WUE of three grasses (foxtail millet, switch grass, yellow bluestem (*Bothriochloa ischaemum* L.)) decreased after drought treatment when compared with the well-watered treatment. Moreover, water stress reduced the photosynthetic rate of velvetleaf (Table 4). CO_2 assimilation by leaves is reduced mainly by stomatal closure, membrane damage and disturbed activity of various enzymes, especially those of CO_2 fixation and adenosine triphosphate synthesis (Farooq et al. 2009). Iqbal and Wright (1998) found that water deficit significantly reduced photosynthetic rate (P) of spring wheat, littleseed canarygrass (*Phalaris minor* Retz.) and common lambsquarters (*Chenopodium album* L.)). The P decrease was mainly due to lower stomatal conductance rate, while changes in the concentration of sub-stomatal CO_2 indicated that other (non stomatal) factors were also responsible, particularly in littleseed canarygrass. Plants display a variety of physiological and biochemical responses at cellular and whole-organism levels towards prevailing drought stress. Abbott et al. (2008) reported that the rapid change in conductance rate and slower response in leaf water potential indicate that stomatal control is an important component of African rue (*Peganum harmala* L.). Wittenmayer and Merbach (2005) reported that ABA also plays an important role in drought-stress adaptation of plants. This hormone causes morphological and chemical changes in plants, ensuring plant survival under water-limited conditions. For example, ABA induces stomatal closure, reduction in leaf surface, and increase in root: shoot ratio.

Conclusion

Our results indicate that water stress greatly affected the growth and physiology of *Abutilon theophrasti* L. plants. However, there were no significant differences between irrigation treatments for root biomass. Earlier onset of reproduction (days to flowerings) was also induced under water stress. Velvetleaf plants possess a variety of development and physiological mechanisms (stomatal control of water loss) which enable them to adapt to water stress. Our results demonstrate that leaf angle in *Abutilon theophrasti* L. is plastic and sensitive to the changing availability of water.

Acknowledgments

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