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Response of climate-growth relationships and water use efficiency to thinning in a *Pinus nigra* afforestation

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ABSTRACT

Thinning is the main forestry measure to increase tree growth by reducing stand tree density and competition for resources. A thinning experiment was established in 1993 on a 32-year-old *Pinus nigra* Arn. stand in central Spain. The response of growth, climate-growth relationships and intrinsic water use efficiency (WUEi) to a stand density reduction were compared between moderate thinned plots and a control plot by a combined analysis of basal area increments (BAI), and C and O stable isotope ratios ($\delta^{13}C_c$ and $\delta^{18}O_c$). BAI in the control plot showed a decreasing trend that was avoided by thinning in the thinned plot. Thinning also partially buffered tree-ring response to climate and trees were less sensitive to precipitation although more sensitive to temperature. $\Delta^{13}C_c$ in the thinned plot was not modified indicating that stomatal conductance (g) and photosynthetic capacity (A) did not change or change in the same direction. However, $\delta^{18}O_c$ decreased in the control plot (unrelated to $\delta^{18}O$ of precipitation) but not in the thinned plot, suggesting a relative increase of temperature and irradiance and/or a decrease of air humidity after reducing the density consistent with an increase in A, g and BAI. As WUEi did not increase in the thinned plot, faster growth in this plot was caused by higher abundance of resources per tree. The trend of WUEi in both plots indicated low-moderate CO_2-induced improvements. Thinning might be a useful adaptation measure against climate change in these plantations reducing their vulnerability to droughts. However, because WUEi was not affected, the positive growth response might be limited if droughts and warming continue and certain thresholds are exceeded.

1. Introduction

Radial growth of trees within forest stands greatly depends on the interactions between competition and environmental conditions (e.g. Piutti and Cescatti, 1997). Crown competition affects the space available for growth as well as the amount of light (energy) that a tree receives whereas root competition determines the amount of water and soil nutrients available for each tree. If water is a limiting resource, and it is predicted to become scarcer, one of the more important measure that forest managers have to modulate the influence of climate on tree growth within stands is by means of more or less intense thinning (e.g. Cescatti and Piutti, 1998) which would make more water available for the remaining trees.

It has been generally considered that a reduction of density decreases global transpiration of the stand although individual tree transpiration might increase (Bréda et al., 1995). Moreover, water availability usually increases as a result of thinning because of the reduction of crown interception or root competition (Sucoff and Hong, 1974; Bréda et al., 1995; Misson et al., 2003). Density reductions also affect positively the amount of incident light, nutrients available (Blanco et al., 2005) as well as the temperature inside the stand (e.g. Tang et al., 2005).

Positive effects of thinning on tree growth are therefore caused by the reduction of crown and belowground competition and to the concentration of potential growth in only a reduced number of selected individuals. Whether this growth acceleration is caused by an improvement of the hydric state of trees, an increase in energy (light) in the canopy or both depends on the interplay between the factors most limiting growth. In dry climates such as the Mediterranean, water availability is considered to be the main limiting factor (Specht, 1981). Although growth increases were reported after thinning without an increase in the water status of trees (Waring and Pitman, 1985), a reduction of water stress improves the general condition of trees (e.g. Kolb et al., 1998) and

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increases growth rates of the remaining trees (Sucoff and Hong, 1974; Donner and Running, 1986; Aussenac and Granier, 1988). If this is the case, it could be recorded in tree-rings as a reduction (values becoming more negative) of the ratio between ^{13}C and ^{12}C stable isotopes of carbon fixed in wood cellulose (δ^{13}C) (e.g. McDowell et al., 2003). Water stress causes stomata closure (Farquhar et al., 1989), reduces stomatal conductance for CO_2 (g) and leads to higher proportion of ^{13}C. However, in dense stands, such as those usually originating from afforestation, light might also be a limiting factor for growth even in high irradiance regions. Therefore in these cases, growth of thinned stands could be enhanced by increasing light availability which could ultimately enhance net assimilation (Warren et al., 2001).

According to the model of Farquhar et al. (1989) carbon discrimination depends on stomatal conductance for CO_2 (g) and on the photosynthetic carbon assimilation (A) as they both regulate the partial pressure of CO_2 in the leaf intercellular spaces (c_i) calculated as

$$c_i = c_a - \frac{A}{g} \tag{1}$$

They both affect discrimination (Δ) expressed as

$$\Delta = a + (b - a) \cdot \frac{c_i}{c_a} \tag{2}$$

where a is the diffusion of carbon in air (4.4‰) and b is the net fractionation in carboxylation by the enzyme ribulose bisphosphate carboxylase/oxygenase (Rubisco; 27‰), and c_a the partial pressure of CO_2 of the atmospheric air (Farquhar et al., 1982). The balance between g and A determines the changes in Δ^{13}C (and in opposite direction of δ^{13}C). In general, A/g are inversely correlated with soil water availability, because g increases more than A (e.g. Dupouey et al., 1993) but this process is also affected by the higher irradiance and possible nutrient availability caused by thinning (e.g. Warren et al., 2001). Thus, a decrease of δ^{13}C (increase in Δ^{13}C) can be caused by an increase of g or a decrease of A relative to the other variable (Farquhar et al., 1989). In order to distinguish between these two possible causes, Scheidegger et al. (2000) suggested the combined use of δ^{13}C and oxygen isotope ratio of organic matter (δ^{18}O). Variations in c_i are inferred from δ^{13}C whereas changes in relative humidity are derived from δ^{18}O because it depends on soil water isotope composition, temperature, and relative humidity (for a review see Yakir, 1992).

The main objective of our study was to assess the growth reactions to thinning of trees in afforested stands of *Pinus nigra* Arn. using a combination of dendrochronological and stable isotope methods. With this study we aim to evaluate whether the effect of reducing the stand density (if any) is caused by an increase on water availability as compared to the pre-thinning period and to a control plot or if water use efficiency is modified by lower competition.

2. Materials and methods

2.1. Study area and field sampling

Our study area was located in central Spain (latitude 41°02′N, longitude 03°04′W) at an altitude of 1050 masl. Trees were in a pure even-aged *P. nigra* subs. Salzmanii var. *hispanica* stand originating from afforestation at an initial stand density of 1600 trees ha^{-1}. The thinning experiment was composed of two control plots (C1 and C2) with no thinning and two thinned plots (T1 and T2) where a moderate thinning from below (removing the trees with smaller diameters) was applied in winter 1993–1994 (trees were 31 years old) removing 28.5% of initial basal area in T1 and 20.5% in T2 (Table 1). All plots have been inventoried four times between 1993 and 2007 (Table 1).

In winter 2006–2007, we sampled 15 trees in three of the four plots (T1, T2, and C1). Control plot C2 was left out of the study because of high natural mortality between 1998 and 2003 (Table 1). Sampled trees were those which had a circumference (k_i) within the range of average plot circumference ($\overline{K_i}$) plus one standard deviation ($k_i = \overline{K_i} + SD_i$) (Misson et al., 2003). Two cores were extracted from each tree with an increment borer, later mounted on wood boards and sanded. Total ring width (TRW) was measured to the nearest 0.01 mm and registered in a computer using the software TSAP (Rinn, 2003). Raw TRW series were visually and statistically crossdated with TSAP by the *Gleichläufigkeit* (sum of equal slopes intervals in per cent), *t*-values and the cross-date index (CDI) which is a combination of both.

2.2. Dendrochronological approach

We derived series of yearly basal area increments (BAI) from raw ring width assuming concentrically distributed tree-rings. BAI were used instead of ring-width directly, because BAI is less dependent on age and thus avoids the need of detrending (Biondi, 1999) which could also remove low frequency variability, more so given the short time span of our series (1960–2006), such as the sudden reduction of stand density. However, we carried out a very conservative detrending with a straight line equal the mean BAI in each series. Basal area increment indices (IBAI) were obtained by dividing yearly BAI values by the mean value of BAI of each tree, $\mathrm{IBAI}_{ij} = \mathrm{BAI}_{ij}/\overline{\mathrm{BAI}}_j$, where BAI_i is the basal area increment of year i (i = 1970, 1994,. . ., 2007) of tree j, and $\overline{\mathrm{BAI}}_j$ is the mean yearly basal area increment for tree j in the period 1993–2007.

2.3. Stable isotope and intrinsic water use efficiency analysis

Stable carbon and oxygen isotope analysis was performed on a subsample of five trees per plot whose tree-ring series most resembled the plot tree-ring chronology from plots C1 and T1 in which the thinning was heavier. We analyzed rings for the period 1986–2005 which corresponded to 8 years before and 12 years after the thinning in order to explore the effect of thinning for a longer period of time. Complete dated rings (including both early-

Table 1
Stand description values of the four plots during the four inventories analyzed. For the first inventory, data before and after the thinning are presented.

Plot		Stand density (trees ha^{-1})					Basal area (m^2 ha^{-1})					Mean DBH[a] (cm)				
		1993 b.th.[b]	1993 a.th.[b]	1998	2003	2007	1993 b.th.	1993 a.th.	1998	2003	2007	1993 b.th.	1993 a.th.	1998	2003	2007
C1	Control	1600	–	1600	1580	1580	30.3	–	34.4	38.5	39.0	15.4	–	16.4	17.4	17.5
T1	Thinned	1590	1020	1020	1020	1020	31.9	22.5	26.4	30.2	32.6	15.8	16.6	18.0	19.3	20.0
C2	Control	1600	–	1590	1320	1310	31.4	–	35.1	33.8	35.3	15.6	–	16.5	17.8	18.3
T2	Thinned	1570	1150	1150	1150	1120	28.3	22.8	26.4	30.0	31.7	14.9	15.7	17.0	18.1	18.8

[a] DBH, diameter measured at breast height (1.30 m).
[b] b.th. = before thinning; a.th. = after thinning.