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Assessing differences in water- and light-use efficiency in two related fir species under contrasting light conditions: gas exchange instantaneous rates *vs.* integrated C fixation and water loss

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ABSTRACT

In this work we examined the differences between two related fir species (*Abies pinsapo* Boiss. and *A. alba* Mill.) with respect to their ability to manage light as a key resource, considering both their C fixation capacity and the “loss” of water through stomata in response to different light regimes. Thus, we carried out three experiments where we measured instantaneous gas exchange rates (net photosynthesis, stomatal conductance to water) under different light conditions. In the first experiment, individuals from both species were subjected to a moderate but constant level of irradiance. In the second one, every individual received a certain light dose through several periods of time characterized by different levels of constant irradiance. Finally, in the third experiment, dark periods of increasing duration were imposed to plants at steady-state of their gas exchange response, under the same level of irradiance employed in the first experiment. We used the time record of the data collected to calculate the total amount of C fixed and the water “lost” in each situation. Both species differed in their intrinsic ability for C fixation and avoidance of water loss, but showed a similar response with respect to the ratio between C fixed and water lost under different circumstances, what suggests that regulation of gas exchange in both species tends to keep this ratio constant under varying light conditions, playing light a critical role as an environmental signal for maximizing water use efficiency.

1. Introduction

Light is perhaps the most heterogeneous factor in time and space of all affecting plant performance (Pearcy, 1999). And so, the light environment experienced by an adult tree from the canopy is quite different from that under evergreen canopies, where long periods of diffuse light are interrupted unpredictably by bright sunflecks and the opening of small gaps or clearings (Pearcy, 1983; Valladares et al., 1997; Lei and Lechowicz, 1998), which alter noticeably the level of irradiance perceived by every individual in the understory. Because of that, it is crucial for tree species to be able to respond satisfactorily to those changes in light supply that can be experienced on different temporal and spatial scales throughout their life cycles.

Of particular attention should be the case of the Mediterranean forests, since the importance of the role played by light supply in these systems has been traditionally underestimated (Valladares et al., 2004), probably because adult trees forming their canopies can receive substantially higher levels of irradiance along the year in comparison to other forest systems. However, light supply in their understory can be sometimes as scarce as in tropical or temperate forests, and their typical temporal and spatial heterogeneity also influences this light supply significantly (Valladares et al., 2004). So, it is sensible to explore to which extent this light heterogeneity can cause changes in the way tree species manage this key resource, especially in comparison to other systems characterized by more homogeneous levels of irradiance.

In this work, we examined the response to different light regimes shown by two different circum-Mediterranean firs that naturally occur in the Iberian Peninsula (López and Amaral, 1986), *Abies pinsapo* Boiss. and *A. alba* Mill. These two species are part of the neo-Mediterranean vegetation, whose origin took place after the immigration and speciation processes that occurred during the establishment of the Mediterranean climate in the region (Scarascia-Mugnozza et al., 2000). In fact, both species seem to derive from a widely-distributed common ancestor (Meyen, 1987;

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Palamarev, 1989; Scaltsoyiannes et al., 1999), which took shelter in mountain ranges around the Mediterranean basin during the last glaciations (Bennett et al., 1991; Tzedakis et al., 2002; Willis and Niklas, 2004). Successive migration and fragmentation processes in progressively smaller and more isolated populations contributed to the diversification and zoning of this ancestral species (Farjon and Rushforth, 1989), what originated the different circum-Mediterranean fir species existing nowadays.

A. pinsapo is a relict, endemic tree which grows in small and isolated populations between 1000 and 1800 m.a.s.l. in N-facing, steep slopes and ravines of some coastal mountain ranges of southern Spain. Although its forests habitually receive a large amount of total annual precipitation (over 1000 mm), the species is clearly subjected to typical Mediterranean climatic conditions, with *ca.* 80% of all that precipitation falling between October and May, besides a long and severe summer drought and great inter-annual variations in the rainfall pattern. For its part, silver fir (*A. alba*), the most widespread fir species in Europe, appears over a broader geographical range including more than twenty countries (Farjon, 2014), and through a wide range of ecological conditions (Konnert and Bergmann, 1995), forming vast forests in many mountain ranges across Europe, from the East Carpathians to the Pyrenees, and from the Beskids in Poland to the mountains in northern Greece. It preferentially occurs under cool climatic conditions, with low temperature amplitudes and relatively high annual precipitation, finding the most favourable climatic conditions at lower elevation (Robakowski et al., 2004). This species finds its south-western limit in the Pyrenees and in mountain ranges nearby (Oliva and Colinas, 2007; Farjon, 2014), far from natural populations of *A. pinsapo*. These populations are frequently above 1200 m.a.s.l., on highly productive soils, like the bottom of a valley, or in N-NW facing slopes on relatively deep soils (Vigo and Ninot, 1987).

Although both species tend to live under humid bioclimates (Aussenac, 2002), as they rely on high consumption of water resources, populations of both species also suffer a recurrent summer drought, being *A. pinsapo* apparently subjected to it to a greater extent. In this sense, during the speciation process mentioned above, different sets of traits related to water-use efficiency may have been selected in order to confer on these species a better performance under the different water supply conditions they stand. As for the light environment, the remarkable shade tolerance exhibited by *A. alba* (Robakowski et al., 2004) suggests that the levels of incident irradiance experienced by this species must be very low, although this aspect can be modulated by the species' composition of its stands (Robakowski et al., 2004). Besides, it suggests that these levels of irradiance must be noticeably lower than those experienced by natural populations of *A. pinsapo* at its current locations. In this latter species, although it has been described a considerable capacity for surviving under dense canopies (Arista, 1995), it has also been stated the noticeable dependence of natural regeneration processes on gap opening and the increased level of irradiance obtained as a result (Arista, 1995).

Due to all the above, we have performed a set of experiments in order to test if both species differ in their ability to deal with changes in the light dose received, resulting from variations in the levels of incident PAR or the way light supply changes over time. In this sense, we state a double hypothesis: on one hand, we expect to find differences between instantaneous rates and the final effect of reaching and maintaining these rates in time ("time integrated variables"), since gas exchange response when facing changes in light supply conditions is not immediate, existing physical and biochemical mechanisms involved that modulate the induction time, and so, the temporal evolution of this response would be the key to explain findings obtained with both groups of variables. On the other hand, we also expect to find differences between both species in terms of their gas exchange and the total amount of C fixed and water "lost", being these differences probably related to the ecological conditions (water and light supply regimes) these species experience at their current locations.

2. Material and methods

2.1. Plant material

We used 6 year-old juvenile individuals from both *A. pinsapo* and *A. alba* species. *Abies pinsapo* saplings, grown in the tree nursery "La Resinera" (Arenas del Rey, Granada, Spain), were kindly provided by Red de Viveros de Andalucía (Consejería de Medio Ambiente, Junta de Andalucía). These saplings were developed from seeds collected in Sierra de Las Nieves Natural Park (province of Málaga, Spain), where most pinsapo forests are located (3027 ha). *Abies alba* saplings were obtained from a commercial tree nursery (Viveros Star Plant, Breda, Gerona, Spain), which certified their provenance (Pyrenees). Until being used in the experiments, all saplings were kept for over a year at the facilities of the University of Jaén Experimental Garden. They remained outdoors all this time and, during the summer, they were protected from the excess of heat and irradiance by a neutral shade cloth which reduced incident irradiance by a 75% approximately. *A. alba* saplings were maintained in their original 6 L containers, with a 1:1 mixture of forest soil and peat (v:v), while *A. pinsapo* saplings were transferred from the original plastic bags to 5 L plastic pots, filled with a 2:2:0.75 mixture (v:v:v) of sieved and air-dried forest soil, peat and perlite. All of them were suitably watered to avoid great seasonal changes by using sprinkler irrigation twice a day (except on the coldest days of winter, to avoid damages in the roots by frostbite). Besides, we changed their position periodically, to prevent unintended effects derived from that.

2.2. Experimental design

The three experiments were carried out in an *in vivo* growth chamber at the scientific facilities of the University of Jaén. Environmental conditions within the chamber were kept constant all the time, with a mean temperature of about 20–22 °C, an air humidity of 50–60%, and a 12:12 photoperiod. In each experiment, irradiance treatments consisted of a low level of irradiance, of about 30–50 μmol m^{-2} s^{-1} PAR ("low irradiance" hereafter), and a moderate level, *ca.* 350 μmol m^{-2} s^{-1} PAR ("high irradiance"). In both cases, irradiance was supplied by conventional fluorescent lamps. In the low irradiance treatment, incident irradiance was conveniently reduced by interposing several layers of neutral shade cloth. 4–5 individuals per species were randomly assigned to each treatment, where they remained for nine months. Within each treatment, individuals were rotated weekly, to avoid effects derived from their position in the chamber. Although water availability was not included in the experimental design, we monitored soil volumetric water content (SVC) throughout every experiment, to ensure that all individuals were suitably watered. For that, we estimated SVC for each individual with a portable moisture measurement instrument based on the time domain reflectometry method (TDR100, Campbell Scientific, Inc., Logan, Utah, USA). We compensated for increasing evapotranspiration under high irradiance by adjusting irrigation intensity and frequency based on previous trials for each irradiance treatment.

Gas exchange measurements (net photosynthesis and stomatal conductance to water) were carried out by using a portable infrared gas analyser (IRGA) LI-6400 coupled to a LI-6400-05 conifer chamber, all from LI-COR Inc. (Lincoln, Nebraska, USA). These