

Response of biomass allocation patterns to thinning in *Pinus halepensis* differs under dry and semiarid Mediterranean climates

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Abstract

• **Key message** To implement adaptive management in post-fire-regenerated Aleppo pine forests, we developed specific biomass equations in two early-thinned climatically contrasting stands. We found thinning enlarged biomass components, although climate primarily

constrained biomass accumulation and biomass allocation.

• **Context** The increase in burnt surface by wildfires in the Mediterranean Basin has triggered the proliferation of large unmanaged forested areas, particularly Aleppo pine stands in drier and lower altitudinal areas. These young naturally regenerated stands require specific biomass models for accurate carbon stock quantification.

• **Aims** The aim of this study is to analyse the effects of climate (dry vs. semiarid), age and forest management (early thinning) on biomass accumulation and biomass allocation of young *Pinus halepensis* components: stem, crown (crown wood, needles and cones) and roots.

• **Methods** We sampled 251 individual Aleppo pine trees across an age sequence of 5–16 years old to develop component biomass equations.

• **Results** We observed that biomass allocation differed with climate, age and tree density. The crown was the largest biomass fraction, followed by root fraction and stem fraction. At the most limiting site (semiarid climate), we found major reproductive efforts, which may be shaped by adaptive traits to recurrent fires or recurrent drought episodes.

• **Conclusion** Climate was the first limiting factor to constrain biomass accumulation and biomass allocation. Thinning played a key role in promoting positive effects on biomass components at both sites, which were enlarged under less stressful site conditions (dry climate). These results may help managers understand how altering stand density promotes more resilient forests.

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Contribution of the co-authors All co-authors contributed significantly to this manuscript. Francisco R. López-Serrano, Daniel Moya and Enrique Hernández-Tecles sampled in the field, carried out the tests described in methods, analyzed the results and contributed to edit the manuscript. Eva Rubio, Francisco R. López-Serrano and Raúl Sánchez-Salguero contributed to the data analysis, to the writing and the editing of the manuscript. Jorge De las Heras, Francisco R. López-Serrano and Daniel Moya devised and designed the experiment, coordinated the research project and supervised the work. R. Alfaro-Sánchez was primarily responsible for conducting the field work, data analysis, preparing figures, writing the manuscript and coordinating and implementing contributions from all co-authors.

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1 Introduction

In recent decades, the recurrence and severity of forest fires have increased significantly in the Mediterranean Basin and they are expected to further increase in the near future (Pausas 2004; Pausas and Fernández-Muñoz 2012). Changes in the fire regime are due to the impact of climate and land use changes, which trigger hazardous fuel accumulation (Lloret 2004). One direct consequence of recurrent forest fires is the enlargement of those areas undergoing natural regeneration, which, in Spain, has covered some 280,000 ha of Aleppo pine (*Pinus halepensis* Mill.) forests since 1993 (MAGRAMA 2012). Young post-fire pine stands require silvicultural management to reduce intraspecific competition for growth-limiting soil resources, i.e. water and nutrients (De las Heras et al. 2012), and to reduce the immaturity risk (Zedler 1995). The main objective of forest management in low-productivity Mediterranean terrestrial ecosystems should be not only conservation through the promotion of resilience and resistance to disturbances, such as droughts and wildfires, but also climate change mitigation by enhancing carbon storage capacity (Bravo et al. 2008). However, predicting the effect of post-fire treatments on the resilience of forest stands in the face of climate change is a major challenge for forest managers.

P. halepensis is a post-fire obligate seeder that presents early cone production (3–6 years after regeneration) as one of its main adaptation features to fire-prone areas (Thanos and Daskalidou 2000). This species allocates many resources to produce cones with viable seeds at very early ages, which helps reduce the immaturity risk of facing recurrent fires (Ne'eman et al. 2004). It is plausible that Aleppo pine has inherited advantageous post-fire regeneration traits (Keeley et al. 2012), but it is difficult to distinguish between adaptations to fire from adaptations to other disturbances, in other words, the so-called “dual life history strategy” (Ne'eman et al. 2004).

Very few long-term research works on post-fire rehabilitation have focused on implementing management in growth models (Lavorel et al. 1998; Vicente-Serrano et al. 2010; Ruiz-Benito et al. 2013). Previous studies carried out on young post-fire-regenerated Aleppo pines stands have reported 1–8.5 Mg C ha⁻¹ stored in living pine biomass (age of 16), which were dependent on climate and silvicultural treatments (Alfaro-Sánchez et al. 2014). Accordingly, there it is necessary to consider the interactions between climate and silvicultural treatments in specific young *P. halepensis* biomass models to improve carbon sequestration estimations (López-Serrano et al. 2005; De las Heras et al. 2013). Nevertheless, young tree stands have been ignored when general carbon sequestration approaches have been carried out (Montero et al. 2005). We still lack solid datasets to evaluate how negatively adverse climatic conditions and competition affect biomass and how this becomes one of the best-adapted tree species (*P. halepensis*) to fire and Mediterranean

climate conditions. For instance, if rising temperatures magnify drought severity and lack of management increases competition, this would constrain carbon stocks and biomass allocation (Kazanis et al. 2012). For this reason, understanding the effects of forest management (competition) on biomass estimations could improve fire risk predictions in the Mediterranean environment.

Regarding allocation patterns, the concepts and mechanisms involved in the ecophysiological processes underlying allocation to different biomass components are not well understood and are not, therefore, included in practical growth forest models (Landsberg and Sands 2011). Changes in the allocation of biomass components have been previously related to factors such as tree age, size and the competitive status, supported by the pipe model theory and functional carbon balance (Vanninen 2004). Following functional carbon balance (Brouwer 1983), we expected root partitions to increase under limited nutrient or water availability, i.e. more fine roots and less foliage (Guo and Gifford 2002). Nevertheless, the influence of climate, together with the interaction with silvicultural treatments on biomass allocation, is poorly understood, particularly allocation of biomass to cones, also called the “reproductive effort” (Prairie and Bird 1989; Ne'eman et al. 2011). Hence, a better understanding of biomass accumulation and allocation patterns would foster appropriate silvicultural decisions for forest managers (Rubilar et al. 2013).

The main objective of this study was to analyse the effects of climate, age and forest management on biomass accumulation and biomass allocation of young *P. halepensis* components (stem, crown (crown wood, needles and cones) and roots) in an age sequence from 5 to 16 years. By considering that allocation patterns differ within tree species (Vanninen 2004), we hypothesised that inherited adaptive traits to fire regimes in *P. halepensis*, such as precocious and copious cone production, could also shape biomass allocation patterns, particularly at younger stages, and that these patterns could be modulated by climate and competition.

2 Material and methods

2.1 Study site and silvicultural treatments

The study areas were located in south-eastern Spain, close to the villages of Yeste and Calasparra, in two post-fire *P. halepensis* stands naturally regenerated after the wildfires that occurred in the summer of 1994. Before the wildfires, the study areas were composed of mature stands, mainly of *P. halepensis*, from natural and planted origins, mixed with *Pinus pinaster* Ait. and *Quercus ilex* L. subsp. *ballota* (the latter was found only at Yeste).

At Yeste, average annual rainfall and temperature were 595 mm and 13.6 °C, respectively, whereas they were 340 mm and 16.5 °C, respectively, at Calasparra (data provided

by the Spanish National Meteorological Agency (AEMET)). The ombrothermic index (Rivas-Martínez et al. 1999) revealed an upper dry type at Yeste (hereafter the dry site) and a lower semiarid type at Calasparra (hereafter, the semiarid site).

In 1999, 18 permanent rectangular plots (10×15 m) were established in low-slope locations (<5 %) of the two natural regenerated sites, and the primary densities of Aleppo pine saplings were 8200 saplings ha⁻¹ at the dry site and 79,000 saplings ha⁻¹ at the semiarid site. Different silvicultural treatments were applied to these plots, which included two factors: age and final tree density (Gonzalez-Ochoa et al. 2004; Moya et al. 2008). The acronyms for treatments were indicated by the number of years elapsed since the wildfire until treatments were applied, i.e. stand age and respective tree density (T_{x-y} , where x is the application year and y is the tree density). The first factor had three levels: thinning applied at post-fire year 5 (in 1999, hereafter T_5), at post-fire year 10 (in 2004, hereafter, T_{10}) and at both dates (in 1999 and 2004, hereafter, T_{5+10}). The second factor, final tree density, was grouped as follows: high tree density (1600 and 9500 trees ha⁻¹, i.e. treatments T_{5-1600} , T_{5-9500} and $T_{10-1600}$) and moderate tree density (800 trees ha⁻¹, i.e. treatments T_{5-800} , T_{10-800} and T_{5+10}). A very high tree density group comprising the non-thinned or control plots, hereafter T_C , was also considered. Climate differences determined the contrasting natural post-fire recruitments, which conditioned the silvicultural treatments design. Consequently, at the semiarid site (with a very high sapling recruitment per hectare), we omitted the application of the most drastic treatment (T_{5-800}) to avoid the risk of stand decay. Instead, we carried out a treatment that left a higher tree density (T_{5-9500}). At each site, the permanent plots were randomly assigned to these seven groups, i.e. six thinning treatments and the control group. Three replicates per group were obtained.

2.2 Plot inventories

The permanent plots were inventoried at both sites in 1999 and 2010, corresponding to tree ages 5 and 16, respectively. For the plots with a tree density lower than or equal to 1600 trees ha⁻¹, all the trees were tagged and monitored. For the plots with a higher tree density, only a random sample of 24 trees per plot was monitored. In order to estimate the dry biomass tree components (other than cones) at the plot level, we measured the stem diameter at 30 cm above the ground, d , for each tagged tree (see Alfaro-Sánchez et al. 2014 for further details). Next, we applied appropriate regression equations (see the following sections) to estimate the individual dry biomass component of each tagged tree (b'_i), where subscript i stands for the tree component (i.e. stem, crown branches, needles and roots) and superscript ' indicates that the dry biomass is an estimated value. In order to obtain the dry cone biomass at the tree level, the individual maximum length, L , and width, D , of all the female cones (immature, mature and

serotinous) of each tagged tree were measured. Then, the individual dry biomass of each cone was estimated by regression equations. After adding all the dry cone biomasses of each tagged tree, the dry cone biomass at the tree level (b'_{CO}) was finally obtained

2.3 Destructive samplings

2.3.1 Tree level

The dry above-ground biomasses of individual pine trees were obtained from the destructive samplings carried out in 1999, 2001, 2008 and 2010, which corresponded to the tree ages of 5 (1999) to 16 years (2010). From each silvicultural treatment, we sampled at least nine pine trees distributed along all the diameter classes (Table 1(A)).

From each individual felled tree, d was measured. The total fresh weights of the felled tree components (stem, b_{ST-f} and crown, b_{C-f}) were recorded on a 60-kg field scale (sensitivity 20 g) and a 6-kg table scale (sensitivity 0.2 g) for light material. To estimate the dry biomass of woody material, we sampled

Table 1 Main characteristics of biomass sampling for dry and semiarid sites of (A) trees and (B) cones

A					
Site	Treatment	Age	n	d	
Dry					
	T_C	5, 7, 14, 16	31	0.7–6.8	
	T_{5-1600}	7, 14, 16	35	1.8–10.7	
	T_{5-800}	7, 14, 16	26	1.7–13.2	
	$T_{10-1600}$	14, 16	16	2.3–11.5	
	T_{10-800}	14, 16	21	1.8–11.5	
	T_{5+10}	14, 16	19	1.5–11.2	
Semiarid					
	T_C	5, 7, 16	28	0.4–2.7	
	T_{5-9500}	7, 16	24	0.5–5.9	
	T_{5-1600}	7, 16	24	0.7–7.2	
	$T_{10-1600}$	16	9	1.0–5.6	
	T_{10-800}	16	9	0.6–5.6	
	T_{5+10}	16	9	1.4–7.6	
B					
Site	Age	CO_{Age}	n	D	L
Dry					
	12, 15, 17, 19	9–17	408	15–42	26–92
Semiarid					
	12, 15, 17, 19	9–17	318	12–36	22–94

n number of sampled trees or cones, d tree diameter at 30 cm above the ground (min-max, cm), CO_{Age} age of cones (year), D width of female cones (mm), L length of female cones (mm), T_C non-thinned plots (control), T_{5-9500} thinning in 1999 to a final density of 9500 trees ha⁻¹, T_{5-1600} thinning in 1999 to a final density of 1600 trees ha⁻¹, T_{5-800} thinning in 1999 to a final density of 800 trees ha⁻¹, $T_{10-1600}$ thinning in 2004 to a final density of 1600 trees ha⁻¹, T_{10-800} thinning in 2004 to a final density of 800 trees ha⁻¹, T_{5+10} thinning in 1999 to a final density of 1600 trees ha⁻¹ and thinning in 2004 to a final density of 800 trees ha⁻¹

three stem subsamples (slices), b_{ST} , from each tree, which were taken to the laboratory and dried in an oven (105 °C, 48 h, Pardé and Bouchon 1994) to obtain humidity (%) values on a dry basis. Double random sampling, with ratio estimators Z_i and K_i , was conducted to calculate the total dry biomass components of the crown, b_C (De Vries 1986). The first group of ratio estimators, Z_i , was used to calculate the fresh biomass of the twigs, b_{TW-f} and dry wood of branches, b_{BR} , at the crown level. To accomplish this, eight branches from each tree were randomly sampled and the total fresh weight, W_{C-f} from each one was recorded.

Subsequently, all the twigs on the sampled branches, W_{TW-f} were removed and weighed. A similar procedure was carried out for the wood of branches, W_{BR-f} . The dry biomass of the wood of the branches, W_{BR} , was obtained by subtracting humidity on a dry basis from W_{BR-f} . To estimate the total fresh biomass of twigs and that of the wood of branches, the ratio estimators (Z_i) were calculated as follows:

$$Z_1 = \frac{W_{TW-f}}{W_{C-f}}$$

$$Z_2 = \frac{W_{BR}}{W_{C-f}}$$

Thus, the total fresh biomass of twigs was calculated as $b_{TW-f} = Z_1 \times b_{C-f}$ and the total dry biomass of the wood of branches obtained was $b_{BR} = Z_2 \times b_{C-f}$. The second group of ratio estimators, K_i , was defined to separately obtain the dry biomass of twigs: i.e. the wood of twigs and needles. From all the twigs removed from the eight branches per tree, six random sets were selected composed of one, two, four, six, eight and ten twigs, respectively (31 sampled twigs in all). The fresh weight of each twig set, w_{TW-f} was recorded. Then, woody twigs and needles, w_{WTW} and w_N , respectively, were separated, which were dried (85 °C for 24 h) and weighed (Pardé and Bouchon 1994). The ratio estimators were calculated as follows:

$$K_1 = \frac{w_{WTW}}{w_{TW-f}}$$

$$K_2 = \frac{w_N}{w_{TW-f}}$$

In order to assess the dry biomass of twigs at the crown level, b_{TW} , needles, b_N , and woody twigs, b_{WTW} , the total fresh biomass of twigs was multiplied by the K_i ratio estimators:

$$b_N = K_1 \times b_{TW-f}$$

$$b_{WTW} = K_2 \times b_{TW-f}$$

Finally, the total dry crown wood biomass, b_{CW} , was obtained as the sum of the wood of twigs, b_{TW} , and the wood of branches, b_{BR} (i.e. $b_{CW} = b_{TW} + b_{BR}$), while the total dry crown biomass, b_C , was obtained as the sum of the dry crown

wood biomass and the dry needle biomass (i.e. $b_C = b_{CW} + b_N$). To estimate total dry above-ground and dry root biomass, the regression models developed in Alfaro-Sánchez et al. (2014) were applied.

2.3.2 Cone level

Immature, mature and serotinous cones from each site were randomly selected and cut in 2007, 2009, 2011 and 2013, which correspond to the tree ages (CO_{Age}) of 13 (2007) to 19 years (2013) (Table 1(B)). The total fresh weight, maximum length (L) and width (D) of each cone were recorded. The dry cone biomass was estimated similarly to the dry biomass of the woody material (see the previous section).

2.3.3 Biomass allocation ratios

Changes in the allocation patterns of the different tree components were studied from the ratios obtained between the dry biomass components. Firstly, all the component dry biomass ratios from the destructive sampling were analysed. However, only the ratios that provided new insights into the biomass allocation patterns were considered; i.e. $R_N = b_N/b_A$; $R_{ST} = b_{ST}/b_A$ and $R_{C-ST} = b_C/b_{ST}$. Secondly, the analysis of the ratios was extended to the whole plots by calculating the estimated dry biomass component ratios and by applying the developed biomass equations to each monitored tree of the two plot inventories, which were as follows: $R'_{ST} = b'_{ST}/b'_A$, $R'_{CW} = b'_{CW}/b'_A$, $R'_N = b'_N/b'_A$, $R'_R = b'_R/b'_A$ and reproductive effort $R'_{CO} = b'_{CO}/b'_A$ (Prairie and Bird 1989).

2.4 Statistical analysis

Each dry biomass (hereafter biomass) component model, other than cones (i.e. stem b_{ST} , crown b_C , crown wood biomass—branches and twigs b_{CW} —and needles b_N), was developed by multiple regression analyses, where both the categorical (treatment at each site) and continuous (d) variables were considered following the methods of Alfaro-Sánchez et al. (2014). We chose the quadratic model, as opposed to the logarithmic model, because (i) young trees (unlike adult ones) have no homoscedasticity problems; therefore, log transformation in the dependent biomass variable is not required; (ii) it was the model that maximised the goodness-of-fit statistics; (iii) whereas predictions for smaller size-classed individuals go beyond the range when log models are used (negative values), the quadratic model blocks this possibility.

Biomass models were simplified using a forward stepwise regression method and following the general linear statistic test (F test; Neter et al. 1996). Dry cone biomass (hereafter cone biomass) models were developed by multiple regression analyses where both the categorical (site) and continuous

(maximum length L and width D of the cone) variables were considered. To select the best models, the highest adjusted determination coefficients (R^2_{adj}), the lowest sum of squares error (SEE) and lack of collinearity in the predictor variables were taken into account (Table 2).

One-way ANOVAs were run to analyse the effect of *site* at post-fire year 5 for the estimated biomass components per tree, b'_{ST} , b'_{CW} , b'_{N} and b'_{CO} , and the estimated variables regarding biomass allocation, R'_{ST} , R'_{CW} , R'_{N} and R'_{CO} . Root biomass and biomass allocation to roots were not analysed at post-fire year 5 because the developed regression models were not valid for those diameter classes (see Alfaro-Sánchez et al. 2014). All the response variables were examined for a normal distribution of errors and for homogeneity of variance. To accomplish both the normality and homoscedasticity assumptions of the variables, log transformations were applied. The Tukey-Kramer HSD test was used for post hoc comparisons.

Generalised linear mixed model (GLMM) analyses were performed to evaluate the effect that factors age and treatment had on the estimated biomass components per tree and for the variables regarding biomass allocation at the plot level. Independent GLMMs were fitted for each site. The plot factor was included as a random effect to account for the spatial autocorrelation among trees within plots at each age. Those models with the lowest Akaike's information criterion (AIC) values were selected. The equivalent models in terms of statistical explanatory power (those within two AIC units of the best model) were also reported. The R^2 of the model fit of the observed versus the predicted was used as a goodness-of-fit measure. Generalised linear model (GLM) analyses were performed to evaluate the effects of the treatment factor at the plot level for b'_{R} and R'_{R} for the 16-year-old data. Independent GLMs were fitted per site. For the model selection, the same procedure as that presented for GLMMs was followed. The models were fitted using the packages *lme4* (Bates et al. 2014) and *MuMIn* (Barton 2013) in the R package, version 3.1 (Development Core Team 2013).

3 Results

3.1 Biomass models

For each above-ground biomass component (crown wood, needles, crown and stem), the complete model was simplified into four homogeneous groups, whose intercept and slope values significantly differed (Table 2(A)). Thus, four regression equations were obtained in the form of $\sqrt{Y} = a_0 + a_1 \cdot d^2$ based on the data for all the ages, including d as a significant predictive variable for four particular interactions of factor site and treatment ($P < 0.05$; 95 % $> R^2_{\text{adj}} > 87$ %).

All the F statistic values that test the null hypothesis, for which the simplified models explained a similar variance to that of the complete model, were smaller than the F statistic for the level of significance and degrees of freedom of our data, which verified that $F \leq 0.66 < F(0.95; 16, 227)$ for the above-ground biomass components (Table 2(A)).

These biomass equations were valid for the whole range of d values recorded at each site, i.e. the [0.7, 13.2]-cm range at the dry site and the [0.4, 7.6]-cm range at the semiarid site (Tables 1 and 2(A)). Some overlapping between ranges of diameters from different ages was noted although, for a given equation, the large diameter classes generally corresponded to older individuals (Fig. S1). The regression model parameters showed lower intercept and higher slope values for the individual pine trees occurring in control stands, mainly at the semiarid site, which emphasises the effect of climate (Fig. S1; Table 2(A)).

The developed cone biomass model included factors *site*, D and L as the significant predictive variables. Thus, two regression models in the form $Y = a_0 + a_1 \cdot L \cdot D^2$ were obtained, one per site, based on the data for all the ages ($P < 0.05$; $R^2_{\text{adj}} = 88$ %; Table 2(B)).

3.2 Effect of climate, age and treatments on biomass per tree

The between-site ANOVA analyses revealed significantly higher values at post-fire year 5 of \bar{b}'_{ST} , \bar{b}'_{CW} and \bar{b}'_{N} at the dry site, while the \bar{b}'_{CO} values were similar at both sites for this age (Table 3). The comparison made of the alternative GLMMs revealed those that best fitted the above-ground biomass components for each site at the plot level, i.e. \bar{b}'_{ST} , \bar{b}'_{CW} , \bar{b}'_{N} and \bar{b}'_{CO} , when considering the effect of factors age and treatment. For the below-ground biomass components (\bar{b}'_{R}), the comparison made of the alternative GLMs revealed those that best fitted this component for each site at the plot level when considering the treatment factor (Table 4). At the dry site, the best fitting models ($R^2 \geq 0.40$; Table 4(A)) included factors age and treatment as the explanatory variables for \bar{b}'_{ST} , \bar{b}'_{CW} , \bar{b}'_{N} and \bar{b}'_{CO} and the treatment factor for \bar{b}'_{R} . At the semiarid site, the best fitting models ($R^2 \geq 0.63$; Table 4(B)) included factors age and treatment as the explanatory variables for \bar{b}'_{ST} , \bar{b}'_{CW} and \bar{b}'_{N} and factor treatment for \bar{b}'_{R} . For variable \bar{b}'_{CO} , only the age factor was significant ($R^2 = 0.04$; Table 4(B)).

Regarding the effects of silvicultural treatments at the dry site, the biomass components of the pine trees occurring in plots with the same tree density, but with different treatment application dates (i.e. T_{5-800} vs. T_{10-800} or T_{5+10} and T_{5-1600} vs. $T_{10-1600}$), were compared (Fig. 1). At post-fire year 16, \bar{b}'_{ST} , \bar{b}'_{CW} , \bar{b}'_{N} and \bar{b}'_{R} for T_{5-800} almost doubled the value for T_{10-800} and were 1.7-fold higher than the value for T_{5+10} . No differences were found between T_{5-1600} and $T_{10-1600}$. The

Table 2 Biomass equations for (A) crown wood (b_{CW}), needles (b_N), crown (b_C) and stem biomass components (b_{ST} , g) according to the diameter at 30 cm above the ground (d , cm) for four particular interactions of factors site and treatment (Eqs. 1–4) and (B) for cone biomass (b_{CO} , g) according to both the length and width of female cones

A		Site	Treatment				
Eq. 1	Dry		T_C	$\sqrt{b_{CW}} = 8.78 + 0.96 \cdot d^2$	$\sqrt{b_N} = 9.43 + 0.83 \cdot d^2$	$\sqrt{b_C} = 12.93 + 1.27 \cdot d^2$	$\sqrt{b_{ST}} = 7.19 + 0.89 \cdot d^2$
	Semi-arid		$T_{5-9500}; T_{5-1600}; T_{10-1600}; T_{10-800}; T_{5+10}$				
Eq. 2	Dry		$T_{5-1600}; T_{10-1600}; T_{10-800}; T_{5+10}$	$\sqrt{b_{CW}} = 16.47 + 0.49 \cdot d^2$	$\sqrt{b_N} = 16.48 + 0.43 \cdot d^2$	$\sqrt{b_C} = 23.38 + 0.66 \cdot d^2$	$\sqrt{b_{ST}} = 12.34 + 0.59 \cdot d^2$
Eq. 3	Dry		T_{5-800}	$\sqrt{b_{CW}} = 19.66 + 0.42 \cdot d^2$	$\sqrt{b_N} = 19.81 + 0.38 \cdot d^2$	$\sqrt{b_C} = 28.10 + 0.57 \cdot d^2$	$\sqrt{b_{ST}} = 17.06 + 0.51 \cdot d^2$
Eq. 4	Semi-arid		T_C	$\sqrt{b_{CW}} = 2.44 + 2.31 \cdot d^2$	$\sqrt{b_N} = 2.89 + 2.07 \cdot d^2$	$\sqrt{b_C} = 3.81 + 3.10 \cdot d^2$	$\sqrt{b_{ST}} = 2.92 + 2.07 \cdot d^2$
R^2_{adj}				87	88	89	95
MAE				4.727	4.119	5.814	3.113
SEE				6.499	5.594	7.881	4.416
B		Dry site	$b_{CO} = 3.30 + 0.000284 \cdot L \cdot D^2$				
	Semi-arid site		$b_{CO} = 2.57 + 0.000284 \cdot L \cdot D^2$				
	R^2_{adj}		88				
	SEE		2.930				
	MAE		2.377				

The goodness-of-fit estimators (adjusted determination coefficient (R^2_{adj}), standard error of estimation (SEE) and mean absolute error (MAE)) are shown b_{CW} crown wood biomass, b_N needle biomass, b_C crown biomass, b_{ST} stem wood biomass, b_{CO} cone biomass, d mean diameter at 30 cm above the ground (cm), D individual width of female cones, L individual length of female cones

Table 3 Mean (standard error) estimated biomass components \bar{b}'_{ST} , \bar{b}'_{CW} , \bar{b}'_N and \bar{b}'_{CO} (g) and ratios \bar{R}'_{ST} , \bar{R}'_{CW} , \bar{R}'_N and \bar{R}'_{CO} (on a per unit basis) at five post-fire years for each site

Site	\bar{b}'_{ST}	\bar{b}'_{CW}	\bar{b}'_N	\bar{b}'_{CO}	\bar{R}'_{ST}	\bar{R}'_{CW}	\bar{R}'_N	\bar{R}'_{CO}
Dry	169 (8)*	224 (10)*	216 (8)*	2.3 (0.4)	0.265 (0.001)	0.3643 (0.0003)*	0.370 (0.001)	0.0034 (0.0005)
Semiarid	22.0 (1.1)	26.3 (1.4)	27.7 (1.2)	2.1 (0.3)	0.2859 (0.0003)*	0.338 (0.001)	0.376 (0.001)*	0.028 (0.004)*

\bar{b}'_{ST} mean estimated stem biomass of all the trees per plot (g), \bar{b}'_{CW} mean estimated crown wood biomass (g), \bar{b}'_N mean estimated needle biomass (g), \bar{b}'_{CO} mean estimated root biomass (g), \bar{R}'_{ST} mean estimated stem biomass divided by the mean estimated above-ground biomass, \bar{R}'_{CW} mean estimated crown wood biomass divided by the mean estimated above-ground biomass ratio, \bar{R}'_N mean estimated needle biomass divided by the mean estimated above-ground biomass, \bar{R}'_{CO} the reproductive effort as the mean estimated cone biomass divided by the mean estimated above-ground biomass

* $P < 0.05$, significant differences between sites

values of \bar{b}'_{ST} , \bar{b}'_{CW} , \bar{b}'_N and \bar{b}'_R for T_{5-800} tripled those for T_{5-1600} . At the semiarid site, \bar{b}'_{ST} , \bar{b}'_{CW} , \bar{b}'_N and \bar{b}'_R of the pine trees occurring in plots with the same tree density (i.e. T_{10-800} vs. T_{5+10} , and T_{5-1600} vs. $T_{10-1600}$) were compared (Fig. 1). No differences were found between T_{10-800} and T_{5+10} , but T_{5-1600} was 1.5-fold higher than $T_{10-1600}$, nor between the values of \bar{b}'_{ST} , \bar{b}'_{CW} , \bar{b}'_N and \bar{b}'_R for T_{10-800} or T_{5+10} and that for T_{5-1600} .

The highest \bar{b}'_{CO} was attained with treatment T_{5-800} at the dry site and with T_{10-800} at the semiarid site, while the lowest \bar{b}'_{CO} was found in the non-thinned plots at both sites (Fig. 1). At the dry site, no differences were found for \bar{b}'_{CO} between T_{5-800} and T_{10-800} , nor between T_{5-1600} and $T_{10-1600}$, but the value of T_{5-800} and T_{10-800} doubled that of T_{5-1600} , $T_{10-1600}$ and T_{5+10} . At the semiarid site, the cone biomass of T_{10-800} was 1.5-fold greater than that of T_{5+10} , and $T_{10-1600}$ was 1.7-fold greater than T_{5-1600} . T_{10-800} was 2.4-fold greater than $T_{10-1600}$.

3.3 Effects of climate, age and treatments on biomass allocation

From the destructively sampled trees, it was found that the individuals in the lowest diameter class exhibited high variability for ratios R_{ST} (from ~0.15 to 0.60) and R_N (ranging from ~0.20 to 0.55), whereas those individuals in the highest diameter class (>4–6 cm) presented a limit value for these ratios: i.e. R_{ST} came close to 0.40 and 0.30 at the dry site and the semiarid site, respectively, and R_N came close to 0.25 and to 0.30 at the dry site and the semiarid site, respectively (Fig. 2).

From the destructive sampled tree data, relationships between b_C and b_{ST} were obtained for the moderate, high and very high tree density groups (Fig. 3). The results showed a high correlation between b_C and b_{ST} . Hence, a less pronounced slope was found at the dry site (1.42) than at the semiarid site (2.56), which indicates that the individuals at the dry site allocated more biomass in stems and less in crowns. For the lowest b_C and b_{ST} values, tree density had

no clear effect on the slope values, whereas the slopes decreased with b_{ST} at both sites for the high and very high tree densities. Conversely for the highest b_C and b_{ST} values, the regressions showed limiting slope values.

At the plot level and between sites, the ANOVA analysis revealed significantly higher values at five post-fire years for \bar{R}'_{ST} at the dry site and \bar{R}'_{CW} , \bar{R}'_N and \bar{R}'_{CO} at the semiarid site (Table 3). The comparison made of alternative GLMMs revealed those that best fitted the biomass allocation ratios (Table 4). At the dry site, the best fitting models for \bar{R}'_{ST} , \bar{R}'_{CW} and \bar{R}'_N ($R^2 \geq 0.68$; Table 4(A)) included factors age and treatment as the explanatory variables. For \bar{R}'_R , the best fitting model ($R^2 = 0.43$; Table 4(A)) included the treatment factor as the explanatory variable. For \bar{R}'_{CO} , two models showed a similar explanatory power ($AIC \leq 2$; $R^2 \leq 0.10$; Table 4(A)), one was included as explanatory variable factor age and the alternative one was the treatment factor.

At the semiarid site, the best fitting models for \bar{R}'_{ST} and \bar{R}'_{CO} included factors age and treatment as the explanatory variables ($R^2 = 0.25$ and $R^2 = 0.58$, respectively; Table 4(B)). For \bar{R}'_{CW} and \bar{R}'_N , the best fitting models included the age factor as the explanatory variable ($R^2 = 0.73$ and $R^2 = 0.47$, respectively; Table 4(B)), whereas for \bar{R}'_R , the best fitting model included the treatment factor ($R^2 = 0.84$; Table 4(B)).

In general, a significant increase in \bar{R}'_{ST} was found over time at the dry site (average values from 0.27 to 0.34), whereas it remained constant at the semiarid site (~0.29) (Table 3; Fig. S2). Ratio \bar{R}'_{CW} marginally decreased over time at the dry site (from 0.36 to 0.35) but increased over time at the semiarid site (from 0.34 to 0.37). At both sites, \bar{R}'_N was higher at the semiarid site than at the dry one and decreased over time (from 0.37 to 0.31 at the dry site and from 0.38 to 0.35 at the semiarid site). \bar{R}'_{CO} also increased over time at the dry site (average values from 0.003 to 0.03) but lowered at the semiarid site (from 0.03 to 0.01) (Table 3; Fig. S2).

The results showed that thinning at the dry site prompted a significant increase in the \bar{R}'_{ST} and \bar{R}'_{CO} ratios of the individual pine trees (maximum for T_{5-800} and T_{10-800} , respectively) and a significant decrease in \bar{R}'_{CW} and \bar{R}'_N

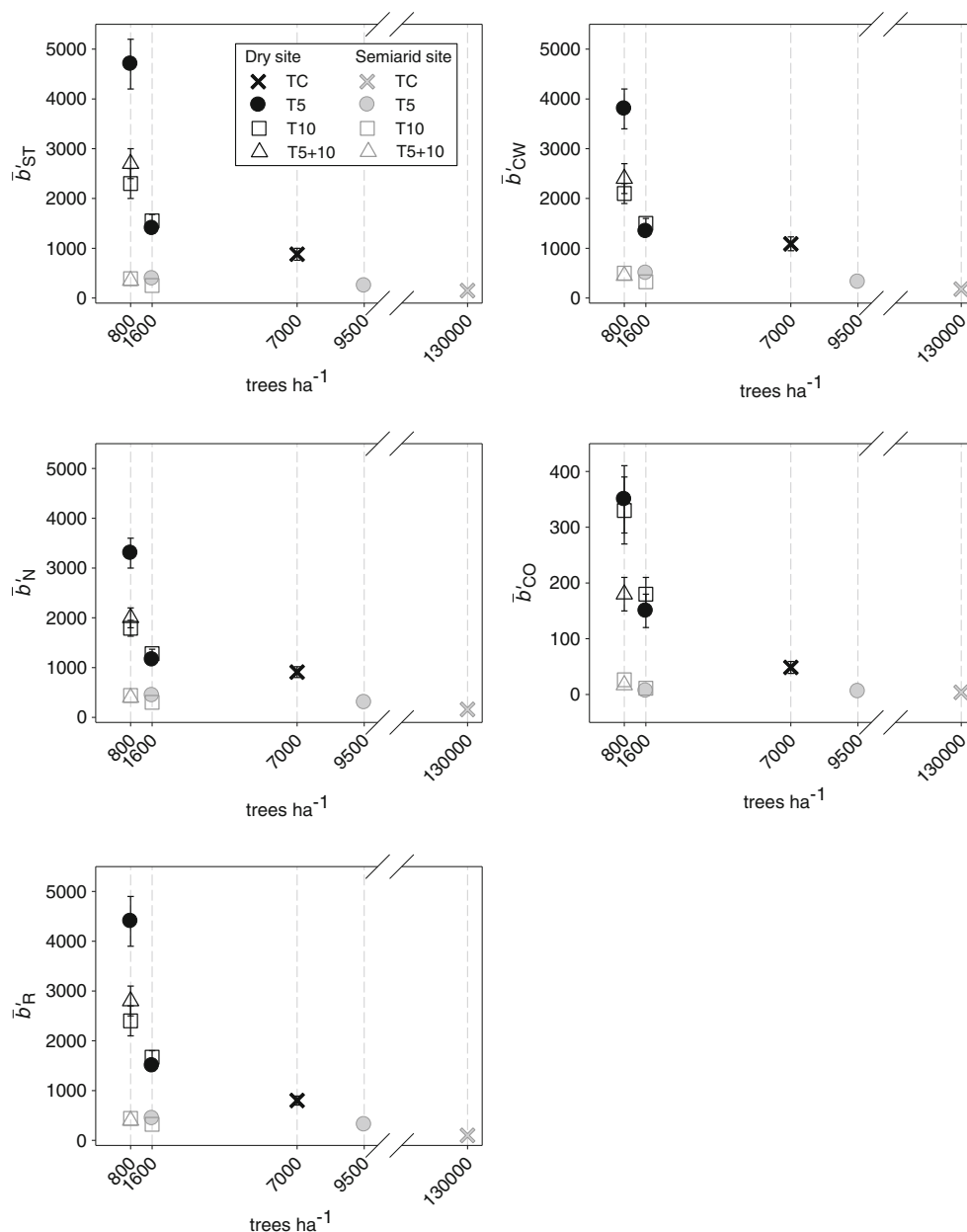
Table 4 Coefficients (standard error) obtained in the best-fitted GLMMs for log-transformed estimated biomass components \bar{b}'_{ST} , \bar{b}'_{CW} , \bar{b}'_N , \bar{b}'_{CO} and \bar{b}'_R (g) and ratios \bar{R}'_{ST} , \bar{R}'_{CW} , \bar{R}'_N , \bar{R}'_{CO} and \bar{R}'_R (on a per unit basis) developed for the dry site (A) and semiarid site (B) according to fixed (age, treatment) and random (σ^2_{Plot}) effects

A Dry site										
Fixed effect	$\log(\bar{b}'_{ST})$	$\log(\bar{b}'_{CW})$	$\log(\bar{b}'_N)$	$\log(\bar{b}'_{CO})$	$\log(\bar{b}'_R)$	$\log(\bar{R}'_{ST})$	$\log(\bar{R}'_{CW})$	$\log(\bar{R}'_N)$	$\log(\bar{R}'_{CO})$	$\log(\bar{R}'_R)$
(Intercept)	4.91 (0.09)	5.23 (0.09)	5.24 (0.08)	2.07 (0.15)	6.41 (0.19)	-1.325 (0.008)	-1.009 (0.002)	-0.998 (0.008)	-4.22 (0.14)	-1.150 (0.020)
Age 16	1.73 (0.10)	1.63 (0.09)	1.46 (0.08)	1.8 (0.3)	n.i.	0.132 (0.010)	0.032 (0.003)	-0.138 (0.009)	0.52 (0.13)	n.i.
$T_{10-1600}$	0.47 (0.15)	0.28 (0.13)	0.32 (0.12)	0.9 (0.3)	0.8 (0.3)	0.115 (0.015)	-0.073 (0.004)	-0.041 (0.013)	n.s.	0.65 (0.21)
T_{5-1600}	0.66 (0.15)	0.47 (0.13)	0.47 (0.12)	0.8 (0.3)	0.7 (0.3)	0.125 (0.015)	-0.063 (0.004)	-0.061 (0.013)	n.s.	0.44 (0.24)
T_{5+10}	1.02 (0.16)	0.75 (0.15)	0.76 (0.13)	1.1 (0.3)	1.3 (0.3)	0.174 (0.016)	-0.091 (0.005)	-0.087 (0.014)	n.s.	0.23 (0.25)
T_{5-800}	1.03 (0.17)	0.68 (0.16)	0.79 (0.14)	1.5 (0.3)	1.7 (0.3)	0.188 (0.017)	-0.150 (0.005)	-0.057 (0.015)	n.s.	0.21 (0.25)
T_{10-800}	0.77 (0.16)	0.53 (0.15)	0.56 (0.13)	1.5 (0.3)	1.2 (0.3)	0.150 (0.016)	-0.088 (0.005)	-0.067 (0.014)	n.s.	0.95 (0.22)
Random effect										
σ^2_{Plot}	0.13	0.11	0.09	0.11	n.i.	0.0010	0.00004	0.0010	0.12	n.i.
AIC	1536.4	1385.8	1245.4	1053.5	687.7	-1830.3	-3553.7	-2069.6	924.6	925.0
R^2	0.71	0.70	0.71	0.54	0.40	0.75	0.72	0.68	0.04	0.10
B Semiarid site										
Fixed effect	$\log(\bar{b}'_{ST})$	$\log(\bar{b}'_{CW})$	$\log(\bar{b}'_N)$	$\log(\bar{b}'_{CO})$	$\log(\bar{b}'_R)$	$\log(\bar{R}'_{ST})$	$\log(\bar{R}'_{CW})$	$\log(\bar{R}'_N)$	$\log(\bar{R}'_{CO})$	$\log(\bar{R}'_R)$
(Intercept)	2.89 (0.05)	3.06 (0.05)	3.16 (0.05)	2.26 (0.14)	4.08 (0.11)	-1.252 (0.002)	-1.084 (0.003)	-0.980 (0.004)	-2.06 (0.11)	-1.63 (0.03)
Age 16	1.71 (0.09)	1.74 (0.09)	1.56 (0.08)	0.37 (0.13)	n.i.	0.044 (0.004)	0.0868 (0.0017)	-0.085 (0.003)	-1.77 (0.23)	n.i.
$T_{10-1600}$	0.78 (0.12)	0.86 (0.12)	0.89 (0.11)	n.s.	1.64 (0.16)	-0.066 (0.006)	n.s.	n.s.	-0.2 (0.3)	0.66 (0.04)
T_{5-1600}	1.23 (0.12)	1.29 (0.12)	1.28 (0.11)	n.s.	1.90 (0.16)	-0.039 (0.006)	n.s.	n.s.	-0.9 (0.3)	0.59 (0.04)
T_{5+10}	1.01 (0.14)	1.07 (0.14)	1.08 (0.12)	n.s.	1.82 (0.17)	-0.049 (0.007)	n.s.	n.s.	-0.4 (0.3)	0.61 (0.04)
T_{10-800}	0.93 (0.16)	0.98 (0.16)	1.01 (0.14)	n.s.	1.87 (0.19)	-0.051 (0.008)	n.s.	n.s.	-0.2 (0.3)	0.60 (0.05)
T_{5-9500}	0.83 (0.12)	0.92 (0.12)	0.94 (0.11)	n.s.	1.60 (0.16)	-0.069 (0.006)	n.s.	n.s.	-0.7 (0.3)	0.68 (0.04)
Random effect										
σ^2_{Plot}	0.03	0.03	0.03	0.13	n.i.	6×10^{-5}	10^{-4}	2×10^{-4}	4×10^{-9}	n.i.
AIC	1473.3	1466.3	1286.0	536.8	603.4	-3392.3	-3647.9	-2770.8	573.6	-541.0
R^2	0.81	0.82	0.84	0.04	0.63	0.25	0.73	0.47	0.58	0.84

See Tables 1 and 3 for acronyms. Age 5 and T_C were considered the reference level

\bar{b}_R mean root biomass (g), \bar{R}_R mean root biomass divided by the mean above-ground biomass, n.i. not included, n.s. not significant

Fig. 1 Mean biomass components (\bar{b}'_{ST} , \bar{b}'_{CW} , \bar{b}'_N , \bar{b}'_{CO} , \bar{b}'_R , g) at the plot level in 16-year-old trees (y axis). Tree density of the plots (trees ha⁻¹) is displayed on the x axis. The application year of treatments is represented by black-coloured symbols for the dry site and grey-coloured symbols for the semiarid site (see Tables 3 and 4 for acronyms). T_C non-thinned plots (control), T_5 thinning in 1999, T_{10} thinning in 2004, T_{5+10} thinning in 1999 to a final density of 1600 trees ha⁻¹ and thinning in 2004 to a final density of 800 trees ha⁻¹



(maximum for T_{5-800} and $T_{5-800}T_{5+10}$ and T_{10-800} , respectively). Thinning at the semiarid site prompted a significant increase in the \bar{R}'_{CO} ratio (maximum for T_{10-800}) and a non-significant effect on the \bar{R}'_{ST} , \bar{R}'_{CW} and \bar{R}'_N ratios. The results for \bar{R}'_R revealed a higher \bar{R}'_R at the dry site than at the semiarid site. The lowest \bar{R}'_R percentages were found for the individuals from the control stands (0.33 at the dry site and 0.20 at the semiarid site) at both sites (Table 4; Fig. S2).

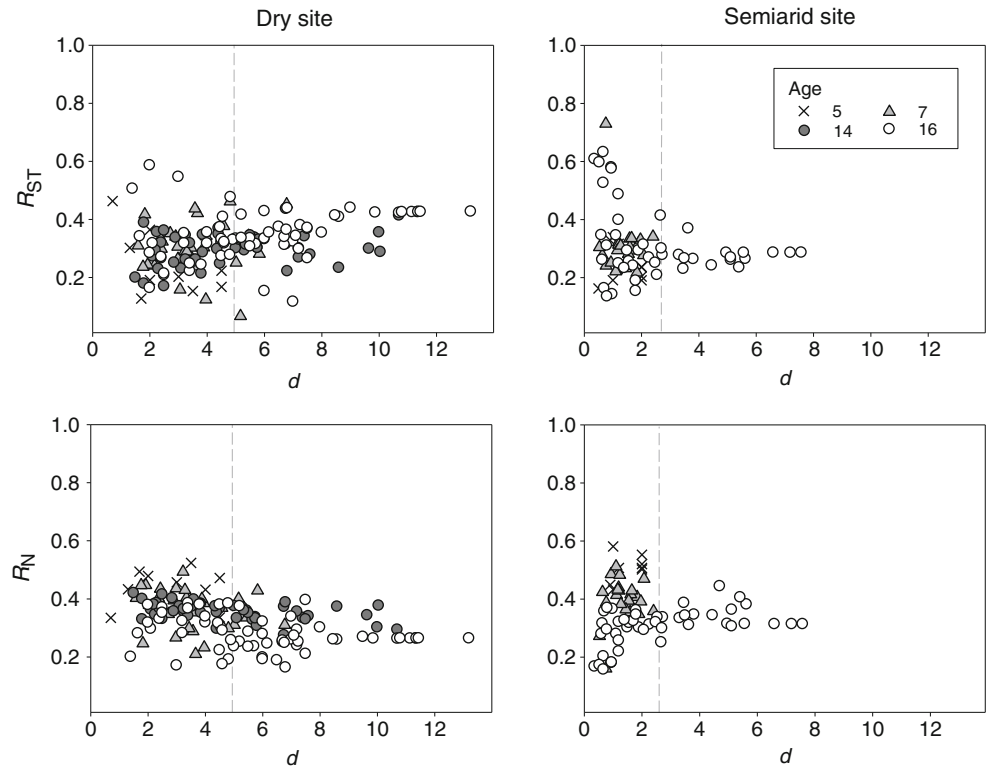
4 Discussion

Our results present a set of biomass equations that allowed the biomass components for young *P. halepensis* trees to be

estimated under two contrasting climate conditions (dry and semiarid sites) and considering the silvicultural treatments and size-age effects, which have not been previously considered in formerly fitted biomass models (López-Serrano et al. 2005; Montero et al. 2005; Ruiz-Peinado et al. 2011).

Our analyses also corroborated that biomass allocation ratios cannot be modelled in terms of d with high performance (López-Serrano et al. 2005). The destructive sampling results revealed very high correlations between the measured biomass components, i.e. crown and stem. Such dependences evidence the non-local condition of the processes involved in the growth of a given component (Landsberg and Sands 2011).

Fig. 2 The stem biomass allocation ratios (R_{ST}) and needle biomass allocation ratios (R_N) obtained from the destructive sampling data (y axis) versus diameter at 30 cm above the ground (d , cm) (x axis) for the dry and semiarid sites. Tree ages of the destructive samples are displayed



The dependence of the biomass equations on young trees according to particular climate and treatment interactions has been clearly proved (Landsberg and Sands 2011; De las Heras et al. 2013). Consequently, specific biomass models should be applied for homogeneous areas in terms of the tree density and cutting age of potential pre-commercial thinning (Tobin and Nieuwenhuis 2007; Correia et al. 2010).

Our results revealed a greater individual pine biomass at the dry site than at the semiarid one due to the more favourable ecological conditions, which confer higher plastic responses (Chambel et al. 2007; Bravo et al. 2008). The effect of treatment at the semiarid site was also attenuated due to the harsh conditions at this location, which was more notable for biomass accumulation than for biomass allocation.

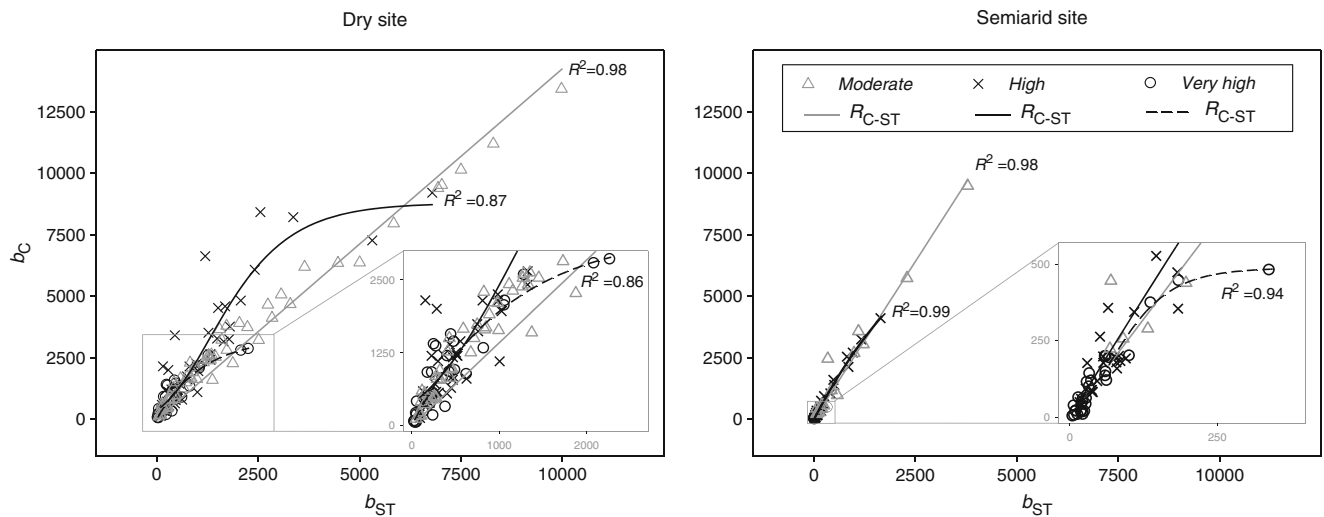


Fig. 3 Relationships between crown biomass components (b_C , g) (y axis) and stem biomass components (b_{ST} , g) (x axis), obtained from the destructive sampling data, for the dry and semiarid sites plotted as quadratic functions to illustrate the differences for the moderate

(treatments T_{5-800} , T_{10-800} and T_{5+10}), high (treatments T_{5-9500} , T_{5-1600} and $T_{10-1600}$) and very high (non-thinned plots T_C) tree density groups

Although both sites are representative of fire-prone communities, the tendency to allocate more biomass to the crown (heavy loading of dead branches and needles) at the semiarid site may promote more flammable canopies (Keeley et al. 2012).

As a result of thinning, suppressed trees allocated more biomass to the stem than those individuals in lower tree density stands. We particularly identified the concomitant growth of the crown and stem biomasses (linearly related) for the individual pine trees that faced less intraspecific competition (moderate tree density). However, for fierce intraspecific competition, we observed that the biomass allocated to the stem progressively increased, mainly at very high tree densities, whereas the biomass allocated to the crown concurrently decreased due to high intraspecific competition until the canopy completely closed. This tendency has been identified in previous studies as an adaptive mechanism to cope with strong competition in the juvenile phase (Zianis et al. 2011).

At the plot level, our results revealed that the stem ratio increased with age at the dry site and that this effect was enlarged in the trees in thinned plots. However, at the semiarid site, this ratio remained constant during the age sequence studied in both the thinned and non-thinned plots, whereas the needle ratio lowered at both sites. This agrees with the fact that biomass components, which accumulate during a tree's life span, such as stem and coarse roots, increasingly contribute to above-ground biomass storage with age. However, the opposite is true for those biomass components, which are not completely cumulative, such as needles and fine roots (López-Serrano et al. 2005; Landsberg and Sands 2011; Xie et al. 2012). The fact that the needle ratio lowered as the stand became older has been described to result from the formation of new wood structures and from the maintenance of older ones (Montès et al. 2004). We found a similar needle ratio to that reported by Montès et al. (2004) for a 10-year-old *P. halepensis* stand and also the same tendency to lower with age. Accordingly, the needle ratios obtained for younger stands are higher than those obtained by López-Serrano et al. (2005) for adult Aleppo pines (i.e. between 0.04 and 0.12).

On average, young Aleppo pines allocated more resources to the crown ($\bar{R}'_C \sim 0.68$) than to the stem ($\bar{R}'_{ST} \sim 0.32$) at post-fire year 16, unlike the mature Aleppo pine estimations, with roughly 50 % ratios of biomass being allocated to the crown and stem (Ruiz-Peinado et al. 2011). Regarding the biomass allocated to roots, yearly changes in the root/shoot ratios, or even a decline in the biomass allocated to roots with age, are possible (Albaugh et al. 2006), although standard root extraction techniques should be considered given the increasing possibility of underestimation when tackling large trees (Adegbidi et al. 2002), which could attain ca. 40 % (Robinson 2004). We found similar ratios for young Aleppo pine trees

($\bar{R}'_R \sim 0.37$) to those found for open adult Aleppo pine trees in close areas (0.35, unpublished results) using the same extraction technique for roots, which contrasts with the lower root/shoot ratios obtained by Ruiz-Peinado et al. (2011) for mature Aleppo pines (0.23). This finding further supports the notion that differences in root/shoot ratios for age should be cautiously taken (Rubilar et al. 2013).

Olivar et al. (2014) found that suppressed trees undergo higher drought stress and lower growth rates than dominant trees as a result of stronger competition that roots face for soil resources. Accordingly, we report lower root/shoot ratios for suppressed trees than dominant trees, mainly in the pine trees that occur in the control plots at both sites and similarly to other species of the genus *Pinus* (Albaugh et al. 2006; Rubilar et al. 2013). This finding is opposite to the functional carbon balance model (Brouwer 1983), which suggested that plants growing with limited soil resources (nutrients or water) should allocate a higher biomass to roots than to above-ground components.

After thinning treatments, the pine trees growing under low intraspecific competition (in low-tree-density plots) were consistently less water stressed than those under high competition (in non-thinned plots); consequently, more coarse roots are expected. Conversely, the pine trees in the non-thinned plots were forced to increase allocation to fine roots at the expense of coarse roots in order to improve their ability to capture scarce resources under stress conditions (Albaugh et al. 1998; Rubilar et al. 2013). The lower root/shoot ratio found in the suppressed trees could arise from the approach selected to estimate the root/shoot ratios, which included both coarse and fine roots.

To the best of our knowledge, this is the first attempt to calculate the cone biomass of young *P. halepensis* individuals using specific biomass equations that are extrapolated to complete, accurate cone inventories (but see Ne'eman et al. 2011). We herein report very early and abundant cone production at our study sites (starting at 3 years old), probably triggered by an adaptive trait to face high fire recurrence or recurrent drought episodes (Naveh 1990; Agee 1998; Tapias et al. 2001; Ne'eman et al. 2004; Espelta et al. 2011), but with very different tree sizes at reproduction onset.

We noted a higher proportion of cone biomass vs. above-ground biomass 5 years after the fire at the semiarid site, if compared to the dry site. However, the opposite trend found at post-fire year 16 denotes the high reproductive effort made by the trees from the semiarid site in early stages (Haymes and Fox 2012), which may have affected growth and allocation of other biomass fractions in subsequent years, i.e. less biomass allocated to the stem to favour the crown. In fact, the high reproductive cost at the expense of growth in early stages can be a strategy developed to face short-term survival (Stearns 1976).

Hence, both the risk of mortality and its predictability drive reproduction onset among the same species (Kozłowski 1992) as a result of local selective pressure (Harper and White 1974). However, reproductive efforts may be moderated by other different factors, such as higher initial tree density, forest management, microsite effects, individual variation, resource availability or recurrent drought events (Obeso 2002; Espelta et al. 2011; Alfaro-Sánchez et al. 2015), as the low deviance explained by our models revealed, particularly at the dry site.

In previous studies, *P. halepensis* has shown high heritability of reproductive allometry (Santos-del-Blanco et al. 2010). Therefore, we agree with the prime importance of forest species for phenotypic plasticity in future adaptations given the natural selection of this trait (Anderson et al. 2012; Chevin et al. 2013). On the whole, Aleppo pine displays a good genetic control of reproductive traits to face selective pressure (Santos-del-Blanco et al. 2013), as we found at the semiarid site, where pine trees are forced to invest available resources, primarily during reproductive growth. At the dry site, however, we found the most usually reported tendency, i.e. investing primarily in growth and secondarily in reproduction (Goubitz et al. 2002; Moya et al. 2008).

5 Conclusions

Our results reveal the high intraspecific variability of *P. halepensis* when different ecological factors are considered in biomass accumulation terms. Climate was the main limiting factor to constrain biomass accumulation and biomass allocation. Early thinning also enhanced the biomass components per tree, which was maximum in the plots with less tree densities. However, the positive effects of tree density reduction were more marked at the dry site than at the semiarid site, particularly for biomass accumulation than for biomass allocation.

In general, crown was the largest biomass fraction, followed by root fraction and stem fraction. Nevertheless, age, tree density reduction and climate factors modify these proportions. The reproductive effort was greater at the most limiting site (the semiarid site) in early stages, probably triggered by specific traits of this species to face short-term survival under recurrent fire regimes or drought episodes. Further testing using other populations should be considered to determine if biomass allocation patterns in young Aleppo pine trees are shaped mainly by adaptive traits to fire or by other disturbances, such as limiting resources or drought events.

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