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# Effects of salt stress on plant water status, leaf gas exchanges and chlorophyll fluorescence of *Pistacia atlantica* Desf. versus *Pistacia vera* L.

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## Abstract

The productivity of agricultural systems and the ecological distribution of plants are strongly influenced by salinity in arid and semi-arid regions. In this context, two pistachio species, *Pistacia vera* L. (*P. vera*) and *Pistacia atlantica* Desf. (*P. atlantica*), have been exposed to NaCl (between 0 and 80 mM) to study the effect of salinity on plant water status, chlorophyll fluorescence and leaf gas exchanges. A specific pattern of response to salinity has highlighted different mechanisms of tolerance. Reductions in stomatal conductance (gs), photosynthesis (A) and total chlorophyll content (TCC) are similar to reductions in the relative water content (RWC) for both species and the NaCl treatments. The shape of the multiphasic fluorescence kinetics curves (OJIP) varies according to the severity of stress, indicating an earlier effect upon addition of NaCl for *P. vera*, but later in *P. atlantica*. The dynamic functioning of PSII depends on the toxicity by NaCl, altering plant water status, light conversion and $CO_2$ assimilation by the mesophyll. The impact of salinity is clear at J and especially at I and P, which greatly increases for high NaCl concentrations, reflecting a decrease in the photochemical efficiency of PSII and electron transport. The chlorophyll fluorescence in *P. atlantica* reflects a lower sensitivity to salinity due to the maintenance of higher cell turgor, chlorophyll content and assimilation of $CO_2$ than *P. vera*, explaining the agricultural practice based on its use as rootstock for *P. vera* for a better rusticity.

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**Introduction**

Salinity of soils and irrigation water is one of the main factors limiting plant growth and productivity (Flowers, 2004; Parida and Das, 2005). Many reports stated that salt stress decreases plant water content, due to osmotic stress and cell dehydration related to the accumulation of salt (Munns, 2002; Sairam *et al.*, 2002). However, some plants tend to maintain the cell turgor through the osmotic adjustment mechanism for different species (Porcel *et al.*, 2012, Duarte *et al.*, 2013).

Under salt stress, the partial or total closure of stomata, in order to preserve the plant water status, is always accompanied by limitations in leaf gas exchanges, which causes reductions in stomatal conductance, photosynthesis and transpiration (Agastian *et al.*, 2000; Abbaspour *et al.*, 2012; Kchaou *et al.*, 2013; Zorrig *et al.*, 2013). In this context, Abbruzzese *et al.* (2009) reported that salt stress affects stomata density and guard cell length, leading to a decrease of stomatal conductance and hydraulic status of the plant.

The inhibition of photosynthesis, as a function of NaCl concentration, was reported in varieties of rice (*Oryza sativa* L.) (Mishra *et al.*, 1991; Tiwari *et al.*, 1997), where the $Na^+$ and $Cl^-$ reduce the ability of $CO_2$ assimilation, altering the photosynthetic apparatus, mainly by a decrease in the maximum Rubisco carboxylation rate (Tattini and Traversi, 2009; Tattini *et al.*, 2009). Limitations in photosynthesis were also attributed to changes in carboxylation efficiency or ability to regenerate the ribulose bisphosphate (Ranjbar *et al.*, 2002; Parida *et al.*, 2003). Additionally, Zorrig *et al.* (2013) reported a damage in the ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco), phosphoenolpyru-vate carboxylase (PEPC) in *Arabidopsis thaliana* under salt stress.

In recent years, the technique of chlorophyll fluorescence has become ubiquitous in the study of abiotic stress on photosynthesis (Maxwell and Johnson, 2000; Baker and Rosenqvist, 2004; Baker, 2008; Kalaji *et al.*, 2011), such as the salinity (Misra *et al.*, 2001; Qiu *et al.*, 2003; Duarte *et al.*, 2013). Indeed, this technique has been extensively used in vivo as a non-destructive method for early diagnosis, added to the used tools (Stirbet and Govindjee, 2011).

The light absorbed by the antenna is not completely converted into chemical energy and the rest is emitted as heat and fluorescence. At ambient temperature, chlorophyll fluorescence emission comes mainly from the PSII light harvesting antenna, which represents 90% (Govindjee and Spilotro, 2002). The fluorescence emission by the PSI is low, which represents 10 to 20% of the total emission. Moreover, only the fluorescence emitted by PSII is variable with time (Govindjee, 1995). Thus, the fluorescence emission reflects the energy losses during the excitation transfer to the reaction centers. Hence, by measuring the chlorophyll fluorescence, information on changes in the efficiency of photochemical reactions can be gained (Maxwell and Johnson, 2000; Papageorgiou and Govindjee, 2004).

The fluorescence induction kinetics curve presents different intermediate stages known as O, J, I and P, introduced by Strasser and Govindjee, (1991, 1992), indicating different states of oxydo-reduction of PSII electron acceptors, QA, QB and plastoquinone.

Little is known about the effect of salinity on the photochemical efficiency of PSII and results are frequently controversial. Some studies showed that in higher plants, salt stress inhibits the activity of PSII (Everard *et al.*, 1994), reducing the photons use efficiency in the reaction of PSII (Lu and Vonshak, 1999; Duarte *et al.*, 2013), while others reported that salt stress has no effect on PSII (Brugnoli and Bjorkman, 1992; Morales *et al.*, 1992).

*Pistacia atlantica* Desf. (Atlas pistachio), belongs to the *Anacardiaceae* family, is a wild dioeciously tree, with semi-evergreen leaves, an extensive root system and a remarkable vigor and longevity. *P. vera* L. is also from the *Anacardiacae* family, a crop specie, mainly in arid and semi-arid areas. Moreover, these

species are of important economical, medicinal and ecological interests (Tomaino *et al*., 2010). *P. atlantica*, despite its adaptation to unfavorable environmental factors, as salinity (Chelli-chaabouni *et al*., 2010; Benhassaini *et al*., 2012), drought (Gijón *et al*., 2010) and nematode, and its good performance as rootstock for pistachio varieties, is nowadays endangered. In arid and semi-arid Tunisia areas, *P. atlantica* exists as isolated aged trees. Even thought that *P. vera* grafted on *P. atlantica* showed a better vigor and production of plants, a mechanism remains not understood. In this context, several hypotheses were reported: The rootstock can affect the vegetative tree growth through hormonal effects (Kamboj *et al*., 1999), mineral nutrition (Jones, 1971) or water status (Olien and Lakso, 1986; Gijón *et al*, 2010), or an improvement of adaptation to abiotic constraints, as salinity and drought.

The seedling stage is considered as the most salt sensitive phase in woody plants (Shannon *et al*., 1994), as *Pistacia* species, where little is reported about the *P. vera* and *P. atlantica* establishment. The present work was planned to: a) study the effect of increasing concentrations of NaCl on leaf gas exchanges, chlorophyll content and chlorophyll fluorescence in *P. vera* and *P. atlantica*, b) discuss the relationship between the plant water status, the chlorophyll content, the $CO_2$ assimilation and chlorophyll fluorescence under salt stress, and c) to study the functional regulation of PSII under salt stress in both species.

**Materials and methods**

The seeds of *P. vera* (Mateur Variety) from Sidi Aïch (West-Central of Tunisia), and those of *P. atlantica* from Meknassy (East-Central of Tunisia) were collected in August 2009.

*Preparation of plants and conduct of the trial*

Production plants were conducted in the laboratory at 22°C and 10h/14h light/obscurity. To avoid tegumentary inhibition, seeds of *P. atlantica* underwent mechanical scarification (Pulping). The outer shells of *P. vera* were also removed.

The plants (four leaves stage) were transplanted into conical pots (one plant per pot), with 15 and 13 cm of diameter and depth, respectively. The contents of the pots are well washed pure sand to avoid the interference of trophic factor. All pots received two irrigations per week (200 ml) until obtaining vigorous plants aged for 70 days.

*Treatments applied*

Since Sodium Chloride (NaCl) is the major source of salt in the soil and irrigation water, it has been used to induce a salt stress: 0, 20, 40, 60 and 80 mM NaCl, respectively 0, 1.17, 2.34, 3.51 and 4.68 g of salt per liter of nutrient solution with two irrigations per week. Individuals received a Hoagland solution.

The salt treatment was applied for two months (May-June 2010) and the culture was placed under an ambient temperature between 27 and 30°C, a relative humidity of around 70% and a photoperiod of 14 h/10 h light/obscurity.

*Parameters studied*

Several physiological parameters were measured at different stages of development, arbitrarily chosen along the experiment.

*Relative water content*

Measuring the relative water content (RWC) in the leaf was performed as follows: The leaf was cut and weighed to determine their fresh weight (FW) and then placed in distilled water (5°C). After 24 h, the leaf is removed, wiped with the filter paper and weighed at full turgor (TW). Then, it was placed in an oven at 80°C during 48 h and then weighed again to determine the dry weight (DW) using the approach developed by Clarke and McCaig (1982). The equation was the following:

$$RWC = (FW - DW) / (TW- DW) \times 100$$

FW: Fresh Weight

DW: Dry Weight

TW: Turgor Weight

*Photosynthetic gas exchanges*

The leaf gas exchanges measurements were performed on attached fully expanded leaves (the third leaf after leaf emergence) by an LCi portable photosynthesis system (ADC Bioscientific Ltd.), with two differential infrared gas analyzers for $CO_2$ and water vapor, and a measuring chamber of gas exchanges. The measurements were performed at a Photosynthetic Active Radiation (PAR) sets (1000 µmol photon $m^{-2}$ $s^{-1}$) at midday. Various parameters were measured: The net photosynthesis rate (A, expressed in µmol $CO_2$ $m^{-2}$ $s^{-1}$) and on the basis of the increase in water vapor gets transpiration rate (E, mol $H_2O$ $m^{-2}$ $s^{-1}$). From the rate of transpiration, leaf temperature ($T_{leaf}$) and pressure of water vapor in the leaf chamber, the stomatal conductance (gs, mol $H_2O$ $m^{-2}$ $s^{-1}$) was calculated.

*Total chlorophyll content*

The total chlorophyll content (TTC) was measured using a Chlorophyll Content Meter device (CCM 200) on attached leaves; those used for gas exchanges measurements. The instrument measures two energy absorption bands in the red and infrared, corresponding, respectively, to the amount of chlorophyll in the leaf and the absorbance of the cells. The instrument used to measure an index called CCI (Chlorophyll Content Index) that appears on the screen of the device corresponding to a rate of total chlorophyll present in the leaf.

*Chlorophyll fluorescence*

The chlorophyll fluorescence measurements were made on leaves which used for gas exchanges measurements, using a portable chlorophyll fluorometer (OS-30P; Opti-science, Inc., NH, USA). After a calibration of the device, initiating the measurement time (30 s), the light intensity (700 µS), special plastic clips were attached to leaves and OJIP transients were measured. The mode OJIP gives fluorescence kinetics of multiphase transition O, J, I and P with:

O: Minimum fluorescence level,

J: Intermediate level of fluorescence, which corresponds to the gradual reduction of QA,

I: Intermediate level of fluorescence, which corresponds to the maximum reduction of QA,

P: Maximum fluorescence level.

*Statistical analysis*

The analysis of variance (ANOVA) was performed according to a factorial model with fixed factors using the statistical package SPSS (version 11.5). The Sigma Plot software (version 11.0) was used to develop the figures and regressions between variables, using average values with standard deviations. OJIP data transfer was made by the software OS-30P and presented on a logarithmic time scale in abscises time axis.

**Results**

*Relative water content*

Untreated species maintained high RWC. Under salt stress, clear differences between the two species were observed and the RWC was significantly reduced ($p<0.001$), especially for *P. vera* at high NaCl concentrations. RWC has been as lower as the salt stress was more severe. At the contrary, *P. atlantica* showed high RWC values for all salinity treatments (Fig. 1).

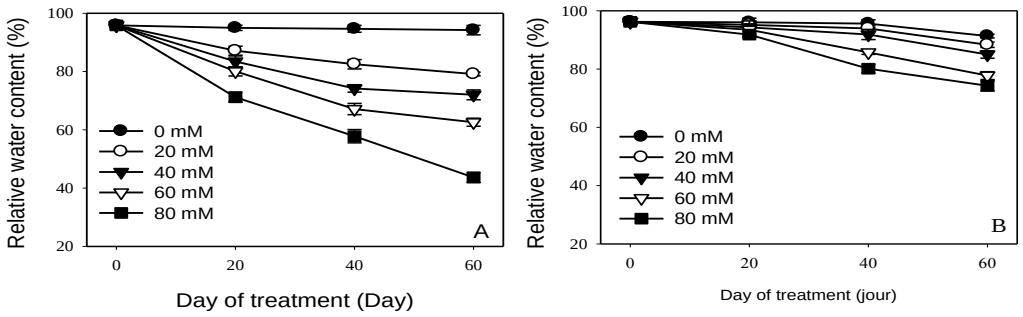


**Fig. 1.** Relative Water Content variation in *Pistacia vera* (A) and *P. atlantica* (B) plants under salinity (n=6).

*Leaf gas exchanges*

Along the experiment, the control seedlings of both species increased gs. Under salt stress, gs was significantly reduced for both species ($p<0.001$) (Fig. 2). Indeed, gs became low while salinity increased. The significant reductions were observed at 80 mM of NaCl, where reductions in gs reached 93 and 100% for *P. vera* and *P. atlantica* respectively at the end of the experiment.

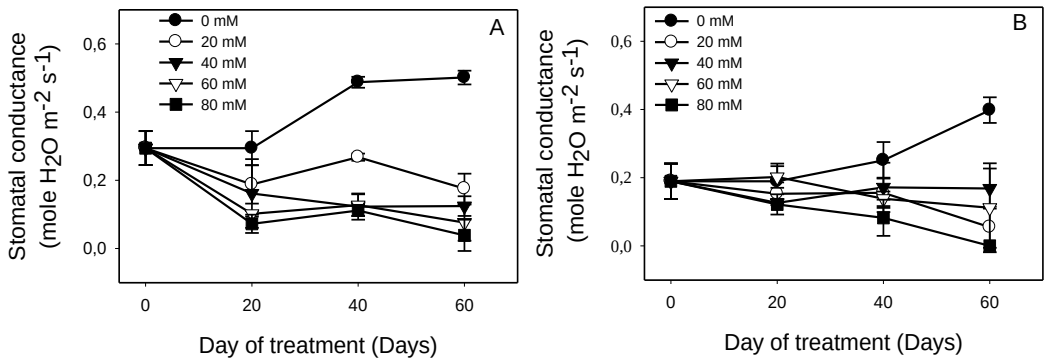


**Fig. 2.** Stomatal conductance variation in *Pistacia vera* (A) and *P. atlantica* (B) plants under salinity (n=6).

In *P. atlantica* and *P. vera,* the control seedlings maintained higher A, whereas under salt stress, both species reduced significantly A ($p<0.001$) for NaCl treatments. Indeed, A is reduced while the severity of salinity increased (Fig. 3). The high reduction occurred for 80 mM of NaCl with no photosynthesis for *P. vera*, but remained at low levels in *P. atlantica* (Fig. 3). The impact of salt stress and duration of treatment on A became significant at the end of the experiment ($p<0.001$).

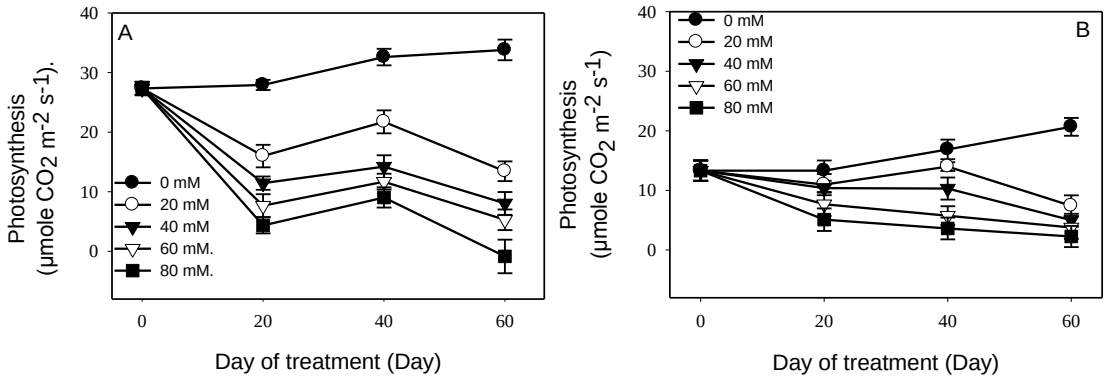


**Fig. 3.** Photosynthesis variation in *Pistacia vera* (A) and *P. atlantica* (B) plants under salinity (n=6).

*Total chlorophyll content*

In control seedlings, TCC increased in *P. vera* to 59 against a slight increase in *P. atlantica*. The NaCl decreased TCC ($p<0.001$) (Fig. 4) and the differences between species are significant ($p<0.001$). Thus, *P. atlantica* maintains higher TCC than *P. vera* (Fig. 4). The reductions reached 75% for *P. vera*, against only 54% for *P. atlantica* at 80 mM.

*Chlorophyll fluorescence*

In *P. vera* (Fig. 5), after 18 days of salinity, fluorescence intensity is higher while the applied concentration of NaCl increased. After 24 days of treatment, an increase in fluorescence at 20 and 40 mM of NaCl is observed. However, for 60 and 80 mM of NaCl, salinity decreased exclusively the transitions I and P. These trends are similar for those observed after 36 days of treatment.

Along the experiment, fluorescence increased, except for 80 mM, where fluorescence is maintained at 50. In contrast, *P. atlantica* (Fig. 6), with higher fluorescence than *P. vera* from the beginning, did not show clear differences between the treatments during the first month of experimentation.

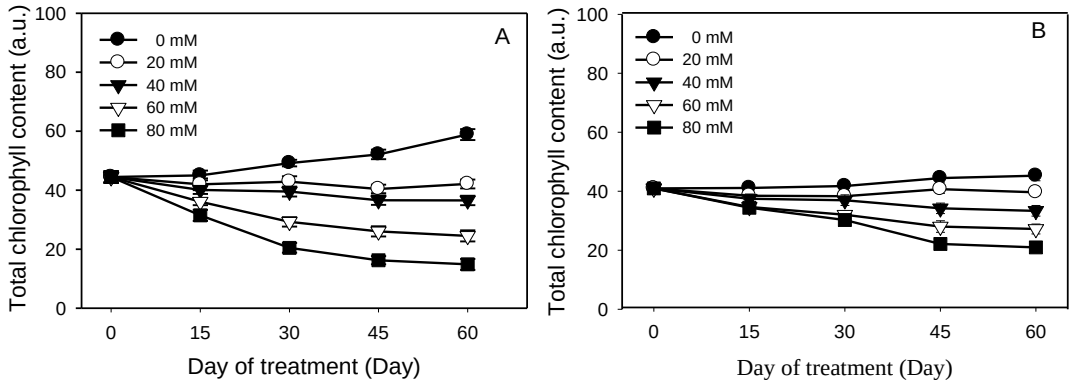


**Fig. 4.** Variation of the total chlorophyll content in seedlings of *P. vera* (A) and *P. atlantica* (B), subject to five increasing concentrations of NaCl (n=6).

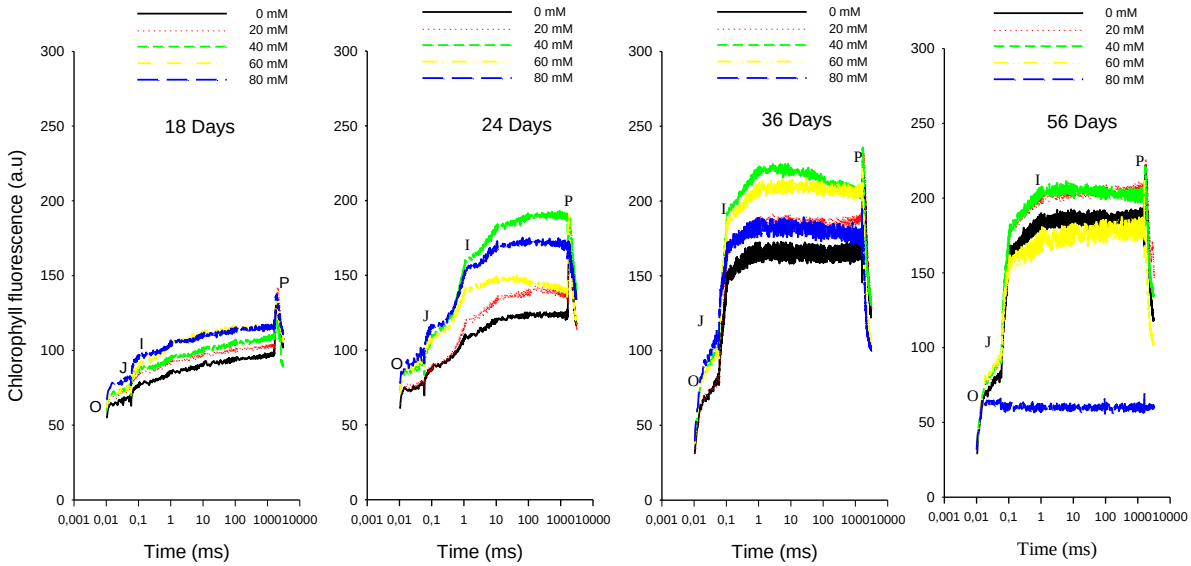


**Fig. 5.** Polyphasic rise of Chla fluorescence transients (OJIP) in *P. vera* subjected to five increasing concentrations of NaCl (n=6).

In both species, the major effect of salinity is observed in P instead of O which remains unchanged for all salinity treatments (Fig. 7). At the end of the test, there is a decrease in fluorescence, particularly at 80 mM, to minimal fluorescence intensity. At this level of stress, steps J and I disappeared from the OJIP curve for *P. atlantica*, and the three phases J, I and P disappeared for *P. vera*. These variations characterize a step called K in *P. vera*, which reflects a changes induced by excess NaCl on PSII. The statistical analysis showed highly significant effects of NaCl treatments and species on O and J ($p<0.001$) and NaCl treatments, species and stages of development on I and P ($p<0.001$).

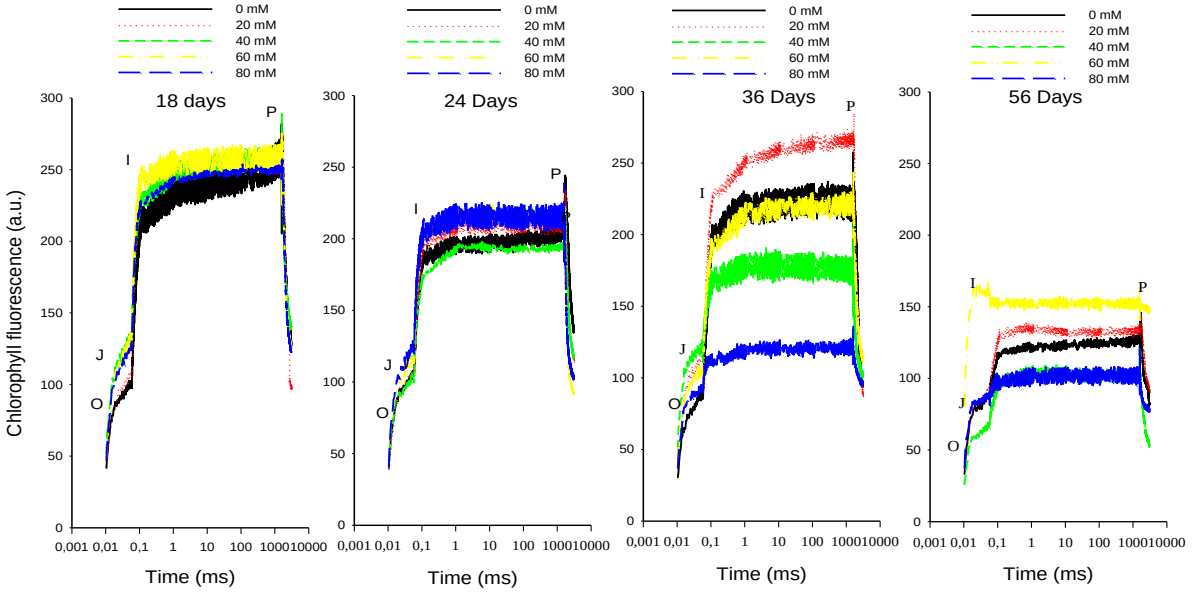


**Fig. 6.** Polyphasic rise of Chla fluorescence transients (OJIP) in *P. atlantica* subjected to five increasing concentrations of NaCl (n=6).

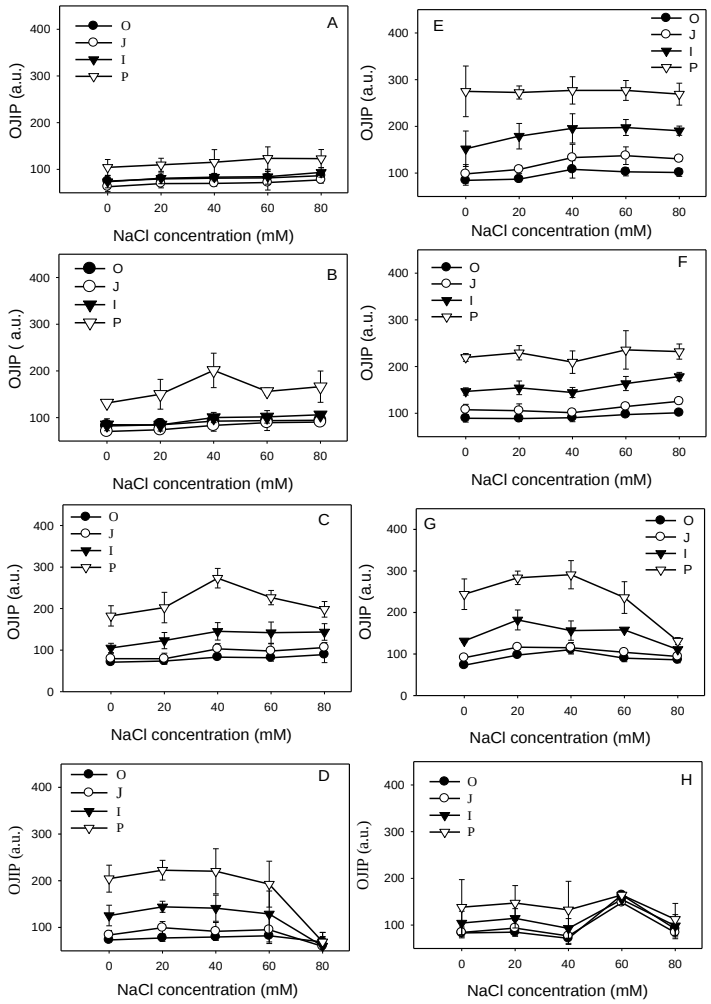


**Fig. 7.** Variation of the transition values multiphase (OJIP) in *P. vera* (A, B, C, D) and *P. atlantica* (E, F, G, H) along the experiment (n=6).

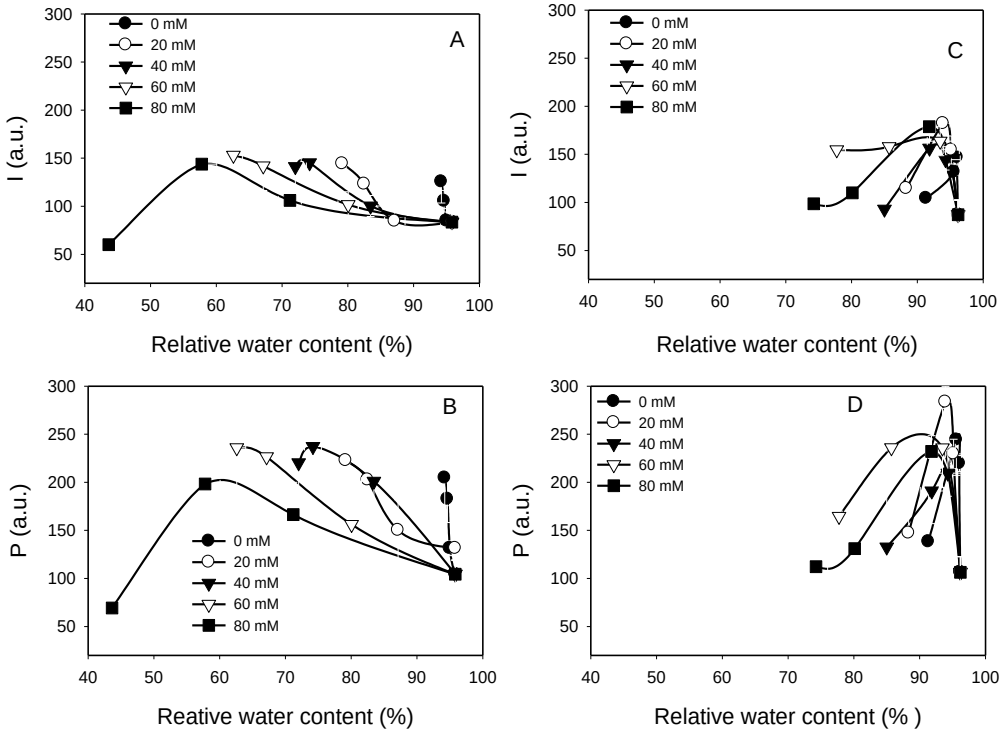


**Fig. 8.** Relationships between relative water content and chlorophyll fluorescence for *P. vera* (A, B) and *P. atlantica* (C, D) (n=6).

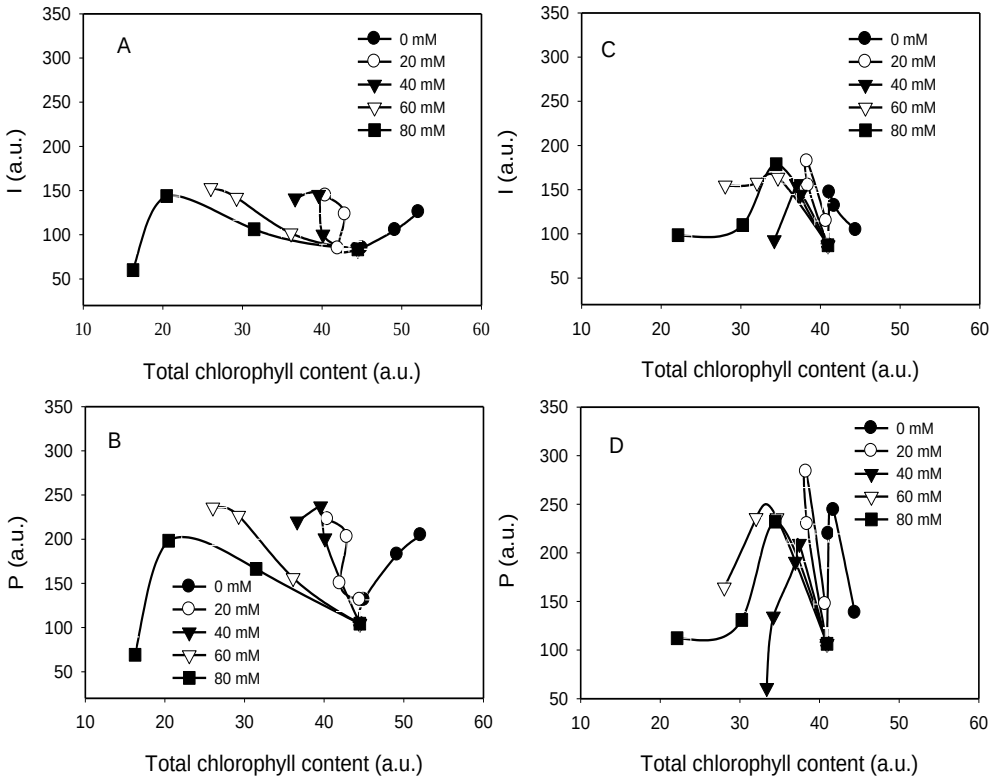


**Fig. 9.** Relationships between total chlorophyll content ant chlorophyll fluorescence for *P. vera* (A, B) and *P. atlantica* (C, D).

**Discussion**

*Plant water status*

From the point of view of cell turgor, RWC depends largely on species (Duarte *et al*., 2013). Indeed, under salinity plant water status is affected in *P. vera*, whereras, *P. atlantica* maintained high leaf turgor. RWC reduction is due to an increase in osmolarity in the cytoplasm causing osmotic stress and cellular dehydration. A more favorable hydration status in *P. atlantica* reveals a mechanism limiting transpiration (Ben Ahmed *et al*., 2008; Porcel *et al*., 2012) due to osmotic adjustment, which maintains the osmotic balance between the cytoplasm and vacuole preventing the efflux of water from the cytoplasm. This is achieved by compartmentalization of salt ions in the vacuole and/or synthesis and accumulation of osmoprotectors without interfering with the metabolism of the plant (Munns, 2002; Parida and Das, 2005; Ben Ahmed *et al*., 2008). In this context, pistachio species and particularly *P. atlantica* proved to accumulate osmoprotectors under salt stress (Chelli-Chaabouni *et al*., 2010). Several studies reported the increase of proline content in plants exposed to a certain salinity levels, depending on the species (Amirjani, 2010; Nazarbeygi *et al*., 2011). The osmotic adjustment was also attributed to the potassium ion (Kamel and El-Tayeb, 2004), often deficient in the presence of NaCl (Ben Ahmed *et al*., 2008; Tavakkoli *et al*., 2011). Indeed, the low nutrient supply to the cambium and low potassium ion content in the shoot leads to a decrease of xylem differentiation under salt stress of vessel lamina of salt-sensitive poplar species (Escalante-Pérez *et al.,* 2009). Therefore, maintaining a favorable tissue hydration improves stress tolerance via the maintenance of the metabolic activity, the root growth and delayed the leaf senescence.

*Chlorophyll content and photosynthesis*

Salt stress reduced all parameters of leaf gas exchanges, but the reductions also depend on species and the severity of salinity. A specific pattern of response for each species has highlighted different mechanisms of tolerance. Thus, upon addition of NaCl in the soil, stomatal closure limits $CO_2$ diffusion, required for carboxylation reactions (Parida and Das, 2005; Tabatabaei, 2006; Ben Ahmed *et al*., 2008) and transpiration. This alters the activity of chloroplast through a damage of the collection system and energy conversion (Everard *et al*., 1994). Certainly, the absorption of NaCl competes with other elements, particularly resulting in $K^+$ deficiency (Chelli-Chaabouni *et al*., 2010; Zorrig *et al*., 2013), disrupting the activity of PSII. Thus, a close correlation has been established between the reduction of photosynthesis and $K^+$ deficiency (Tabatabaei, 2006). This reduction can be explained by the disruption caused by metabolic stress and ionic perturbations of the structure and functioning of the photosynthetic apparatus to which they are associated. Reductions in A, E and gs are similar to RWC decreases for *P. vera* and *P. atlantica*. Studies have shown that lowering gs is controlled by an hormonal message from the roots, the abscisic acid (ABA) (Zhu *et al*., 2005; Dodd and Perez-Alfocea, 2012; Zorb *et al*., 2013), which affects stomatal movements, reducing Ci, and consequently inhibiting photosynthesis (Wilkinson and Davies, 2002) and leaf expansion (Munns *et al*., 2006). However, *P. vera* exhibits greater reductions than *P. atlantica*, reflecting a considerable sensitivity to salinity. In contrast, the favorable water status for *P. atlantica* didn't improve the photosynthesis activity, which depends more on gs and TCC, severely reduced by salinity (Ranjbar *et al*., 2002; Tabatabaei, 2006). In this context, reductions in A were an adaptative mechanism rather than a destructive consequence of salt stress (Ben Ahmed *et al*., 2008), in conformity with other results on *P. vera*, (Ranjbar *et al*., 2002; Tavallali *et al*., 2008; Karimi *et al*., 2009) and *Olea europea* (Tabatabaei, 2006; Ben Ahmed *et al*., 2008).

The quantification of photosynthetic pigments is based on a non-destructive sample showing that excess of NaCl reduced the TCC in both species. Under salinity stress, TCC decreases (Mousavi *et al*., 2008; Dhanapackiam and Ilyas, 2010), a consequence of chlorophyll photo-oxidation by oxy-radicals and the disruption of the chloroplast ultra-structure (Hernandez *et al*., 1999) or increasing the activity of

chlorophyllase and chlorophyll degradation (Ranjbar *et al.*, 2002; Parida *et al.*, 2003). However, *P. vera* is more sensitive to salinity for chlorophyll content. Reductions in RWC, A and TCC are similar for each species, marking a specific general pattern of response to salt stress. Thus a positive correlation between chlorophyll content and photosynthesis was observed.

*Functional stability of the PSII under salt stress*

The study of fluorescence permits to evaluate the rapid and non-destructive effect of stress on photosynthesis (Stirbet and Govindjee, 2011). The shape of the multiphase curves (OJIP) of the fluorescence kinetics is depending on the severity of salinity and species. *P. vera* shows a gradual increase in fluorescence at high chlorophyll content, reflecting an inhibition of $CO_2$ assimilation, which causes a greater dissipation of energy and a photo-inhibition of reaction centers of PSII, and decreases in the photochemical efficiency (Baker, 1991). The decrease in fluorescence in both species, particularly at 80 mM of NaCl, was due to a lack of electron donor (Lazár, 1999).

Variation of transitions O, J, I and P as a function of RWC (Fig. 9) showed that O remains unchanged by increasing salt stress in both species**.** In *P. vera*, while RWC progressively decreases, the fluorescence intensity increases progressively for all NaCl treatments. The increase in excess of excitation light intercepted by the PSII collector antennas as fluorescence may be explained by the fact that salt stress caused an increase in the rates of reduced QA and QB, resulting in a blockage of electron transfer in the electron transport chain.

At the beginning of the experiment and at high values of TCC, an increase in fluorescence intensity is associated with reduction in A. On the contrary, at the end of the experiment, the reduction of fluorescence is associated with a decrease of A (Fig. 8). The decrease in photosynthetic activity is linked to reducing effects of NaCl on the activity of PSII (Mishra *et al.*, 1991; Tiwari *et al.*, 1997). The correlation between chlorophyll content and fluorescence can be explained by the fact that salt stress induced a significant reduction of Chla and Chlb content (Ranjbar *et al.*, 2002; Karimi *et al.*, 2009), attributed mainly to the reduction of chl*a*, a major component of the reaction centers and antenna of PSII, by increasing the cholorophyyllase activity: the chlorophyll degrading enzyme (Ranjbar *et al.*, 2002), inducing the destruction of the chloroplast structure and the instability of pigment protein complexes, disturbing A and fluorescence especially for *P. vera*. Jamil *et al.* (2007) reported that the photochemical efficiency of PSII had a positive relationship with chlorophyll content in radish seedlings under salinity.

**Conclusion**

Under salt stress, the physiological and morphological changes largely depend on the species and the severity of salt stress. The dynamic functioning of PSII depends largely on the toxicity by NaCl, altering plant water status, the conversion of light energy and the $CO_2$ assimilation by the mesophyll.

*P. atlantica* has maintained higher RWC, TCC and A than *P. vera*. The study of chlorophyll fluorescence reflects a lower sensitivity of *P. atlantica* under salinity, even for 80 mM of NaCl. This account for the rusticity of *P. atlantica* justifies the agricultural practice based on its use as rootstock for *P. vera* to improve survive under salinity.

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