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Y. Monnier, B. Vila, Anne Bousquet-Mélou, B. Prévosto, C. Fernandez. Fertilization and allelopathy modify Pinus halepensis saplings crown acclimation to shade. Trees - Structure and Function, 2011, 25 (3), p. 497 - p. 507. hal-00637640

HAL Id: hal-00637640
https://hal.science/hal-00637640

Submitted on 2 Nov 2011

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Fertilization and allelopathy modify *Pinus halepensis* saplings crown acclimation to shade

Yogan Monnier[1, 2] · Bruno Vila[1] · Nicolas Montes[1] · Anne Bousquet-Mélou[1] · Bernard Prévosto[2] · Catherine Fernandez[1]

(1) Institut Méditerranéen d'Ecologie et de Paléoécologie (IMEP, UMR CNRS 6116), Aix-Marseille Université, Centre St-Charles, 3 place Victor Hugo, 13331 Marseille cedex 03

(2) CEMAGREF, UR EMAX, 3275 Route de Cézanne CS 40061, 13182 Aix en Provence Cedex 5

corresponding author : Yogan Monnier

e-mail : yogan.monnier@yahoo.fr

tel : 04-88-57-69-74 Fax : 04-91-10-85-40

Abstract

Pinus halepensis Mill. is a Mediterranean pioneer forest species with shade intolerance features. The purpose of this study is to better understand how stand fertility and allelopathic properties of adult trees influence shade acclimation of saplings. Crown growth and morphological plasticity were studied under different light, fertilization, and allelopathic conditions in a nursery experiment. We tested whether shade-acclimation capacity increases with fertilization, and is affected by autotoxicity due to pine leachates. We examined stem diameter, and crown characteristics (length, width, shape and density) in a factorial experiment with two levels for each tested factor: light (full and 20 % reduced light), fertilization (low and high rate of NPK fertilizer) and allelopathy (control and allelopathic leachates uptake). In our study, shading induced a significantly higher crown length, width and surface. Fertilization strongly increased crown length and vertical expended crown shape (the ratio crown length/crown width). Leachates uptake reduced crown length and density, highlighting an autotoxicity phenomenon. We concluded that *P. halepensis* saplings presented a shade avoiding syndrome and that the crown shade-acclimation response increased with fertilization but was severely compromised by autotoxicity. We finally discuss the role of fertilization and allelopathy in early *P. halepensis* acclimation ability.

Key words: crown plasticity, growth, light, fertilization, allelopathy, shade-avoidance

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Introduction

Acclimation to shade is achieved by a remarkable variability in many structural features of plants including biomass allocation, physiological and morphological changes from leaf to whole plant scale (Delagrange et al. 2004; Givnish 1988; Kennedy et al. 2007; Messier and Nikinmaa 2000; Portsmuth and Niinemets 2007; Wang et al. 2006). At crown-level, several morphological changes are involved in the structural acclimation to the prevailing light environment. Plants exposed to high irradiance are frequently subjected to photoinhibition particularly under adverse conditions (Long et al. 1994) as in arid or Mediterranean-type environments. In this situation, plants exhibit a strategy based on the avoidance of excessive irradiance by structural features that reduce the leaf area directly exposed to the sun (Pearcy et al. 2005; Valladares and Pearcy 1998). This plastic response leads to foliage aggregation, highly branching and "bushy" growth form (Ali and Kikuzawa 2005; Shukla and Ramakrishnan 1986). By contrast, when plants grow in dense stands, decreased light availability leads plants to follow two principal strategies: shade tolerance and shade avoidance (Grime 1979; Henry and Aarssen 1997). "Shade-avoidance" means that a plant grown under low irradiance may maximize future light interception by a strong vertical growth (King 1990). This phenomenon involves a highly plastic response with accelerated extension growth, strong elongation of internode and petiole, and a strengthened apical dominance among other processes (Grime 1979; Smith and Whitelam 1997). All these morphological adjustments correspond to the concept of 'foraging for light' (Ballare et al. 1997), and result from modification of light quality strongly related to decrease of light quantity (Pecot et al. 2005). The proximity of neighbouring plants is detected by both biogenic volatile organic compounds and light receptors (sensing red and far-red light ratio and blue light), then shade avoidance responses occurre with the involvement of phytohormones (Franklin 2008; Kegge and Pierik 2010; Pierik et al. 2004; Stamm and Kumar 2010).

The "shade avoiders" are commonly ruderal herbs and pioneer tree species present in early to intermediate stage of succession, where the probability of encountering high irradiance with vertical growth is still reasonably high (Henry and Aarssen 1997; Smith 1982). Hence, emerging seedlings of early successional species show a high elongation rate and a strong shade avoidance response to weak proximity signals, in order to rapidly overtop their neighbours and colonize canopy gaps (Gilbert et al. 2001).

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In this study we focus on a Mediterranean pioneer forest species, *Pinus halepensis* Mill. with intolerant-shade features (Puértolas et al. 2009; Zavala et al. 2000) allowing high growth rate under high light conditions. *P. halepensis* naturally regenerates within disturbed and relative open habitats, such as forest clearings, burned areas and abandoned agricultural lands (Buhk et al. 2006). In developing forests, *P. halepensis* predominates as an early recruit in secondary vegetation succession leading to monospecific dense stands where natural regeneration is absent or difficult (Prévosto and Ripert 2008). Causes of regeneration failure in these fire-free stands have been much less widely studied than post-fire regeneration. Light plays an important role in recruitment and growth beneath tree canopy for shade intolerant species like *P. Halepensis* (Zavala et al. 2000). However, *P. halepensis* growth responses to light availability during regeneration are still not well-defined. While Thanos (2000) reports a positive influence of light on germination, some authors observe that light availability does not have any effect on either germination (Broncano et al. 1998) or early seedling development measured a few days after germination (Fernandez et al. 2008). Broncano et al. (1998) noted similar growth rates (growth was evaluated through a volume index) under shaded (10 % full sunlight) compared to unshaded conditions on 8-month old *P. halepensis* saplings, while saplings reacted to shading by increasing elongation (stem height per stem basal diameter). In order to clarify the effects of irradiance on early pine aerial development, we analyzed the response of some crown structural parameters to shade.

In Mediterranean environments, in addition to water availability, soil nutrient content is also a frequent limiting factor for plant development (Sardans et al. 2005) including *P. halepensis* (Sardans et al. 2004). Soil nutrient availability can directly influence growth and biomass allocation, altering structural development of aerial parts of the plant (Ingestad and Agren 1991). More precisely, nutrient uptake strongly affects shoot length growth and foliar area production (Niinemets et al. 2002), changing acclimation capacity to shade (Coomes and Grubb 2000; Kobe 2006). In understory conditions soil nutrients were shown to exert a lower influence on growth, emphasizing the importance of considering light acclimation combined with nutrient effects (Broncano et al. 1998; Kobe 2006; Kranabetter and Simard 2008; Portsmuth 2006).

More recently, allelopathy was found to be implicated in renewal of forest stands (Mallik 2008). *P. halepensis* is known to release allelopathic compounds (Fernandez et al. 2006) with autotoxic effects affecting its own seedlings' initial growth (Fernandez et al. 2008). Autotoxicity may have important ecological implications such as the reduction of overcrowding and intraspecific competition for light water and nutrients (Singh et al. 1999). In our case, autotoxicity processes may be consistent with the pioneer and fast-expensive strategy of *P. halepensis*, avoiding long-term establishment at the same place and favouring an escape-strategy. Hence

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allelopathic compounds (mainly phenolic acids) could influence aerial development of *P. halepensis* and impact light acclimation of saplings beneath the forest canopy. The allelopathic compounds interfere with seedling growth by causing plant growth inhibition, and nitrogen (N) immobilization (Inderjit et al. 2004; Inderjit 2006; Northup et al. 1995). Moreover, allelochemicals can affect development of roots tissue (Schenk 2006), leading to a decrease in nutrient uptake by the plant (Inderjit and Duke 2003; Yamasaki et al. 1998). *P. halepensis* leachates may therefore directly interfere with seedling acclimation capacity through the release of organic compounds and indirectly through soil nitrogen immobilization and/or decreasing uptake rates.

The objectives of this study were to better understand how stands fertility and allelopathic properties of adult trees influence shade acclimation of regenerating subjects. Both morphological and growth parameters (i.e., stem diameter, crown dimensions, crown shape, and foliar density) were studied under different light, fertilization, and allelopathic conditions in a nursery experiment. We tested two hypotheses: (1) does shade-acclimation capacities increase with fertilization and (2) does leachates of *P. halepensis* have a negative impact on shade acclimation of *P. halepensis* saplings, due to allelopathic properties?

Materials and methods

Experimental design and treatment application

The experiment was conducted in the administrative plant nursery of “Les Milles” (Departmental Directorate of Agriculture and Forestry of the Bouches-du-Rhône), in Aix-en-Provence, Southern France. The seeds were harvested in a Mediterranean pinewood, in the Luberon Massif. In May 2006, the experiment was established with 1-year-old nursery-grown *P. halepensis* seedlings of uniform size germinated and grown on an irrigated and fertilized artificial soil. Seedlings were transplanted one per pot, in 10 l plastic pots filled with a draining substrate made of 25% calcareous sand, 25% siliceous sand, and 50% mineral soil from Provence Granulat quarry. This substrate was chosen in order to prevent allelopathic features of an organic substrate. The seedlings were grown outdoors during one year and regularly drip irrigated to prevent water stress. The factorial experimental design included three factors: (i) light availability, (ii) nutrient availability and (iii) presence of

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allelopathic compounds. For light availability, half of the pots were in full sunlight (high light, L+), and the other half under a shade cloth (EMIS france, ref. 1077) so as to reproduce light conditions under a dense pine wood canopy (Broncano et al. 1998; Maestre and Cortina 2004). Shade cloth was placed 2.5 m above ground to cover the entire plot area, and four additional net pieces on all plots orientations were placed vertically. Shade cloth transmittance, R:FR ratio and blue light describe the light conditions under the shading treatment. Transmittance and light quality, both under the shade and in the sun, were measured with a spectrometer (SpectrcoVio C5210-C5220, Lab. Junior kit-SV2100, Korea Materials & Analysis Corp. K-MAC). We measured the shade cloth light transmittance of total light spectra, defined as the ratio of photon flux density (PFD) beneath the shade cloth to the PFD in full sunlight. Transmittance below the shading nets was 23%. Light quality was modified with shade cloth. Following Gasque and Garcia (2004) the red to far red ratio was measured at 660/730 nm respectively. R:FR was 1.54 for full light treatment (HL) and 1.11 for low light treatment (LL) similarly to values observed under *Pinus halepensis* cover (Gasque and García-Fayos 2004). Following Aphalo and Lehto (1997) photon flux density of blue light was measured at 450nm. Photon flux density of blue light under the shade cloth was 22% of the one measured under full light conditions. With regard to fertilization, two rates of fertilizer were supplied once by week with irrigation; the first composed of 75mg N, 8.2mg P and 20.74mg K (low fertilization, F-) and the second five times higher (high fertilization F+). Such process and fertilization rates are already used in greenhouse experiment with Aleppo pine saplings (Diaz et al. 2010). Finally, the allelopathic factor was tested through the use of leachates (Fernandez et al. 2008). Monthly, 25 kg of *P. halepensis* needles were harvested in a *P. halepensis* forest (circa 20 years old pine) near Aix-en-Provence, on the Arbois plateau. Needles were macerated in 250 l of water during 48 hours, in dark conditions (Yu et al. 2003) in order to obtain leachates at 10% fresh weight, corresponding at 5 % dry weight (Fernandez et al. 2006). In this way, 0.5 l of leachates was brought to half the pots (A+), while water was brought to the other half (A-).

Each treatment results from the combination of the two levels of the three factors (L, F, A). The resulting 8 treatments each contained 20 pots (=replicates) except the treatments with the lowest level of fertilizer with only 10 plants leading to a total of 120 pots for the whole experiment. Treatments were arranged in blocks, four under the shade cloth and four in full light, in 50 m². Stem diameter, crown dimensions, crown shape and foliar density were used as response variables to analyse growth and morphological plasticity.

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142 **Growth measurements and crown descriptors**

143 Plasticity and crown morphological parameters were estimated on two-years old *P. halepensis* saplings using an
144 original and non-destructive method based on digital image analysis, previously tested on *P. halepensis* by
145 Montès et al. (2004).

146 The sampling procedure consisted in taking photographs of each individual, in March 2007, two years after the
147 beginning of the experiment. Because of a possible axial asymmetry of saplings, two pictures were taken from
148 orthogonal viewpoints, using a 3 megapixel digital camera. Using an image analysis software (Adobe®
149 Photoshop® CS2), photographs were then converted in three luminance levels (black for the surface area of the
150 sapling, grey for the outline and white for background of the image). For each sapling, the mean of the two
151 orthogonal views provide d a basis for deducing, from the number of pixels of each category, crown length (CL),
152 crown width (CW), surface area of the crown (CS) and crown outline (CO) (Fig. 1). Total height was not
153 considered as this dimension was very close to crown length due to branch insertion starting almost at stem base
154 for all the saplings. These parameters combined with stem diameter measurements (February 2007) were used to
155 make morphological and architectural trait descriptors: elongation (CL/D), crown shape (CL/CW), and crown
156 density (CS/CO^2) which is an isometric indicator of crown openness. These plant parameters were compared for
157 each treatment.

158

159 **Statistical analysis**

160 Multi-way ANOVA was used to analyze stem diameter, crown length, crown width, elongation, crown shape,
161 crown surface and crown density as dependent variables, with light, fertilization and allelopathy levels, as the
162 main factors. In case of significant interactions, one-way ANOVA was used to test differences. Afterwards, a
163 Tukey test ($P<0.05$) was used to test differences between mean values of treatments. Normality and
164 homoscedasticity were tested by Shapiro-Wilks' and Bartlett's tests, respectively. Due to violation of ANOVA
165 assumptions for treatment at low fertilization level with no leachates uptake, the effect of the light factor on
166 sapling growth variables was determined after a Kruskall–Wallis test. Allometric relationships between crown
167 length, crown surface and crown density were determined through regressions. Changes in allocation pattern
168 between treatments were assessed by comparison of the slopes and intercepts of regression lines using ANOVA.
169 All tests were performed using Statgraphics Centurion XV (StatPoint, Inc., USA) software.

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Results

All morphological parameters were significantly influenced by light, in interaction with fertilization and macerates (ANOVA, $P<0.0001$; Table 1).

Effects of shade on aerial development and allometric relations

Crown length, elongation, crown width, vertical expended crown shape, and crown surface increased under low light (L-) conditions ($P < 0.001$) (Fig. 2). Conversely, stem diameter and crown density decreased under low light conditions but the difference was only significant for crown density ($P = 0.059$ for stem diameter). Under high light (L+) and low light (L-) conditions crown surface increased with crown length with a strongly significant dependence ($P <0.005$; $R^2 = 0.29$ and $P = 0.001$; $R^2 = 0.80$ respectively; Fig. 3). The level of irradiance did not influence the relationship between crown surface and crown length (differences between regression slopes, $P = 0.139$). Crown density was significantly higher in L+ than in L- ($P <0.001$).

Fertilization effects in interaction with light (without allelopathy).

In treatments without allelopathy, there were significant interactions between light and fertilization effects on crown length, elongation, crown shape, crown surface ($P < 0.001$). In L+ conditions, no differences between the two fertilization levels for all parameters were noted whereas under L- conditions, higher fertilization led to higher values ($P < 0.001$, Tukey test) (Fig. 4). In contrast, crown density and width were never significantly affected by fertilization level ($P >0.05$). With regard to interaction, the increase observed for crown length, elongation, shape surface and width under shading conditions was much greater when the level of fertilization was high. High level of fertilization thus enables pines to have a more pronounced growth effect in low light and hence be more plastic.

Influences of allelopathic leachates in interaction with fertilization in low light conditions

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There were significant interactions between leachates and fertilization effects on crown length, crown surface and crown density ($P < 0.001$). The increase of crown length, elongation shape surface and density due to high fertilisation was totally cancelled when allelopathic compounds were present (Fig. 5). For the lowest fertilization level, growth is low and leachates supply did not affect crown length and crown surface, but decreased crown density ($P = 0.007$, Tukey test; Fig. 5). With high rate of fertilization, growth is high and leachates did not affect crown density but decreased crown length, crown surface, and vertical expended crown shape ($P < 0.001$, Tukey test). Our results showed negative effects of leachates on aerial development, except on crown width.

Discussion

Morphological effects of shade acclimation

Shade acclimation has first been studied with standard level of nutrients (F-) and without leachates (A-). In this treatment, all morphological parameters of *P. halepensis* were positively and significantly influenced by shade except stem diameter, which decreased but not significantly. This negative impact of shade on stem diameter has been previously observed by Jose et al. (2003) on *Pinus palustris* Mill. seedlings, a shade intolerant pine species (Knapp et al. 2008). Moreover, Puertolas et al. (2009) reported similar trend on *P. halepensis* seedlings. In our study, the non-significant light influence on diameter is certainly due to the early age of saplings, the short-term length of the experiment and delayed response of stem increment to the treatment. Crown length (CL), crown elongation (CL/D), and crown shape (CL/CW) significantly increased in shade treatment. We found greater crown length in shade than under high light conditions which is consistent with previous studies where shade intolerant species showed similar or higher height growth in lower light availability during the first seasons (Chen and Klinka 1998; Groninger et al. 1996; Kennedy et al. 2007). Similar height variations have also been measured for *P. halepensis* (Puértolas et al. 2009) and for another early successional species, *Pinus sylvestris* L., which responded to shade with an increase in stem height (Dehlin et al. 2004). Enhancement of height growth in shade for light-demanding species could reflect a strategy of light-seeking by species adapted to the exploitation of high-resource environments (Walters et al. 1993). This growth strategy is common for shade-intolerant species to avoid shading by neighbouring vegetation (Ballare 1999; Grime 1979). In addition to the decrease of light quantity, neighbour plant canopy can also strongly modify light quality with a strong reduction of blue and

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red light absorbed by photosynthetic pigments and an increase of ethylene levels (Kegge and Pierik 2010; Pecot et al. 2005). The low R:FR, Blue light depression and a stimulated foliar ethylene emissions induce shade avoidance responses, such as enhanced stem elongation (Franklin 2008; Kegge and Pierik 2010; Pierik et al. 2004). This "shade avoidance" strategy involves maximizing light interception through architectural traits that contribute to a competitive advantage by strong vertical growth (Henry and Aarssen 1997; King 1990; Smith and Brewer 1994). As demonstrated by our results, the elongation (CL/CW) increase with light quantity decrease for *P. halepensis*., which has also been previously mentioned by Broncano et al. (1998) and for other species (Chen and Klinka 1998; Kennedy et al. 2007). This finding emphasizes the stronger shade avoidance response (Smith and Whitelam 1997). In addition to shade cloth effects on light quality, both density of plantation and proximity of neighbours may play a role by stimulating the shade avoidance signals and stem elongation (Anten et al. 2005; Pierik et al. 2004).

We also found crown width enhancement with decreasing light, which may be considered to be advantageous for foraging for light patches along horizontal gradients under forest canopies (Chen et al. 1996; Hutchings and Dekroon 1994). Under limited light conditions, a growth strategy that promotes lateral crown expansion might be favourable in enabling saplings to minimize self-shading and to improve light interception (Givnish 1988; Sterck et al. 2003). In our study, saplings have higher ratios of crown length to crown diameter in shade compared with higher light conditions, indicating that crowns shape were proportionally more vertically expanded in shade than in higher light. Such results differ from the positive relationship between this ratio and light availability generally observed in many studies for light-demanding tree species (Beaudet and Messier 1998; Chen et al. 1996; Klinka et al. 1992). These differences can be imputed to the strong interactions between light intensity and tree height, this last factor being in our case a strong determinant of architectural responses variability. Although shade avoiding syndrome increases both crown length and crown diameter, the former increases more than the latter, therefore saplings showed a more vertical expanded crown shape in shade. The crown surface increased while crown density decreased in shade only indicating a higher crown openness under shade conditions. Under L+ conditions, crown density was higher, indicating a higher proportion of hidden biomass within the crown, while in low light, most of the branching becomes apparent which enhances, with the same biomass allocation, photosynthetic capabilities. Results of crown surface and density analyses showed that high irradiance leads seedlings of shade-intolerant species to adopt a 'bushy' form whereas under shade conditions the crowns are more slender and vertically extended to prevent self-shading (Henry and Aarssen 1997; Henry and Aarssen 2001; King 1990; Shukla and Ramakrishnan 1986; Steingraeber et al. 1979).

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253

254 **Fertilization effects on light acclimation**

255 Fertilization has frequently been described as a factor that can change allocation and aerial development in
256 interaction with light availability (Coomes and Grubb 2000; Grubb et al. 1996; Kobe 2006; Portsmuth and
257 Niinemets 2007). It has been suggested that light-dependent growth and plasticity depend on nutrient availability
258 (Burton and Bazzaz 1995; Lortie and Aarssen 1996; Portsmuth and Niinemets 2007). In our study, for several
259 parameters involved in crown shade acclimation, fertilization effect differed largely in light and shade
260 conditions. In L+, nutrient uptake had no effect on morphological parameters, in line with the results of
261 Portsmuth and Niinemets (2007) on others shade-intolerant species (given nevertheless that they reported results
262 on growth rate and not morphological parameters). Conversely, under low light conditions, our results showed
263 that architectural parameters (except crown width and crown density) were strongly influenced by nutrients in
264 contrast with general conclusions of Portsmuth and Niinemets (2007) based on works of Poorter and Nagel
265 (2000). The latter have found that nutrient requirement is higher and growth is more responsive to nutrients at
266 higher irradiance. To explain these results, Poorter and Nagel (2000) noted that higher irradiance implies a
267 higher rate of photosynthesis per unit leaf mass, but also a higher rate of water uptake due to increased
268 transpiration and a higher nutrient uptake because growth is stimulated. They showed, in accordance with the
269 functional equilibrium model, that biomass was more preferentially allocated to plant parts related to limited
270 resource. Hence, the fraction of biomass allocated to roots increased proportionally with irradiance at non-
271 limited nutrient level. In the same way, under L- conditions, nutrient increase improved primarily the fraction of
272 biomass invested in the stems, and changed the morphological development of aboveground parts of the plant as
273 detected in this study for crown descriptors. In our study, the increase observed for crown length, elongation,
274 shape surface and width in shading conditions versus high light conditions was much greater when nutrient
275 availability was high. High level of fertilization thus allows pines to have a more pronounced growth effect in
276 low light and therefore be more plastic. Comparable variations in aerial components of pioneer species have
277 been observed in *P. sylvestris* (de la Rosa et al. 1984). Increased aerial growth response to shade under more
278 fertile conditions implies a competitive advantage over neighbouring plants through pre-emptive capture of light
279 resources, especially under high-fertilization conditions, where competition from other seedlings is likely to be
280 intense.

281

282 **Interactions with allelopathic phenomenon**

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Major allelopathic effects on crown development were conspicuous under shade conditions in interaction with nutrient availability. At lower rate of fertilization, leachates supply only reduced crown density whereas in high fertilization, leachates supply reduced crown length, surface and elongation ratio (H/D). Such inhibition of crown development may be caused by phenolic acids by (1) nitrogen immobilization (Inderjit et al. 2004; Inderjit 2006; Northup et al. 1995), (2) root and vegetative tissue degradation by cytotoxicity, (Schenk 2006) and/or a complex process of interactions with microorganisms and mycorrhizae. Some authors reported that growth inhibitor effects caused by leachates supply were eliminated by addition of fertilizers (Einhellig 1999; Inderjit 2006). Similarly to Inderjit et al. (2004), we noted that the main phytotoxic effects occurred at high level of fertilization. Nitrogen addition could increase microbial populations that could influence qualitative and quantitative availability of phenolic compounds (Inderjit et al. 2004). These phenolic compounds can form recalcitrant complexes with proteins and modify nutrient availability (Hättenschwiler and Vitousek 2000) which could lead to a detrimental influence on sapling growth. It should be noted that many phenolic compounds are present in *P. halepensis* leachates (Fernandez et al. 2009). Interactions with ectomycorrhizae may also explain the absence of effect of leachates supply at low soil fertility. While a high fertilization had been described to be nefast for *P. halepensis* ectomycorrhizae, at low fertilization level ectomycorrhizae can develop (Diaz et al. 2010) and may detoxify phenolic compounds like described on different species (Zeng and Mallik 2006). To our knowledge, no study looked at plant crown architectural response to allelopathy. Crown length inhibition observed in this study under F+ conditions led to a decrease of elongation and vertical expanded crown shape, modifying strongly crown morphology and seedlings' acclimation ability to shade, confirmed by crown surface decrease. In fact, plastic adjustments of crown morphology due to higher fertilization are cancelled with leachates supply. Hence, allelopathy, and more precisely autotoxicity, severely affected *P. halepensis* saplings' acclimation to low irradiance during the first years. Autotoxicity in *P. halepensis* has already been noted in germination and initial growth (10-days-old seedlings) under laboratory conditions (Fernandez et al. 2008). With our experiment, we confirmed the autotoxic effects of *P. halepensis* needles leachates on sapling development. This study highlights the negative effects of allelopathy on *P. halepensis* saplings acclimation to shade and complex interactions with fertility conditions. By affecting height growth in non-limited soil fertility conditions, autotoxicity could have an impact on saplings acclimation to limited light beneath the canopy, and potentially on regeneration of *P. halepensis* stands.

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Acknowledgments This study was funded by the CNRS within the framework of the Zone Atelier "Arrière-pays Méditerranéen". We thank the staff of the administrative plant nursery of Les Milles (Departmental Directorate of Agriculture and Forestry of the Bouches-du-Rhône, France), particularly Patrice Brahic for his useful comments and all the staff for technical assistance. We would also like to thank Michal Paul for proofreading the english, Nicolas Faivre and Chrisinte Scoffoni for their comments that improve the manuscript, and Sylvie Dupouyet, Stéphane Greff, Caroline Lecareux, Céline Pernin and the DFCV team who assisted us with collection of needles and for leachates confection and watering.

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Tables and Figures caption

Table 1 ANOVA results for stem diameter (D), crown length (CL), crown elongation (CL/D), crown shape (CL/CW), crown width (CW), crown surface (CS) and crown density (CD) as a function of light (L), fertilization (F) and allelopathy (A) and their interactions. Significant effects ($\alpha = 0.05$) are in bold

Fig 1 Schematic representation of a sapling, and the measured variables: stem diameter (D), crown length (CL), crown width (CW), crown surface (CS), crown outline (CO)

Fig 2 Means and standard errors for crown length (CL), crown elongation (CL/D), crown width (CW), crown shape (CL/CW), crown surface (S) and crown density (CD) in high light (L+) and low light (L-) are presented only for the low ferrtilization (F-) and without allelopathy (A-) . Contrasting letters refer to significant differences (post hoc Tukey test $P< 0.05$)

Fig 3 Relationship between crown surface (CS) and crown length (CL) as a function of light level. The responses of surface to height have been compared in high light (L+) and low light (L-) treatment

Fig 4 Interactions, means and standard errors for light and fertilization effects on crown length (CL), crown elongation (CL/D), crown width (CW), crown shape (CL/CW), crown surface (S) and crown density (CD) in treatments without allelopathy (A-). Contrasting letters refer to significant differences (Tukey test $P< 0.05$)

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508 **Fig 5** Interactions, means and standard errors for allelopathic and fertilization effects on crown length (CL),

509 crown elongation (CL/D), crown width (CW), crown shape (CL/CW), crown surface (S) and crown density (CD) in

510 low light treatments (L-). Contrasting letters refer to significant differences (Tukey test $P< 0.05$)

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	Stem diameter (D)		**Crown length (CL)**		**Crown width (CW)**		**Elongation (CL/D)**		**Crown shape (CL/CW)**		**Crown surface (CS)**		**Crown Density (CS/CO²)**	
Source	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Light (L)	10.00	**0.002**	148.98	**0 .000**	104.36	**0 .000**	178.82	**0 .000**	13.25	**0.000**	106.81	**0 .000**	233.84	**0 .000**
Fertiliser (F)	0.71	ns	23.57	**0 .000**	2.72	ns	14.22	**0.001**	36.33	**0 .000**	0.56	ns	5.89	**0.039**
Allelopathy (A)	9.96	**0.002**	2.36	ns	4.89	**0.029**	0.07	ns	0.41	ns	0.36	ns	8.58	**0.008**
Interactions														
LxF	0.57	ns	0.15	ns	10.79	**0.001**	0.01	ns	5.58	**0.020**	7.54	**0.007**	0.40	ns
LxA	1.89	ns	22.16	**0 .000**	2.81	ns	12.5	**0.001**	35.02	**0 .000**	6.45	**0.013**	2.47	ns
FxA	4.83	**0.030**	0.73	ns	1.91	ns	3.12	ns	1.07	ns	4.69	**0.032**	1.50	ns
LxFxA	15.18	**0.000**	47.7	**0 .000**	0.79	ns	18.01	**0 .000**	35.13	**0 .000**	18.71	**0 .000**	12.17	**0.006**

512 **Table 1**

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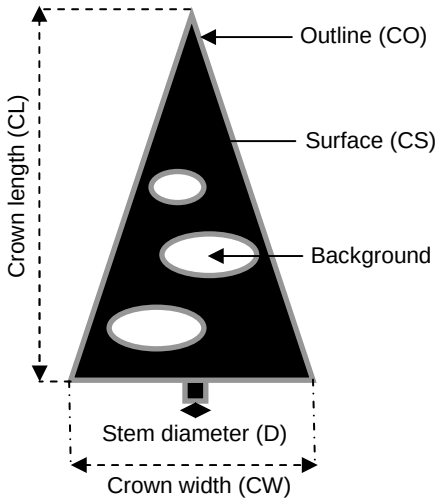

Fig. 1

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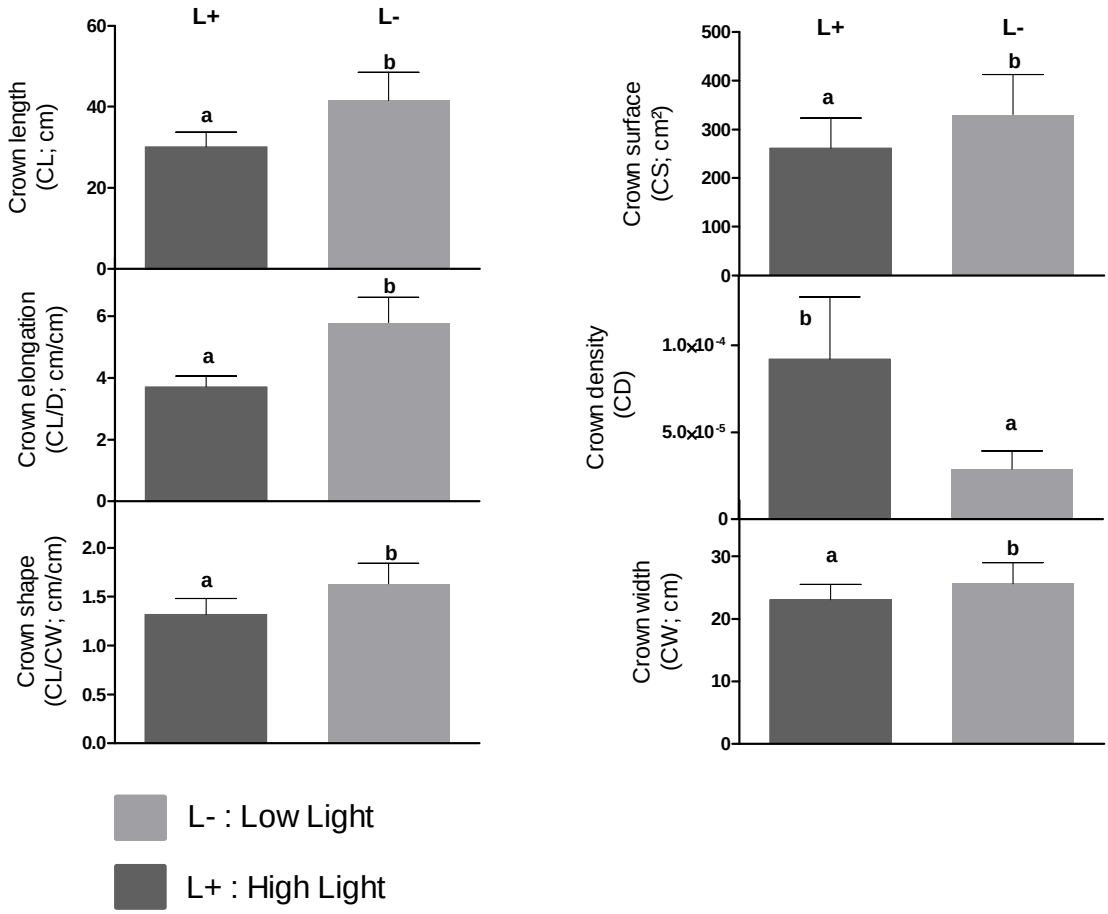

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531

532 **Fig. 2**

533

Monnier Y., Vila B., Montes N., Bousquet-Melou A., Prevosto B. and Fernandez C. (2011) Fertilization and allelopathy modify Pinus halepensis saplings crown acclimation to shade, Trees-Structure and Function, 25, 3, 497-507.
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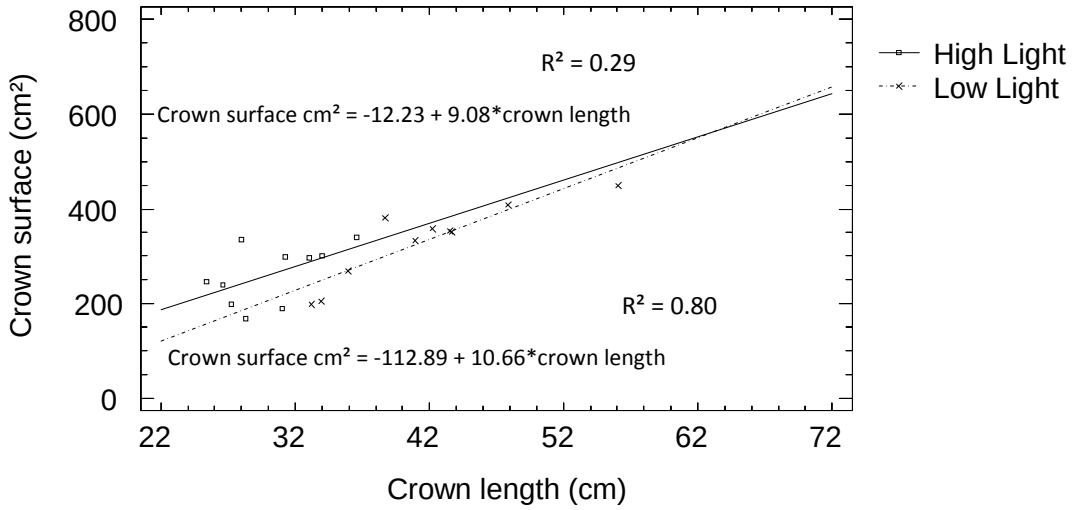

535

536 **Fig. 3**

537

Monnier Y., Vila B., Montes N., Bousquet-Melou A., Prevosto B. and Fernandez C. (2011) Fertilization and allelopathy modify Pinus halepensis saplings crown acclimation to shade, Trees-Structure and Function, 25, 3, 497-507.
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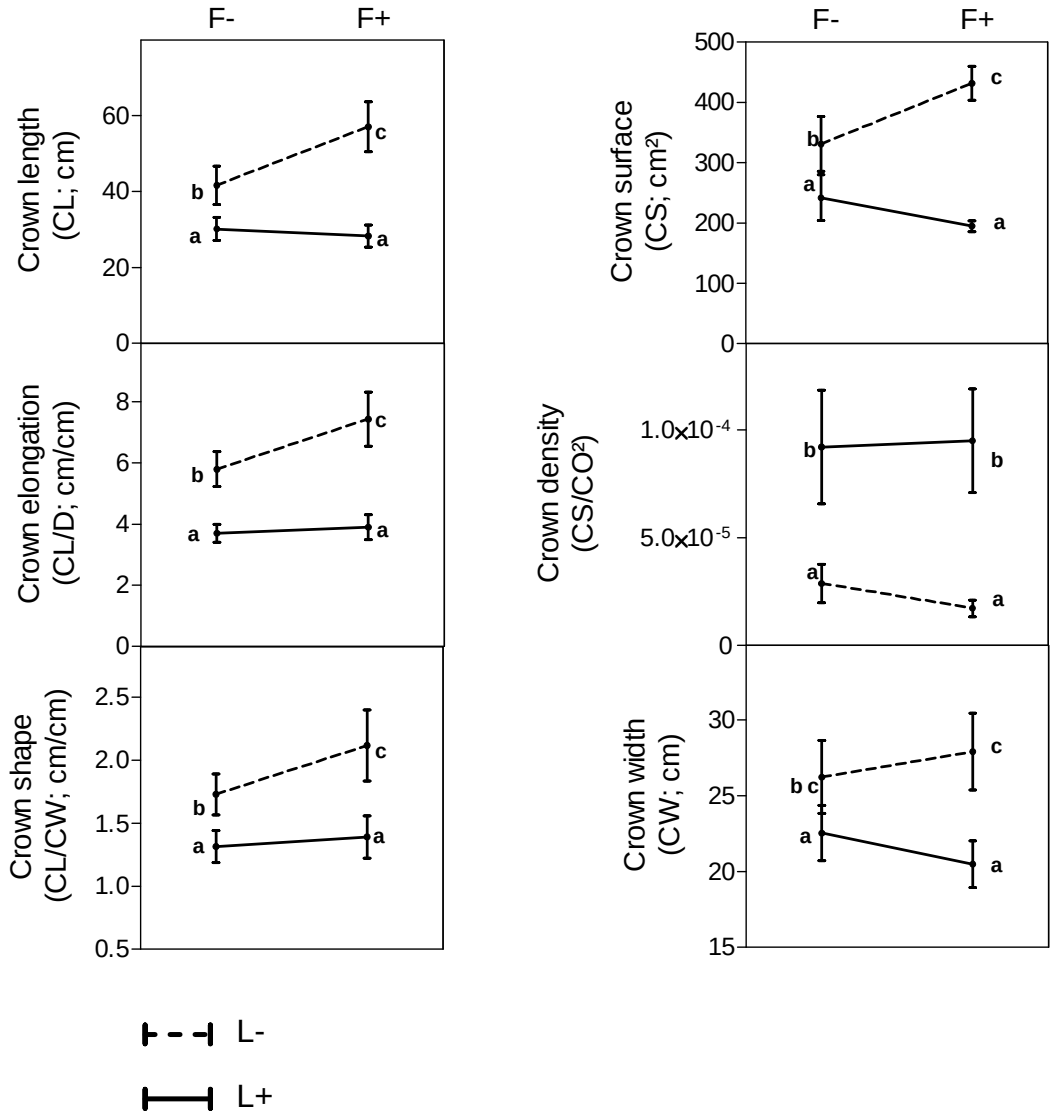

538

539 **Fig. 4**

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Monnier Y., Vila B., Montes N., Bousquet-Melou A., Prevosto B. and Fernandez C. (2011) Fertilization and allelopathy modify Pinus halepensis saplings crown acclimation to shade, Trees-Structure and Function, 25, 3, 497-507.
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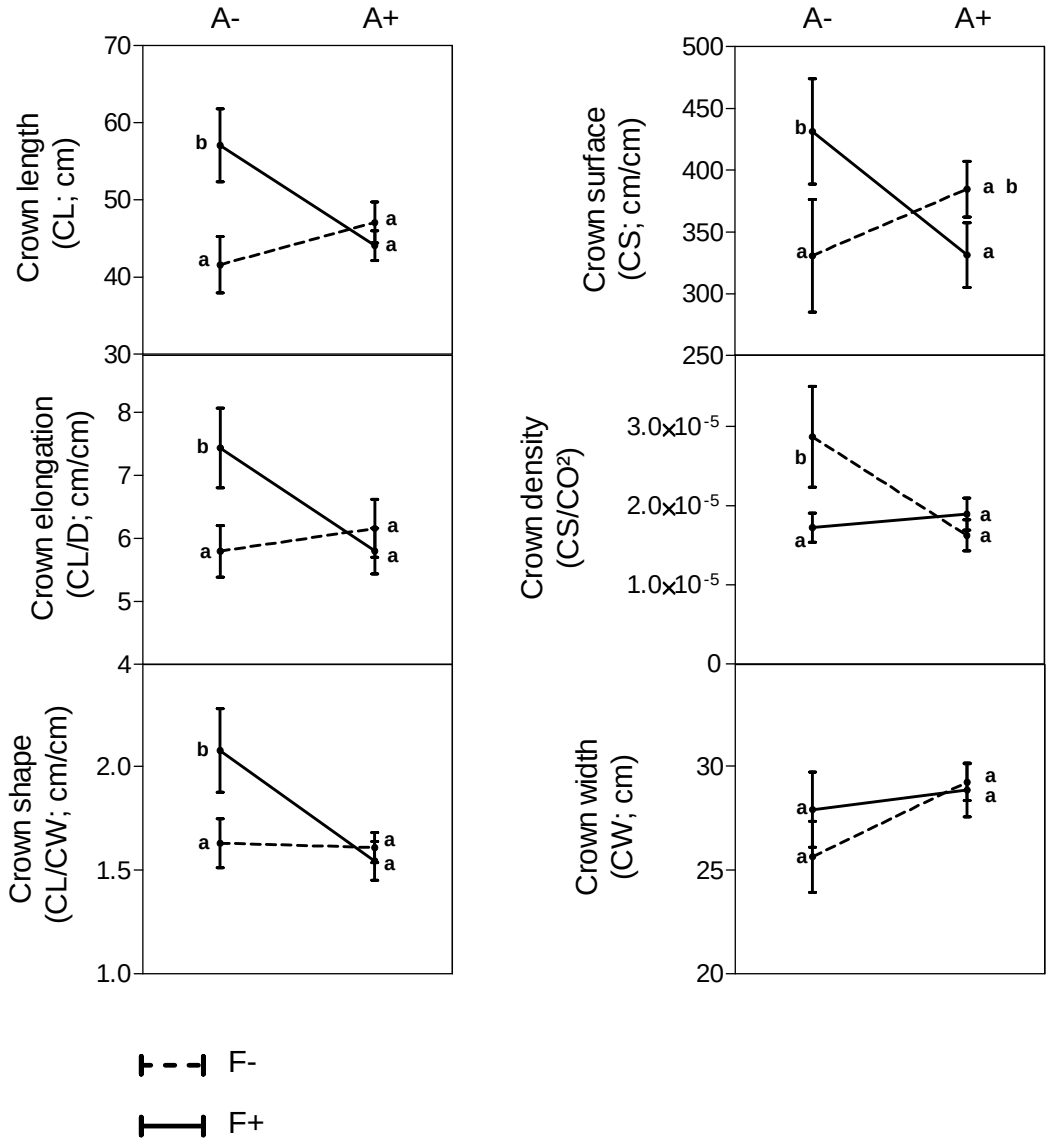

Fig. 5