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Photosynthetic activity of poikilochlorophyllous desiccation tolerant plant *Reaumuria soongorica* during dehydration and re-hydration

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Abstract

Diurnal patterns of gas exchange and chlorophyll (Chl) fluorescence parameters of photosystem 2 (PS2) as well as Chl content were analyzed in *Reaumuria soongorica* (Pall.) Maxim., a perennial semi-shrub during dehydration and re-hydration. The net photosynthetic rate (P_N), maximum photochemical efficiency of PS2 (variable to maximum fluorescence ratio, F_v/F_m), quantum efficiency of non-cyclic electron transport of PS2, and Chl content decreased, but non-photochemical quenching of fluorescence and carotenoid content increased in stems with the increasing of drought stress. 6 d after re-hydration, new leaves budded from stems. In the re-watered plants, the chloroplast function was restored and Chl *a* fluorescence returned to a similar level as in the control plants. This improved hydraulic adjustment in plant triggered a positive effect on ion flow in the tissues and increased shoot electrical admittance. Thus *R. soongorica* plants are able to sustain drought stress through leaf abscission and keep part of Chl content in stems.

Additional key words: carotenoids; chlorophyll fluorescence; drought stress; non-photochemical quenching; photosystem 2; quantum efficiency; relative water content; stomatal conductance.

Introduction

The desiccation-tolerant or resurrection plants can survive drying to a point when the water content may be no more than 5–10 % of dry mass. Upon watering the plants rapidly revive and are restored to their former state (Scott 2000). In vascular plants, desiccation tolerance of the vegetative tissue has been demonstrated in only 350 species, making up less than 0.2 % of the total flora (Proctor and Tuba 2002). Desiccation-tolerant plants may be subdivided into homoiochlorophyllous and poikilochlorophyllous. The homoiochlorophyllous desiccation-tolerant plants retain their chlorophyll (Chl) content during desiccation, whereas in poikilochlorophyllous ones the desiccation results in the loss of Chl which must be re-synthesized following re-hydration (Tuba *et al*. 1998).

Photosynthesis is one of the most important and water stress sensitive processes in all non-desiccation tolerant green plants. Reports on the effect of drought on photosystem 2 (PS2) function are contradictory and the site and exact mechanisms of PS2 injury are still unclear. Damage of the oxygen evolving complex and PS2 reaction centres reaction centres (Skotnica *et al*. 2000) has been observed. Other studies have shown that PS2 is resistant to water deficit, being either unaffected or affected only under severe drought (Lu and Zhang 1998). However, almost nothing is known about the characteristics of photosynthetic recoverable system in the desiccation tolerant plants during dehydration and re-hydration.

Resurrection plants provide very suitable model for the study of photosynthetic activity during dehydration and re-hydration (Drazic *et al*. 1999, Deng *et al*. 2003). In *Reaumuria soongorica*, one of the resurrection plants, the fully mature leaves can lose up to 95 % of their water content and die, but the stem remains alive. Upon re-watering, the stems are re-hydrated and produce new leaves. *R. soongorica* is an extreme xerophytic semi-shrub of Tamaricaceae, being the constructive and dominant species of the desert grasslands in China (Xu *et al.* 2003). *R. soongorica* desert is a typical zonal vegetation in the central Asia, which is distributed from the western Erdos, Alashan, Hexi Crridor, Beishan, Qaidam Basin, Gashun Gobi to Tarim Basin and Junggar Basin in China (from the east to the west), and forms the vast

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and distinctive landscape of the salt desert (Liu and Liu 1996).

We studied the effect of desiccation and re-hydration on the net photosynthetic rate, PS2 activity, and the content of Chl in *R. soongorica.* We tried to describe the response of photosynthetic system of this poikilochlorophyllous desiccation-tolerant plant during dehydration and re-hydration.

Materials and methods

Plants: The research was conducted from March to August, 2006 in the Botanical Garden of Lanzhou University. The 2-year-old *R. soongorica* plants were transplanted from the field to individual 3 000 cm^3 plastic pots with the original soil. The potted plants were transferred to a field tunnel with the same depth as the height of pots. The bottoms of the plastic pots were mulched with plastic to avoid the root spreading into ground and thereby absorbing moisture from it. A rain shed was made over pots and covered with plastic to avoid precipitation. On 14 May 2006, the plants were well watered. 20 pots were selected for drought treatment at the following 53 d until all leaves shed. Thereafter, water was applied in 7-d intervals for the following 40 d.

Soil and leaf relative water contents (RWC): Soil water content was calculated from the difference between the initial and dried soil masses. The RWC of the leaves and stems were calculated as RWC = [(FM − DM)/(TM − DM)]×100 % (FM − fresh mass, DM − dry mass, TM − turgid fresh mass).

Gas exchange and Chl fluorescence: Leaf gas exchange (a gas exchange system *Li-6400*) and Chl fluorescence (a pulse-modulated fluorescence monitor system *FMS-2*; *Hansatech*, UK) were monitored on the shoots every two hours from predawn to 19:00 in all plants. Net photosynthetic rate (P_N), stomatal conductance (g_s), photosynthetic photon flux density (PPFD), maximal photochemical efficiency (F_v/F_m), quantum efficiency of non-cyclic electric transport of PS2 (Φ_{PS2}), and non-photochemical quenching of fluorescence (NPQ) were measured.

Pigment contents: Chl *a*, Chl *b*, and total carotenoids (x+c) were extracted from leaves and stem with 80 % acetone. The pigment contents were determined spectrophotometrically according to Lichtenthaler (1987) and the data were calculated per leaf DM.

Results and discussion

Leaf and soil water contents did show large differences. During drought stress, soil water content changed from 90.00 to 2.54 % at 0−10 cm and from 93.00 to 3.46 % at 10−25 cm, and leaf water content changed from 79.00 to 4.66 %. Re-hydration induced rapid recovery of soil RWC, but the stem RWC did not recover until budding of new leaf (Fig. 1*B,D*). *R. soongorica* has characteristics typical of a resurrection plant (Scott 2000).

Photosynthesis: *R. soongorica* was exposed to multiple environmental stresses, including water deficit, high irradiance, and high air temperature. Maximal irradiance and temperature were about 1 100 $\mu mol\ m^{-2}\ s^{-1}$ and 42 °C, respectively (data not shown). P_N declined significantly ($p<0.05$) with the increasing drought (Fig. 2*A*). Diurnal time courses of P_N of *R. soongorica* displayed typical double-peak curve model, especially under well-watering and moderate drought. However, under severe drought stress diurnal courses of P_N exerted a single-peak curve. During re-hydration, diurnal time courses of P_N of *R. soongorica* recovered form single-peak curve to double-peak curve model (Fig. 2*B*). The photosynthetic performance of *R. soongorica* was consistent with the results of other researchers (Xu *et al.* 2005, Jia *et al.* 2006, Liu *et al.* 2007). On the other hand, after re-watering of the soil for 6 d, P_N was restored to the initial state (Fig. 2*B*). This means that within a short time this plant was able to restore its metabolic processes. This was particularly conspicuous in the case of electron transport between the photosystems. After re-watering, the studied parameters of Chl *a* fluorescence reached 86–90 % of control values, so a nearly complete reactivation of photosynthetic processes took place. Hence the photosynthetic apparatus in *R. soongorica* is very resistant to water stress.

Electron transport in PS2: Water stress had slight effect on the F_v/F_m at 42 d and this ratio declined significantly after all leaves have shed, especially at noon (Fig. 2*C*). Stems of shed leaves (RWC lower than 5 %) decreased F_v/F_m by about 45 % due to the larger decline of F_m. Following 3 d of re-hydration, F_v/F_m increased considerably but it was still lower than that of control and reached its normal level only after the emergence of new leaves (Fig. 2*D*). Kinetics of Chl fluorescence induction is used as a monitor in photochemical activities of photosystems (Lu *et al.* 1994). Stresses affecting PS are often accompanied by a decline in F_v/F_m which reflects the maximal efficiency of excitation capture of a dark-adapted plant and is correlated with the number of functional PS2 reaction centres (Öquist and Chow 1992, Osmond 1994). Significant declines of F_v/F_m were observed in *R. soongorica* leaves and stems in the dark after dehydration and re-hydration cycle, suggesting that the maximum capacity of the primary reaction of photosynthesis may be impaired.

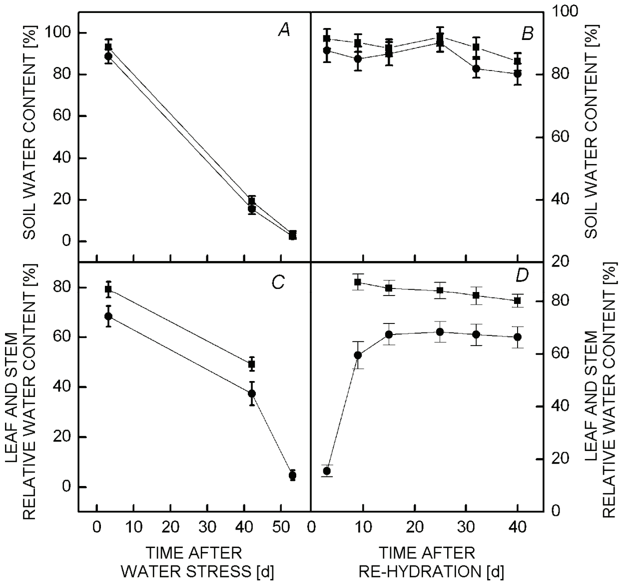

Fig. 1. Changes in soil water content (*A*) during water stress and (*B*) during re-hydration in 0−10 cm (●) and 10−25 cm (■) layers, and in leaf (●) and stem (■) relative water content (*C*) during water stress and (*D*) during re-hydration. Means ± SE (*n* = 9).

Φ_{PS2} was much more influenced by desiccation than F_v/F_m (Fig. 2*E*). In leaves of *R. soongorica,* Φ_{PS2} declined from about 0.80 to 0.45 with change of RWC from 80.0 to 4.5 %. Upon re-hydration, the values of Φ_{PS2} almost restored normal control level upon the emergency of a new leaf (Fig. 2*F*).

The thermal energy dissipation, expressed as NPQ, increased about 1 and 2 times when the leaf RWC was reduced from 80 to 50 and 4.5 %, respectively. and it was still higher than the control after 9 d of re-hydration (Fig. 2*G,H*).

Φ_{PS2} is a parameter closely correlated with the quantum yield of non-cyclic electron transport (Genty *et al.* 1989). The values of Φ_{PS2} were near to 0.35 and NPQ was near to 0.7 at the end of desiccation, indicating that there was hardly a linear electron transport and most of the PS2 reaction centres were closed. The dehydrated plants were in dormant state, all physiological processes nearly ceased.

Pigment contents: Chl *a* and *b* in leaves were lost during dehydration but Car content in stem significantly increased (Table 1). 6 d after the new leaf emergency, Chl recovery started upon re-hydration in leaf and Car content declined to normal. Cars and anthocyanins protect against light damage (Hopkins 1992). Decline in Car content during dehydration of *R. soongorica* is parallel with the dismantling of the photosynthetic apparatus to prevent light-interactions. Anthocyanins accumulate in plant vacuoles in response to irradiance and temperature stresses and may mask Chl and/or act as filters preventing excess photon absorption by the leaf (Hopkins 1992). They may also play an anti-oxidant role (Larson 1988). Also the decline in Chl content in the leaves of *Xerophyta viscosa* is accompanied by the accumulation of anthocyanins (Sherwin and Farrant 1998). The processes of dismantling the photosynthetic apparatus and the synthesis of anthocyanins may be linked to the protection of plants against UV-radiation and damage resulting from oxygen free radical generation during desiccation (Smirnoff 1993, Sherwin and Farrant 1998).

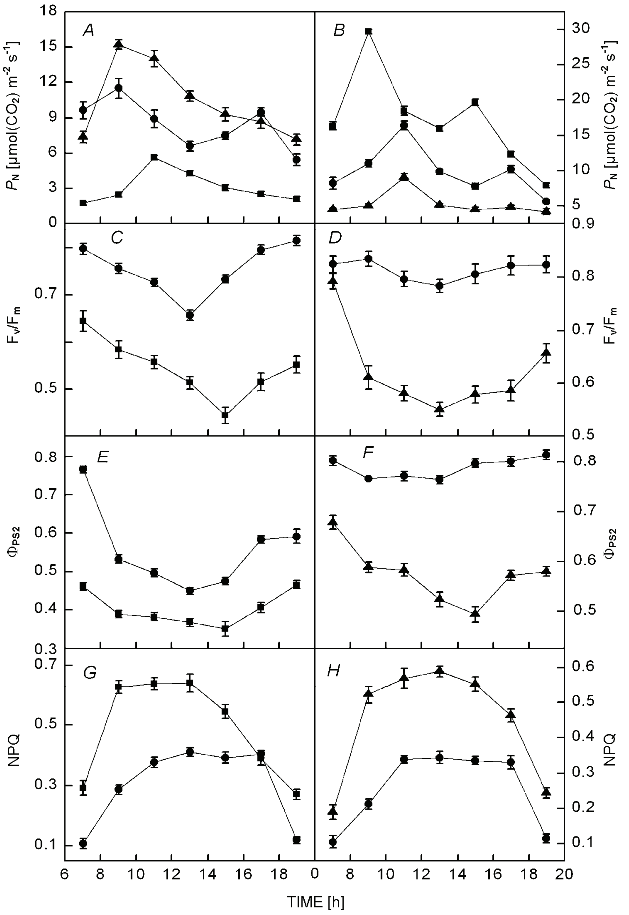

Fig. 2. Diurnal time courses of (*A*) net photosynthetic rate (P_N), (*C*) maximum photochemical efficiency of photosystem 2 (F_v/F_m), (*E*) quantum efficiency of non-cyclic electric transport of PS2 (Φ_{PS2}), and (*G*) non-photochemical quenching of fluorescence (NPQ) during dehydration or (*B*), (*D*), (*F*), and (*G*) during re-hydration, respectively. ▲, ●, and ■ indicate 3, 42, and 53 d after water stress and 3, 9, and 25 d after re-hydration, respectively. Means±SE (*n* = 8).

R. soongorica has characteristics typical of a poikilochlorophyllous resurrection plant. It survives the loss of 95 % of its water and during drying about 80 % Chl is lost and the thylakoid membranes are dismantled accompanying leaf shed. Leaf shedding that reduces the surface area exposed to light during dehydration and in the dry state is one strategy of this plant to cope with such

Table 1. Chlorophyll (Chl) *a* and *b*, and carotenoid (Car) contents [g kg^{-1}(DM)] of *R. soogorica* leaves and stems during progressive drought and resurrection process. Means±SE of three independent observations. Values within columns followed by the same letter(s) are not significantly different ($p<0.05$). WS − water stress, RH − re-hydration.

			Chl *a*	Chl *b*	Chl *a*+*b*	Car
WS	3	leaf	1.322±0.220a	0.565±0.040a	1.887±0.112a	0.253±0.001a
		stem	0.552±0.041d	0.221±0.007d	0.773±0.065d	0.083±0.004c
	42	leaf	1.556±0.215b	0.692±0.009b	2.247±0.108b	0.312±0.006b
		stem	0.310±0.009e	0.217±0.017d	0.527±0.023e	0.155±0.204d
	53	stem	0.300±0.005e	0.213±0.012d	0.513±0.048e	0.178±0.222d
RH	3	stem	0.335±0.002e	0.200±0.006d	0.536±0.035e	0.162±0.203d
	9	leaf	0.998±0.008c	0.498±0.048c	1.497±0.127c	0.267±0.002a
		stem	0.521±0.014d	0.192±0.034d	0.713±0.038d	0.095±0.004c
	15	leaf	1.385±0.147a	0.563±0.034a	1.948±0.128a	0.235±0.014a
		stem	0.525±0.080d	0.227±0.043d	0.752±0.011d	0.093±0.004c
	25	leaf	1.514±0.114b	0.628±0.054a	2.242±0.137b	0.253±0.004a
		stem	0.511±0.033d	0.250±0.006d	0.761±0.080d	0.085±0.003c
	32	leaf	1.573±0.121b	0.620±0.038a	2.194±0.300b	0.245±0.008a
		stem	0.541±0.075d	0.213±0.012d	0.755±0.016d	0.097±0.005c
	40	leaf	1.529±0.103b	0.577±0.065a	2.108±0.118b	0.233±0.006a
		stem	0.555±0.084d	0.211±0.062d	0.769±0.028d	0.083±0.003c

stress. Reflective irradiated surfaces further reduce the amount of photons absorbed and possibly facilitate temperature control. The leaf shed and the loss of Chl in this species may be necessary to prevent excess photon absorption. The cost to a poikilochlorophyllous species like *R. soongorica* is in the longer recovery associated with repair and re-synthesis once water becomes available.

We found that the decrease in soil water content and the increase of water deficit in leaves were associated with disturbances in the photosystem activities resulting in changes in Chl *a* fluorescence and content of photosynthetic pigments. In a study of Kamińska-Różek and Pukacki (2004) with Norway spruce, severe drought resulted in a degradation of cytoplasmic membranes and a decrease in contents of phospholipids and polyunsaturated fatty acids. The reduced Chl fluorescence parameters during drought indicate that photosynthesis was less effective (Babani *et al.* 1996, Van Heerden *et al.* 2003).

In summary, the plant studied here withstands damage caused by drought by a combination of avoidance and protective mechanisms. Both utilize leaf shedding to reduce the irradiated surface area and retain chloroplast integrity and a considerable amount of Chl in stems during dehydration and in the dry state. Intermediate stages of dehydration and re-hydration are seen as critical, as limited water prevents full physiological activity but enables deleterious reactions to proceed. During these stages protection is afforded by activities of Chl fluorescence.

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