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Effects of drought stress induced by polyethylene glycol on pigment content and photosynthetic gas exchange of *Pistacia khinjuk* and *P. mutica*

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Abstract

The effects of drought stress induced by polyethylene glycol, PEG (molecular mass 6000) on some ecophysiological characteristics of two wild pistachio species, Mastic and Khinjuk (*P. mutica* and *P. khinjuk*) selected as root stocks for production of edible pistachio trees (*P. vera*) in Iran and Turkey, were studied. Net photosynthetic rate (P_N), stomatal conductance (g_s), chlorophyll (Chl) fluorescence parameters, leaf water potential (Ψ_l), leaf osmotic potential (Ψ_π), leaf osmotic adjustment ($\Delta\Psi_\pi$), and Chl *a* and *b* were measured. All parameters were influenced by increase in concentra-tion of PEG in the nutrient solutions. P_N, g_s, and Chl *a* were significantly higher in *P. mutica* than in *P. khinjuk* but, compared to the control treatment, *P. khinjuk* showed a higher resistance to drought stress than *P. mutica*.

Additional key words: chlorophyll content; net photosynthetic rate; osmotic adjustment; stomatal conductance; water use efficiency.

Introduction

Mastic and khinjuk pistachio (*Pistacia mutica* L. and *P. khinjuk* L.) are two wild pistachio species which are growing together with almond, oak, and other forest trees at altitudes between 600-3 000 m (Sheibani 1995). They are distributed in Iran, Turkey, Syria, northern Iraq, and southern Jordan (Zohary 1995). *P. mutica* has been selected as a rootstock for edible pistachio trees (*P. vera*) in many parts of Iran (Sheibani 1987). *P. khinjuk* is another well-known species in pistachio nut production and it is also used as a rootstock (Dahab *et al.* 1975).

Polyethylene glycols (PEG) with molecular mass of 6000 and above are non-ionic, water-soluble polymers which are not expected to penetrate intact plant tissues rapidly (Chazen *et al.* 1995). PEG solutions are often used to induce water stress in higher plants (*e.g.*, Leidi 1993, El-Shahaby 1994, Ashraf and O'Leary 1996, Nepomuceno *et al.* 1998). Dodd and Davies (1996) reported the inhibitory effects of PEG on barley (*Hordeum vulgare* L.) growth through high accumulation of abscisic acid. Johnson *et al.* (1996) mentioned that PEG-generated osmotic stress (-1.6 to –2.0 MPa) significantly reduced cell turgor pressure in *Colophospermum mopane* (Fabaceae). Drought stress generated by polyethylene glycol induces significant reduction in P_N and turgor pressure in white spruce (*Picea glauca*) seedlings (Jiang *et al.* 1995). Also Zhang and Kirkham (1995) stated that osmotic stress generated by PEG (-0.57 MPa) reduced photosynthetic rate, leaf water potential, osmotic potential and transpiration rate in sunflower (*Helianthus annuus* L.) plants.

The objectives of the present study were to determine if drought stress induced by PEG affects ecophysiological parameters in two pistachio species and if it does, to evaluate the influence of the stress on fluorescence emission, Chl content, P_N, g_s, and water use efficiency. Also, both species will be compared in relation to their drought tolerance.

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Abbreviations: Chl - chlorophyll; *E* - transpiration rate; F_0 - minimal fluorescence yield; F_m - maximal fluorescence yield; F_v - variable fluorescence yield; q_n - non-photochemical quenching; q_p - photochemical quenching; g_s - stomatal conductance; P_N - net photosynthetic rate; PAR - photosynthetically active radiation; PEG - polyethylene glycol; WUE - water use efficiency; Ψ_l - leaf water potential; Ψ_p - leaf pressure potential; Ψ_π - leaf osmotic potential; $\Delta\Psi_\pi$ - osmotic adjustment; Ψ_s - osmotic potential of the nutrient solution.

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Materials and methods

Plants: Seeds of *Pistacia khinjuk* and *P. mutica* were obtained from the Natural Resources Research Institute of Charmahal-Bakhtiary, Iran. The seed outer shells were scarified by sulphuric acid following Mahmood (1979). Seeds were then sown in pots containing sand and peat. Seedlings were grown in the greenhouse at 27±5 °C, relative humidity 65±10 %, and natural irradiance for 21 months. Plants were transplanted on 11 February 1999 to vermiculite with minimal root disturbance. They were simultaneously irrigated using a circulating system consisting of water-pump, gutter, and reservoir containing the nutrient solutions. Treatments made at three levels of drought stress (Ψ_s = -0.5, -1.0, and -1.6 MPa) induced by PEG 6000 were compared against a control (Ψ_s = -0.1 MPa). Drought stress levels were chosen with respect to the climatic conditions of the lands where the species are native and similar studies have been carried out, such as that by Nepomuceno *et al.* (1998). A preliminary experiment to compare PEG 6000 and PEG 10 000 showed that the former had no side effects on pistachio plants. In order to prevent adverse effect of PEG 6000 on oxygen availability to plant roots (Plaut and Federman 1985), the nutrient solutions were continuously aerated. The concentration of PEG 6000 [g kg^{-1}(water)] for each drought stress level was determined using the equation of Burlyn and Merrill (1973).

Osmotic potential of the nutrient solution was decreased by -0.15 MPa per day until final Ψ_s was reached. The final Ψ_s for each drought treatment was kept for three weeks. The plants were fertilised by adding a modified (50 %) Hoagland nutrient solution (see Picchioni and Miyamoto 1990). The volume of each treatment solution in the container was maintained daily with the addition of tap water. A total of 32 pistachio plants were used in this experiment.

Methods: Leaf water and osmotic potentials were measured three weeks after reaching the final stress treatments, on the fourth leaf from the top of plants. From each plant (stressed and non-stressed plants) two leaf disks (0.25 cm^2) were punched early in the morning. Leaf water potential was directly determined using the thermocouple psychrometer (Spanner 1951) on one of the two leaf disks. The second group of leaf disks was wrapped in aluminium foil and was frozen (-18 °C) in order to collapse the cell wall and the semi-permeable membranes. The leaf osmotic potential was then determined after thawing these leaf disks, also using the thermocouple psychrometer.

Chl fluorescence parameters were measured four times within the experimental period (weeks 1, 2, 3, and 4 after reaching the final stress levels), using a portable PAM-fluorometer (*H. Walz*, Effeltrich, Germany) and *DA-2000* software. Fluorescence parameters were measured on four plants of each treatment after a dark adaptation of 30 min. Minimal fluorescence (F_0), maximal fluorescence (F_m), the ratio of variable fluorescence to maximal fluorescence (F_v/F_m), photochemical quenching (q_p), and non-photochemical quenching (q_n) were recorded on the adaxial surface of the fourth leaf from the top.

At the end of the greenhouse experiments a fully extended leaf from each plant was collected. The leaves were wrapped in aluminium foil to avoid degradation of pigments by light. Half-gram samples were taken from the collected leaves. They were then pulverised with liquid nitrogen. Subsequently, 0.25 g of each sample was extracted by 80 % acetone and put in the freezer at -5 °C for 24 h. Pigments were determined according to Lichtenthaler (1987) by means of spectrophotometer analysis (*Uvikon 930*).

P_N, E, and g_s were measured according to Samson *et al.* (1997) on the same leaves as the leaf water potential using a CO_2 and H_2O gas exchange apparatus (*ADC 225 MK3*) at an irradiance of 500±20 µmol(PAR) m^{-2} s^{-1}, 60 % relative humidity, 23 °C, and 390-425 µmol(CO_2) mol^{-1}.

Results

Leaf water potential (Ψ_l) and leaf osmotic potential (Ψ_π): Both Ψ_l and Ψ_π of the two species were significantly affected by Ψ_s indicating that PEG indeed induced drought stress on the plants. Overall, *P. mutica* showed more negative Ψ_l and Ψ_π than *P. khinjuk*. No significant difference was found in Ψ_l and Ψ_π at Ψ_s higher than -0.5 MPa. Significant deviation from the control started at Ψ_s –1.0 MPa and increasingly continued at Ψ_s -1.6 MPa (Fig. 1*A*,*B*). The leaf pressure potential (Ψ_p) was maintained almost constant (0.35 and 0.43 MPa for *P. khinjuk* and *P. mutica*, respectively). The degree of osmotic adjustment ($\Delta\Psi_\pi$), calculated as the difference of Ψ_π between the stressed and control plants, for all stress levels increased by more negative Ψ_s.

Chl fluorescence and Chl content: Exposure of pistachio plants to drought stress led to a significant effect in non-photochemical quenching (q_n) as well as Chl *a* and *b* contents (Table 1). The study indicates an increasing and a decreasing trend for q_n and Chl content, respectively. Non-photochemical quenching showed a significant augmentation (1.21 times the control) only at Ψ_s = -1.6 MPa. The value of q_n in *P. khinjuk* was lower than that of *P. mutica* for all stress levels (Table 1). Other Chl fluorescence parameters were not affected.

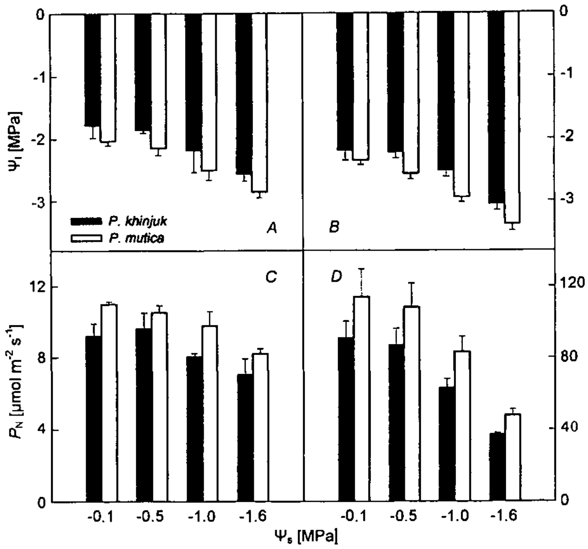

Fig. 1. Leaf water potential (Ψ_l) (*A*), leaf osmotic potential (Ψ_π) (*B*), net photosynthetic rate (P_N) (*C*), and stomatal conductance (g_s) (*D*) in *P. khinjuk* and *P. mutica* at control (-0.1 MPa) and three levels of drought stress (-0.5, -1.0 and -1.6 MPa) induced by PEG 6000 (Ψ_s). Each bar represents the mean of four observations ± SE.

Significant decrease in Chl *a* content started at Ψ_s = -1.0 MPa and continued with further decrease of Ψ_s down to -1.6 MPa while a significant reduction in Chl *b* was only observed at Ψ_s of -1.6 MPa. *P. mutica* was characterised with higher Chl *a* concentration and *P. khinjuk* revealed higher Chl *b* content. The trend of reduction in Chl *a* and *b* in both species was parallel, which was reflected in the nearly constant Chl *a*/*b* ratio (Table 1). Analysis of variance confirmed a significant difference of Chl *a*/*b* between the species, with the higher value for *P. mutica*.

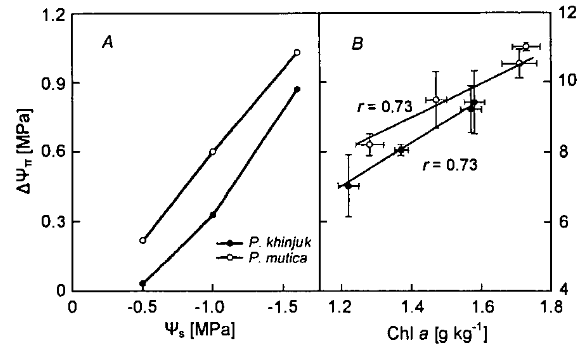

Fig. 2. Osmotic adjustment ($\Delta\Psi_\pi$) at different drought stress (Ψ_s = -0.5, -1.0, and -1.6 MPa) (*A*), and (*B*) the relation between chlorophyll *a* (Chl *a*) content and net photosynthetic rate (P_N) in *P. khinjuk* and *P. mutica*. Regression models for *P. khinjuk* and *P. mutica* are P_N = 6.18 (Chl *a*) - 0.40 and P_N = 4.87 (Chl *a*) + 2.16, respectively.

Table 1. Chlorophyll *a* and *b* contents [g kg^{-1}(f.m.)], non-photochemical quenching (q_n), and water use efficiency, WUE [mmol(CO_2) mol^{-1}(H_2O)] in *P. khinjuk* and *P. mutica* at control (-0.1 MPa) and three drought stress levels (-0.5, -1.0, and -1.6 MPa) induced by PEG 6000. Means ± SE (*n* = 4). Different letters express significantly different results between drought stress levels (Ψ_s) in the same species (a, b, c) or between species with same drought stress level (r, s).

Species	Ψ_s [-MPa]	Chl *a*	Chl *b*	Chl *a*/*b*	q_n	WUE
P. khinjuk	0.1	1.57±0.03a/r	0.75±0.04a/r	2.10±0.16a/r	0.248±0.010a/r	18.80±1.35a/r
	0.5	1.58±0.03a/r	0.75±0.02a/r	2.10±0.03a/r	0.250±0.000a/r	19.66±1.27a/r
	1.0	1.37±0.01b/r	0.69±0.01b/r	2.10±0.06a/r	0.264±0.010a/r	18.34±0.59a/r
	1.6	1.22±0.02c/rs	0.61±0.05b/r	2.00±0.14a/r	0.303±0.000b/r	18.01±0.99a/r
P. mutica	0.1	1.73±0.03a/s	0.69±0.00a/s	2.50±0.07b/s	0.259±0.010a/r	18.01±2.65a/r
	0.5	1.71±0.03a/s	0.66±0.03a/s	2.57±0.20b/s	0.263±0.010a/r	17.13±1.48a/r
	1.0	1.47±0.03b/s	0.60±0.02b/s	2.48±0.10b/s	0.279±0.000a/r	18.34±2.04a/r
	1.6	1.28±0.03c/rs	0.52±0.03b/s	2.47±0.08b/s	0.312±0.010b/r	18.31±0.47a/r

P_N, g_s, and water use efficiency (WUE): P_N and g_s decreased with decreasing Ψ_s for both species (Fig. 1*C*,*D*). Relative to the control plants, both species showed a similar decrease of 42 and 75 % for P_N and g_s, respectively, when Ψ_s was -1.6 MPa. Stomatal conductance differed significantly at Ψ_s = -1.0 and -1.6 MPa, while P_N was only significantly different at Ψ_s = -1.6 MPa. The performances of P_N and g_s in *P. mutica* were significantly superior to that of *P. khinjuk* either in drought-stressed and control plants. *P. mutica* showed higher stomatal frequency and larger stomata (values not shown), which might account for the higher g_s compared to *P. khinjuk*. WUE was calculated as the ratio of P_N over *E*. Analysis of variance did not show any significant difference in value of WUE, neither between the various levels of stress nor between the two species (Table 1).

Discussion

By decreasing the Ψ_s, both Ψ_l and Ψ_π decreased and this could be caused by an accumulation of osmolytes at cellular level (Nepomuceno *et al.* 1998). Higher values of Ψ_l and Ψ_π were found in *P. khinjuk* compared to *P. mutica* which illustrates that the former species tolerates a higher drought stress.

An increasing trend of $\Delta\Psi_\pi$ with decreasing Ψ_s of the nutrient solution was observed (Fig. 2*A*). This behaviour has been described as a mechanism developed for the plant to survive in dry conditions (Herralde *et al.* 1998), and can be attributed to the active accumulation of solutes in the cell sap or through passive solute accumulation resulting from reduced cell volume (Morgan 1984). *P. mutica* exhibited a higher $\Delta\Psi_\pi$ (0.62) than *P. khinjuk* (0.41), which reflects the ecological adaptations to the land where they are native. The former species is native in semi-arid to arid area while the latter one is native in arid area (Abrishami 1995), and the period of dry season in the regions where *P. mutica* is native is shorter than in the areas where *P. khinjuk* is distributed. Wong *et al.* (1985) stated osmotic adjustment might delay stomatal closure. Therefore the lower $\Delta\Psi_\pi$ in *P. khinjuk* than in *P. mutica* could be effective in stomatal closure, thus reducing transpirational water losses which is important to survive in arid environments.

At Ψ_l of -3 MPa, a Ψ_p of approximately 0.4 MPa was maintained. In many fruit tree species, a decreasing Ψ_l is accompanied with the loss of Ψ_p. For example, Sean *et al.* (1998) showed that ber (*Ziziphus mauritiana* Lamk.) leaves reached zero Ψ_p at a Ψ_s of -2.3 to -2.5 MPa. Therefore maintaining Ψ_p in the species studied here could be an effective tool in tolerating drought stress.

Non-stomatal restrictions on CO_2 assimilation under drought stress can be assessed through measuring Chl fluorescence parameters. Non-photochemical quenching (q_n), which is related to the energetic state of the chloroplast, shows that the energetic state of this organelle increased as a consequence of drought stress. The other fluorescence parameters such as q_p show that the redox state of photosystem 2 was not affected by drought stress. Our results for q_n are consistent with the findings of, *e.g.*, Lichtenthaler and Rinderle (1988) and Eastman and Camm (1995) on spruce needles. Nevertheless, fluorescence parameters change also during vegetation season (for *P. lentiscus* see Karavatas and Manetas 1999).

Imposition of drought caused a reduction in Chl content in both pistachio species. The reduction in Chl *a* content was higher than in Chl *b*, which is mainly due to sensitivity of the former parameter to environmental stress, especially to salt and drought stress (Reddy and Vora 1986). Our findings agree with the results of Sayed (1996) on *Zygophyllum qatarenase* and Luquez *et al.* (1997) on soybean (*Glycine max*).

Photosynthetic performance in *P. mutica* is superior to that of *P. khinjuk* in unstressed and stressed conditions, and this could be related to the difference in Chl *a* content between the species (Luquez *et al.* 1997) (Fig. 2*B*). With respect to the effect of drought treatments, the control-compared values of P_N show that *P. mutica* is more affected by stress compared to *P. khinjuk*. Both stomatal and mesophyll limitations could reduce P_N in both species. The decrease in g_s at decreasing Ψ_s (Fig. 1*D*) and the accompanied decrease in P_N (r = 0.61) (Fig. 1*C*) illustrates the stomatal limitations. The maintenance of WUE with decreasing Ψ_s, in both species, could be an illustration of the presence of mesophyll resistance (Behboudian *et al.* 1986). Also the reduction in Chl content (especially Chl *a*) and alteration in energy state of the chloroplast (as increasing q_n) were non-stomatal limitations, which reduce P_N. Our results with P_N and g_s (Fig. 1*C,D*) are in agreement with the findings of Goldhamer *et al.* (1984) on *Pistacia vera* and Loreto *et al* (1993) on *Quercus ilex* and *Pistacia lentiscus*.

In conclusion, drought stress induced by PEG-6000 promoted significant differences in stressed plants *versus* control plants in their water relations and gas exchange. Both pistachio species have the capacity to maintain a relatively high P_N with decreasing Ψ_s down to at least −1.0 MPa. *P. khinjuk* has a relatively greater drought resistance than *P. mutica*, and it is relatively more suited for arid environments.

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