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RESEARCH PAPER

Impact of fresh and saline water flooding on leaf gas exchange in two Italian provenances of *Tamarix africana* Poiret

R. Abou Jaoudé, G. de Dato, M. Palmegiani & P. De Angelis

Department for Innovation in Biological, Agro-food and Forest Systems (DIBAF), University of Tuscia, Viterbo, Italy

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Correspondence
R. A. Jaoudé, Department for Innovation in Biological, Agro-food and Forest Systems (DIBAF), University of Tuscia, via S. Camillo de Lellis snc, 01100 Viterbo, Italy.
E-mail: raj@unitus.it

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ABSTRACT

In Mediterranean coastal areas, changes in precipitation patterns and seawater levels are leading to increased frequency of flooding and to salinization of estuaries and freshwater systems. *Tamarix* spp. are often the only woody species growing in such environments. These species are known for their tolerance to moderate salinity; however, contrasting information exists regarding their tolerance to flooding, and the combination of the two stresses has never been studied in *Tamarix* spp. Here, we analyse the photosynthetic responses of *T. africana* Poiret to temporary flooding (45 days) with fresh or saline water (200 mm) in two Italian provenances (Simeto and Baratz). The measurements were conducted before and after the onset of flooding, to test the possible cumulative effects of the treatments and effects on twig aging, and to analyse the responses of twigs formed during the experimental period. Full tolerance was evident in *T. africana* with respect to flooding with fresh water, which did not affect photosynthetic performances in either provenance. Saline flooding was differently tolerated by the two provenances. Moreover, salinity tolerance differently affected the two twig generations. In particular, a reduction in net assimilation rate (−48.8%) was only observed in Baratz twigs formed during the experimental period, compared to pre-existing twigs. This reduction was a consequence of non-stomatal limitations (maximum carboxylation rate and electron transport), probably as a result of higher Na transport to the twigs, coupled with reduced Na storage in the roots.

INTRODUCTION

In the Mediterranean region, changes in precipitation patterns as a consequence of climate change are leading to an increased frequency of torrential rainfall, thus increasing flooding occurrence (Alpert *et al.* 2002). Moreover, the increase in global average temperatures is causing widespread melting of snow and ice, resulting in a rise of sea level, which could provoke the salinization of irrigation water, estuaries and freshwater systems (IPCC 2007). Therefore, Mediterranean coastal areas, salt marshes and estuaries, where plant existence is already limited because of other stress factors (drought, high temperatures, marine aerosol), may be primarily affected by both flooding with fresh and salt water. Coastal plants have evolved many physiological, morphological and reproductive strategies to survive flooding and salinity; however, their ability to adapt to multiple stressors (*e.g.* flooding with saline water) is lower compared to their tolerance to a moderate increase in a single stressor (Day *et al.* 2008).

Tamarix spp. are naturally distributed in Mediterranean coastal areas, salt marshes and riverbanks of temporary and perennial streams, and are often the only woody species growing under such extreme conditions (Aránzazu Prada & Arizpe 2008). *Tamarix* spp. show high adaptability to different environments and high tolerance to adverse conditions (Ginzburg 1967; Bar-Nun & Poljakoff-Mayber 1974; Brotherson & Field 1987; Cleverly *et al.* 1997; Di Tomaso 1998; Glenn *et al.* 1998; Horton *et al.* 2001; Tallent-Halsell & Walker 2002; Zhang *et al.* 2002; Gries *et al.* 2003; Xu & Li 2006). However, although considered halophytic, a reduction in *Tamarix* growth rates under concentration of 100 mM NaCl or more has been reported in the literature (Waisel 1961; Kleinkopf & Wallace 1974; Glenn *et al.* 1998). Moreover, contrasting results exist regarding their tolerance to flooding with fresh water and to water level fluctuations (Horton 1960; Sprenger *et al.* 2001; Vandersande *et al.* 2001; Tallent-Halsell & Walker 2002; Gries *et al.* 2005; Stromberg *et al.* 2007; Meritt & LeRoy-Poff 2010), although the effects of flooding with saline water on photosynthesis and growth have never been studied in these species.

Soil salinity may result in a decrease in plant growth as a result of (i) a reduction in soil water potential, (ii) nutrient ion imbalance due to disturbance of essential intracellular ion concentrations and (iii) toxicity caused by excess Na^+ and Cl^- accumulation (Munns *et al.* 1995; Maathuis & Amtmann 1999; Mansour 2000). In fact, at high cellular NaCl concentrations, both stomatal (increased resistance to CO_2) and non-stomatal (reduced mesophyll conductance, electron transport and RuBisCO activity) limitations to photosynthesis have been reported (Bongi & Loreto 1989; Delfine *et al.* 1998; Lovelock & Ball 2002; Nandy (Datta) *et al.* (2007). Leaf sensitivity also depends on leaf age: in old leaves, high salinity increases maintenance costs because leaf aging and salt

stress both reduce photosynthetic rates and salt accumulation capacity (Suárez & Medina 2005). Flooding is a common environmental condition in many coastal areas (Colmer & Flowers 2008). Flooding events trigger a series of biological, chemical and physical mechanisms on habitats that completely alter soil capacity to support plant growth by: (i) reducing O_2 diffusion and supply to the roots; (ii) increasing mineral solubilisation; (iii) promoting anaerobic metabolism of roots and microbes, which leads to the formation of phytotoxic compounds; and (iv) causing breakdown of aggregates, clays deflocculation and destruction of cementing agents (Blom & Voesenek 1996; Kozlowski 1997). Under scarce or no O_2 availability in soil, an increase in ethylene synthesis in tolerant species and its accumulation in roots trigger aerenchyma formation (Drew *et al.* 2000). This tissue provides an interconnected system of air channels, enabling oxygen to diffuse among or ventilate plant organs (Blom & Voesenek 1996), and remove carbon dioxide, ethylene and methane from roots and soils (Colmer 2003). Moreover, many tolerant species are able to form adventitious roots when their primary root system cannot function properly (Visser *et al.* 1995). Together with waterlogging, salinity can cause severe damage to plants (Barrett-Lennard 2003), combining the harmful effects of both stresses. In particular, salinity may compromise flood tolerance mechanisms (Salter *et al.* 2008), preventing adventitious root formation (Akilan *et al.* 1997; Salter *et al.* 2008) and increasing Na^+ and Cl^- concentrations in the foliage of plants under flooding conditions (Marcar *et al.* 2002).

In this study, the photosynthetic responses to temporary flooding with fresh and saline water (200 mM) were assessed in two Italian provenances of *T. africana* Poiret. We used the A/C_i curve approach (Farquhar *et al.* 1980; von Caemmerer & Farquhar 1981) to evaluate the impact of the treatments on both stomatal conductance and carboxylation rate. The measurements were conducted before and after the onset of flooding, to test the possible cumulative effects of the treatments and examine twig aging, and to analyse the responses of twigs formed during the experimental period.

The subjects tested in this work are:

1 General tolerance of *T. africana* to flooding conditions;
2 Different impacts of flooding alone or in combination with salinity;
3 The more important effect of treatments on twigs exposed for the entire period compared to twigs formed during the experimental period;
4 Differences in ability to cope with the imposed stress between the two populations.

MATERIAL AND METHODS

Two provenances of *T. africana* Poiret were collected in November 2008 from two sites in southern Italy. Among the collected material, three genotypes at each site were selected from the shores of the salty Lake Baratz (BAR) (40°40′ N, 8°13′ E; northwest Sardinia; 1.3 km from the sea) and near the mouth of the River Simeto (SIM) (37°24′ N, 15°04′ E, eastern Sicily; 2.0 km from the sea), which are both characterised by a similar mean soil salinity of 5–6 $dS \cdot m^{-1}$ (Martinelli 1998; Ferrara & Pappalardo 2004). The BAR site has a mean annual temperature of 16.9 °C and annual rainfall of 573 mm (meteorological station of Alghero Fertilia, 40°38′ N 8°17′ E; altitude 24 m a.s.l.; period of observation 1971–2000). In SIM, the mean annual temperature is 17.6 °C and annual rainfall is 447 mm (meteorological station of Catania Sigonella, 37°24′ N 14°55′ E; altitude 22 m a.s.l.; period of observation 1971–2000). In both sites, a long dry period (from May to September) is common.

The selected genotypes were replicated six times through cuttings, which were planted in 1.6-dm^3 pots (10.5 × 10.5 × 22 cm) containing sand (35%) and loamy soil (65%). The cuttings were grown in a greenhouse for 6 weeks and were subsequently transplanted in 2.6-dm^3 pots (17.5 × 17.5 × 25 cm) containing the same soil mixture. The pots were inserted into nine plastic boxes (60 × 40 × 40 cm) in groups of four (two provenances per two randomly selected genotypes) and grown for 2 months in a growth chamber under a photosynthetic photon flux density of 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$, 60% relative humidity, with a photoperiod of 12 h and a day/night temperature of 25/15 °C. The plants were watered three times a week with fresh water. Two weeks before the beginning of the experiment, a modified half-strength Hoagland solution was supplied. The nine boxes were divided into three blocks, each composed of three treatments. The treatments were: (i) daily irrigation with fresh water (control – C), (ii) flooding with fresh water (F) and (iii) flooding with fresh water added with 200 mM NaCl (FS). Flooding levels were maintained 3 cm above the soil surface and kept constant for 45 days by adding fresh or saline (200 mM NaCl) water once a week. Moreover, a proportional amount of Hoagland solution (0.5 × concentration) was provided to all treatments (C, F and FS) once a week, according to plant N requirement. To estimate this amount, the tenth youngest twig was selected from the highest (dominant) sprout and twig length growth was determined each week. Thereafter, the twig was cut and the dry weight determined by placing in an oven at 70 °C until no further weight change occurred. To estimate weekly twig growth, considering constant twig water content over 7 days, the initial twig dry weight was calculated as:

$$DW_i = DW_f / TL_f * TL_i \quad (1)$$

where DW_i is the initial twig dry weight in g, DW_f is the final twig dry weight in g, TL_i is the initial twig length in cm and TL_f is the twig length in cm after 1 week of growth. Thus, weekly twig growth was estimated as:

$$DWG = DW_f - DW_i \quad (2)$$

where DWG is the twig dry weight growth in g. Weekly plant growth was estimated by multiplying twig growth by the total number of twigs of the dominant sprout, by the total number of sprouts per plant, and by a correction factor of 0.5 (to prevent overestimating plant N requirement, as non-dominant sprout length was always lower compared to the dominant sprout). Total dry weight growth was then multiplied by twig N content (on average 1.5%; determined as reported below).

Two weeks after the beginning of the experiment, adventitious roots had formed at the base of the stem of all plants flooded with both fresh and saline water. No differences in adventitious roots biomass were observed between plants flooded with fresh and saline water.

Gas exchanges and chlorophyll fluorescence measurements

Two plants (one SIM and one BAR) per treatment and per block were analysed for gas exchange and fluorescence. As *T. africana*, similar to *Cupressus* spp., has scale-like leaves surrounding a central branchlet, it was not possible to perform the gas exchange measurements on a single leaf. Therefore, measurements were performed on green twigs. Gas exchange was measured 1 day before the beginning of the experiment (time 0) on one young green twig (YT0; the tenth twig from the apical bud); on day 45 after the onset of the experiment, gas exchange was measured on one young twig (YT45; the tenth twig from the apical bud, formed after the onset of the treatment) and on one pre-existing old twig (OT45; YT0, the neighbouring twig to that time 0). All twigs were selected from the dominant sprout of each plant (n = 3).

Gas exchange was measured using a portable infrared gas analyser (LI-6400; LI-COR Biosciences, Inc., Lincoln, NE, USA) equipped with a conifer chamber (LI-6400-05). The cuvette temperature was set at 25 °C, while air flow rate was adjusted (400–600 $\mu mol \cdot s^{-1}$) to maintain a constant VPD (1.5 ± 0.2 kPa). Artificial light was generated with a halogen incandescent lamp and transmitted to the cuvette through a fibre-optic (FL-400 with 400-F; Walz, Effeltrich, Germany). With the objective of determining the saturating photon flux, which was set at 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, light curves were run before the beginning of the measurements. Net assimilation rate (A) change in response to intercellular [CO_2] variation (C_i) was determined for ambient CO_2 concentrations (C_a) of 400, 300, 250, 200, 150, 50, 400, 500, 650, 750, 850 and 1000 $\mu mol \cdot mol^{-1}$ as suggested in Long & Bernacchi (2003); a values were recorded as soon as C_a was stable (cv <0.7%; Ainsworth *et al.* 2002). Net assimilation rates (A_{400}) and stomatal conductance (g_s) measured at a C_a value of 400 $\mu mol \cdot mol^{-1}$ were considered as the assimilation and stomatal conductance at growth chamber CO_2 concentration. Intrinsic water use efficiency (A/g_s) was calculated as the ratio between A_{400} and g_s. The maximum carboxylation rate (Vc_{max}) and maximum rate of electron transport (J_{max}) were estimated according to Farquhar *et al.* (1980). Following A/C_i curves and 5 min of adaptation to dark conditions, dark respiration (R_d) was measured at a C_a of 400 $\mu mol \cdot mol^{-1}$. After gas exchange measurements, the twigs were cut off and their fresh weight determined. The twigs were then scanned and the images analysed with the software Skyroot (Llandrindod Wells, Powys, UK) in order to obtain total twig length. The twig area (silhouette) was estimated by multiplying the twig length by the mean twig diameter (0.7 mm). A small twig portion was dried at 70 °C for dry weight estimation, while the rest of the twig was dark-adapted for 15 min for chlorophyll fluorescence measurements.

Chlorophyll fluorescence was measured with a PAM 2000 fluorimeter (Walz) on the same samples used for gas exchange measurements. Small portions of the twig were placed close to each other to fill the entire surface of the fluorimeter clip. The photochemical efficiency was estimated from the quantum yield of PSII in dark-adapted twigs (F_v/F_m). Additional far-red light (735 nm) was used to estimate ground state fluorescence (F_0). The fluorescence yield (Φ_{PSII}; *i.e.* quantum yield of PSII in the light) was measured with a saturating pulse of white light.

Twig and roots characteristics

After drying in oven at 70 °C to constant weight, YT45 and OT45 used for gas exchange and fluorescence measurements were inserted into a plastic tube containing 50 ml deionised water. The tubes were shaken at 500 rpm for 20 min. The liquid phase was then separated from the twigs using filter paper. Electrical conductivity (EC) of the liquid phase, which is proportional to the amount of dissolved NaCl secreted by salt glands, was measured at a 20 °C using a conductimeter (HI9811; Hanna Instruments Inc., WoonsocKet, RI, USA) equipped with an electrode probe (HI1285; Hanna Instruments Inc., WoonsocKet, RI, USA). The EC value was expressed as $dS \cdot m^{-1} \cdot g^{-1}$ of twig dry weight without salt. The salt mass, calculated as the difference in dry weight before and after twig washing, and EC were linearly related ($R^2 = 0.896$). YT45 and OT45 nitrogen ([N]) and carbon ([C]) concentrations were determined using an elemental analyser (NC Soil Analyser, FlashEA 1112 series; Thermo Electron Corp., Waltham, MA, USA).

At the end of the experiment, the plants were harvested and belowground roots (BGR) were collected, washed and dried at 70 °C to constant weight. YT45, OT45 and BGR sodium (Na) concentration was determined according to the AAS-flame technique (C_2H_2/Air; Varian SpectrAA, 220 FS; Varian Inc., Palo Alto, CA, USA).

RESULTS

Twig photosynthetic activity changes over time

After 45 days of treatment, a reduction in net assimilation rate (A_{400}), maximum rate of carboxylation (Vc_{max}), maximum rate of electron transport (J_{max}), dark respiration (R_d), stomatal conductance (g_s) and ground state fluorescence (F_0) was observed in all treatments, including twigs grown under control conditions (Table 1). However, intrinsic water use efficiency (A/g_s), as well as quantum yield of PSII in the dark (F_v/F_m) and in the light (Φ_{PSII}) did not change over time.

Flooding with fresh water (F)

After 45 days under flooding with fresh water, A_{400} was not affected by the treatment, showing values similar to plants grown under control conditions, in both provenances and twig types (average 17.3 $\mu mol\ CO_2\ m^{-2} \cdot s^{-1}$; Fig. 1a). Similarly, Vc_{max} (78.8 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$), R_d (3.12 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$) and g_s (0.40 $mol \cdot H_2O \cdot m^{-2} \cdot s^{-1}$) were not affected by the continuous flooding condition (Fig. 1b–d), with no interaction between provenances and twig types. The intrinsic water use efficiency (A/g_s) was 42.9 $\mu mol \cdot CO_2/mol \cdot H_2O$ as the mean of the provenances and twig types (Fig. 1e). The parameters reflecting functionality of the photosynthetic light reactions (J_{max}, F_v/F_m, Φ_{PSII} and F_0) were also not influenced

Table 1. Absolute values and relative changes (RC) of the analysed photosynthetic parameters [net assimilation rates (A_{400}), maximum carboxylation rate (Vc_{max}), dark respiration (R_d), stomatal conductance (g_s), intrinsic water use efficiency (A/g_s), maximum rate of electron transport (J_{max}), quantum yield of PSII in the dark (F_v/F_m) and in the light (Φ_{PSII}) and ground state fluorescence (F_0)] measured in the two provenances (SIM and BAR) before the beginning of the experiment, on the tenth twig from the apical bud (YT0), and after 45 days from the beginning of the treatment, on a YT0 neighbouring twig (OT45). A repeated ANOVA (R-ANOVA) was performed to test time effect on twig photosynthetic responses (*P < 0.05; **P < 0.01; ***P < 0.001). RC were analysed by ANOVA to evaluate the main effects of provenance (P), treatment (T) and their interaction (P × T).

	A400 ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$)		Vc_{max} ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$)		R_d ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$)		g_s ($mol \cdot H_2O \cdot m^{-2} \cdot s^{-1}$)		A/g_s ($\mu mol \cdot CO_2 / mol \cdot H_2O$)		J_{max} ($\mu mol \cdot e^- \cdot m^{-2} \cdot s^{-1}$)		F_v/F_m		F_{PSII}		F_0	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
SIM																		
C																		
YT0	17.1	3.2	100.1	17.5	4.4	0.5	0.39	0.07	44.2	2	235	50.6	0.77	0.01	0.35	0.02	0.032	0.009
OT45	15.4	3.9	73.7	12.2	1.8	0.9	0.33	0.12	63.2	23.2	161.7	32.8	0.78	0.02	0.3	0.03	0.027	0.002
RC (%)	−9.7		−26.4		−60		−15		43		−31.2		0.3		−14		−16.3	
F																		
YT0	17	3.7	78	16.8	3.5	0.9	0.47	0.1	36.6	4.5	180.5	37.5	0.77	0.01	0.26	0.04	0.056	0.004
OT45	12.9	3.6	58.1	14.4	1.1	0.1	0.31	0.09	42.7	6.3	117.1	29.9	0.81	0	0.42	0.1	0.032	0.006
RC (%)	−24		−25.5		−67.6		−33.6		16.6		−35.1		5.5		65.6		−42.9	
FS																		
YT0	17.4	4.7	101.5	37.3	3.7	1.2	0.29	0.03	58.3	10.5	256.7	108.5	0.79	0.01	0.25	0	0.045	0.002
OT45	12	2.8	75	10.4	2.2	0.9	0.16	0.04	78	9.2	145.2	37.2	0.77	0.05	0.35	0.02	0.02	0.003
RC (%)	−31.2		−26.1		−41.9		−45.1		33.6		−43.4		−3		40.3		−55.2	
BAR																		
C																		
YT0	18.4	1.9	104	10.4	2.9	0.8	0.48	0.02	37.2	5	228.3	12.3	0.76	0.01	0.31	0.09	0.047	0.001
OT45	13.5	1.2	59.9	4.1	1.8	0.5	0.36	0.08	40.9	8	130.4	5.7	0.81	0	0.31	0.01	0.033	0.009
RC (%)	−26.8		−42.4		−39.8		−25.4		9.9		−42.9		6.6		−2.1		−31	
F																		
YT0	23.7	2.6	148	7.3	5.9	1.4	0.37	0.08	68	10.8	363	29.8	0.78	0.02	0.36	0.02	0.047	0.01
OT45	16	0.6	78.7	0.6	2.6	0.2	0.3	0.02	53	5.7	191.5	4.2	0.76	0.06	0.29	0.14	0.023	0.007
RC (%)	−32.4		−46.8		−55.8		−17.9		−22.1		−47.3		−2.1		−19.1		−51.8	
FS																		
YT0	15.7	3.5	104.7	23.6	6.1	0.4	0.22	0.01	70	15.2	253.5	64.9	0.76	0.02	0.43	0.05	0.049	0.001
OT45	13.9	0.9	77.6	9.4	3.5	0.7	0.3	0.08	56.6	18.4	156.4	17.6	0.81	0.03	0.3	0.09	0.021	0.008
RC (%)	−11.6		−25.9		−42.6		32.1		−19.1		−38.3		6.9		−30.1		−56.2	
R-ANOVA	**		**		***		*		n.s.		***		n.s.		n.s.		***	
ANOVA																		
P	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	
T	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	
P × T	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	

n.s., not significant.

Post-hoc analysis was performed using Fisher's LSD test. Lowercase letters refer to the comparison of RC among the treatments. Values are means of n = 3 ± SE.

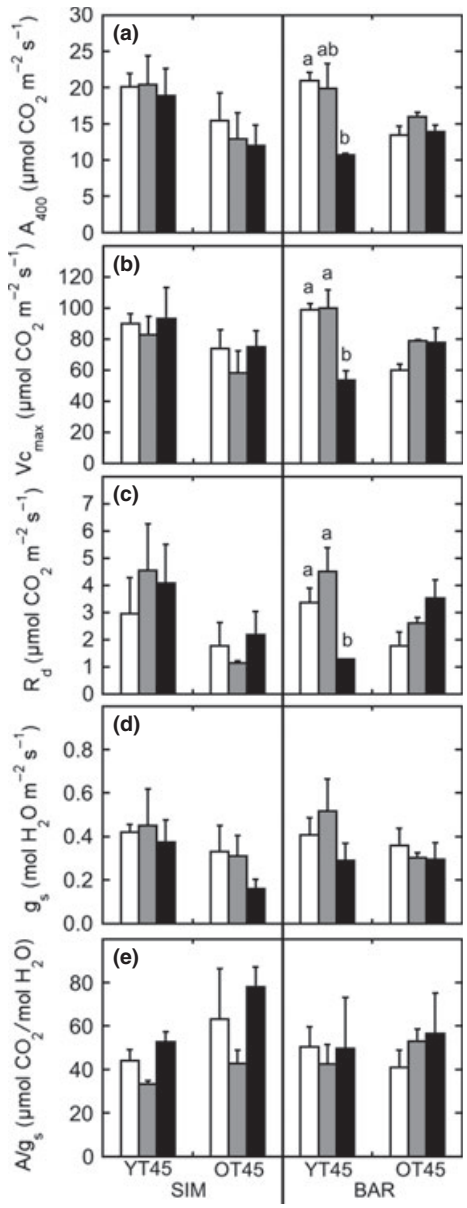

Fig. 1. Net assimilation rates (A_{400}) (a), maximum carboxylation rate (Vc_{max}) (b), dark respiration (R_d) (c), stomatal conductance (g_s) (d) and intrinsic water use efficiency (A/g_s) (e) measured after 45 days from the beginning of the experiment on the tenth twig from the apical bud (formed after the beginning of the treatment; young twig, YT45) and on a pre-existing twig (the tenth twig from the apical bud at time 0, formed before the beginning of the experiment; old twig, OT45) in the two provenances Simeto (SIM) and Baratz (BAR), under control (C; white bars), flooding with fresh water (F; grey bars) and flooding with saline water (FS; black bars). ANOVA was performed on all parameters to test the effect of treatments, twig development and their interaction after 45 days from the beginning of the experiment. The *post-hoc* analysis was performed using Fisher's LSD test. Lowercase letters refer to the comparison among treatments. Statistical significance was considered for $P < 0.05$. Values are means of $n = 3 \pm SE$.

by F in both provenances and twig types (Fig. 2a–d); the mean values were, respectively, 187.4 $\mu mol \cdot e^{-} \cdot m^{-2} \cdot s^{-1}$, 0.77, 0.35 and 0.025 as an average for both twig types.

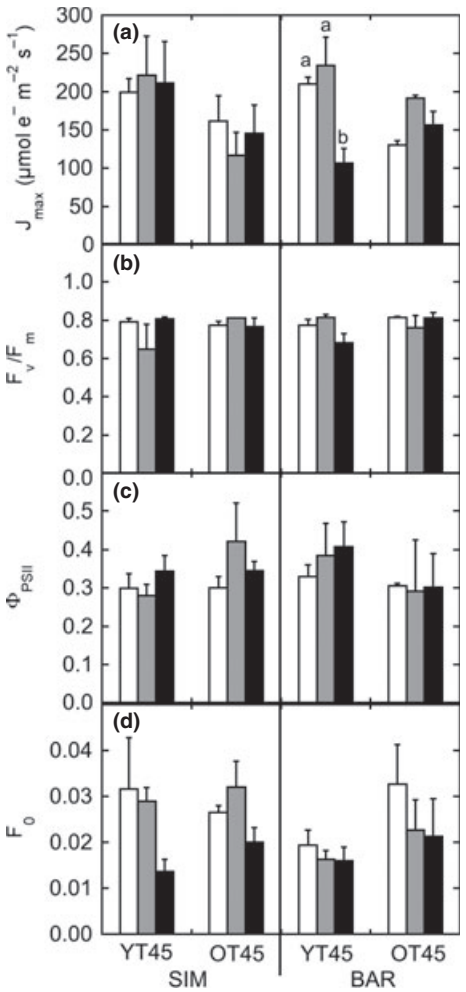

Fig. 2. Maximum rate of electron transport (J_{max}) (a), quantum yield of PSII in the dark (F_v/F_m) (b) and in the light (Φ_{PSII}) (c), and ground state fluorescence (F_0) (d) measured after 45 days from the beginning of the experiment on the tenth twig from the apical bud (formed after the beginning of the treatment; young twig, YT45) and on a pre-existing twig (the tenth twig from the apical bud at time 0, formed before the beginning of the experiment; old twig, OT45) in the two provenances Simeto (SIM) and Baratz (BAR), under control (C; white bars), flooding with fresh water (F; grey bars) and flooding with saline water (FS; black bars). ANOVA was performed on all parameters to test the effect of treatments, twig development and their interaction after 45 days of treatment. The *post-hoc* analysis was performed using Fisher's LSD test. Lowercase letters refer to the comparison among the treatments. Statistical significance was considered for $P < 0.05$. Values are means of $n = 3 \pm SE$.

After 45 days of flooding, BAR young twig [C] (48.0%) was significantly higher compared to the control (45.0%; $P < 0.01$), while no effects were detected in old twigs (Table 2). In contrast, [N] (Table 2) was not affected by the treatment, being on average similar in both provenances and twig types (1.96%). The amount of CO_2 fixed by photosynthesis per unit of twig N was not influenced by treatment or plant provenance, and was on average 7.45 $\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1} \cdot g \cdot N^{-1}$. Flooding did not affect the amount of salt present on the twig surface (Fig. 3). The average electrical conductivity (EC) of the washing solution was 1.3 $dS \cdot m^{-1} \cdot g^{-1}$, with no

Table 2. Carbon ([C]) and nitrogen ([N]) content measured in the two provenances Simeto and Baratz (SIM and BAR) after 45 days from the beginning of the experiment on the tenth twig from the apical bud, formed after the start of treatment (young twig, YT45) and on a pre-existing twig (the tenth twig from the apical bud at time 0, formed before the start of the experiment; old twig, OT45) under control (C), flooding with fresh water (F) and flooding with saline water (FS). ANOVA was performed on all parameters to test the effect of treatments, twig development and their interaction after 45 days of treatment.

	YT45			OT45		
	C	F	FS	C	F	FS
SIM						
[C] %						
mean	47.2	48.3	48.9	45.6	47.1	46.6
SE	0.5	0.4	0.6	0.4	0.3	0.5
[N] %						
mean	0.9	1.14	0.76	0.47	0.27	0.76
SE	0.31	0.43	0.18	0.26	0.07	0.17
BAR						
[C] %						
mean	44.7a	47.9b	47.4b	45.7	45.2	46
SE	0.6	0.1	1.3	0.2	1	1.4
[N] %						
mean	0.97	1.76	1.67	0.72	1.49	1.38
SE	0.19	0.7	0.89	0.37	0.52	0.46

The parameters expressed as percentage were transformed using the arcsine of the square root of the analysed parameter divided by 100. *Post-hoc* tests were performed using Fisher's LSD. Lowercase letters refer to comparison among the treatments. Statistical significance was considered for $P < 0.05$. Values are means of n = 3 ± SE.

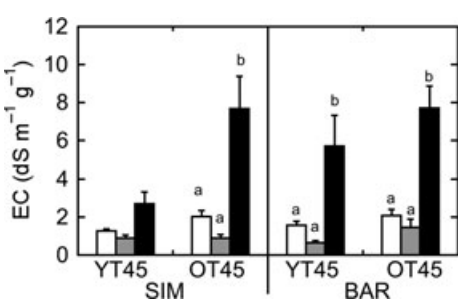

Fig. 3. Electrical conductivity (EC) of the washing solution per unit of twig biomass measured after 45 days from the beginning of the experiment on the tenth twig from the apical bud (formed after the beginning of the treatment; young twig, YT45) and on a pre-existing twig (tenth twig from the apical bud at time 0, formed before the beginning of the experiment; old twig, OT45) in the two provenances Simeto (SIM) and Baratz (BAR), under control (C; white bars), flooding with fresh water (F; grey bars) and flooding with saline water (FS; black bars). ANOVA was performed on all parameters to test the effect of treatments, twig development and their interaction after 45 days of treatment. The *post-hoc* analysis was performed using Fisher's LSD test. Lowercase letters refer to the comparison among the treatments. Statistical significance was considered for $P < 0.05$. Values are means of n = 3 ± SE.

difference between SIM and BAR. Sodium concentration (Na; Fig. 4) of twigs and belowground roots under F was similar to the control in both provenances, being on average 3.5 and

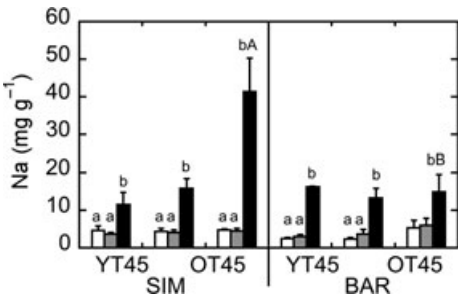

Fig. 4. Sodium (Na) content of the tenth twig from the apical bud, formed after the beginning of the treatment (young twig, YT45), of a pre-existing twig (tenth twig from the apical bud at time 0, formed before the beginning of the experiment; old twig, OT45) and of belowground roots (BGR) measured in the two provenances Simeto (SIM) and Baratz (BAR), under control (C; white bars), flooding with fresh water (F; grey bars) and flooding with saline water (FS; black bars). ANOVA was performed on all parameters to test the effect of treatments, twig development and their interaction after 45 days of treatment. The *post-hoc* analysis was performed using Fisher's LSD test. Lowercase letters refer to the comparison among the treatments. Statistical significance was considered for $P < 0.05$. Values are means of n = 3 ± SE.

5.1 mg·Na·g^{-1}, respectively. Na content was similar in the two twig types.

Flooding with saline water (FS)

Photosynthetic activity was unaffected by flooding with saline water in SIM YT45, OT45 and BAR OT45, as demonstrated by gas exchange and fluorescence parameters. Only in young twigs of the Baratz provenance was A_{400} reduced by 48.8% ($P < 0.05$) in response to the treatment (Fig. 1a). This reduction was coupled with a similar decrease in Vc_{max} (−45.8%; $P < 0.05$; Fig. 1b) and R_d (−62.2%; $P < 0.1$; Fig. 1c). The decrease in A_{400} was accompanied by an adjustment of g_s, as demonstrated by the maintenance of A/g_s (Fig. 1d,e). Vc_{max} reduction was coupled with a decrease in J_{max} (Fig. 2a); however, chlorophyll fluorescence was not affected by the treatment; F_v/F_m, Φ_{PSII} and F_0 were similar to control and, respectively, 0.76, 0.35 and 0.018 (Fig. 2b–d).

Carbon concentration was on average similar in the control (45.8%) and treated plants (47.1%) (Table 2), although a higher [C] was found in BAR YT45 compared to the control ($P < 0.05$; Table 2). [N] did not vary in response to treatment in YT45 and OT45 of both provenances and was on average 0.95 (Table 2). Consequently, the amount of CO_2 fixed by photosynthesis per unit twig N was reduced under FS ($P < 0.01$); according to the *post-hoc* test, the reduction was significant only in BAR YT45. The amount of salt present on the twig surface increased significantly after 45 days under flooding with saline water ($P < 0.001$; Fig. 3), and the electrical conductivity of the washing solution was on average 5.9 dS·m^{-1}·g^{-1} in FS and 1.7 dS·m^{-1}·g^{-1} in the control. Old twigs secreted more salt than young ones (7.7 and 4.2 dS·m^{-1}·g^{-1} in OT45 and YT45, respectively; $P < 0.001$), but not in the BAR provenance. Moreover, the quantity of salt secreted by BAR YT45 was 52.8% higher than that secreted by SIM YT45 ($P < 0.05$). Twig Na content was influenced by the treatment, being significantly higher under FS

(14.1 $mg \cdot g^{-1}$) compared to the control (3.4 $mg \cdot g^{-1}$; $P < 0.001$; Fig. 4). Twig Na content of treated plants was similar in YT45 and OT45 of both provenances, although BAR YT45 Na content was slightly higher than that of SIM YT45 ($P = 0.07$). Accordingly, Na content in BGR was significantly higher under FS ($P < 0.001$) in both provenances, although SIM roots were characterised by a higher Na content (41.3 $mg \cdot g^{-1}$) compared to BAR roots (14.8 $mg \cdot g^{-1}$; $P < 0.001$; Fig. 4).

Vc_{max} and J_{max} measured under C, F and FS were linearly related in SIM YT45 ($R^2 = 0.808$) and OT45 ($R^2 = 0.927$), as well as in BAR twigs ($R^2 = 0.9218$ and $R^2 = 0.7080$, respectively, for YT45 and OT45). Furthermore, slopes and intercepts of the four linear regressions were similar, and one equation fitted all the data ($R^2 = 0.882$; Fig. 5). In contrast, Vc_{max} was not significantly dependent on twig N in both provenances and twig types (data not shown). A_{400} varied in accordance with N in the SIM provenance, in YT45 ($R^2 = 0.6822$; $P < 0.05$) and OT45 ($R^2 = 0.7919$; $P < 0.01$); in BAR, these two parameters were not significantly correlated ($R^2 = 0.3869$ in YT45 and $R^2 = 0.4473$ in OT45).

DISCUSSION

Independent of the treatment, there was a loss of photosynthetic activity in aging twigs, as previously reported (Ethier *et al.* 2006; Katahata *et al.* 2007). A high tolerance of both *T. africana* provenances to continuous flooding with fresh and saline water was observed in this study: at the end of the experiment, all plants were still alive.

Seedling tolerance and adventitious root formation have been reported in *T. aphylla* and *T. ramosissima* in response to flooding with fresh water (Ginzburg 1967; Sprenger *et al.* 2001), and *Tamarix* spp. are frequently the dominant species in floodplains (Irvine & West 1979; Pedrotti & Gafta 1996; Sala & Smith 1996). Adventitious root and aerenchyma formation represent adaptations to alleviate the anoxic stress induced by flooding (Visser *et al.* 1995; Blom & Voesenek 1996; Drew *et al.* 2000; Colmer 2003; Evans 2004). However, Vandersande *et al.* (2001) found a lower flooding tolerance in *T. ramosissima* compared to other riparian species as a consequence of reduced development of adventitious root systems, indicating that flooding tolerance in *Tamarix* can differ among species according to their ability to produce aerial roots. In this study, flooding with fresh water did not affect stomatal conductance and gas exchange, as generally observed in non-tolerant plants (Chen *et al.* 2005; Rengifo *et al.* 2005; Fernandez 2006). In our experiment, continuous flooding with saline water did not affect photosynthetic activity of young and old Simeto twigs, and old Baratz twigs. High tolerance to flooding with saline water represents an adaptive trait in species that occupy estuarine environments (like *Tamarix* spp.), and is frequently associated with the regulation of foliar Na, Cl and K concentrations (Carter *et al.* 2006), as also reported in saline environments (for recent reviews see Flowers & Colmer 2008; Munns & Tester 2008). Contrary to expectations, net assimilation rates and maximum rates of carboxylation and electron transport were strongly reduced in young Baratz twigs after flooding with saline water. These reductions were not associated to an increase in dark respiration, as observed by Loreto *et al.* (2003), or to a reduction in twig [N]. Moreover, the absence of a decrease in quantum yield of photosystem II in both light and dark conditions, as expected after a reduction in maximum rate of electron transport, suggests the absence of a direct effect of salt on photosystems. A decrease in plant assimilation rate and growth under saline conditions has been reported in both glycophytes (Bongi & Loreto 1989; McLeod *et al.* 1999; Centritto *et al.* 2003; Loreto *et al.* 2003) and halophytes (Ueda *et al.* 2003; Parida *et al.* 2004; Nandy (Datta) *et al.* 2007). In most cases, the decline in photosynthetic activity was linked to reduced stomatal conductance. In our study, flooding with saline water did not reduce stomatal conductance, allowing salt to be transported to the twigs. Fur-

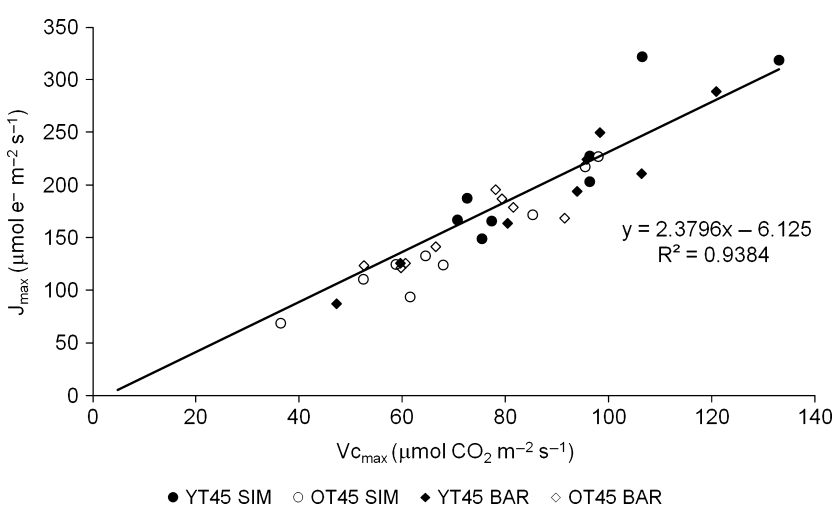

Fig. 5. Correlation between maximum carboxylation rate (Vc_{max}) and maximum rate of electron transport (J_{max}) obtained from net assimilation rate (A) *versus* intercellular CO_2 concentration (C_i) curves of both SIM (black symbols) and BAR (white symbols) provenances in young (squares) and old (circles) twigs, under control, flooding with fresh water and flooding with saline water. The software Prism 4 (GraphPad) was used to evaluate whether the slope and the intercept of Vc_{max} and J_{max} linear equations for both provenances and twig types were different from each other. R^2 and P values refer to the global fit.

thermore, stomatal conductance was, on average, lower in old twigs, so that the additional salt accumulation in these twigs was much slower than the initial uptake into new twigs (Cram *et al.* 2002). Finally, the higher quantity of Na collected from the surface of young Baratz twigs compared to Simeto twigs, was mirrored in lower Na storage in the roots in this provenance (see Fig. 4).

In conclusion, our results suggest that increased salt transport through the symplast and apoplast routes (Thomson & Liu 1967) could be the cause of the reduction in RuBisCo activity in young Baratz twigs. These results are in accordance with Delfine *et al.* (1998) and Munns *et al.* (2006), who suggested that photosynthetic activity (especially RuBisCO, see the reduction in Vc_{max}) is not inhibited when salt concentrations remain below a certain threshold. Therefore, the root/-shoot ratio could be an important driver of the different impacts of salinity observed at the provenance level, representing the plant equilibrium between water demand (loss) and water acquisition (and solute transport). Further comparative studies on salinity tolerance in *Tamarix* spp. should also consider this observation.

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