



Managing drought-sensitive forests under global change. Low competition enhances long-term growth and water uptake in *Abies pinsapo*

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ABSTRACT

Understanding forest responses to the current climate change requires to investigate the effects of competition, buffering or enhancing process of forests decline. Here we attempt to place intra-specific competition in a climate change context, using as experimental system the drought-sensitive fir *Abies pinsapo*. We conducted a decade-long (2004–2015) investigation at four permanent plots (two thinned plots and two controls), where all trees were identified, tagged and mapped. Experimental thinning was performed attempting to enhance stand structure diversity by (1) reducing tree competition, (2) increasing the equitability of size classes (i.e. diversity) and (3) randomizing tree spatial pattern. We focus on tree basal area increment and sap flow density, as regards microclimate and competition, to quantify the extent to that thinning alleviates drought in the remaining trees. The results support that lower competition fosters short- to long-term tree-level physiological responses, specifically, improved growth and water uptake in the remaining trees. Density reduction provides a promising strategy for minimizing climate change effects on drought-sensitive tree species by improving resources availability to the remaining trees. Nevertheless, our results also support a higher air temperature and soil water depletion according to density reduction, suggesting that lower competition might also increase soil and understory evapotranspiration. Adaptive management, as the experimental thinning reported here, may increase tree-level resources availability, but the long-term stand-level effectiveness of this approach at sustaining forest ecosystem functioning remains uncertain.

1. Introduction

Increasing variability and uncertainty regarding future environmental conditions provide new challenges for forest management (Franklin et al., 2002; Puettmann, 2011; Messier et al., 2013; Ameztegui et al., 2017). Rising temperatures and changes in precipitation patterns may translate into shifting species composition and changing processes and functions of forest ecosystems over broad geographic regions (Breshears et al., 2005; Goetz et al., 2012; Vayreda et al., 2012). Increases in drought frequency and intensity are expected to elevate mortality rates for those drought-sensitive tree species, as widespread tree mortality has been documented in forests worldwide (Allen et al., 2010).

Despite climate change appears as a main driver of this worldwide reported forest die-off, usually related to tree growth decline and widespread mortality, the modulating effect of stand structure has been

also widely recognized (Floyd et al., 2009; Lines et al., 2010; Moreno-Gutiérrez et al., 2012; Martínez-Vilalta et al., 2012). Competition is a critical demographic concern for determining tree growth and mortality, forest dynamics and, consequently, ecosystem function and carbon cycling (Canham et al., 2006; Ruíz-Benito et al., 2013; Fernández-de-Uña et al., 2015; Ford et al., 2017). Specifically, trees subjected to higher competition show lower radial growth and are more prone to die following extreme drought events (Carnwath and Nelson, 2016; Diaconu et al., 2017; Gleason et al., 2017).

In southern Europe, increasing tree mortality has been related not only to increased drought, but also reduced forest management, which has potentially led to increased competition between trees (Gómez-Aparicio et al., 2011; Vayreda et al., 2012; Sánchez-Salguero et al., 2015a). Competition for resources (primarily for irradiance, water and nutrients) is a key biotic factor that affects the growth and functioning of plants at the individual, population and community levels (Carnwath

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and Nelson, 2016). In forests, competition affects tree mortality, size structure and species composition (Canham et al., 2006; Anderegg et al., 2016). Increasing stand density causes a decrease in soil water availability, which induces stomatal closure to prevent hydraulic failure and results in carbon uptake reduction by photosynthesis (Breda et al., 2006; McDowell, 2011). As a result, the response of drought-sensitive dense forests to a warmer and drier climate in future will likely be modified by competitive relationships among trees, which may potentially affect species composition and cause a need to change forestry practices (Puettmann, 2011; Ameztegui et al., 2017).

As regards the course involved in this recent large-scale forest decline, drought-induced tree mortality drives the functional and structural dynamics of forest ecosystems, both as a sink/source of carbon and nutrients, and as a mechanism of change in forest structure and species diversity (Galiano et al., 2010; Anderegg et al., 2012; McDowell et al., 2013; Rigling et al., 2013). However, managing stand structure, including sizes diversity and tree spatial patterns, may boost the adaptive capacity of drought-sensitive tree species (D'Amato et al., 2013; Giuggiola et al., 2013; Sohn et al., 2013; Elkin et al., 2015; Aldea et al., 2017). Hence, it seems mandatory to investigate stand structure effects, buffering or enhancing process of forests decline (Sohn et al., 2016; Diaconu et al., 2017; Gleason et al., 2017; Ameztegui et al., 2017).

Our study concerns the responsiveness of individual trees to changing climate variables with respect to their competitive status in the local neighbourhood. Here we attempt to place intra-specific competition in a climate change context, assessing the effects of forest structure under drought stress. We focus on tree growth and water fluxes to quantify the extent to that changing stand structure (by an experimental thinning) might alleviate drought stress in the remaining trees. We used *Abies pinsapo* forests as experimental system. This drought-sensitive Mediterranean fir was subjected to centuries of intense perturbation, by grazing and logging by the local inhabitants (Linares and Carreira, 2009). From the middle 20th Century onwards, *A. pinsapo* forests underwent the abandonment of traditional uses, increasing stand density during recent decades (Linares and Carreira, 2009). Nowadays, episodic *A. pinsapo* decline and mortality has been related to dry site conditions and high stand density (Linares et al., 2010).

We aim to test the main hypothesis that density-dependent factors and structural diversity, as a legacy of previous forest management, are among the main determinants of forest growth and climate sensitivity through the effect of competition. Our specific aims are: (1) to quantify the extent to that stand density alters microclimate, as regards soil water availability, air temperature and vapour pressure deficit; (2) to investigate how stand density modulates climate-growth sensitivity; and (3) to analyze the inter-annual patterns of sap flow and secondary growth of individuals subjected to contrasting competition, dealing to spatially-explicit assessment of their competitive environment.

2. Material and methods

2.1. Study species and thinning design

The study was carried out at natural stands of *Abies pinsapo* Boiss., a drought-sensitive fir, located near the lower elevation limits of the altitudinal species distribution range (Sierra de las Nieves Natural Park; 36°43'N, 4°57'W, 1200 m, aspect NW, slope ca. 40%; Linares et al., 2010). *A. pinsapo* forests in the study area were subjected to intense grazing and logging by the local peoples up to about the middle 20th Century (Supporting Information, Fig. S1). During the second half of the 20th Century, until present, these forests were protected, while they underwent the abandonment of traditional uses (Linares and Carreira, 2009). The suppression of the perturbation regime initiates the processes involved in stand regeneration, leading currently to near-to even-aged dense stands (Linares and Carreira, 2009). Often, these stands maintain their even-aged structure until the next major disturbance occurs, as seems to be the case of extreme drought events and diseases, observed since the onset of the 1990s decade (Linares and Carreira, 2009; Navarro-Cerrillo et al., 2014). As a consequence, the studied stands were mainly formed by medium to small trees, generally spindly, with vigour suppressed by canopy closure (Linares et al., 2010).

We selected four circular plots, about 1300 m² surface and 100 m apart, where all trees with more than 3 cm diameter at 1.3 m from the ground (DBH) were identified (tree species; tree status: alive, dead, stump), tagged and mapped, and DBH was measured (Table 1). The studied stands were dominated by *A. pinsapo* (mainly 5–25 cm DBH) and scattered *Pinus halepensis*; mean stand density were 1335 trees ha⁻¹, while mean total basal area were 29.7 m² ha⁻¹ (Table 1). Two plots were randomly selected for thinning while the others were kept as control.

Experimental thinning was designed and performed in October 2004, attempting to enhance stand structure diversity by (1) reducing tree competition, (2) increasing the equitability of size classes (i.e. diversity) and (3) randomizing tree spatial pattern (Franklin et al., 2002). To achieve this objective of enhance stand structure diversity, the thinning was focused on the size classes with the highest tree density (Fig. 1). Thus, the diversity of size classes (the range of DBH sizes) was preserved, while equity of basal area for each size class was newly achieved (Fig. 1). Finally, the selection of trees to be felled were randomized to generate a heterogeneous spatial structure, where horizontal and vertical variability provided contrasting regeneration niches, enhanced gap colonization and boosted canopy cover recovery (Franklin et al., 2002; Pretzsch et al., 2012). Furthermore, spatial heterogeneity provided trees subjected to different competitive status. The thinning accounted for about 50% of the basal area, and about 45% of stand density (Table 1, Fig. 1). Trees felled during the thinning treatment were sawed and bring out from the stands. We obtained 184 stem DBH cross-section samples to investigate secondary growth and

Table 1

Main characteristics of the studied plots located at the lower elevation limit of *Abies pinsapo*. Values between parentheses show the standard error.

| Treatment | Plot | Location | | | Pre-thinning | | | After-thinning | | | | |
|-----------|------|------------|-----------|-----------|---------------|------------------------------------|---------------------------|----------------|------------------------------------|---------------------------|----------------------|-------------------------|
| | | Latitude | Longitude | Elevation | DBH | Basal area | Stand density | DBH | Basal area | Stand density | Basal area reduction | Stand density reduction |
| | | (N) | (W) | (m) | (cm) | (m ² ha ⁻¹) | (trees ha ⁻¹) | (cm) | (m ² ha ⁻¹) | (trees ha ⁻¹) | (%) | (%) |
| Control | C1 | 36°43' 28" | 4°57' 59" | 1173 | 11.8 (0.5) | 34.1 | 2085 | – | – | – | – | – |
| | C2 | 36°43' 29" | 4°58' 10" | 1232 | 14.2 (0.9) | 28.8 | 1146 | – | – | – | – | – |
| Thinned | T1 | 36°43' 27" | 4°58' 01" | 1181 | 17.2 (0.8) | 28.7 | 995 | 15.6 (1.0) | 14.4 | 581 | 50.0 | 41.6 |
| | T2 | 36°43' 26" | 4°58' 01" | 1188 | 14.8 (0.8) | 27.2 | 1114 | 12.7 (1.2) | 12.4 | 581 | 54.4 | 47.9 |

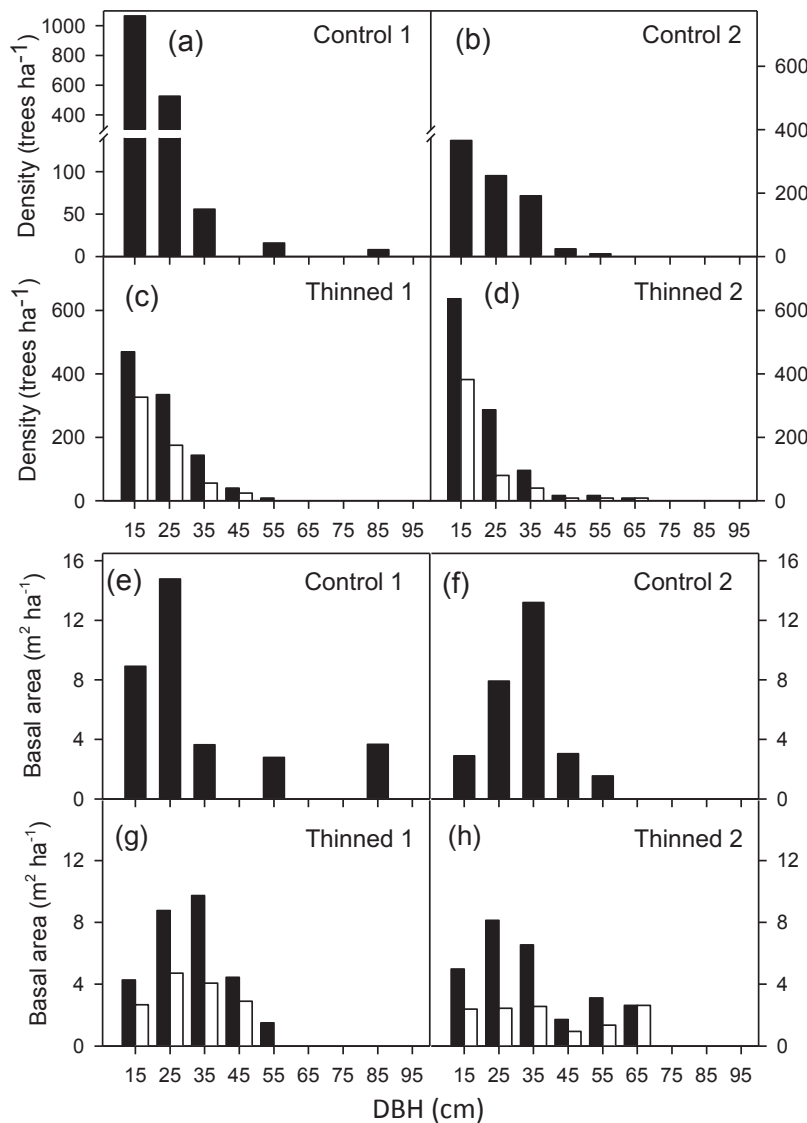


Fig. 1. Size classes distribution (stem diameters at 1.3 m; DBH) of control (Control 1 and 2) and thinned (Thinned 1 and 2) plots at the lower elevation limit of *Abies pinsapo*. Upper panels (a, b, c and d) represent the stand density, while bottom panels (e, f, g and h) represent the basal area. Data correspond to the stand structure prior (black bars) and after (white bars) the thinning.

sapwood area (see the method Section 2.3 below). Heartwood was not observed by visual inspection in any cross-section sample. In addition, *A. pinsapo* had a very thin bark within the range of ages studied here (< 5 mm, data not shown). As a consequence, we considered the whole basal area as sapwood for further analyses.

2.2. Microclimate measurements

Air temperature (T, °C) and relative air humidity (RH, %) were measured hourly and recorded using two dataloggers per plot (HOBO sensors; Onset Co., USA). Dataloggers were placed at a height of 1 m above the ground, inside a PVC box 15 cm diameter, open at the bottom to allow a proper air circulation through the sensors, and covered with insulating polyurethane foam to avoid direct sun heating. Vapour pressure deficit (VPD, kPa) was estimated using T and RH data as follows (Castellvi et al., 1997). Saturated vapour pressure (SVP, kPa) was estimated from T as:

$$SVP = 0.66 * e^{(0.06 * T)} \quad (1)$$

VPD was then obtained from SVP and RH as:

$$VPD = \frac{(100 - RH)}{100} * SVP \quad (2)$$

Volumetric Soil water content (SWC, %) was estimated from the

dielectric constant of the soil (DC, mV), measured by four probes per plot (ECH2O model EC-20 sensors, Decagon Device, Inc) buried at 30 cm, and recorded hourly using a datalogger per plot (Cavadevices, Inc.). Conversion from the probes output values to the SWC was performed, according to Decagon Devices specifications (http://manuals.decagon.com/Application%20Notes/13492_Calibration%20and%20Evaluation%20of%20an%20Improved%20Low-Cost%20Soil%20Moisture%20Sensor_Print.pdf), by the following linear relationship:

$$SWC = 0.119 * DC - 40.1 \quad (3)$$

where DC is the output (mV) of the sensor when excited at 2.5 V.

Hydrological year was set from October to September, and it was divided into a wet season (October–April) and a dry season (May–September) based on SWC and VPD measurements.

2.3. Secondary growth measurements

Secondary growth prior to 2004 were measured by standard dendrochronological methods, using the 184 DBH cross-sections obtained in the thinned plots, and 20 wood cores, sampled by a Pressler increment borer, from each control plot (see Linares et al., 2009, 2010). Further annual secondary growth was estimated measuring changes in tree girth by band dendrometers (D1 Permanent Tree Girth, UMS,

Germany). Selected trees covered a range of diameters between 6 cm and 44 cm DBH, accounting for whole tree sizes distribution within the plots. Mean DBH of trees equipped with dendrometers was 18.9 ± 0.9 (standard error, SE) cm. Band dendrometers were mounted in winter 2004 around the stem at ca 1.3 m. The bark was carefully smoothed with a rasp before attaching the dendrometer. Readings were not exactly periodic. For most years the sampling were done monthly between October and March, and biweekly between April and September. In any case, measurements were fully available for the beginning of the growing season in spring (April–May) and after the growing season in autumn (September–October). Dendrometer measurements were corrected using the linear thermal expansion coefficient provided by the manufacturer ($\alpha = 75 \times 10^{-6} \text{ K}^{-1}$). Annual secondary growth was calculated as the basal area increments (BAI), computed as the difference of basal area (cm^2) recorded at the year (j) minus the basal area recorded at the year (i):

$$BAI = \frac{\pi}{4} (DBH_j^2 - DBH_i^2) \quad (4)$$

Individuals without growth during at least one year were discarded in the subsequent sampling, while some dendrometers could not be maintained along the whole study period by the shortage of the full dendrometer girth length, due to tree growth. Control plots accounted 37 dendrometers (26 in C1 and 11 in C2). At the end of the study period (year 2015), 34 dendrometers were maintained (25 in C1 and 9 in C2). Thinned plots accounted 24 dendrometers (12 in T1 and 12 in T2). At the end of the study period, 19 dendrometers were maintained (11 in T1 and 8 in T2). To upscale BAI values obtained at tree level to stand level, we correlated BAI and DBH values in thinned and control plots and estimated the BAI of each tree; basal area increment per hectare and year results from the sum of the individual BAI of all trees within each plot.

2.4. Competition intensity

Competition intensity (CI) was estimated using a distance-dependent competition index (Linares et al., 2009, 2010).

$$CI = \sum_{j=1}^{N(R)} (DBH_j/DBH_i)/\text{dist}_{ij} \quad (5)$$

where the degree of competition of the i tree was computed as the sum of the N quotients, for all j neighboring trees surrounding it within a radius of $R = 8$ m, between the ratio DBH_j/DBH_i and the distance between the i and the corresponding j trees (dist_{ij}). The rationale was that trees surrounding by a high number of neighbors (N), higher in size (DBH_j/DBH_i) and close in distance (dist_{ij}), were subjected to high competition (Eq. (5)). The value of 8 m for the threshold radius above which neighbors were regarded as not competing was estimated in preliminary tests comparing CI figures obtained with several distances (from 1 to 10 m radiuses) and the long-term (1945–2004) radial growth expressed as BAI (Linares et al., 2010). For selected trees in the thinned plots, we registered their CI prior to thinning, in order to check for differential responses to competition release (Linares et al., 2009, 2010).

2.5. Sap flow measurements

Sap flow was measured with heat dissipation probes (Granier, 1985) manufactured in the laboratory of the Department of Land, Environment, Agriculture and Forestry of the University of Padova (Italy). Granier's sensors are composed of two needles (3 cm length) containing each one a thermocouple (1 cm length). On the outside, probes have a heating winding. Every probe is positioned in the xylem, inside a metal sleeve (1.1 cm length) to homogenize heat transference (<http://intra.tesaf.unipd.it/people/carraro/sapflow.pdf>).

Sap flow gauges were installed in June 2009 at DBH of the north facing of the bole and covered with reflective insulation to avoid the influence of natural temperature gradients in the bole. To avoid changes in the magnitude of sap flow measured by the same sensors over long periods, due to sensor malfunction, wounding, or resin production, inserted sensors were replaced annually or bi-annually with new ones at new positions on the tree (Moore et al., 2010). Circuits to powering the probes were composed by 12 V batteries supplies by a solar panel; data were collected by a CR1000 datalogger (Campbell Scientific Inc., Logan, UT, USA). Method is based on temperature differences between the upper (heated) probe and the lower one, vertically separated 15 cm. Maximum temperature difference takes place at zero sap flow, while minimum temperature differences denotes maximum heat dissipation due to active sap flow. Then, we calculated daily values of maximum temperature difference (no flow) to calculate the sap flow density as follows:

$$SFD = 4.284 * \left(\frac{\Delta T_{\max}}{\Delta T} - 1 \right)^{1.231} \quad (6)$$

where SFD is the sap flow density ($\text{dm}^3 \text{ dm}^{-2} \text{ sapwood h}^{-1}$), ΔT is the temperature difference at any sampling (30 min intervals, daily) and ΔT_{\max} is the daily maximum temperature difference; equation coefficients were obtained empirically (<http://intra.tesaf.unipd.it/people/carraro/TDP.asp>). Punctual sap flow measurements were corrected for radial variability in sap flow density (Clearwater et al., 1999; Poyatos et al., 2007). We applied a whole-tree correction coefficient to obtain mean sap flux per sapwood area (Ford et al., 2004), using a Gaussian-type function that relates tree diameter and sap flow, decreasing the flow from the outermost to the innermost sapwood (Supporting Information, Fig. S2):

$$CF = 1 * e^{-0.5 * \left(\frac{x-1}{\beta} \right)^2} \quad (7)$$

where the correction factor (CF) ranges between 0 and 1, x is the sapwood depth measured from the cambium and β is the slope of the function. Based on Ford et al. (2004) we used a value of $\beta = 10$. A maximum of 12 trees per treatment (six per plot) were measured simultaneously. Sap flow measurements were divided into wet and dry seasons, as it was defined in the Section 2.2. Energy supply was not able to be maintained during some winters due to too low solar radiation receive in the solar panels, therefore, wet season could not include winter months some years. Anyway, all comparisons were performed among plots for similar time periods.

To upscale sap flow values obtained at tree level to stand level, we multiplied the mean sap flow of a given period by the sapwood of each tree within the plot (dm^2) and the corresponding CF according to its DBH. Stand-level sap flow was then obtained as the sum of the estimated SFD of each tree within the plot.

$$SFD_{\text{STAND}} = \sum_{i=1}^{N(\text{plot})} (BA * SFD * CF) * \frac{10,000}{PS} \quad (8)$$

where SFD_{STAND} is the sum of the estimated sap flow of the N trees within the plot, during a given time span, per hectare ($\text{dm}^3 \text{ ha}^{-1} \text{ day}^{-1}$), BA is the basal area of each tree (dm^2), SFD is the mean daily sap flow density, during a given time span, based on tree with probes ($\text{dm}^3 \text{ dm}^{-2} \text{ sapwood day}^{-1}$), CF is the correction factor according to each tree DBH, defined in Eq. (7), and PS is the plot surface area (m^2).

2.6. Statistical analyses

The Kolmogorov-Smirnov and Levene tests were used to assess normality and homoscedasticity, respectively. To perform simple comparison among independent groups of observations we used one-way analysis of variance (ANOVA) for data showing normal distribution

of the residuals. The Kruskal–Wallis test by ranks was used when normal distribution of the residuals might be not assumed, as a non-parametric method. Environmental conditions (T, HR, VPD and SWC) were statistically tested by a Student *T* test designed for paired comparison for dependent samples (dependency was assumed as regards sampling date). Repeated measures of BAI and SFD were tested for homogeneity of variance and for the assumption of compound symmetry of the variance-covariance matrix using the Bartlett-Box *F*-test and the Mauchly criterion, respectively. Given that our dataset do not fulfill the parametric statistic assumptions, we used test statistics available for heteroscedastic semi-parametric multivariate data and repeated measures designs to compare BAI and SFD in trees with different thinning treatments (Friedrich et al., 2017). The between-subject factor was thinning treatment (control versus thinning), whereas the competition intensity (CI) and tree size (DBH) were considered as covariates. Sampling date was regarded as the within-subject factor. Statistical analyses were performed in R (R Core Team, 2017); Package ‘MANOVA.RM’. Data are shown as mean \pm standard error (SE) throughout the text. Significant threshold was fixed for $p < 0.05$.

3. Results

Volumetric soil water content (SWC) during the wet season (October–April) was on average 31.4%, showing similar values among control and thinned plots. However, during the dry season (May–September) SWC was on average 23.9%, showing usually lower values in the thinned plots, compared to the control ones; these differences in mean SWC during the dry period were statistically significant in seven of the eleven measured years (Fig. 2; Supporting Information, Table S1).

Mean air temperature (T) and vapour pressure deficit (VPD) were significantly higher in the thinned plots all over the study period (Fig. 2; Supporting Information, Table S1). T during the wet season was on average 7.3 °C in the control plots and 8.0 °C in the thinned plots, while T during the dry season was 17.7 °C and 18.2 °C, in control and thinned plots, respectively. VPD during the wet season was on average 0.34 kPa in the control plots and 0.39 kPa in the thinned plots, while VPD during

the dry season was 1.03 kPa and 1.10 kPa, in control and thinned plots, respectively (Fig. 2; Supporting Information, Table S1).

The mean precipitation was 1358 mm (Fig. 3c). Annual precipitation was below the mean for the period 1991–1995, 2005–2008 and 2012; 1995 and 2012 were extreme (below two standard deviations) drought years while 1996 and 2010 were extreme (above two standard deviations) rainy years (Fig. 3c). Trees basal area increment (BAI) was similar among plots prior to the thinning. Mean BAI for the period 1990–2004 was on average 4.7 cm² year⁻¹, showing similar inter-annual variability, including sudden growth reductions according to drought event in 1995, 2005 and 2012 (Fig. 3a). Following the thinning in 2004, mean BAI was significantly higher in the thinned plots, compared to the control ones, with mean values for the period 2005–2015 of 9.3 cm² year⁻¹ and 4.2 cm² year⁻¹, in thinned and control plots, respectively (Fig. 3a). Monthly and seasonal sap flow density (SFD) was significantly higher for thinned plots (Fig. 3b, Table 2). The effect of thinning (the ratio between thinned and control values) was higher in those years with annual precipitation below the mean, while prior to thinning, both control and thinned plots showed a BAI ratio near to 1 (Fig. 3c).

Daily SFD was significantly related among trees located within control and thinned plots, while the slope of this relationships shows smaller SFD values (on average 28% smaller) for control trees over all the measured period (2009–2014; Fig. 4a). During the wet season (October–April) mean SFD was commonly higher than in the dry season (May–September) and it was related to VPD, showing a steady SFD rise as VPD did from 0.1 kPa to 0.4 kPa, while VPD values above 0.4 kPa were related to lower SFD (Supporting Information, Fig. S3). During the dry season, SFD decreased linearly as air temperature increased (Supporting Information, Fig. S3), while no significant relationships were found regarding SWC.

The annual mean tree SFD and BAI obtained in thinned and control plots for the period 2009–2014 illustrated both higher secondary growth and transpiration at the remaining trees within the thinned plots (Fig. 4b). Nevertheless, when SFD and BAI values were extrapolated to the whole plot, the stand BAI was commonly lower in the thinned plots; alike, the estimation for stand SFD was usually lower in the thinned plots (Supporting Information, Fig. S4).

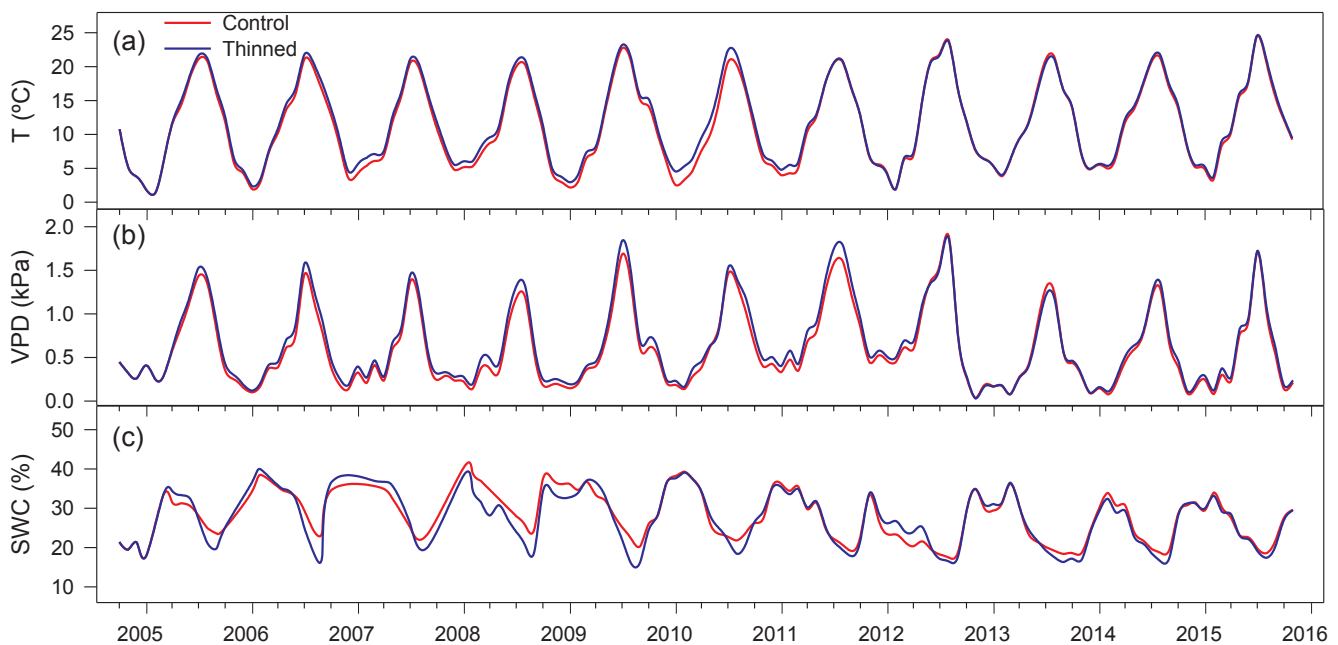


Fig. 2. Microclimatic conditions: air temperature, T (a), air vapour pressure deficit, VPD (b), and volumetric soil water content, SWC (c), measured by sensors connected to dataloggers in control and thinned plots (two plots per factor). Hourly data were averaged at monthly scale (see statistical analysis at Supporting information, Table S1). The on-line color version represents data from thinned plots in blue and data from control plots in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

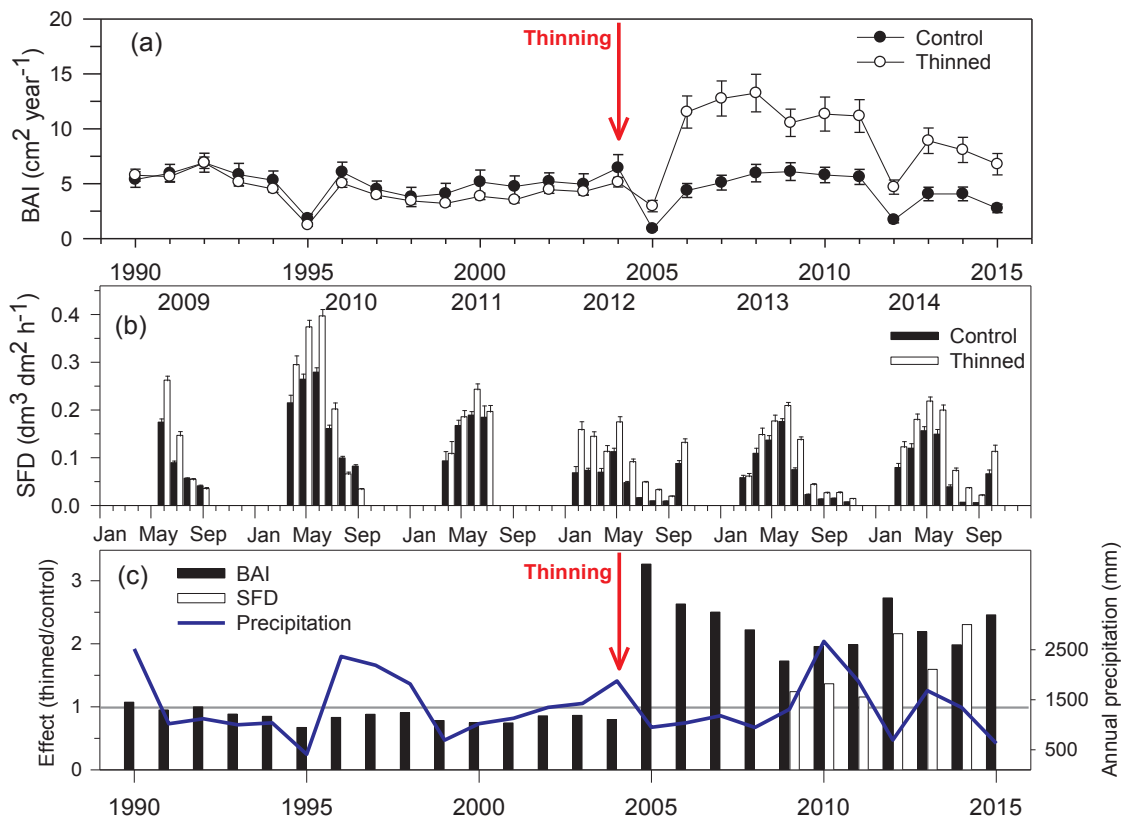


Fig. 3. Annual basal area increment (BAI) for the period 1990–2015 (a), and monthly sap flow density (SFD) for the period 2009–2014 (b) measured in control and thinned plots (two plots per factor). The effect of thinning (c) was computed as the ratio between thinned and control values; the horizontal line indicates similar values among thinned and control plots (the ratio is equal to 1) as well as the mean value of total annual precipitation during the showed period (1990–2015; 1358 mm). Vertical arrow indicates the year of thinning; error bars indicate the standard error.

Table 2

Sap flow density (SFD) measured in control (C) and thinned (T) plots (two plots per factor). Data show the mean and the standard deviation (Std. dv.); nd: not available data. Statistical differences were tested separately for wet (October–April) and dry seasons (May–September) between control and thinned plots by pair comparison for dependent samples; m: marginally significant, $p < .1$.

| Year | Season | Treatment | SFD ($\text{m}^3 \text{dm}^2 \text{h}^{-1}$) | Std. dv. | p |
|------|--------|-----------|--|----------|-----|
| 2009 | Wet | C | nd | nd | |
| | | T | nd | nd | |
| | Dry | C | 0.081 | 0.043 | |
| | | T | 0.111 | 0.080 | *** |
| 2010 | Wet | C | 0.215 | 0.060 | |
| | | T | 0.295 | 0.068 | *** |
| | Dry | C | 0.187 | 0.093 | |
| | | T | 0.233 | 0.160 | *** |
| 2011 | Wet | C | 0.094 | 0.083 | |
| | | T | 0.109 | 0.105 | m |
| | Dry | C | 0.179 | 0.063 | |
| | | T | 0.212 | 0.075 | *** |
| 2012 | Wet | C | 0.072 | 0.041 | |
| | | T | 0.132 | 0.067 | *** |
| | Dry | C | 0.039 | 0.046 | |
| | | T | 0.074 | 0.067 | *** |
| 2013 | Wet | C | 0.087 | 0.052 | |
| | | T | 0.115 | 0.070 | *** |
| | Dry | C | 0.085 | 0.072 | |
| | | T | 0.119 | 0.084 | *** |
| 2014 | Wet | C | 0.055 | 0.061 | |
| | | T | 0.085 | 0.083 | *** |
| | Dry | C | 0.072 | 0.078 | |
| | | T | 0.110 | 0.092 | *** |

*** $p < .001$.

The BAI for the period 2005–2015 was, at tree-level, strongly related to the competition intensity (CI; Fig. 5) as well as the climate-growth sensitivity (Fig. 6). Mean BAI decreased exponentially as CI increased, supporting that trees located within the thinned plots showed higher growth rates according to released competition strength (Fig. 5). Growth sensitivity, estimated as the slope of the climate-growth relationships, was higher in trees subjected to lower competition, showing a positive relationship with mean SWC of the hydrological year and the wet season, and a negative relationship with mean T of the dry season (Fig. 6).

4. Discussion

4.1. Tree-level effects of structure management on drought-sensitive species

The interactive effects of drought and competition are still insufficiently understood as regards forest response to global climate change (Ruíz-Benito et al., 2013; Elkin et al., 2015; Sánchez-Salguero et al., 2015a; Carnwath and Nelson, 2016; Ford et al., 2017). Short- to long-term physiological process underlying growth and water balance responses to thinning present a significant challenge to our understanding, although this knowledge seems crucial to define forests adaptation strategies under a climate change scenario (Messier et al., 2013). Tree-level responses to competition removal are grounded on limiting-resources ecological theory (Sohn et al., 2016; Ford et al., 2017). Trees under low competition often present higher soil water content, soil-to-canopy hydraulic conductance, stomatal conductance and photosynthetic rates than trees subjected to high competitive stress (Breda et al., 2006). *A. pinsapo* is a drought-sensitive fir, whose xylem water potential need to keep within a non-damaging range to prevent hydraulic failure (Sánchez-Salguero et al., 2015b). During the drought

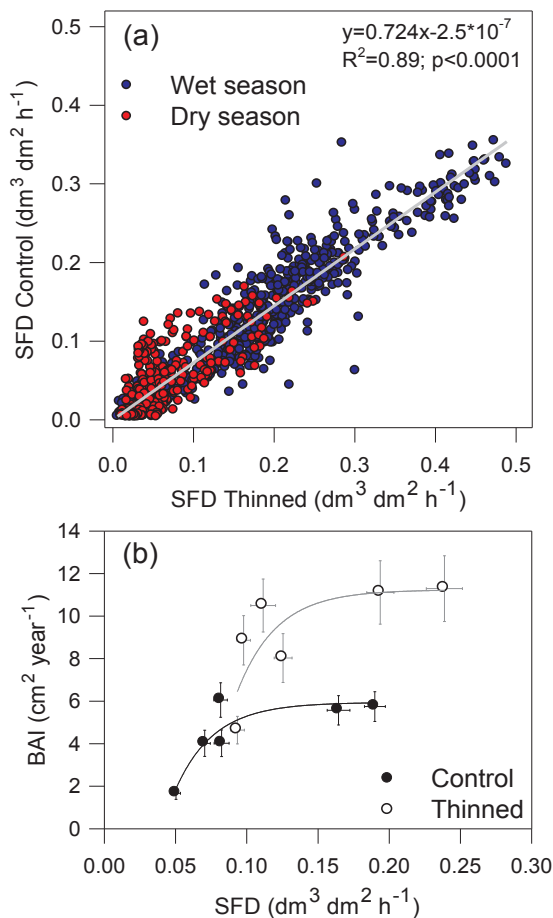


Fig. 4. (a) Daily mean sap flow density (SFD) obtained in thinned (X axis) and control (Y axis) plots. The on-line color version represents SFD data separately for the wet season (October–April, blue); and the dry season (May–September, red). Inset show the parameters and statistics of a linear regression performed for the whole dataset. (b) Annual mean sap flow density (SFD) and basal area increment (BAI) obtained in thinned (white dots) and control (black dots) plots for the period 2009–2014. Curves show polynomial regressions (Control: $R^2 = 0.81$, $p = .08$; Thinned: $R^2 = 0.62$, $p = .10$; $n = 6$ years, 2009–2014). Error bars indicate the standard error.

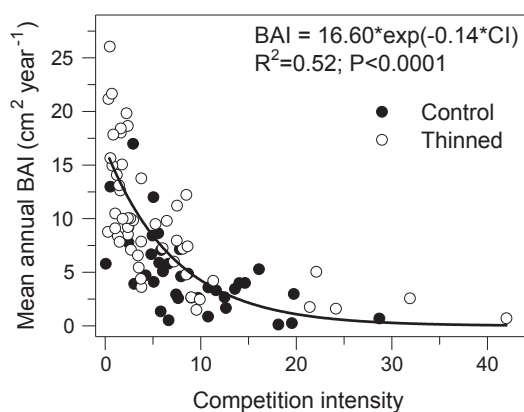


Fig. 5. Tree-level relationship obtained between competition intensity (CI) and the mean annual basal area increment (BAI) for the period 2005–2015 in trees from control (black; $n = 38$) and thinned (white; $n = 52$) plots. Inset show the parameters and statistics of an exponential regression curve performed for the whole dataset. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

period, *A. pinsapo* displayed significant stomatal closure according to reduced SFD, as a mechanism to reduce water loss and to prevent needles wilting. Nonetheless, low stomatal conductance to water

vapour also reduces carbon uptake, and therefore, photosynthesis rates (Linares et al., 2009; Sánchez-Salguero et al., 2015b). Improving carbon uptake by thinning should decrease *A. pinsapo* mortality by allowing the remaining trees to produce enough carbohydrates for metabolism and defenses against biotic attacks (McDowell et al., 2008).

Despite the widespread endorsement of different thinning strategies, few empirical studies have evaluated the long-term effectiveness of this approach to mitigate current climate change impacts in drought-sensitive forests (Sohn et al., 2013; Elkin et al., 2015; Ford et al., 2017). Here, the mitigating effects of management on drought stress were supported by both secondary growth and transpiration of the remaining trees in the thinned plots. We demonstrate that sudden growth declines (Fig. 3a) were linked with drought (Fig. 3c), but significantly modulated by competition (Figs. 5 and 6). This pattern was also reliable regarding SFD, comparing the wet and the dry season at the intra-annual scale. Thus, the remaining trees in the thinned plots were able to maintain higher transpiration, despite this improvement was still limited under drought conditions (Fig. 3b; Table 2). Besides, the differences in BAI among trees subjected to contrasting competition were reduced by drought (Fig. 6).

These results suggest that the use-efficiency of resources, as light or soil water and nutrients, by the remaining trees in the thinned plots increases as those resources availability does (Aldea et al., 2017). In our study, SWC in the thinned plots were sometimes lower than in the control plots (Fig. 2). However, since the number of trees in the thinned plots was reduced, the tree-level water availability might be higher, even SWC was lower. According to that, our results support that transpiration rates, measured as the quantity of ascending water in the stem, were higher in the remaining trees in the thinned plots (Fig. 4b).

Nevertheless, environmental conditions during the drought period were likely harsher in the thinned plots. Indeed, thinned plots showed slightly higher mean air temperature and related VPD, while SWC at the end of the dry season was on average lower, compared to the controls (Supporting Information, Table S1). These results suggest that the improved secondary growth of the remaining trees within the thinned plots relies on carbon source stored as reserves likely prior to, or at the early, growing season (Hartmann et al., 2015). This hypothesized allocation of carbon to secondary growth (mainly as earlywood; Linares et al., 2009), may be founded on fall and winter photosynthesis, released by the higher light availability in the canopy, opened by thinning (Aldea et al., 2017). If so, then the linkage between relieved competition and enhanced growth on water-limited ecosystems could rely on improving carbon and water uptake when water is not limiting, instead of buffering the impacts of drought itself when water shortage occurs. Supporting this hypothesis, fall and winter photosynthesis has been postulated in drought-prone ecosystems as a mechanism that replenishes carbon storage pools that have been reduced during stressed summer drought conditions (Hartmann et al., 2015).

Tree responses to environmental conditions could even be in opposite directions for trees under different competitive stress within the same stand (Sánchez-Salguero et al., 2015a; Ford et al., 2017). We found a higher sensitivity (expressed as the rates of change in growth and water transpiration per unit of change in the environmental conditions; i.e., the slope; Fig. 6) on competitively advantaged trees. By opposite, disadvantaged trees support an interactive effect of climate and competition, coping with water shortage and neighbourhood shading (Figs. 5 and 6; Canham et al., 2006). Trees subjected to lower competition are more sensitive to water availability (positive response), likely because they allocate more resources to growth (Pretzsch et al., 2012; Gleason et al., 2017). On the one hand, the greater exposure of remaining trees in the thinned plots to environmental conditions could have resulted in a greater climate sensitivity compared to more sheltered trees beneath closed stands (Breda et al., 2006). Anyway, the most significant effect of thinning seems to be that remaining trees, whose canopies were better exposed to light, responded more effectively and more quickly to the environment by increasing water uptake and

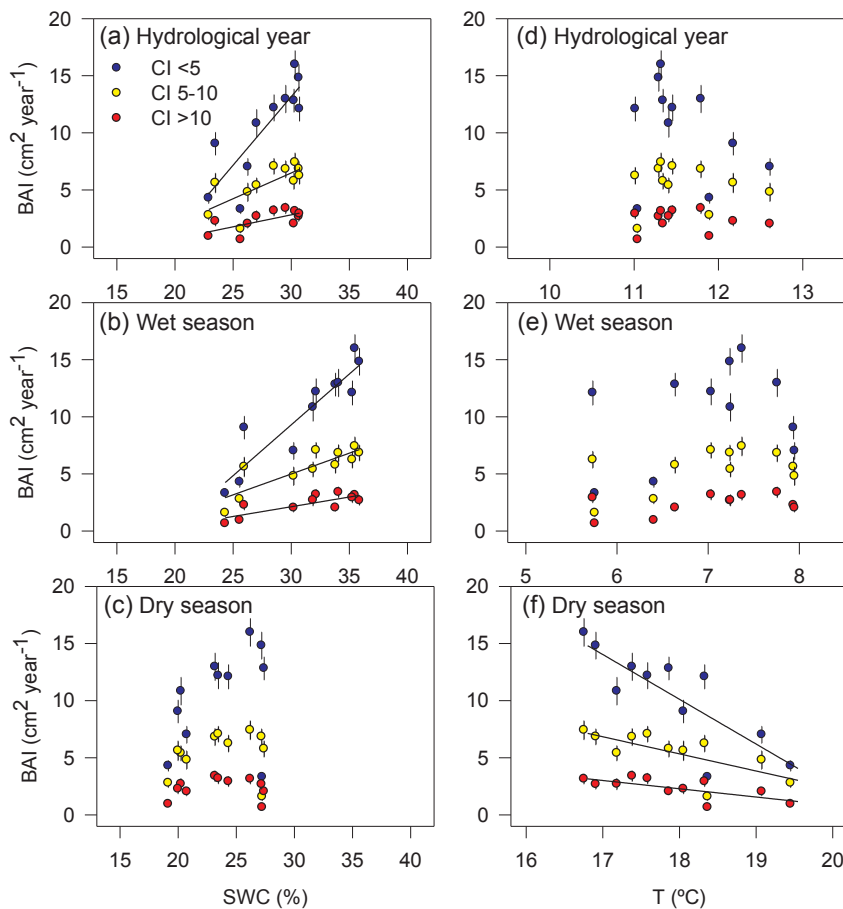


Fig. 6. Linear regressions obtained between the average microclimatic conditions of volumetric soil water content (SWC) and air temperature (T) and the annual basal area increments (BAI) of trees subjected to contrasting competition intensity (CI). CI values were divided in three categories: trees with a CI higher than 10 (red in the on-line color version), trees with a CI between 5 and 10 (yellow in the on-line color version), and trees with a CI lower than 5 (blue in the on-line color version). Error bars indicate the standard error. SWC (a, b and c) and T (d, e and f) were averaged for hydrological year (October–September, a and d); wet season (October–April, b and e); and dry season (May–September, c and f). Only significant regressions ($p < .05$) are showed. Slopes of the regressions for $CI < 5$ were statistically different to those of $CI 5-10$ and $CI > 10$; slopes of $CI 5-10$ and $CI > 10$ were not statistically different (two-slopes comparison test). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

allocating resources to stem growth (Fig. 3; Giuggiola et al., 2016).

By opposite, transpiration (SFD) and growth (BAI) of trees subjected to high competition were, on average, reduced (Fig. 4). Trees growing within high stand density prevent water loss by stomata closure during longer periods than those growing at lower stand density (Linares et al., 2009; Sánchez-Salguero et al., 2015b). Limited water availability might lead to hydraulic failure (McDowell, 2011), while continued metabolic demand for carbohydrates, as well as increasing respiration rates linked to temperature rise, led to increasing carbon starvation likelihood (Adams et al., 2009; Reich et al., 2014).

This contrasting responsiveness of individual trees to climate, with respect to their competitive status, posits that drought effects are related to forest attributes, such as stand density, sizes diversity, and spatial pattern (Gómez-Aparicio et al., 2011; Martínez-Vilalta et al., 2012; Fernández-de-Uña et al., 2015). In turn, managing stand structure may potentially be able to modulate such climate-related drivers (Sohn et al., 2016). Our results support that thinning provides a promising strategy for minimizing climate change effects on drought-sensitive tree species by improving resources availability to the remaining trees. Nonetheless, despite it is widely acknowledged that stand density reduction fosters individual tree growth, several stand-scale concerns remain poorly understood.

4.2. Stand-level effects of structure management on drought-sensitive tree species

Competition for resources is a well-recognized key biotic factor that affects stand-level mortality, sizes structure, and species composition (Canham et al., 2006; Lines et al., 2010; D'Amato et al., 2013; Carnwath and Nelson, 2016). Here, we illustrate that stand structural variables, as a legacy of previous forest management, are among the main

determinants of forest growth and, consequently, they should be taken into account in the expected future dynamics, including climate sensitivity and carbon stock trends (Gómez-Aparicio et al., 2011; Vayreda et al., 2012; Ruíz-Benito et al., 2013; Ford et al., 2017).

The structural pattern observed in *A. pinsapo* seems consistent with the expected self-thinning dynamics related to the recent abandonment of forest management, with the consequent increase in stand density and competition (Linares and Carreira, 2009). The studied stands were near to even-aged, with lefty-shaped diameter distribution (i.e., dominated by the lower sizes; Fig. 1). In turn, the performed thinning attempted to mimic uneven-aged stands properties, such as the presence of tiny even-aged clumps with scattered overtopping individuals (Franklin et al., 2002). Despite stand density declines as size classes increased, to the point where the largest size classes were quite scattered, thinned plots presented more balanced stand structure, compared to controls (Fig. 1). As a result, thinned plots should allow for greater light penetration and encourages deeper crowns and greater vertical structure, furthermore lowering mean competition for resources (Fig. 5). We promoted as long as possible an irregular canopy that includes small gaps, where regeneration should be favoured in the near future (Beckage et al., 2000; Dobrowolska and Veblen, 2008).

Stand density reduction performed by experimental thinning will temporarily diminish leaf area at the stand scale (D'Amato et al., 2013; Sohn et al., 2016; Giuggiola et al., 2016). The corresponding decline of total stand photosynthesis leads to declines in gross and net primary productivity at thinned stands over some time period (Dore et al., 2012; Stuart-Haëntjens et al., 2015). Afterward, stand-level productivity may likely recover as remaining trees and understory vegetation react to thinning increasing individual-scale production, according to enhanced water uptake and light use efficiency (Goetz et al., 2012; Stuart-Haëntjens et al., 2015). Eddy covariance measurements performed in a

Pinus ponderosa-dominated ecosystem in northern Arizona showed that a thinned site reduced its carbon sink strength, compared to undisturbed-control site, only for the first two years after the treatment (Dore et al., 2012). Thereafter, in the third and fourth years, annual carbon sink strength of the thinned site was higher than the undisturbed site, suggesting that thinning reduced aridity and drought limitation to carbon uptake (Dore et al., 2012; Sohn et al., 2016). This results contrast to our estimates of stand-level BAI (Supporting Information, Fig. S4a), those values were on average lower in the thinned plots, despite significant tree-level higher growth rates over the study period.

As regards changes in water fluxes following experimental thinning, density reduction should reduce stand-level transpiration (Anderegg et al., 2016). Lower leaf area itself will drive this decrease in transpiration, which should also lead to increases in soil moisture (but see also Miller et al., 2011). Alike stand-level BAI, our estimates of stand-level SFD were usually lower in the thinned plots (Supporting Information, Fig. S4b). That is, the sum of the lower growth and sap flow rates of a larger number of trees within the control plots was higher than the sum of the higher growth and sap flow rates of a smaller number of trees within the thinned plots. Nonetheless, these estimated stand-level differences diminished in drought years, as for instance 2005 and 2012, because the growth and sap flow rates in the control plots declined more than those of the thinned ones, suggesting higher resistance in the thinned stands (D'Amato et al., 2013; Diaconu et al., 2017; Supporting Information, Fig. S4).

Water availability is a major limitation to forest productivity in Temperate and Mediterranean mountains (Breda et al., 2006; Linares and Carreira, 2009; D'Amato et al., 2013; Gleason et al., 2017). As a consequence, changes in the water losses from soil evaporation induced by thinning might be a major concern for the hydrology of drought-prone forest ecosystems (Zhang et al., 2001; Adams et al., 2012; Ameztegui et al., 2017). The experimental design of the thinning performed here enhanced spatial variability, according to the goal of increasing stand structure diversity. Thus, spatial variability in soil evaporation should be larger in the thinned plots, compared to controls (Huxman et al., 2005; Moreno-Gutiérrez et al., 2012). It is known that, in water-limited forests, soil evaporation fluxes in sun-exposed areas may be up to two times those in shaded areas (Raz-Yaseef et al., 2010). This spatial variability in soil evaporation is related to radiation, which may be about 90% higher in exposed compared to shaded sites, and correlates with SWC (Raz-Yaseef et al., 2010). Regarding the thinned plots, SWC should be higher in exposed areas during the wetting season, but higher in shaded areas during the drying season (Giuggiola et al., 2016). By opposite, as regards the control plots, SWC was higher during the drought season, likely related to higher fraction of shaded areas, while the higher canopy cover of dense stands may increase intercepted precipitation and transpiration, reducing groundwater infiltration (Huxman et al., 2005; Adams et al., 2012; Ameztegui et al., 2017).

Alternatively, it should be noted that thinning might be also changing the composition of understory plant functional types within forest ecosystems over time (Beckage et al., 2000; Anderegg et al., 2012). Studies performed on drought-prone forests dominated by *Pinus sylvestris* in the inner Alpine region reported higher soil water content when the understory vegetation was removed (Giuggiola et al., 2016). That is, the water loss via water consumption and transpiration by the understory vegetation of our thinned plots might exceed the loss of water due to higher insolation and soil evaporation (Matsushima and Chang, 2007; Giuggiola et al., 2016). Such community-level shift can lead to significant impacts on the ecosystem carbon and water dynamics (Zhang et al., 2001; Anderegg et al., 2012; Poyatos et al., 2014; Dieleman et al., 2015).

In our study case, drought sensitive understory species may suffer from high temperature stress due to canopy opening (Dobrowolska and Veblen, 2008). As a result, stand subjected to lower competition may shift to different functional and structural dynamics due to alterations in canopy structure and resources availability (Matsushima and Chang,

2007). Notwithstanding, carbon uptake could be greater in thinned stands if we take into account the contribution of gap communities dominated by shrubs and graminoids (Ward et al., 2013). Indeed, recent studies showed that warming-induced changes in carbon fluxes were more correlated with corresponding changes in C4 grass abundance, than with soil temperature or moisture (Niu et al., 2013). In the specific case of water-limited fir forests, canopy opening seems to favor these changes in forest structure and species diversity (Dobrowolska and Veblen, 2008). Indeed, field data, obtained in our study area, suggest that *A. pinsapo* gaps created by root rot fungi-related mortality led to increasing Mediterranean-type scrubs (Navarro-Cerrillo et al., 2014), but also seedling and saplings of different tree species, suggesting potential vegetation shifts from near to even aged *A. pinsapo* fir stands towards mixed forests (Beckage et al., 2000; Galiano et al., 2010; Rigling et al., 2013).

5. Conclusions

Our results place forest structure in a climate change-driven context and outline the combined effects of competition and drought on tree carbon and water balances. Hence, we demonstrate that the effect of drought on individual trees was mediated by their competitive status, regarding the local neighbourhood. Trees responsiveness to microclimate depends largely on whether they were subjected to competition. These results support that stand density reduction provides a promising strategy for minimizing the effects of rising temperatures and changes in precipitation patterns on drought-sensitive tree species; specifically, by improving growth and water uptake in the remaining trees. Nevertheless, our results also support a higher temperature and water depletion according to density reduction, suggesting that lower competition might also increase soil and understory evapotranspiration. Adaptive management, as the experimental thinning reported here, may increase tree-level resources availability, but the long-term effectiveness of this approach at the stand-level remains uncertain.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.10.017>.

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