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Research article

Effect of phosphorus concentration on the photochemical stability of PSII and CO_2 assimilation in *Pistacia vera* L. and *Pistacia atlantica* Desf.

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ABSTRACT

A greenhouse pot experiment was conducted at the faculty of sciences of Gafsa to evaluate the effect of phosphorus treatment on two pistachio species. The seedlings of *Pistacia vera* and *Pistacia atlantica* were subjected to six levels of phosphoric acid (P_2O_5) (0, 5, 15, 30, 60 and 120 ppm). Stomatal conductance, net photosynthesis, chlorophyll fluorescence (OJIP) and total chlorophyll content were measured after 1, 2, 3, 6, 8, 9 and 12 weeks of treatment. During the experiment, phosphorus application at 5 ppm increased photosynthesis and stomatal conductance, relative to the treatment 0 ppm only in *P. atlantica*. However, phosphorus supply at 60 and 120 ppm induced toxicity leading to an inhibition of CO_2 photo-assimilation rate, an alteration of photosystem II (PSII) structure and function and reduction in leaf chlorophyll content in both species. The (OJIP) transient showed complex changes in O-J, J-I and I–P phases of fluorescence. Due to phosphorus toxicity, both donor and acceptor sides of PSII were damaged, electron transport perturbed and chlorophyll pigment reduced which resulted in the fall of CO_2 photo-assimilation rate, followed by mortality in both species.

1. Introduction

Phosphorus (P) is essential for the normal growth and development of plants. Indeed, P plays an essential role not only in the synthesis of proteins, nucleotides, and enzymes but also in photosynthesis as an ATP (Marschner, 1993; Lewis et al., 1994). P is also involved in the regulation of metabolic pathways (Theodorou and Plaxton, 1993). Soil P is found in different forms, such as organic (20–80%) and mineral P. Pi is the form of P available to plants (Pi) (Schachtman et al., 1998). Although soils may contain relatively high quantities of total P, only a small proportion is immediately available to plants. (Vance et al., 2003). Therefore, to overcome the P deficiency, phosphate fertilizers are applied to the soil (Naeem et al., 2010). However, phosphorus may become toxic when accumulated by plants to high concentration (Silber et al., 2002).

Plants respond differently to P supply depending on concentration and species. Indeed, P deficiency can reduce photosynthesis (Jacob and Lawlor 1991, 1992; Ghannoum and Conroy, 2007; Suriyagoda et al., 2010). Stomatal or biochemical factors are among the mechanisms of photosynthesis decrease under low P (Lauer et al., 1989; Lima et al., 1999; Fujita et al., 2004; Salehi and Hajiboland, 2008). Therefore, several authors reported limitation in RuBP regeneration in P deficient plants due to smaller ATP content (Rao et al., 1987; Rao and Terry, 1989; Jacob and Lawlor, 1992; Carstensen et al., 2018). Net photosynthesis decrease may also be limited by the reduction in Rubisco amount and activity due to P deficiency (Brooks, 1986; Brooks et al., 1988; Lauer et al., 1989; Usuda and Shimogawara, 1991; Jacob and Lawlor, 1992; Sawada et al., 1992). P deficiency may also decrease leaf chlorophyll and protein contents (Plesniar et al., 1994; Usuda, 1995).

Adequate phosphorus increased photosynthesis as P concentration increased, but, it gradually decreased at high levels (Naeem and Khan, 2009; Naeem et al., 2010; Zhu et al., 2012; Taliman et al., 2019).

Nevertheless, high internal phosphorus concentrations may lead to P toxicity depending on species (Dai et al., 1999). Certain plant species such as *Verticordia plumosa* L. suffer from P toxicity at lower concentrations than most other plant species (Silber et al., 2002). The mechanism of P toxicity in plants is little understood, P toxicity is associated with P–Zn interactions, either in the soil or in the plant (Loneragan and Webb, 1993). Zn is a major constituent of enzymes essential to photosynthesis, such as the carbonic anhydrase (Assche and Clijsters, 1983). Notably, in tomato plants, reduction in photosynthesis had been explained by an overexpression of AtHXK1. HXK is involved in the regulation of photosynthesis (Dai et al., 1999; Jang and Sheen, 1997; Xiao et al., 2000).

Total chlorophyll content declined in plants grown under low P. Naeem et al., (2010) and Zhu et al., (2012) reported a significant

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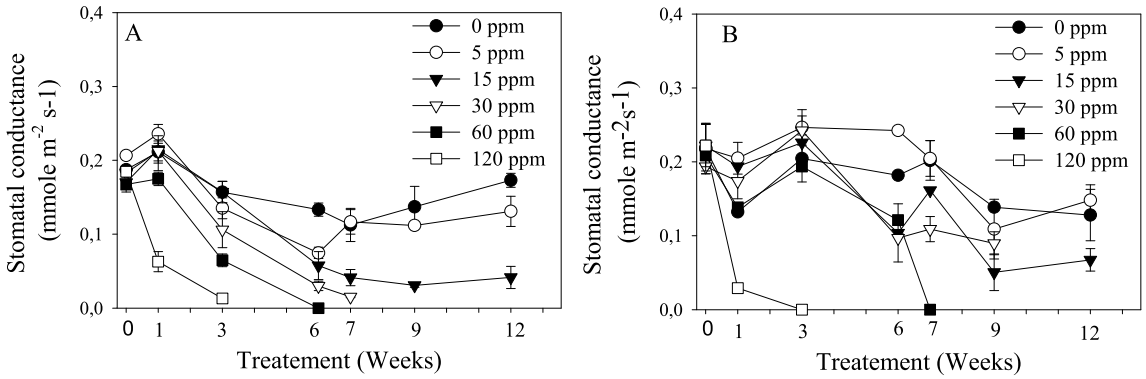

Fig. 1. Effect of six level of phosphorus on stomatal conductance of the seedlings of *P. vera* (A) and *P. atlantica* (B) during the experiment (n = 6).

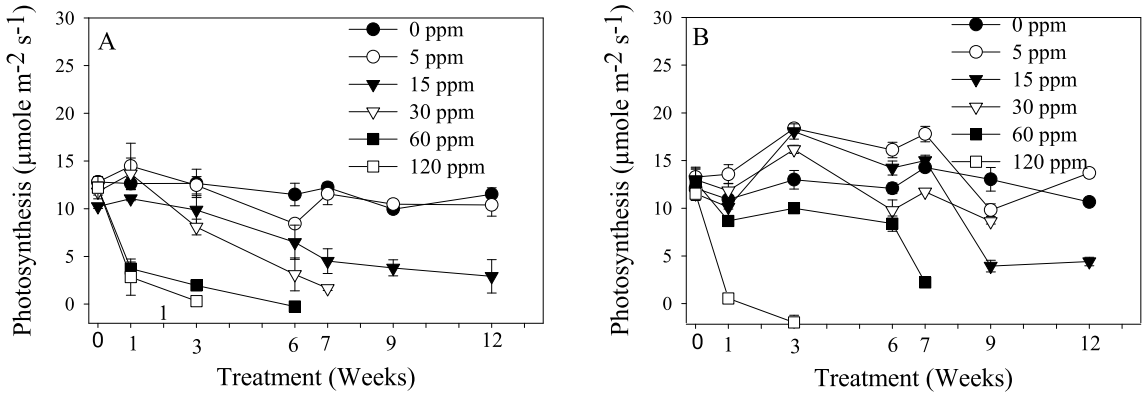

Fig. 2. Effect of six level of phosphorus on net photosynthesis of the seedlings of *P. vera* (A) and *P. atlantica* (B) during the experiment (n = 6). Bars denote the standard errors.

increase in total chlorophyll content as P increased.

Chlorophyll fluorescence is a fast and non-destructive method for studying plant physiology. This tool is required in plant stress detection (Bąba et al., 2016; Kalaji et al., 2017a), such as nutrient deficiency/excess (Kalaji et al., 2018; Samborska et al., 2018). The fast phase is called OJIP, where O is for origin, the first measured minimal level, J and I are intermediate levels, and P is the peak. OJIP transient has been reported to reflect changes in the redox state of quinone A (QA) and the reduction of the photosynthetic electron transport chain. The OJIP transient is characterized by three phases OJ, JI and IP. The OJ phase represents the reduction of the acceptor side of PSII. The JI phase describes the reduction of the PQ and the IP phase represents the fractional reduction of the acceptor side of PSI or the last step in the reduction of the acceptor side of PSII and the amplitude of the IP phase is an indicator of PSI content (Stirbet and Govindjee, 2011).

P. vera L. is an important nut crop, usually propagated by grafting on seedlings of many *Pistacia* species. *P. atlantica* a wild endangered species exists as isolated aged trees in arid and semi-arid areas. Despite its adaptation to hostile environments such as salinity (Ferguson et al., 2005), drought (Ben Hamed et al., 2016) and nematode tolerance and its good performance as rootstock compared to *P. vera*, it is, nowadays, rarely used as rootstock for pistachio varieties, probably because of seeds lack and the low germination capacity. Since *P. atlantica* is adapted to arid environment and an important rootstock for *P. vera,* it can be used to rehabilitate soils where phosphorus is extracted as soon as it tolerate excess phosphorus. So determining limits of P tolerance is of prime importance. In this context, appears the importance of the study of physiological responses of *P. vera,* and *P. atlantica* to different phosphorus levels, ranging from deficient to toxic concentrations. Thus, this work was planned to i) study comparatively the effect of phosphorus on the physiological behavior of *P. vera* and *P. atlantica,* ii) to identify physiological mechanisms of excess phosphorus tolerance and iii) to find rehabilitant species for the phosphorus extraction soils.

2. Materials and methods

2.1. Culture condition

The experimentation was carried out on seedlings of *P. vera* and *P. atlantica* subjected to six levels of phosphorus. The seeds of *P. vera* (Mateur cultivar) were collected from Gafsa (South East Tunisia) during 2011, and those of *P. atlantica* were collected during the same year from wild trees in Meknassy (Centre-West Tunisia). Before the setting in germination, the seeds of *P. atlantica* were subjected to a mechanical scarification. Initially, the production of the plants was led under controlled conditions of the laboratory; the temperature was 25 °C and the photoperiod was 14/10 h light/obscurity. The sowing was carried out on 27 September 2011. Seeds were germinated on pure washed sand. Germination took place after 10 days for *P. atlantica* and 7 days for *P. vera* (Ben Hamed et al., 2016).

After one month of growth, the individuals were transplanted in plastic culture pots of 9 cm in diameter and 55 cm in depth. The content of the pots are pure and really washed sand. The density of the individuals was an individual per pot for each studied species. The test related to 2 species, 6 treatments of phosphorus of 10 repetitions each one, giving a total of 120 pots. All the pots received the same amount of watering (100 ml), twice per week.

2.2. Experimental design

Phosphorus treatment was applied on 11 April 2012 during three months. Six increasing concentrations of P_2O_5 were applied: 0; 5; 15; 30; 60; 120 ppm of P_2O_5, at a rate of two watering per week. The volume of irrigation was 15 mm for each pot. The experimentation was

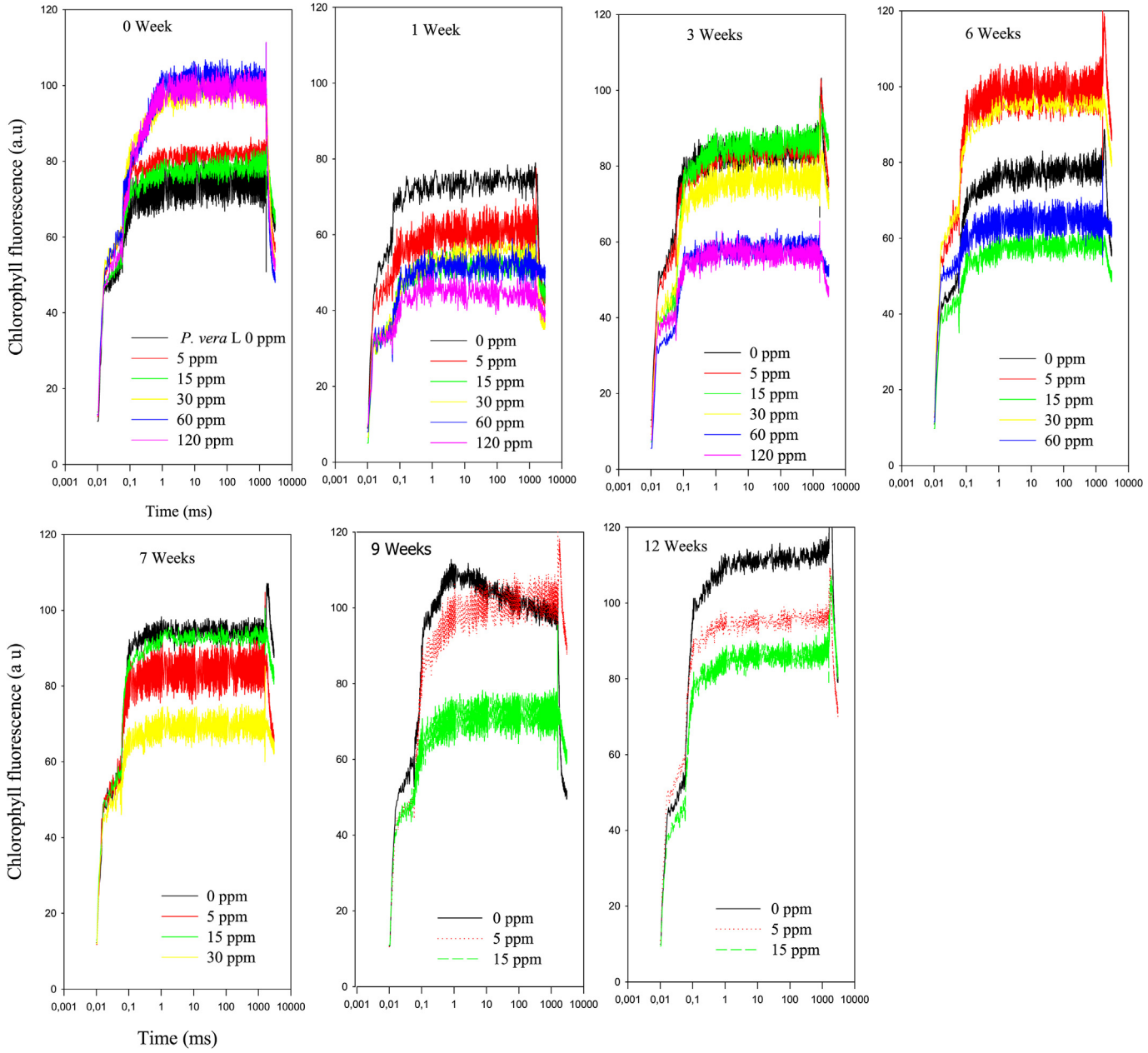

Fig. 3. Effect of different concentrations of phosphorus on chlorophyll fluorescence (OJIP) in *P. vera* in light adapted leaves along 12 weeks of treatment (n = 6).

conducted during April and May 2012. The temperature ranged between 15 and 23 °C.

2.3. Measurements

2.3.1. Leaf gas exchanges

Net photosynthesis rate (A, μmol m^{-2} s^{-1}) and stomatal conductance rate (gs, mol H_2O m^{-2} s^{-1}) were assessed on six leaves of the same physiological age, the third leaf after the first leaf of emergency. Measurements were estimated by a portable system LCi of photosynthesis (ADC BioScientific Ltd, USA), equipped with infra-red analyzers gas differential for CO_2 and the vapor of water and a measuring chamber of the gas exchange. The basis of measurement consists of placing the leaf in the leaf chamber and after a phase of stabilization, the system makes it possible to record the values of the leaf gas exchanges. Measurements of the leaf gas exchanges were taken with an active photosynthetic radiation fix (1000 μmole photon m^{-2} s^{-1}). During the experiments, eight measurements of leaf gas exchange were monitored: Just before the induction of the treatment and 1, 2, 3, 6, 8, 9 and 12 weeks after treatment with six repetitions per phosphorus treatment. Measurements were taken from 9 h to 11 h of the morning on sunny days.

Chlorophyll fluorescence Measurements.

2.3.2. OJIP transient

The measurements of chlorophyll fluorescence were made on the same leaves used for gas exchanges measurements, using a portable chlorophyll fluorometer (OS–30P; Opti science, Inc., NH, USA). The device was calibrated by initiating the measurement time (30 s), the light intensity (700 μS). Thereafter, special plastic clips were attached to leaves and OJIP transients were measured. The mode OJIP gives fluorescence kinetics of multiphase transition O (Minimal fluorescence level), J, I (Intermediate level of fluorescence) and P (Maximal fluorescence). Measurements were taken both at an actinic light and after dark-adaptation of 30 mn. In both states, 6 measurements were monitored. These measurements were taken just after leaf gas exchange

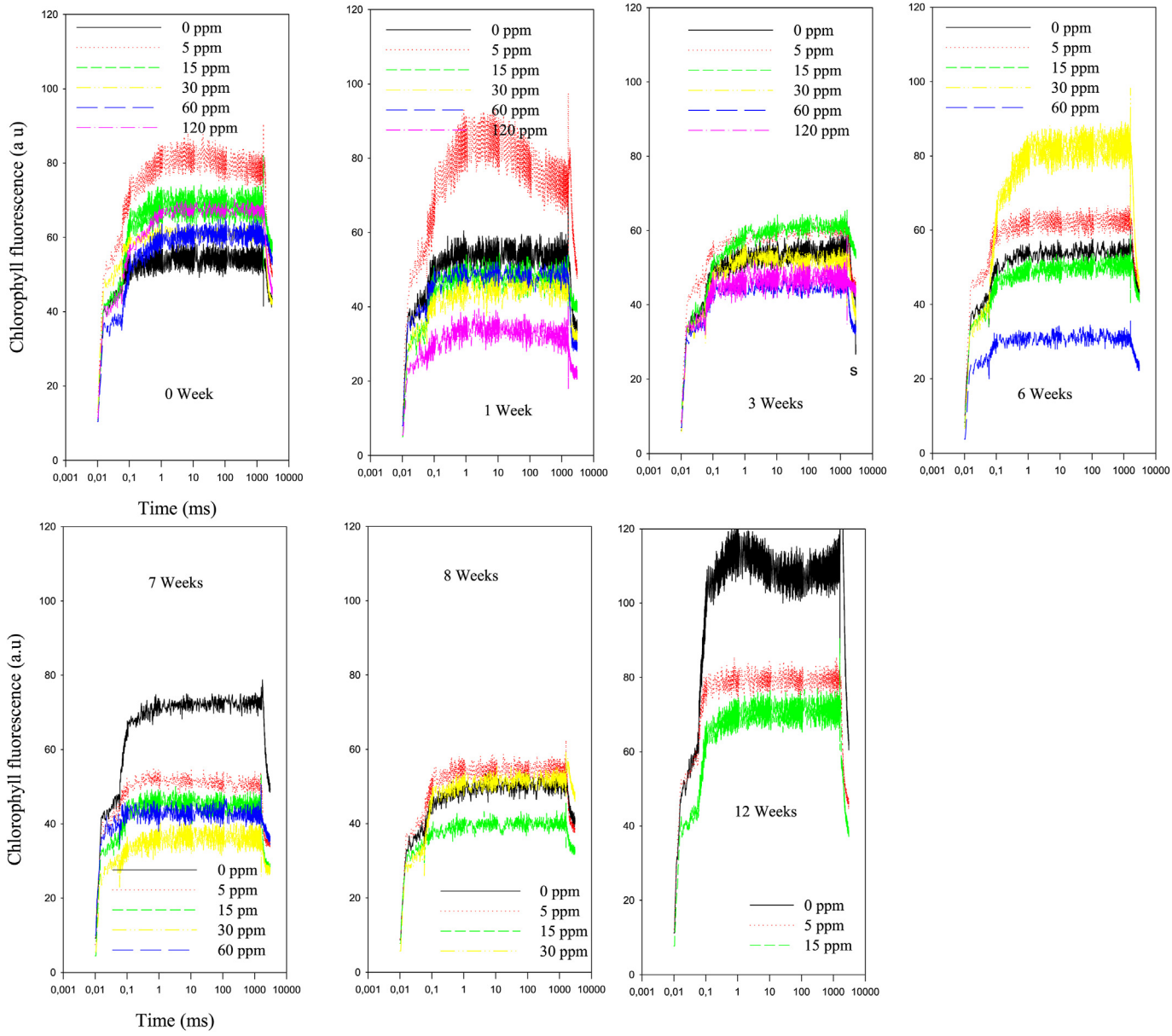

Fig. 4. Effect of different concentrations of phosphorus on chlorophyll fluorescence (OJIP) in *P. atlantica* in light adapted leaves along 12 weeks of treatment (n = 6).

measurements.

2.3.3. Total chlorophyll content

The total chlorophyll content was measured on the same leaves (6 leaves) used for leaf gas exchanges measurements, using chlorophyll Meter (CCM 200, Opti-Sciences, USA). Measurements were taken just after photosynthesis and fluorescence measurements from 9 h to 11 h. This parameter was monitored after 1, 2, 3, 6, 8, 9 and 12 weeks of treatment.

2.4. Statistical analysis

Variance analysis of data (one-way ANOVA) was performed using SPSS software Version 11.5 (*SPSS Institute Inc., Cary, NC, USA*). Means are presented with standard errors of the mean and significance is expressed at $p < 0.05$.

3. Results

3.1. Effect of different phosphorus levels on leaf gas exchanges

All plants subjected to high phosphorus level (120 ppm) exhibited a clear decrease of stomatal conductance in the two studied species since the first week of treatment (Fig. 1). This decrease reached 80 and 100% in *P. vera* and *P. atlantica* respectively. Nevertheless, for the treatment 60 ppm, net photosynthesis was significantly reduced *in P. vera* 1 week after treatment. However, *P. atlantica* maintained gs values near those of control treatment until six weeks of treatment. Thereafter, it decreased significantly. Also, the treatment 5 ppm marked differences between species: It increased stomatal conductance only in *P. atlantica* by 28% about 3 weeks of treatment.

Concerning net photosynthesis, the same trend of variation was observed (Fig. 2). High phosphorus level (120 ppm) decreased net photosynthesis. However, the concentration 5 ppm improved A in treated plants compared to the control ones.

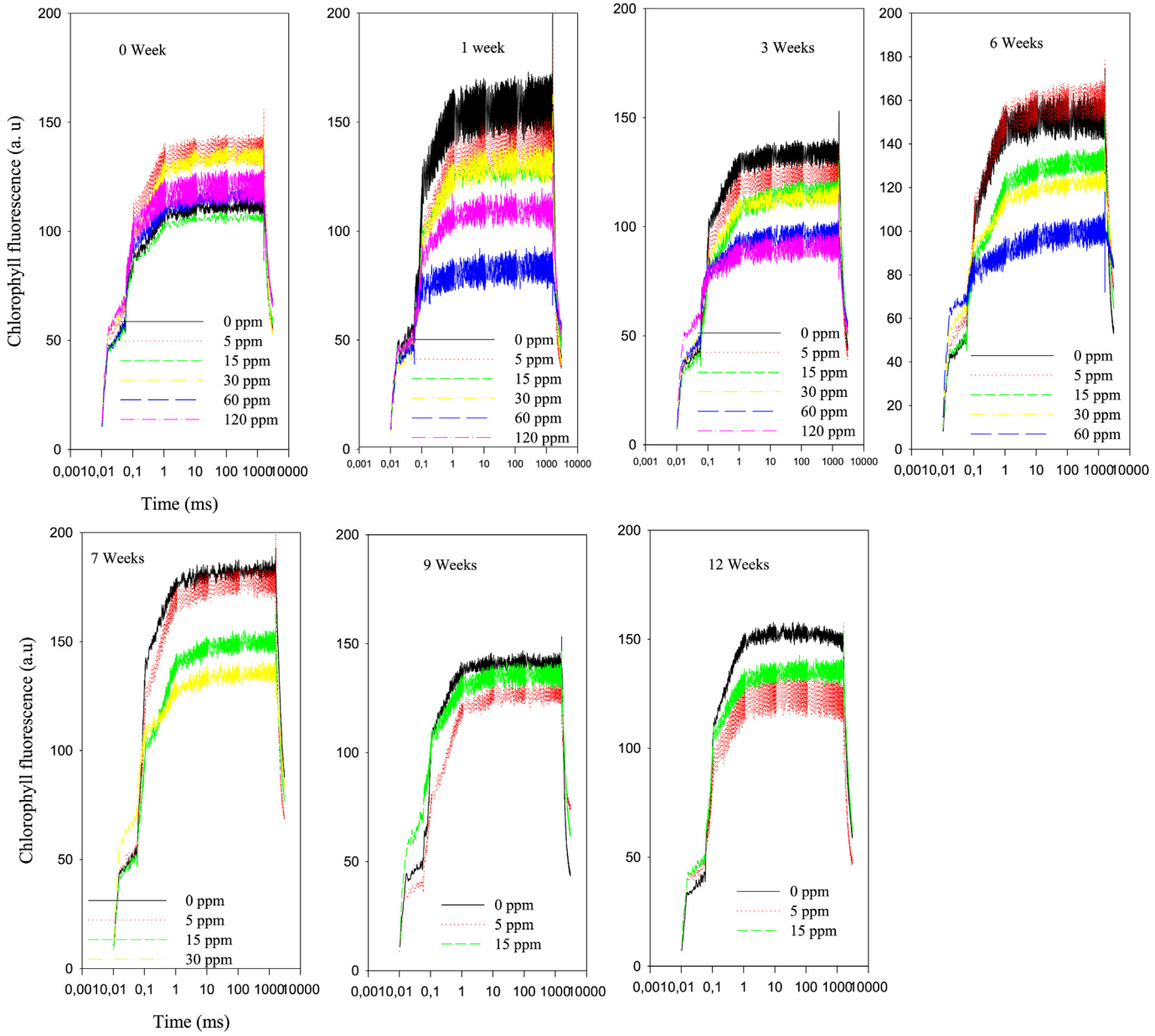

Fig. 5. Effect of different concentrations of phosphorus on chlorophyll fluorescence (OJIP) in *P. vera* in dark adapted leaves along 12 weeks of treatment (n = 6).

3.2. Effect of different phosphorus levels on chlorophyll fluorescence transient (OJIP)

OJIP transients in light and dark-adapted leaves (Figs. 3–6) showed a typical polyphasic rise with the major phases of fluorescence rise from O to P with two intermediate steps, J and I. Measurements made on chlorophyll fluorescence demonstrate important differences in OJIP transient in dark as in light test: The fluorescence intensity is higher in leaves adapted to darkness (Fig. 5 and 6) than those light-adapted (Fig. 3 and 4) for both species and all treatments. In the actinic light, (OJIP) transients of P-treated seedlings at high phosphorus levels (60 and 120 ppm) showed a decrease of magnitude of O-J, J-I and I–P phases of fluorescence since 2 weeks of treatment in *P. vera* (Fig. 3). Whereas, in *P. atlantica,* the highest concentration (120 ppm) induced a decrease in OJIP steps after 1 week of treatment (Fig. 4). The concentrations 5 ppm induced a rise in the chlorophyll fluorescence intensity compared to those of the control after 2 weeks in *P. atlantica* in light-adapted leaves (Fig. 3 and 4).

In dark-adapted leaves, (OJIP) transients of leaves of P-treated seedlings with 120 and 60 ppm showed a decrease of magnitude and rise of O-J, J-I and I–P phases of fluorescence after 2 and 3 weeks of treatment in *P. vera* (Fig. 5). However, in *P. atlantica,* the concentration 120 ppm induced decrease in all OJIP steps after 3 weeks of treatment compared to the seedlings subjected to 0 ppm (Fig. 6).

3.3. Effect of different phosphorus levels on total chlorophyll content

The total chlorophyll content showed significant differences between the two studied species and the different treatment ($p < 0.001$) (Fig. 7). Excess of phosphorus induced a reduction of this parameter. The most important reductions are observed in the seedlings subjected to a concentration of 120 ppm. The reduction ratios in *P. vera* and *P. atlantica* after three weeks of treatment are of 48 and 81% respectively. However, the treatment 5 ppm of phosphorus showed a slight improvement of the total chlorophyll content in *P. atlantica* by about 31%.

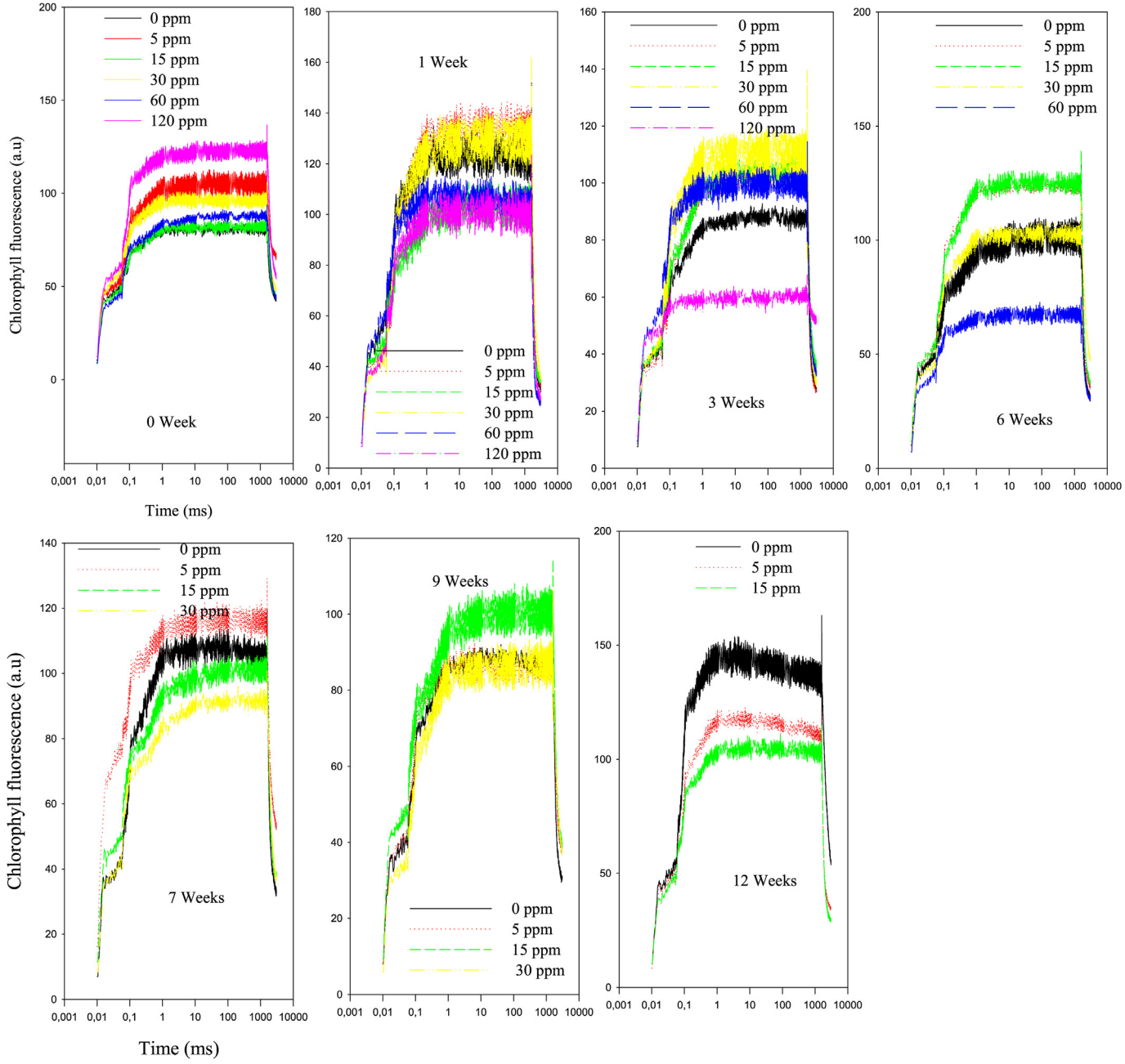

Fig. 6. Effect of different concentrations of phosphorus on chlorophyll fluorescence in *P. atlantica* in dark adapted leaves (OJIP) along 12 weeks of treatment (n = 6).

4. Discussion

Our results show that P is a main nutrient that limits plant growth. Nevertheless, excess in P induces plant toxicity leading to mortality of all treated plants (120 ppm). The toxicity effect of high phosphorus level was detected thought several non-destructive physiological parameters. Indeed, since the first week of treatment, net photosynthesis, stomatal conductance, chlorophyll fluorescence and total chlorophyll content were significantly decreased. The decrease in leaf gas exchange parameters is the consequence of several factors: In fact, the reduction of the stomatal conductance limits the diffusion of CO_2 necessary to the reactions of carboxylation, and thus, reducing net photosynthesis. At high Pi supply, triose-P export competes with ribulose 1,5-bisphosphate (RuBP) regeneration and the rate of photosynthesis can be diminished. Also, reduced leaf area under excess of phosphorus may explain photosynthesis reduction in *P. vera* and *P. atlantica* (Unpublished data). On the other hand, it was reported that P toxicity reduces Zn availability (Loneragan and Webb, 1993). Zn is a major constituent of enzymes essential to photosynthesis, such as the carbonic anhydrase (Assche and Clijsters, 1983). Moreover, Zn is an important element that controls the uptake of P by the roots, and/or transport of P from the roots to the shoots.

In addition to the phosphorus-zinc interaction, there is also evidence that there is a phosphorus-interaction with other cationic micronutrients. Indeed, it has been reported that high phosphorus level limit Mn uptake (Beer et al., 1972; Fageria and Baligar, 1997; Hellin and Alcaraz, 1980; Safaya, 1976; Neilsen et al., 1992; Shane and Lambers, 2005; Pedas et al., 2011). Consequently, it decreases PSII function, since 4 Mn are a component of oxygen evolving complex (OEC) of photosystem II (Pedas et al., 2011; Glatzel et al., 2013). Also, excess P results in a decrease in iron (Fe) uptake (Brown and Tiffin, 1962; Haleem et al., 1992; Singh et al., 1996; Li et al., 2010), Fe is

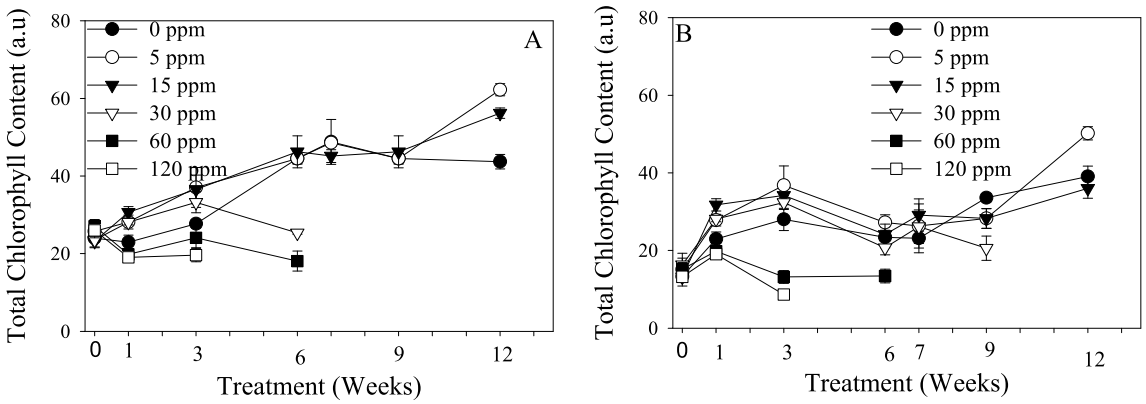

Fig. 7. Effect of six level of phosphorus on total chlorophyll content of the seedlings of *P. vera* (A) and *P. atlantica* (B) during the experiment. Each point is the mean of 6 measurements. Bars denote the standard errors.

included in photosynthetic structure (cytochromes, ferredoxin and several intermediaries of the thylakoid electron transport chain) (Perez et al., 1995). The effect of phosphorus toxicity on the PSII structure and function was detected by chlorophyll fluorescence (OJIP) that seems very sensitive to variation of plant nutrient status. Indeed, in both species, the concentration 60 and 120 ppm induced a decrease in all OJIP steps compared to the control seedlings translating a damage of both donor and acceptor sides of PSII and perturbation of electron transport. Studies dealing with phosphorus toxicity effects on chlorophyll fluorescence are limited.

On the other hand, the interaction of the excess phosphorus with other nutrients causes a nutritional imbalance and disruption of photosynthesis and hence, decreased chlorophyll fluorescence. Indeed, excess of P reduces the absorption of Mn (Shane and Lambers, 2005). Mn is a complex of oxygen evolving complex of *PSII* (Pedas et al., 2011; Glatzel et al., 2013.). Therefore, the function of *PSII* decreased. Also, it reduces the uptake of Fe, Fe is involved in cytochrome structure, ferredoxin and several intermediates of the thylacoid transport chain) (Perez et al., 1995). Reductions of chlorophyll fluorescence were observed since the first week of treatment, reflecting the sensitivity of this parameter to the change in the status of the plant. Only the concentration 5 ppm induces an increase in chlorophyll fluorescence intensity in *P. atlantica* compared to the treatment 0 ppm.

Moreover, excess phosphorus leads to Mg deficiency, in fact, Mg represent a constituent of the Chl molecule and is required for the development of the chloroplast, Hence, Mg deficiency leads to photosynthesis reduction (Terry and Ulrich, 1974). Also, it was reported that N and K were reduced at high phosphorus level. N, a major constituent of Rubisco and chlorophyll pigment (Ripullone et al., 2003), K required in the activation of enzymes by its involvement in adenosine triphosphate (ATP) production and in stomatal activity (Jin et al., 2011). An interaction of P and copper (Cu) has also been reported (Safaya, 1976; Timmer and Leyden, 1980; Rhoads et al., 1992). However, high phosphorus level enhance Na uptake that may reduce photosynthesis (Unpublished data).

The treated seedlings of *P. vera* and *P. atlantica* maintained higher values of total chlorophyll content compared to the control under treatments 5 and 15 ppm. Indeed, phosphorus is associated with multiple organic combinations in fabrics with the chloroplasts. However, those who received very high phosphorus concentrations (60 and 120 ppm) showed a reduction of the total chlorophyll content. The toxicity induced by the excess of phosphorus could be explained by the phosphorus-fer interaction. These results are in agreement with those reported by Naeem et al. (2010) and Zhu et al. (2012).The differences between the two studied species are significant for the treatment 5 ppm. Hence, it improves all the measured parameters only in *P. atlantica*.

Concerning the estimation of total chlorophyll content, Kalaji et al., (2017b) reported that the chlorophyll content fluoremeter CCM200 is among the devices that provide reasonably estimation of total chlorophyll content until optimal nutrient conditions. Nevertheless, under nutrient deficiency, it provides different values for the same plant under the same nutrient deficiency. Our results showed that in pistachio species, the CCM200 showed comparable values for the same plant under the same nutrient deficiency. Thus, the CCM200 showed a high degree of accuracy for phosphorus deficiency.

Rock phosphate is a non-renewable resource and high P input levels in agriculture have led to environmental problems. So improving phosphorus use efficiency of the plants is of prime importance. In this context, many physiological mechanisms are involved in phosphorus use efficiency. These mechanisms can be divided into external and internal phosphorus use efficiency strategies. Internal mechanisms improve P scavenging and uptake, by increasing transport capacity. Others promote a more economical use of P in plant growth, by optimising allocation within the plant. For improving P uptake, root exudates (protons and organic acids, such as citrate, malate, and oxalate) are thought to assist in mobilizing P from fixed sources in the soil (Vance et al., 2003). Hydrolytic enzymes, such as acid phosphatases and ribonucleases, are upregulated in response to low P and upon exudation are able to release P fixed in organic forms in the soil, such as phytate (Vance et al., 2003).

Internal P use efficiency include a series of metabolic modifications; An important aspect is the effective mobilization of P within the plant, such as recycling P from old and senescing plant parts to actively growing tissue and re-use of phosphate from vacuoles as shown in *Brassica* cultivars. At high P, up to 75% of P in leaves can be present as orthophosphate, most of which in the vacuoles (up to 85–95% of cellular P (Akhtar et al., 2008). Nevertheless, upon P limitation photosynthesis is quickly affected, so there are apparently limitations to mobilization of this stored P (Richardson et al. 2011). Another strategy is adapting plant metabolism to a lower P requirement. One way is the replacement of phospholipids by sulfo- and/or galacto-lipids in membranes (Lambers et al., 2006). Under P deficiency stress, anthocyanin is accumulated, that expected to offer protection to photo-inhibitory damage as a consequence of P-limited photosynthesis (Vance et al., 2003).

Hormone and signalling pathways are important integrators of stress responses in plants. Auxin and ethylene initiate lateral root initiation, which is a pivotal response to low P. Gibberellin counteracts auxin effects on lateral root formation. Sugar signalling also interacts with P responsiveness. Decreased photosynthesis in response to low P leads to increased starch formation in shoots (Hammond and White, 2011). In addition, sugar loading into the phloem is increased and thus allocated to roots (Hammond and White, 2011).

5. Conclusion

This study carries out to deduce that excess phosphorus leads to

toxicity in the two studied species. Its early detection is of prime importance. It seems that chlorophyll fluorescence is an important tool for stress detection. The stage of development is sensitive to the excess of phosphorus for both studied species that require low concentrations of phosphorus at this stage. *P. atlantica* showed specific ecophysiological traits that make it more tolerant than *P. vera* to phosphorus, therefore it can be cultivated in the exploited phosphate zones contrary to *P. vera*. Therefore, we suggest phosphorus tests on adult *P. atlantica* plants in fields.

Contribution

This manuscript focus on the ecophysiological responses of two pistachio species (*Pistacia vera* and *Pistacia atlantica*) to phosphorus treatment. The results showed that the supply of phosphorus at 60 and 120 ppm induced toxicity in *P. atlantica* and *P. vera.* The (OJIP) transient showed complex changes in O-J, J-I and I–P phases of fluorescence. However, the treatment 5 ppm improved photosynthesis and stomatal conductance in *P. atlantica*.

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