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Peanut photosynthesis under drought and re-watering

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Abstract

The photosynthetic response of three *Arachis hypogaea* L. cultivars (57-422, 73-30, and GC 8-35) grown for two months was measured under water available conditions, severe water stress, and 24, 72, and 93 h following re-watering. At the end of the drying cycle, all the cultivars reached dehydration, relative water content (RWC) ranging between 40 and 50 %. During dehydration, leaf stomatal conductance (g_s), transpiration rate (E), and net photosynthetic rate (P_N) decreased more in cvs. 57-422 and GC 8-35 than in 73-30. Instantaneous water use efficiency (WUE_i) and photosynthetic capacity (P_{max}) decreased mostly in cv. GC 8-35. Except in cv. GC 8-35, the activity of photosystem 1 (PS1) was only slightly affected. PS2 and ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) were the main targets of water stress. After re-watering, cvs. 73-30 and GC 8-35 rapidly regained g_s, E, and P_N activities. Twenty-four hours after re-watering, the electron transport rates and RuBPCO activity strongly increased. P_N and P_{max} fully recovered later. Considering the different photosynthetic responses of the studied genotype, a general characterisation of the interaction between water stress and this metabolism is presented.

Additional key words: *Arachis*; cultivar differences; photosynthetic electron transport; photosystems 1 and 2; ribulose-1,5-bisphosphate carboxylase/oxygenase; stomatal conductance; transpiration rate; water stress.

Introduction

Water stress is an important factor in determining plant productivity, namely due to its effects on photosynthesis. Word crop production is limited by environmental factors, drought stress being one of the most important factors that affect, among others, the photosynthetic metabolism (Kaiser 1987, Stuhlfauth *et al.* 1990, Di Marco and Tricoli 1993, Jefferies 1994). Under drought, plants reduce stomatal conductance (g_s) in order to diminish water loss which leads to a decrease in CO_2 uptake (Frederick *et al.* 1989). Additionally, under these circumstances, the rate of photon absorption largely exceeds its consumption in the carboxylation reactions (Lawlor 1995, Lauriano *et al.* 2000). Yet several mechanisms for excess energy dissipation have been reported for photosystems PS2 and PS1 (Lauriano *et al.* 2002).

The recovery after re-watering is a fundamental trait of plant survival, reflecting the balance between the need of rebuilding drought-strained structure and their reactivation (Moreira *et al.* 1990). After re-watering, although photosynthesis may increase rapidly (Cornic 1987, Cornic *et al.* 1987), the relevant long-term consequence of water stress seems to be a reduction of growth. Yet, the extent of photosynthesis recovery depends on the genotype, as shown with *Panicum maximum* (Ludlow *et al.* 1980), *Medicago sativa* (Hall and Larson 1982), and *Cajanus cajan* (Lopez *et al.* 1988b). It also depends on the degree of dehydration reached at the end of the drying cycle (Kriedemann and Downton 1981) and has its

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Abbreviations: c_i – internal leaf CO_2 concentration; Chl – chlorophyll; DCPIP – 2,6-dichlorophenolindophenol; $DCPIPH_2$ – reduced 2,6-dichlorophenolindophenol; DPC – 1,5-diphenyl carbohydrazide; E – transpiration rate; g_s – stomatal conductance to water vapour; MV – methyl viologen; OEC – oxygen evolving complex; P_{max} – photosynthetic capacity; P_N – net photosynthetic rate; PS – photosystem; RuBPCO – ribulose-1,5-bisphosphate carboxylase/oxygenase; RWC – relative water content; WUE_i – instantaneous water use efficiency; Δ_t – difference between air temperature and leaf temperature.

basis in the capacity of plants to rebuild the photosynthetic apparatus.

The aim of this work was to evaluate the ability to endure water stress and recovery of the photosynthetic process at photochemical and biochemical levels, for three genotypes of *Arachis hypogaea* (cvs. 57-422, 73-30, and GC 8-35).

Materials and methods

Plants: The effects of drought were evaluated in two-months-old plants of peanut (*Arachis hypogaea* cvs. 57-422, 73-30, and GC 8-35). After germination in Petri dishes, the seedlings were placed in 2 500 cm^3 pots (one plant per pot), filled with a mixture of vermiculite and *Trio-hum* substrate (4/5, v/v). The plants were grown in a glasshouse from June to August, under natural irradiation, without control of temperature. They were kept well watered and fed weekly with a Hoagland nutrient solution; relative water content (RWC) was around 95 %. Drought was imposed by withholding irrigation during 9 d. At the end of this drought cycle, plants reached RWC between 40 and 55 %. These samples were considered as control (C) and severe water stress (S) plants. After S, the plants were re-watered and measurements were further carried out 24, 72, and 96 h after re-watering.

Plant water status: RWC was determined gravimetrically according to Čatský (1960), using samples of 10 leaf discs of 0.5 cm^2 each. The fresh (FM), turgid (TM), and dry (DM) masses were determined. To obtain DM, samples were dried at 80 °C for 24 h.

Gas exchange: Photosynthetic capacity (P_{max}) was determined using a leaf disc oxygen electrode (*LD2/2*, *Hansatech*, Kings Lynn, UK) under an irradiance of 1 500 $\mu mol\ m^{-2}\ s^{-1}$ and temperature of 25 °C. CO_2 concentration for C plants was 6–7 % (obtained through a carbonate/bicarbonate buffer) and for S plants 15 %, to completely overcome the stomatal resistance. Net photosynthetic rate (P_N), stomatal conductance (g_s), and transpiration rate (E) were measured using a portable photosynthetic system *LI-6200* (*LI-COR*, Lincoln, USA). Water use efficiency (WUE_i) was calculated from the ratio P_N/E.

Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity, Hill and Mehler reactions: Carboxylation activity of RuBPCO was determined by the assimilation of $^{14}CO_2$ according to Parry *et al.* (1993). Preparation of sub-chloroplast fractions and the determination of electron transport rates followed the method described by Droppa *et al.* (1987). The Hill reactions associated with or without the oxidising water complex (H_2O–DCPIP and DPC–DCPIP, respectively) and the Mehler reaction ($DCPIPH_2$–MV) were determined using a Clark-type oxygen electrode (*LW2*, *Hansatech*, Kings Lynn, UK), adding chloroplasts to a final concentration equivalent to about 30 µg Chl. The concentration of Chl was determined according to Arnon (1949).

Statistical analysis was performed by two-way ANOVA ($p \leq 0.05$). For mean comparison, a Tukey test was applied, considering a 95 % confidence level. Different letters indicate significant differences: r, s, t among cultivars and a, b, c, d among treatments.

Results

At the end of the of drought cycle, the RWC decreased in all the cultivars, reaching values that may be considered as a severe water stress (Table 1).

The g_s and P_N showed a significant decrease; the most inhibited were cvs. 57-422 and GC 8-35. WUE_i also declined, especially in cv. GC 8-35. c_i become slightly affected in cvs. 57-422 and GC 8-35, whereas in cv. 73-30 it remained unchanged. The highest values of P_{max} were observed in the cvs. 57-422 and GC 8-35 (Table 2). Under stress, P_{max} decreased strongly, mainly in cv. GC 8-35.

In control plants, the highest rate of H_2O–DCPIP reaction was observed in the cv. 57-422, while the highest rate of DCP–DCPIP reaction was observed in the cvs. 57-422 and GC 8-35 (Table 2). The $DCPIPH_2$–MV and RuBPCO activities reached highest values in the cvs. GC 8-35 and 57-422, respectively. The reactions associated with PS2 (H_2O–DCPIP and DPC–DCPIP) decreased under severe drought in all the cvs., whereas the reaction $DCPIPH_2$–MV showed minor variations in the cvs. 57-422 and GC 8-35 (Table 2). In all cvs., the RuBPCO activity was significantly decreased.

Twenty-four hours after re-watering, the RWC of all the cvs. was fully regained (Table 1). At this time, an over-recovery of g_s occurred in the cv. 73-30, while for the cvs. 57-422 and GC 8-35 a partial recovery was observed, representing 67 and 19 % of the C plants, respectively (Table 1).

In all the cvs., the recovery of E was faster than recovery of P_N (Table 1). After re-watering for 24 h, a significant over-recovery was found for E in the cvs. 73-30 and GC 8-35, but the cv. 57-422 showed only a partial recovery. The regain of P_N was faster in cvs. 73-30 and GC 8-35 than in 57-422. In cvs. 73-30 and GC 8-35 a 69 % recovery was found, whereas the cv. 57-422 only showed a 46 % regain. After re-watering for 72 h, a significant over-recovery occurred in cvs. 73-30 and GC 8-35, with the cv. 57-422 totally recovering.

Considering the WUE_i, 24 h after re-watering, a partial recovery was observed (Table 1) in all the cvs.

(representing 56, 39, and 35 % of C plants for cvs. 57-422, 73-30, and GC 8-35, respectively). After 72 h, a regain occurred in cv. 57-422, but the other cvs. showed a partial recovery (*ca.* 83 and 74 % of the control plants for the cvs. 73-30 and GC 8-35, respectively). A partial recovery of c_i was observed in cvs. 73-30 and GC 8-35 (Table 1). As concerns E, an over-recovery occurred in cv. 73-30, while in the cv. 57-422 E slightly recovered (Table 1).

Table 1. Relative water content, RWC [%], stomatal conductance, g_s [mmol(H_2O) m^{-2} s^{-1}], net photosynthetic rate, P_N [µmol(CO_2) m^{-2} s^{-1}], transpiration rate, E [mmol(H_2O) m^{-2} s^{-1}], c_i [cm^3 m^{-3}], and water use efficiency, WUE_i [P_N/E] under control and severe water stress conditions as well as at 24 and 72 h after re-watering. Means ± SE, $n = 5$. *Different letters* indicate significant differences: r, s, t among cultivars and a, b, c, d among treatments.

Cv.		Control	Severe water stress	Time after re-watering	
				24	72
57-422	RWC	94	45-55	95	94
	g_s	$549 \pm 12^{a;r}$	$36 \pm 4^{c;s}$	$91 \pm 9^{b;s}$	$105 \pm 21^{b;t}$
	P_N	$16.2 \pm 0.9^{a;r}$	$0.8 \pm 0.0^{c;s}$	$7.4 \pm 0.2^{b;s}$	$16.1 \pm 1.7^{a;r}$
	E	$6.2 \pm 0.2^{a;r}$	$0.7 \pm 0.0^{c;t}$	$5.5 \pm 0.06^{b;s}$	$4.7 \pm 0.7^{b;s}$
	c_i	$296 \pm 1^{a;r}$	$272 \pm 14^{a;s}$	$235 \pm 1^{b;t}$	$214 \pm 8^{b;t}$
	WUE_i	$2.7 \pm 0.0^{a;r}$	$1.3 \pm 0.0^{c;r}$	$1.5 \pm 0.01^{c;r}$	$3.4 \pm 0.02^{a;r}$
73-30	RWC	93	45-55	95	94
	g_s	$255 \pm 32^{b;c}$	$100 \pm 0^{c;r}$	$337 \pm 52^{a;r}$	$375 \pm 37^{a;s}$
	P_N	$9.0 \pm 0.1^{b;r}$	$1.2 \pm 0.0^{a;r}$	$6.1 \pm 0.2^{c;t}$	$14.0 \pm 0.3^{a;s}$
	E	$5.0 \pm 0.0^{b;s}$	$2.6 \pm 0.0^{c;r}$	$9.1 \pm 0.4^{a;r}$	$9.2 \pm 0.0^{a;r}$
	c_i	$289 \pm 2^{a;s}$	$287 \pm 2^{a;r}$	$285 \pm 9^{a;r}$	$282 \pm 7^{a;r}$
	WUE_i	$1.8 \pm 0.3^{a;s}$	$0.9 \pm 0.0^{b;s}$	$0.7 \pm 0.0^{b;s}$	$1.5 \pm 0.0^{a;s}$
GC 8-35	RWC	93	45-55	94	93
	g_s	$454 \pm 19^{a;s}$	$32 \pm 2^{c;s}$	$304 \pm 21^{b;r}$	$453 \pm 120^{a;r}$
	P_N	$13.0\pm 0.4^{b;s}$	$0.5 \pm 0.0^{d;s}$	$8.8 \pm 0.1^{c;r}$	$18.0 \pm 3.0^{a;r}$
	E	$6.0 \pm 0.1^{b;r}$	$1.5 \pm 0.0^{c;s}$	$10.6 \pm 0.1^{a;r}$	$11.0 \pm 2.0^{a;r}$
	c_i	$299 \pm 1^{a;r}$	$266 \pm 14^{b;)}$	$261 \pm 0^{b;s}$	$258 \pm 2^{b;s}$
	WUE_i	$2.2 \pm 0.1^{a;rs}$	$0.3 \pm 0.0^{c;t}$	$0.8 \pm 0.0^{d;s}$	$1.7 \pm 0.0^{b;s}$

In cvs. 57-422 and GC 8-35, P_{max} fully recovered 72 h after re-watering, but only a partial regain (69 % of the control) was observed in cv. 73-30. During the recovery period, the rate of reaction H_2O–DCPIP of cv. 57-422 was fully recovered 24 h after re-watering. Moreover, only after 72 h of re-watering the cvs. 73-30 and GC 8-35 showed a sharp recovery. After re-watering for 24 h, the rate of the reactions DCP–DCPIP over-recovered in the cvs. 73-30 and GC 8-35, but for cv. 57-422 a recovery was found only after 72 h. The rate of the reaction DCPIPH_2–MV displayed, 24 h after re-watering, an over-recovery (mainly in cvs. 73-30 and GC 8-35).

After re-watering, RuBPCO activity showed an over-recovery in the cvs. 57-422 and 73-30, but only a full regain in cv. GC 8-35.

Discussion

Under control conditions, the differences in g_s among the cvs. were connected to those of E. The cvs. 57-422 and GC 8-35 that showed the highest g_s also displayed the highest E. The c_i did no vary significantly among the cvs. Thus, as differences in g_s were not reflected in c_i, this parameter did not explain the differences in P_N among cvs.

In C plants, the highest P_{max} attained in cvs. 57-422 and GC 8-35 reflected the highest rate of Hill reactions. Additionally, the high rate of the Mehler reaction might also contribute to high P_{max} in cv. GC 8-35.

Under water stress, the lowest water intake justifies the effects on g_s, E, and P_N. Indeed, as previously described (Fischer and Turner 1978, Davies and Pereira 1992), the effect on P_{max}, P_N, and E mediated by water stress is connected to the decrease of WUE_i, further implicating cuticular conductance.

The limiting effect on P_N by non-stomatal factors can be attributed to inhibition of the thylakoid-mediated electron transport activity, implicating a decrease in photosystem activities (Keck and Boyer 1974, Mayoral *et al.* 1981) and inhibition of RuBPCO (Lauriano 2002). Yet according to previous reports (Havaux 1992, Lauriano *et al.* 1997) the pattern displayed by the Mehler reactions indicated that, in general, PS2 was more affected than PS1, probably because the photosystems are connected to metabolic pathways participating in dissipation of excess energy (Harbinson and Foyer 1991, Heber and Walker 1992, Lawlor 1995).

The decreases in the rates of the reactions H_2O–DCPIP and DCP–DCPIP (for cv. 57-422), DCP–DCPIP (for cv. 73-30), DCP–DCPIP, and $DCPIPH_2$–MV (for cv. GC 8-35) seem to justify the observed decline of P_{max} found in these cvs. Additionally, as previously stated for several plant species (Boyer and Bowen 1970, Mohanty and Boyer 1976, Kaiser 1987, Lauriano *et al.* 1997), peanut DCP-DCPIP reactions under stress are also the most affected, inducing an inhibition at the PS2 level.

Table 2. Relative water content, RWC [%], photosynthetic capacity, P_{max} [μmol(O_2) m^{-2} s^{-1}], activities of ribulose-1,5-bisphosphate carboxylase/oxygenase, RuBPCO [μmol(CO_2) m^{-2} s^{-1}] and of reactions H_2O–DCPIP, DCP–DCPIP, and $DCPIPH_2$–MV [mmol(O_2) kg^{-1}(Chl) s^{-1}] under control and severe water stress conditions as well as at 24, 72, and 96 h after re-watering. Means ± SE, $n = 5$. *Different letters* indicate significant differences: r, s, t among cultivars and a, b, c, d among treatments.

Cv.		Control	Severe water stress	Time after re-watering		
				24	72	96
57-422	RWC	94	45-55	95	95	93
	$P_{máx}$	34.0 ± 2.1 $^{b;r}$	11.0 ± 1.2 $^{c;r}$	-	37.0 ± 1.0 $^{b;r}$	42.0 ± 4.0 $^{a;r}$
	RuBPCO	78 ± 6 $^{b;r}$	44 ± 3 $^{c;r}$	96 ± 4 $^{a;s}$	-	-
	H_2O–DCPIP	1.78 ± 0.08 $^{b;r}$	1.17 ± 0.11 $^{d;r}$	1.67 ± 0.08 $^{b;r}$	5.28 ± 0.47 $^{a;s}$	6.94 ± 1.19 $^{a;r}$
	DCP–DCPIP	8.89 ± 0.28 $^{c;r}$	1.56 ± 0.28 $^{e;s}$	6.94 ± 0.28 $^{d;s}$	15.28 ± 1.11 $^{b;r}$	22.50 ± 1.11 $^{a;r}$
	$DCPIPH_2$–MV	27.22 ± 2.22 $^{c;s}$	28.33 ± 1.39 $^{c;r}$	54.72 ± 5.00 $^{b;r}$	103.61 ± 0.55 $^{a;r}$	106.67 ± 2.50 $^{a;s}$
73-30	RWC	93	45-55	94	94	93
	$P_{máx}$	29.0 ± 0.6 $^{b;s}$	9.0 ± 1.7 $^{d;r}$	-	20.0 ± 2.7 $^{c;s}$	37.2 ± 2.6 $^{a;s}$
	RuBPCO	53 ± 2 $^{b;s}$	29 ± 5 $^{c;s}$	123 ± 5 $^{a;r}$	-	-
	H_2O–DCPIP	0.97 ± 0.28 $^{c;s}$	0.78 ± 0.06 $^{c;s}$	1.25 ± 0.06 $^{c;s}$	5.83 ± 0.17 $^{b;rs}$	7.50 ± 0.42 $^{a;r}$
	DCP–DCPIP	4.11 ± 0.28 $^{c;r}$	1.42 ± 0.00 $^{d;s}$	11.11 ± 0.83 $^{b;r}$	11.67 ± 0.56 $^{b;s}$	17.78 ± 0.83 $^{a;t}$
	$DCPIPH_2$–MV	23.89 ± 0.56 $^{c;t}$	21.67 ± 1.67 $^{c;s}$	36.39 ± 1.39 $^{b;t}$	98.89 ± 0.56 $^{b;t}$	102.50 ± 7.72 $^{a;s}$
GC 8-35	RWC	94	45-55	95	92	91
	$P_{máx}$	39 ± 1 $^{b;r}$	8 ± 2 $^{c;rs}$	-	38 ± 4 $^{b;r}$	48 ± 3 $^{a;r}$
	RuBPCO	48 ± 2 $^{b;s}$	27 ± 4 $^{c;s}$	97 ± 3 $^{a;s}$	-	-
	H_2O–DCPIP	0.86 ± 0.11 $^{c;s}$	0.67 ± 0.06 $^{c;s}$	1.44 ± 0.25 $^{b;rs}$	7.50 ± 0.56 $^{a;r}$	8.33 ± 0.69 $^{a;r}$
	DCP–DCPIP	6.11 ± 0.00 $^{d;s}$	2.22 ± 0.00 $^{e;r}$	11.11 ± 0.28 $^{c;r}$	14.17 ± 0.56 $^{b;r}$	20.28 ± 0.83 $^{a;s}$
	$DCPIPH_2$–MV	35.00 ± 0.56 $^{d;r}$	21.11 ± 1.94 $^{e;s}$	45.28 ± 1.67 $^{c;s}$	105.00 ± 0.83 $^{b;r}$	115.28 ± 5.00 $^{a;r}$

After re-watering, the fast and full recovery of RWC allowed only a slow recovery of g_s in cv. 57-422, which is a very normal phenomenon after re-watering. This process must be regarded as a way to plant prevention against new dehydration (Mansfield and Davies 1981, Matos *et al.* 1983, Lopez *et al.* 1988a, Matos 1990). In this context, the fast recovery of g_s in the cvs. 73-30 and GC 8-35 can be attributed to a high reactivity of stomata. The recovery of P_N in cv. GC 8-35 may be related with its high drought tolerance, which is linked to a high membrane stability (Lauriano *et al.* 2000).

Although RWC and g_s were fully regained 24 h after re-watering, the recovery of P_N occurred later, because the re-hydration is only one of the first steps of recovery. According to Tuba *et al.* (1994), P_N recovery is a reflex of assemblage of metabolic events working in order to rebuild, reorganise, and reactivate all the structure damaged during the dehydration process. This proposal also fits in our study, since P_N was fully recovered only after complete regain of electron transport and RuBPCO activities.

After re-watering for 24 h, except for the reaction DCP–DCPIP of cv. 57-422 (where a recovery of 78 % was observed), the other reactions related to photosynthetic electron transport and RuBPCO showed an over-recovery, which lead to a regain of P_{max} with an increase of the re-watering period. The faster recovery of P_{max} found in the cvs. 57-422 and GC 8-35 reinforces the drought tolerance of these two cvs. as observed previously (Lauriano *et al.* 2000). On the other hand, P_N recovered much more than P_{max}, mainly in cv. 73-30, suggesting that after re-watering this cv. shows a lowest tendency for depletion of the newly fixed carbon compounds. Also the recovery of photosynthetic electron flow was much greater than the recovery of P_{max}. Yet, compared to the C plants, for a given value of P_{max} the plants under recovery displayed a much higher electron flow (mainly in cv. 73-30), suggesting that a significant amount of electron was driven, for example, to other metabolic pathways.

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