Forest Systems
26 (2), e06S, 20 pages (2017)
eISSN: 2171-9845
https://doi.org/10.5424/fs/2017262-10583
Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria O. A., M. P. (INIA)

RESEARCH ARTICLE

OPEN ACCESS

Decline in holm oak coppices (*Quercus ilex* L. subsp. *ballota* (Desf.) Samp.): biometric and physiological interpretations

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Abstract

Aim of the study: To analyse the decline in aged holm oak coppice forests as regards above-ground and below-ground fractions and physiological features.

Area of study: Centre of the Iberian Peninsula (Guadalajara province).

Material and methods: 26 pairs of holm oak stools with different vigour but with similar site and structural characteristics within each pair were selected. Morphological (basal area, number of stools, maximum height) and physiological traits (leaf water potential, stomatal conductance) of the standing stools were assessed. Their aerial and underground parts were extracted and different size fractions of both their above and below-ground biomass were quantified. Linear mixed models were built to test the effect of '*Stool vigour*' on the mean behaviour of the measured variables. Additionally, for the aerial part, linear regressions between the weights of the different size fractions and the basal area at breast height were performed using '*Stool vigour*' as a fixed factor.

Main results: For the same site, root depth, and number and diameter of shoots than good vigour stools, poor vigour stools displayed: lower predawn water potential, greater leaf mass per unit of area; lower total leaf area; lower above-ground biomass (in total as well as per fractions); lower fine roots biomass; lower proportion of leaf biomass and a greater proportion of biomass of both all roots and those with diameter 2-7 cm.

Research highlights: The above-ground physiological and morphological characteristics of declined stools are interpreted as poorer adaptation to site conditions. Root system architecture was found to be relevant to explain this behaviour.

Additional keywords: decay; stool; above-ground biomass; below-ground biomass; drought; global change.

Abbreviations used: AB (stool basal area at breast height); AB_G (stool basal area at ground level); AB_{ha} (stool basal area per hectare); B (bad vigour stools); d (shoots mean diameter at breast height); G (good vigour stools); ICP Forest (International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests); LA (mean single leaf area); LAI (leaf area index); LMA (mean leaf mass per unit of area); LW (leaf dry weight); N (stool number of shoots); SAR (cross-sectional area of roots leaving pieces with diameter >7cm); TAW (dry weight of the total aerial part); WAP (dry weight of the woody aerial part); WP_M (midday water potential); WP_P (predawn water potential).

Authors´ contributions: Conception and design of the experiments: RS. Performance of the experiments: RS, JO and JABF. Data analysis: VGS and MJA. Writing the manuscript: RS, VGS, JABF and MJA. Obtaining funding and coordinating the research project: SR.

Citation: Serrada R.; Gómez-Sanz, V.; Aroca, M. J.; Otero, J.; Bravo-Fernández, J. A.; Roig, S. (2017). Decline in holm oak coppices (*Quercus ilex* L. subsp. *ballota* (Desf.) Samp.): biometric and physiological interpretations. Forest Systems, Volume 26, Issue 2, e06S. https://doi.org/10.5424/fs/2017262-10583

Supplementary material : (Tables S0 to S10) accompanies the paper on FS's website.

Received: 07 Oct 2016. **Accepted**: 18 Oct 2017.

Funding: This work was performed within the framework of the project '*Dehesas y Tallares de Encina en la España mediterránea: propuestas de gestión para la sostenibilidad de dos sistemas forestales paradigmáticos*' (*De.Tall.E*: RTA2009-00110-00-00), supported by the Spanish National Institute for Agricultural and Food Research and Technology (INIA).

Competing interests: The authors have declared that no competing interests exist.

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Introduction

Mediterranean coppices of hardwood species generally are natural stands with a simplified structure resulting from their historical management, traditionally aimed at producing firewood and charcoal through clearcutting with short rotations. These stands currently cover large areas in the Mediterranean basin and often show problems of instability due to the abandonment of traditional management (Scarascia-Mugnozza *et al.,* 2000).

Holm oak (*Quercus ilex* L. subsp. *ballota* (Desf.) Samp.) accounts for much of the forested area with this type of stand structure in Spain (Serrada *et al.,* 1992). These coppices are frequently located on low quality sites and have been intensively managed by repeated clearcutting over a long period in the past. This has led to a greatly simplified even-aged coppice structure. The commonly used coppicing rotation length used to be between 20 and 25 years with frequent variation in this period ranging from 15 to 30 years (Serrada, 2011). Moreover, according to some authors (de Olazabal, 1883; Ugarte & Velaz de Medrano, 1921), rotation periods of 5 to 12 years were not infrequent in coppices used for firewood production. After clearcutting, resprouting involves the mobilization of resources (mainly starch) from the stool (Gracia *et al.,* 1999a; Ojeda, 2001), which requires a minimum recovery period between cuttings (López *et al.,* 2009). Therefore, these short rotations frequently resulted in small-sized, low-value products; led to impoverished soil and severely affected the stools, reducing their vigour and shortening their lifespan (Roda *et al.,* 1999; Bravo *et al.,* 2008). This situation got worse when no measures were taken to avoid grazing during a period of sufficient length to allow the root system to recover the reserves employed in resprouting following cutting. Since the 1960's, after this period of intense exploitation, the use of other fuel sources led to the abandonment of this type of forest management, therefore ceasing the treatments on which this type of forestry system is strongly dependent (Serrada *et al.,* 1992). Today, there are large areas of holm oak coppice with serious silvicultural and ecological problems; namely, high number of trees per hectare with low mean diameters and reduced basal areas; slow growth; scarce acorn production; little or no sexual regeneration; very low biodiversity; and high fire risk (Serrada *et al.,* 1992; Bravo *et al.,* 2008). These poor stand conditions together with the progressive ageing of stools (at least as regards the root systems as they were not renewed through cuttings) may account to some extent for the increasing sensitivity to climate observed in holm oak coppices in recent decades (Camarero *et al.,* 2004; Gea-Izquierdo *et al.,* 2009). As reported by various authors (Gracia *et al.,* 1999b; Gracia *et al.,* 1999c; Sabaté *et al.,* 2002; Ogaya & Peñuelas, 2007b), under the current climate change, the decrease in precipitation and the increase in temperatures lead to greater water deficit in Mediterranean forests such as those of holm oak (especially during the increasingly intense summer drought period), which in turn results in lower photosynthetic activity (with lower growth and carbon fixation as a consequence); furthermore, the rise in temperature leads to an increase in the rate of leaf and fine root renewal. The interaction between all these factors together leads to increased consumption of carbohydrate reserves and insufficient supply to the stool. When the effects of climate change are combined with the excessive stand density and ageing due to the abandonment of management practices, there is an increased risk of fire, stands decline and some individuals even die from drought, pests and disease (Camarero *et al.,* 2004; Serrada *et al.,* 2011).

According to the observations of the ICP European Forest network for forest damage monitoring (http://icp-forests.net/), the percentage of crown defoliation (concurrent with tree mortality) has increased significantly over the last two decades in most Mediterranean forests, not only in holm oak coppices, in response to greater water deficit (Carnicer *et al.,* 2011). However, the response of holm oak to climatic events over this period was slightly worse than the mean for other Mediterranean species (Manzano *et al.,* 2013). In this respect, Tognetti *et al.* (1998) argues that, despite the high tolerance of holm oak to extreme drought and its adaptation to warm, dry climates, the Mediterranean coppices of this species operate at the limits, which are easily surpassed under severe drought conditions, hence predisposing these stands to decline.

Despite this theoretical predisposition, when the defoliation and general decay process occur, they do not affect all the stools in the stand to the same degree. Typically, some individuals tend to be much more affected by decay than others, even when they share the same site conditions and visible morphological traits. The weakest stools and sprouts are expected to be the most vulnerable to decline (Rodríguez-Calcerrada *et al.,* 2011), nevertheless it remains unclear in which morphological-physiological traits does this "weakness" exactly lie. In recent decades, much research has focused on both diagnosing coppice status and analyzing possible alternatives for managing coppices in the Mediterranean basin (*e.g.* Ducrey, 1992; Gracia *et al.,* 1997; Serrada *et al.,* 1992; Terradas, 1999; Bravo-Fernández *et al.,* 2008). However, fewer studies have attempted to identify the underlying functional problem in "weak" individuals. Most of the studies dealing with the decline of holm oak at individual tree level have focused mainly on characterizing the effects or symptoms of decay in the aerial part of the stools, both at leaf and xylem level (Tognetti *et al.,* 1998; Camarero *et al.,* 2004; Corcuera *et al.,* 2004), sometimes through water exclusion experiments (Limousin et al., 2009; Barbeta *et al.,* 2013; Pérez-Ramos *et al.,* 2013). However, because holm oak is a species with a strong resprouting capacity and as most of the stools have been managed in a coppice system over a long period of time, it would seem reasonable to assume that the cause of decay of some stools may be at least partially explained by factors relating to the root system (Camarero *et al.,* 2004). Analysing the root systems of adult specimens, particularly in coppice systems, is obviously very complex. The few studies that have addressed this question in depth for either coppices of holm oak or other *Quercus* species (Sanesi *et al.,* 2013), mainly handle some of the following hypotheses to explain, at least partially, the decay of some stools (López *et al.,* 1998; Cañellas & San Miguel, 2000; López *et al.,* 2003; Cotillas *et al.,* 2016; Salomon *et al.,* 2016): i) there is an imbalance between above-ground biomass and below-ground biomass, in favor of the latter; ii) there is an imbalance between below-ground fractions, with excess of coarse roots and scarcity of fine ones; and iii) there is a problem associated with ageing, particularly of the root system and all that this entails.

The results obtained to date, shed light on certain aspects but are not conclusive because of the reduced size of the samples employed among other factors. This study aims to provide answers to some of these issues through an experimental design for the exhaustive analysis of individual stems including the extraction of root systems within a sample of larger magnitude than that used in previous studies. Therefore, a sampling design consisting of pairs of holm oak stools with good and bad vigour condition, across several coppices within the central region of Spain was employed, the main objective being to analyse the situation of decline frequently found in holm oak stools, as well as to find possible explanations related to biometric or physiological aspects of the stools, paying particular attention to the state of the root systems. In particular, on the basis of the good and bad vigour stools identification, the specific objectives of this study were: i) to quantify and characterize the structure and biomass (above and below-ground) of stools with different vigour condition; ii) to analyse the relationship between physiological variables and the vigour of the stools; iii) to study the influence of below-ground biomass on the development and vigour of the stools.

Material and methods

Site description

The study area was located in the centre of the Iberian Peninsula (Guadalajara province), within Territorial Group 4 (southern sub-meseta) according to the study of Iberian holm oak sites, by Sánchez-Palomares *et al.* (2012). The altitude of the study area ranges from 725 to 1217 m.a.s.l. with slopes of less than 5% within all the sampling sites. Mean annual precipitation is 660 mm and mean annual temperature is 12 ºC.

Sampling selection

For the purposes of the study, 26 pairs of holm oak stools (52 single stools altogether) were selected across eight neighbouring forests within the study area. The two stools comprising each pair were chosen so as to fulfil the following criteria (Serrada *et al.,* 2013): i) close proximity in order to avoid differences in soil and climatic conditions; ii) size similarity, mainly in terms of number and diameter of shoots; iii) one (G) had to show good vigour and the other (B), in contrast, had to show signs of decline. The good/bad stool condition was defined in accordance with the IPC Forest methodology for visual assessment of tree condition in the large-scale European network (L1) for forest damage monitoring (Eichhorn *et al.,* 2006 & 2010; SSF-DGDRyPF, 2012). Accordingly, the condition was defined through visual assessment of crown defoliation, with B stools displaying defoliation levels higher than 25% (defoliation levels 2: “moderate” and 3: ”high” of the ICP Forest methodology), whereas defoliation was negligible for the G stools. The term “defoliation” includes both premature loss of foliage and leaf and branch dieback (SSF-DGDRyPF, 2012). The name, location and physiographical/lithological site characteristics for the 26 sampled pairs of stools are presented in Table 1.

Standing stool measurements

All selected stools were morphologically and physiologically characterized. First of all, the amount and diameter of all the stems of every stool were measured both at ground level and at breast height; Stool number (N) and diameter (d) of shoots, Stool basal area at breast height (AB) and Stool basal area at ground level (AB_G) were therefore assessed. In addition, a rectangular plot was defined circumscribing the ground projection of every crown, enlarged by a 0.5 m band around its entire perimeter. The basal area at breast height per hectare (Stool basal area per hectare, AB_{ha}) was calculated over this surface area, which would also be the reference area for the subsequent extraction of the below-ground biomass. Hence, AB_{ha} is intended to reflect the mean density conditions encountered within the stool.

Secondly, prior to the cutting and measurement of the aerial parts, the following physiological measurements were carried out once on every stool during the period of water stress (August 2011): i) leaf water potential: measured on two twigs per stool (6-18 leaves each)

Table 1. Code, location and physiographic features of holm oak analysed pairs of stools.

Code	Township	Forest	X UTM H30EU79	Y UTM H30EU79	Altitude (m)	Bedrock
1GU	Guadalajara	Cañada Real de las Matas	490830	4495614	944	Limestone
2GU	Guadalajara	Cañada Real de las Matas	490791	4495529	948	Limestone
3GU	Guadalajara	Cañada Real de las Matas	491011	4496046	949	Limestone
4GU	Guadalajara	Cañada Real de las Matas	491044	4496028	937	Limestone
5GU	Guadalajara	Cañada Real de las Matas	491260	4496400	955	Limestone
6GU	Guadalajara	Cañada Real de las Matas	492020	4497072	952	Limestone
7BG	Brihuega	UP 42	517360	4511740	1.074	Limestone
8BG	Brihuega	UP 42	517010	4511483	1.063	Limestone
9BG	Brihuega	UP 42	517282	4511850	1.059	Limestone
10MB	Mirabueno	Cañada Real Soriana	526483	4528773	1.068	Limestone
11MB	Mirabueno	Cañada Real Soriana	526502	4528785	1.055	Limestone
12MB	Mirabueno	Cañada Real Soriana	527082	4528981	1.066	Limestone
13FH	Fuentelahiguera	Fuentelfresno	474683	4520143	927	Quartzite
14FH	Fuentelahiguera	Fuentelfresno	474546	4519809	922	Quartzite
15FH	Fuentelahiguera	Fuentelfresno	474188	4518987	916	Quartzite
16CU	Casa de Uceda	UP 248	470146	4522956	890	Quartzite
17CU	Casa de Uceda	UP 248	469469	4523089	885	Quartzite
18TR	Trillo	UP 76	534193	4504510	735	Limestone
19TR	Trillo	UP 76	534387	4503846	727	Limestone
20TR	Trillo	UP 76	532874	4503368	725	Limestone
21CT	Castilforte	UP 219	548965	4494751	1.131	Limestone
22CT	Castilforte	UP 219	548751	4494752	1.133	Limestone
23CT	Castilforte	UP 219	549137	4491548	1.131	Limestone
24RC	El Recuenco	UP 49	556307	4500924	1.202	Limestone
25RC	El Recuenco	UP 49	556320	4500956	1.206	Limestone

selected at the top of the crown, using a Sholander pressure chamber type PMS (C0 Instruments), both just before sunrise (predawn leaf water potential) and at midday when water stress was high (midday leaf water potential); ii) stomatal conductance: measured on three leaves per stool located in the sun-exposed part of the crown at its maximum diameter; mid-morning (9-12 h a.m.); using a leaf porometer model SC-1 (Decagon Devices Inc.).

Leaf morphology parameters for each stool were assessed on the same twigs as those selected for water potential estimations. Leaf area was determined on fresh material using a digital planometer, whereas leaf mass measurements were performed after oven drying at 103 ºC to constant weight. Leaf Mass per unit Area (LMA) was therefore calculated as the averaged ratio between individual leaf mass and Individual Leaf Area (LA). The mean values obtained were used to calculate the Leaf Area Index (LAI) for each stool through the estimated leaf weight (see Table S6).

Cutting and characterization of the above-ground biomass of stools

The cutting and characterization of the aerial biomass was carried out in October 2011. These operations consisted of harvesting the above-ground part of the stool, weighing fresh material by size fractions, accurately measuring heights and collecting samples for each biomass size fraction for mass estimation in the laboratory after oven drying at 103 ºC to constant weight.

The aerial biomass was arranged into size fractions as follows: i) stems > 7 cm in diameter; ii) stems from 7 to 2 cm; iii) stems < 2 cm; iv) leaves. The biomass fractions considered are in accordance with those described in previous works by Montero *et al.* (1999) and Ruiz-Peinado *et al.* (2011, 2012, 2015).

Extraction and characterization of the below-ground biomass of the stools

The below-ground part of the stools was extracted between December 2011 and February 2012 with a high-powered backhoe. The surrounding dug-out earth was manually checked and all the visible roots were collected in sacks or tarpaulins. After air-drying, stools were cleaned using high-pressure water jet and shaker tools to remove all the attached earth and stones. A qualitative analysis was then performed which involved: photographs, checking for the presence or absence of coppicing, presence of shoots from the stool or the roots, presence or absence of taproot and root grafts, limitations due to soil depth. The different fractions of the root system were then separated using a chainsaw and pruning scissors into roots of < 2 cm in diameter, from 2 to 7 cm, and those > 7 cm. The three fractions were then weighed (air dried weight) and corresponding samples were subsequently taken to estimate the oven dried weight. Finally, the perimeter of all the roots leaving the >7 cm diameter pieces was measured around the insertion section in order to assess the aggregated cross-sectional area of all the roots leaving out pieces with diameter larger than 7 cm (SAR). This variable, along with ratios between this section and the different aerial or below-ground biomass fractions, were used to indirectly evaluate the conduction capacity of the stools. The SAR is considered to have an important physiological significance since it reflects the possible flow of crude sap (upwards) and elaborated sap (downwards) and can be understood as the conductive area in the sense proposed by Larcher (1977), whereas the quotients can be interpreted as the relative conducting area or measurement of the supply capacity of the plant to its different parts (Larcher, 1977).

Data analysis

Data analysis focused on providing a detailed characterization of the sampled stools as well as on contrasting the relationship between '*Stool vigour*' at sampling and all the morphological and physiological variables that comprise their characterization (names, brief definitions, units and acronyms of all the studied variables are summarized in Table S0 [suppl]). Some morphological singularities were identified within certain stools of the sample that had to be partially excluded from the analysis (Table S1 [suppl]). Linear mixed models were built to test the '*Stool vigour*' effect on the mean behaviour of the rest of the measured variables. Within these models '*Stool vigour*' (good or bad) was considered as a fixed factor affecting the mean, whereas the '*Sampling pair*' nested into the '*Sampling region*' was considered as a random factor. The significance of this effect was assessed through the comparison of the performance of the models with (M_1) and without (M_0) the '*Stool vigour*' term by means of the respective likelihood tests based on -2Log Likelihood criteria (Eqs. [1]-[3]).

$$M_0\text{: } Yij = \beta_0 + \sigma j + eij \qquad [1]$$

$$M_1\text{: } Yij = \beta_0 + \beta_1 \cdot Xi + \sigma j + eij. \qquad [2]$$

$$\text{L-ratio} = -2 \cdot (\text{logLikelihood}M_1 - \text{logLikelihood}M_0) \qquad [3]$$

where, 'Xi' is the stool vigour (Xi=1 for good vigour 'G', and Xi= 0 for bad vigour 'B'),'β_1' is the stool vigour fixed effect on the mean and 'σj' is the random effect of the *j* stool (sampling pair nested into the sampling region) on the mean.

In the specific case of the aerial part of the stools, linear regressions between the weights of the different size fractions and the basal area at breast height were conducted with the '*Stool vigour*' as a fixed factor. In this way, we attempted to determine whether the development of the aerial part for a certain basal area was different for good and bad stools.

Mixed linear models were implemented using the *lme* function of the *nlme* R package (Pinheiro *et al.*, 2016) according to the procedure proposed by Zuur *et al.* (2009), whereas linear regressions between basal area and biomass fractions were estimated using the *lm* R package.

The detailed characterization of each of the sampled stools (structure, physiological state, leaf morphology, above-ground & below-ground biomass) are provided in Tables S1 to S10 [suppl].

Results

Stools structure variables

The morphological similarity (mean diameter, maximum height and number of shoots) of the pairs of stools chosen was evaluated (Table 2). With regard to the stools vigour effect over the means, only Hmax values showed clear significant differences (p< 0.001) between stool vigour conditions, so that the good stools averaged 0.65 m higher than the bad ones. The good stools also displayed a slightly greater mean basal area at breast height (AB), although this difference was not significant at the 95% confidence level but rather only at 90%. When the correlation between size variables was assessed, AB showed high linear correlation with both basal area at ground level (0.88, p <0.001) and maximum height (0.60, p <0.001), whereas this correlation was weaker between basal area at ground level and Hmax (0.43, p = 0.01). AB is therefore considered to be the best single variable to resume stool size for ulterior analysis of aerial biomass.

Physiological state variables

Despite the fact that the physiological state of the stools was evaluated under homologous conditions of temperature and relative humidity for both groups of stools considered, predawn water potential (WP_P) was found to be significantly lower in the bad vigour stools (-11.2 %) whereas differences in the rest of the variables (lower midday water potential, higher stomatal conductance and lower WP_P - WP_M difference in bad vigour stools) did not show a sufficiently consistent tendency between vigour groups (Table 3).

Leaf morphology variables

Table 4 shows the descriptive statistics for this group of variables and the results of the analysis of the ’*Stool vigour*’ effect. In the case of the bad vigour stools, the leaves were found to have greater mean leaf mass per unit area (LMA, p= 0.025) and lower stool leaf area (TLA, p<0.001) and LAI (p<0.001) whose showed mean values around 50% of the corresponding values for the good vigour stools. On the other hand, no significant

Table 2. Descriptive statistics for stool structure variables together with the estimation of the ‘*Stool vigour*’ fixed effect over the means, after random effects removal (namely ‘*Sampling pair*’ nested into the ‘*Sampling region*’).

Variable (Y)	Stool vigour (Xi)	N	Mean ± SD	Min.	Max.	Stool vigour effect estimation (β_1)		
						β_1	L-ratio	*p*-value
N Stool number of shoots	G	26	3.8 ± 3.1	1.0	10.0	0.23	0.68	0.411
	B	26	3.7 ± 3.2	1.0	11.0			
	All	52	3.8 ± 3.2	1.0	11.0			
d (cm) Shoots diameter at breast height	G	26	9.4 ± 5.2	3.9	24.5	0.64	2.21	0.137
	B	26	8.8 ± 5.1	2.5	25.7			
	All	52	9.1 ± 5.1	2.5	25.7			
AB (cm^2/stool) Stool basal area at breast height	G	26	179.7 ± 109.1	23.8	471.4	25.48	3.05	0.081
	B	26	154.2 ± 113	9.9	518.8			
	All	52	166.9 ± 110.7	9.9	518.8			
AB_g (cm^2/stool) Stool basal area at ground level	G	26	350 ± 190.5	66.5	766.0	25.83	1.09	0.297
	B	26	324 ± 216.8	23.3	832.7			
	All	52	337.1 ± 202.5	23.3	832.7			
AB_{ha} (m^2/ha) Stool basal area per hectare	G	26	43.7 ± 27.8	8.0	119.2	7.96	2.90	0.089
	B	26	35.8 ± 16.8	4.4	69.8			
	All	52	39.7 ± 23.1	4.4	119.2			
h (m) Stool maximum height	G	26	4.8 ± 1.3	2.6	8.0	0.65	**14.47**	**0.000**
	B	26	4.2 ± 1.1	1.4	6.4			
	All	52	4.5 ± 1.3	1.4	8.0			
HD (cm/cm) Stool height to diameter ratio	G	26	60.1 ± 23.9	31.2	130.8	4.28	1.31	0.252
	B	26	55.8 ± 19.6	24.9	93.5			
	All	52	58 ± 21.8	24.9	130.8			

G: good vigour stools; B: bad vigour stools; N: sample size for parameters estimation; SD: standard deviation; significant p-values at 95% confidence level are shown in bold.

differences were found in the mean individual leaf area (LA), thus revealing that bad stools displayed significantly less number of leaves than good ones, although these leaves have similar individual area and greater individual weight than those of the good stools.

Above-ground biomass variables

The averaged weights of all the aerial biomass fractions were found to be significantly lower in the badvigour stools group(Table 5). Thus, the dry weight of theirtotalaerial part (TAW) was 32% lower than that of the stools with good vigour, reaching the differences a similar magnitude in the rest of the woody fractions. In the case of leaf weight (LW), discrepancy was particularly high so that the mean forgoodstoolsalmost doubled that of the bad group, hence endorsing the visual criteria employedfor stool vigour selection.

All these differences may be partly explained by the lower maximum height of the bad vigour stools as well as by their slightly lower basal area. In this regard, when the effect of the stool vigour on the aerial biomasswas analysed taking into account the effect of stool size through regressions for basal area at breast height (Fig. 1), it was observed that: i) the effect of stool vigour on the aerial biomass became significant just for the leaf fraction, whereas the differences found in the rest of the fractionsseemed to be mainly explained by the variation in stool size rather than by stool vigour; ii) the most explanatory models were those for the dry weight of the woody aerial part (WAP) and TAW, which explain almost 88% of the variance; while those which worst explained the variability were those for weight of woody parts of less than 2 cm (WAP-2) and for LW, explaining 66 % and 70 % of the variance respectively.

Therefore the difference in behaviour between the goodvigour and the badvigour stools was clearly highlighted, with good stools showing higher aerial biomass than bad ones. Nevertheless,the biomass of the aerialfractions mostly consisting of thick woody parts (WAP+2, WAP, TAW), wasclosely correlated to the accumulated growth of the stools represented by their basal area, whereassmaller fractions and leaves biomass showed higher unexplained variability. In the case of leaf biomass stool vigour condition was needed in addition to tree size to explain the observed variability although 30% of variance still remained unexplained.

Below-ground biomass variables

Among all the considered root fractions, significant differences between bad and good stools were only found for roots with diameter less than 2 cm (RW2); however, this difference was large, with bad vigour group showing a 30 % lower mean RW2 than the good vigour one. Stump area (SA) and aggregated cross-sectional area of all the roots leaving pieces with diameter larger than 7 cm (SAR), were also lower (-20%) for the bad vigour stools, although only at the 90 % confidence level (p = 0.061) (Table 6). The

Table 3. Descriptive statistics for physiological state variables together with the estimation of the '*Stool vigour*' fixed effect over their means after random effects removal (namely *'Sampling pair'* nested into the '*Sampling region*').

Variable (Y)	Stool vigour (Xi)	N	Mean ± SD	Min.	Max.	Stool vigour effect estimation (β_1)		
						β_1	L-ratio	Sig.
WP_P (MPa) Predawn water potential	G	26	-1.91 ± 0.86	-3.85	-0.80	0.24	5.59	**0.018**
	B	26	-2.14 ± 0.86	-3.55	-0.80			
	All	52	-2.02 ± 0.86	-3.85	-0.80			
WP_M (MPa) Midday water potential	G	26	-3.31 ± 0.61	-4.35	-2.30	0.14	1.30	0.255
	B	26	-3.45 ± 0.57	-4.40	-2.35			
	All	52	-3.38 ± 0.59	-4.40	-2.30			
WP_{DIF} (MPa) $WP_P - WP_M$ difference	G	26	1.4 ± 0.49	0.50	2.65	0.09	0.32	0.572
	B	26	1.31 ± 0.59	0.40	3.00			
	All	52	1.35 ± 0.53	0.40	3.00			
SC (mmol/m^2·s) Stomatal conductance	G	26	106.57 ± 44.63	36.73	216.43	-5.14	0.12	0.733
	B	26	111.7 ± 62.07	54.83	298.57			
	All	52	109.13 ± 53.59	36.73	298.57			

G: good vigour stools; B: bad vigour stools; N: sample size for parameters estimation; SD: standard deviation; significant p-values at 95% confidence level are shown in bold.

Table 4. Descriptive statistics for leaf morphology variables together with the estimation of the '*Stool vigour*' fixed effect over their means, after removing random effects (namely '*Sampling pair*' nested into the '*Sampling region*'). Pairs of stools comprising group 1 (Table S1 [suppl]) were excluded.

Variable (Yi)	Stool vigour (Xi)	N	Mean ± SD	Min.	Max.	Stool vigour effect estimation (β_1)		
						β_1	**L-ratio**	**Sig.**
LA (cm^2) Mean individual leaf area	G	20	1.92 ± 0.74	0.90	3.50	- 0.04	0.02	0.878
	B	20	1.95 ± 0.69	1.00	2.90			
	All	40	1.93 ± 0.7	0.90	3.50			
LMA (mg/cm^2) Mean leaf mass per unit of area	G	20	24.49 ± 2.51	18.50	30.20	- 1.91	5.47	**0.025**
	B	20	26.4 ± 2.65	21.70	30.30			
	All	40	25.45 ± 2.73	18.50	30.30			
TLA (m^2) Total leaf area per stool	G	20	27.08 ± 18.88	4.20	71.80	14.30	15.28	**<0.001**
	B	20	14.53 ± 11.09	2.43	49.06			
	All	40	20.81 ± 16.55	2.43	71.80			
LAI (m^2/m^2) Leaf area index	G	20	6.36 ± 3.62	1.87	15.64	2.73	13.95	**<0.001**
	B	20	3.63 ± 2.76	1.08	11.14			
	All	40	5.00 ± 3.46	1.08	15.64			

G: good vigour stools; B: bad vigour stools; N: sample size for parameters estimation; SD: standard deviation; Significant *p*-values at 95% confidence level are shown in bold.

Table 5. Descriptive statistics for the aerial biomass variables together with the estimation of the '*Stool vigour*' fixed effect over their means, after random effects removal (namely '*Sampling pair*' nested into the '*Sampling region*'). Pairs of stools comprising group 1 (Table S1 [suppl]) were excluded.

Variable (Y)	Stool vigour (Xi)	N	Mean ± SD	Min.	Max.	Stool vigour effect estimation (β_1)		
						β_1	**L-ratio**	**Sig.**
WAP-2 (kg) Dry weight of the woody aerial part with Ø<2 cm	G	20	14.68 ± 6.9	3.40	26.40	4.00	10.99	**0.001**
	B	20	10.68 ± 6.34	2.60	23.10			
	All	40	12.68 ± 6.85	2.60	26.40			
WAP+2 (kg) Dry weight of the woody aerial part with Ø>2 cm	G	20	56.26 ± 31.83	6.40	111.90	18.63	10.44	**0.001**
	B	20	37.63 ± 22.02	9.10	85.90			
	All	40	46.95 ± 28.62	6.40	111.90			
WAP (kg) Dry weight of all the woody aerial part	G	20	70.94 ± 37.74	9.80	136.10	22.63	11.27	**<0.001**
	B	20	48.31 ± 27.49	13.10	100.80			
	All	40	59.63 ± 34.55	9.80	136.10			
LW (kg) Leaves dry weight	G	20	6.91 ± 4.81	1.07	18.31	3.20	13.62	**< 0.001**
	B	20	3.71 ± 2.83	0.62	12.51			
	All	40	5.31 ± 4.22	0.62	18.31			
TAW (kg) Total aerial part dry weight	G	20	77.86 ± 41.79	10.90	153.10	25.84	12.17	**< 0.001**
	B	20	52.02 ± 29.81	14.10	106.90			
	All	40	64.94 ± 38.14	10.90	153.10			

G: good vigour stools; B: bad vigour stools; N: sample size for parameters estimation; SD: standard deviation; Significant *p*-values at 95% confidence level are shown in bold.

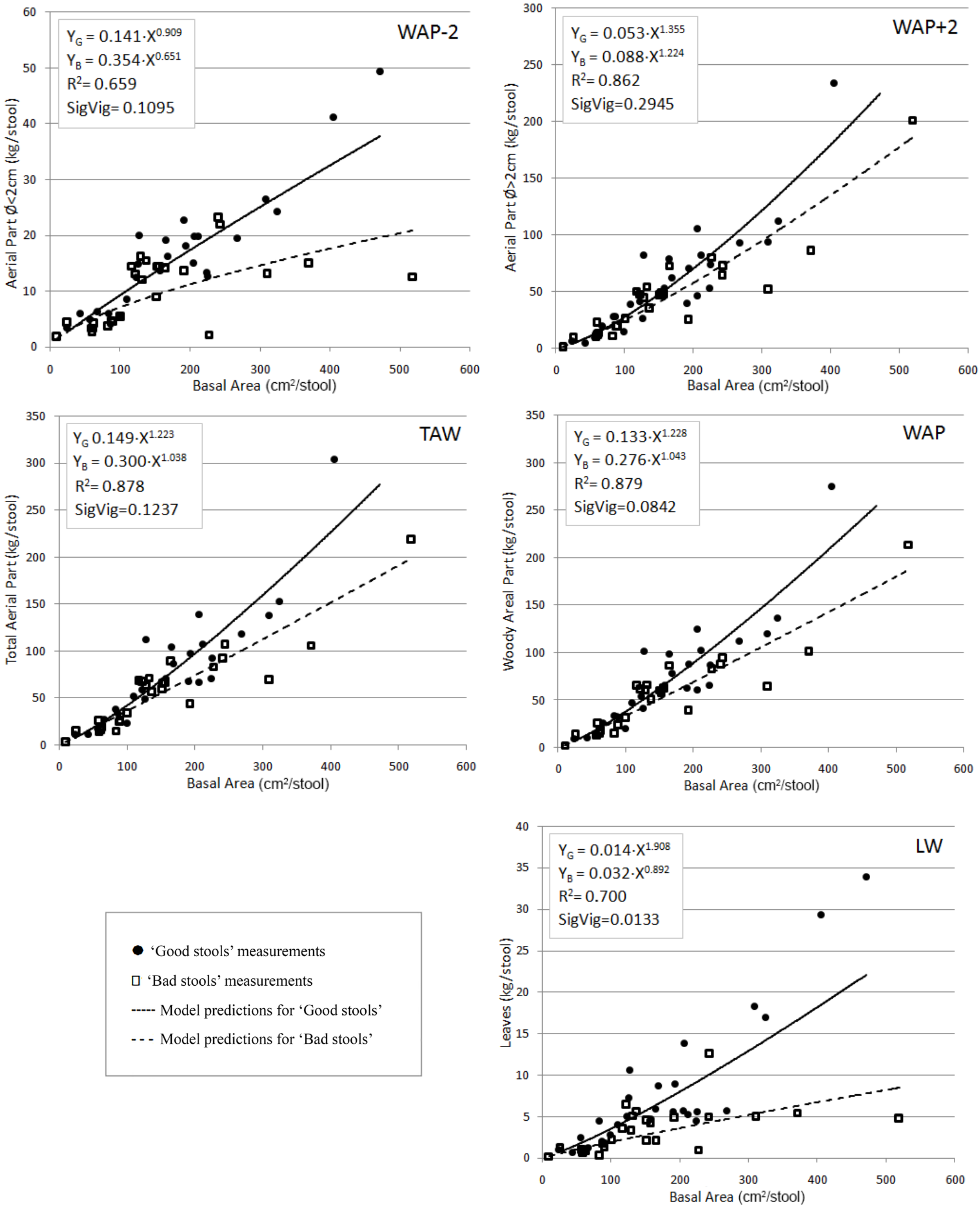

Figure 1. Linear regressions between the stools basal area at breast height and the dry weights of the different size fractions considered for aerial biomass (N=52). '*Stool vigour*' (good or bad) is considered in the models as a fixed factor. Equations of the fitted model for each size fraction are presented at the left corner of every plot, Yg: equation for good stools (stool vigour =1), Yb: equation for bad stools (stool vigour = 0). R^2: adjusted R-squared for the model. SigVig: significance of '*Stool vigour*' effect in the model

relationships between the SAR and the different root fractions (Table 7) showed no significant differences in any of the cases as regards stool vigour. Besides, it should be pointed out that root grafts on pre-existing roots of other stools were observed in several cases.

Variables of the relationship between below-ground and aerial biomass

Ratio parameters were developed between biomass fractions (both aboveground and belowground ones) and stools total dry weight, as well as with their corresponding SAR (Tables 8 & 9). The ratios between SAR and both the total aerial woody biomass and its different fractions showed a strong similarity within the two studied groups of stools, thus revealing that supplying capacity of the plant to its different parts - measured as the relative conducting area per unit of aerial biomass-, did not differ according to stools vigour. By contrast, there were marked and significant differences in relation to LW and TLA; the values for the bad vigour stools were, nonetheless, significantly higher in this case as a consequence of their noticeably lower leaf biomass and area and do not imply further considerations.

Regarding percentages of the different biomass fractions over the total dry weight of the stool (Table 9), it has to be pointed out that:

i) When comparing percentages of aerial fractions biomass instead of absolute values (Table 9), only the leaf fraction (LW%) remained significantly lower for the bad stools at the 95%, however whereas 2-7 cm (WAP2-7%) was also lower but at 90% of confidence level.

ii) With regard to percentages of below-ground fractions, the bad vigour stool group displays a greater significant proportion of root biomass between 2 and 7 cm (RW2-7, p=0.019). Surprisingly the mean values for percentages of RW2 were not significantly different. However, for the same amount of root biomass <2 cm, bad stools tend to show less above-ground biomass than good ones whereas below-ground biomass displayed the opposite trend: for the same amount of root biomass <2 cm, bad

Table 6. Descriptive statistics for below-ground biomass variables together with the estimation of the '*Stool vigour*' fixed effect over the means after random effects removal (namely '*Sampling pair*' nested into the '*Sampling region*'). Pairs of stools comprising group 2 (Table S1 [suppl]) were excluded.

Variable (Y)	Stool vigour (Xi)	N	Mean ± SD	Min.	Max.	Stool vigour effect estimation (β1)		
						β1	L-ratio	Sig.
RW2 (kg) Dry weight of roots with Ø < 2 cm	G	19	12.71 ± 10.75	0.40	47.07	3.78	7.80	**0.005**
	B	19	8.94 ± 7.34	0.48	30.44			
	All	38	10.83 ± 9.28	0.40	47.07			
RW2-7 (kg) Dry weight of roots with 2 cm< Ø <7 cm	G	19	12.71 ± 10.75	0.40	47.07	-0.30	0.02	0.093
	B	19	8.94 ± 7.34	0.48	30.44			
	All	38	10.83 ± 9.28	0.40	47.07			
RW7 (kg) Dry weight of roots with Ø> 7 cm	G	19	12.71 ± 10.75	0.40	47.07	-1.17	0.05	0.829
	B	19	8.94 ± 7.34	0.48	30.44			
	All	38	10.83 ± 9.28	0.40	47.07			
TRW (kg) Total dry weight of roots	G	19	61.33 ± 43.61	4.67	182.06	2.32	0.09	0.767
	B	19	59.01 ± 46.89	1.47	163.01			
	All	38	60.17 ± 44.68	1.47	182.06			
SA (cm^2) Stump area	G	19	376.42 ± 210.74	75.70	763.07	69.44	3.76	0.502
	B	19	306.98 ± 189.13	20.81	745.23			
	All	38	341.7 ± 200.61	20.81	763.07			
SAR (cm^2) Cross-sectional area of roots leaving pieces with Ø> 7cm	G	19	714.95 ± 484.23	176.00	2071.00	127.84	3.50	0.061
	B	19	587.11 ± 435.08	28.00	1437.00			
	All	38	651.03 ± 458.64	28.00	2071.00			

G: good vigour stools; B: bad vigour stools; N: sample size for parameters estimation; SD: standard deviation; significant p-values at 95% confidence level are shown in bold.

Table 7. Descriptive statistics for 'Roots Area: Below-ground biomass' ratios together with the estimation of the '*Stool vigour*' fixed effect over their means after random effects removal (namely '*Sampling pair*' nested into the '*Sampling region*'). Pairs of stools comprising group 2 (described in Table S1 [suppl]) were excluded.

Variable	**Stool vigour (Xi)**	**N**	**Mean ± SD**	**Min.**	**Max.**	**Stool vigour effect estimation (β_1)**		
						β_1	**L-ratio**	**Sig.**
SAR/RW2	G	19	92.55 ± 100.62	20.41	467.66	18.28	0.55	0.464
	B	19	74.27 ± 38.03	25.49	200.00			
	All	38	83.41 ± 75.6	20.41	467.66			
SAR/RW2-7	G	19	51.71 ± 24.11	8.09	118.17	10.36	1.68	0.203
	B	19	41.35 ± 25.14	15.13	130.02			
	All	38	46.53 ± 24.86	8.09	130.02			
SAR/RW7	G	19	27.2 ± 13.72	4.42	70.23	5.69	1.66	0.206
	B	19	21.51 ± 13.54	0.00	55.05			
	All	38	24.35 ± 13.75	0.00	70.23			
SAR/TRW	G	19	13.77 ± 7.5	2.51	40.25	2.28	1.74	0.187
	B	19	11.49 ± 5.28	5.58	26.93			
	All	38	12.63 ± 6.5	2.51	40.25			
SAR/SA	G	19	1.95 ± 0.69	1.02	3.42	0.10	0.19	0.667
	B	19	1.85 ± 0.7	0.80	3.36			
	All	38	1.9 ± 0.69	0.80	3.42			

SAR: aggregated cross-section of roots leaving pieces Ø>7cm; RW2: dry weight of roots with diameter < 2 cm ; RW2-7: dry weight of roots with diameter between 2-7cm; RW7: dry weight of roots with diameter >7 cm; TRW: total dry weight of roots; SA: stump area; G: good vigour stools; B: bad vigour stools; N: sample size for parameters estimation; SD: standard deviation; significant p-values at 95% confidence level are shown in bold.

stools showed higher below-ground biomass than good ones. For this reason, when ratios thin roots biomass to total stool biomass are assessed, above and below trends balanced out, therefore hiding the influence of stool vigour over the thinner roots biomass.

iii) The proportion of total weight corresponding to the aerial part (TAW%) was significantly higher (+10.8%) in the case of the good stools and therefore the proportion of total weight of roots (TRW%) was significantly lower (-12.6%), both at the 90% confidence level. Figs. 2 and 3 show a graphical comparison of total and partial biomass fractions percentages for good and bad vigour stools.

iv) Finally, with regards to the ratio of below-ground to aerial biomass (R:S biomass ratio), an overall mean value of 0.95 was obtained for the whole set of stools; 0.81 for the good vigour stools and 1.09 for the bad vigour stools. The differences between the good and bad stools were only significant at the 90% confidence level (Table 9).

Discussion

Under the current climate change scenario, holm oak coppices undergoing excess of competition among shoots, often display signs of loss of vigour. However, decline does not affect all stems homogeneously and it is common to find stools in close proximity within a stand showing very different vigour condition. One of the hypotheses most frequently put forward in the literature to explain the variation in the decline of stools, is based on the assumption that stools with poor vigour have excess below-ground biomass, particularly an excess of larger size fractions (Ducrey & Huc, 1999; Bravo *et al.*, 2008; Salomon *et al.,* 2016). Over the lifetime of a coppice forest, both the aerial and below-ground parts will grow. The aerial part will be harvested and/or burned from time to time and will recover itself by means of the resprouting mechanism, which requires non-structural carbohydrate and other nutrients which are stored in the root system (Mitchell *et al.,* 1992; Canadell *et al.,* 1999). In contrast, although the effect of coppicing on the root system is scarcely understood (Mitchell *et al.,* 1992), it is evident that the below-ground biomass is never extracted; hence it becomes increasingly large and old. One part of the gross primary production is dedicated to the respiration of the different plant tissues. The rest is the so-called net primary production, which is employed to produce reserves

Table 8. Descriptive statistics for 'Cross sectional area of roots: Above-ground biomass' ratios together with the estimation of the '*Stool vigour*' fixed effect over the means after random effects removal (namely '*Sampling pair*' nested into the '*Sampling region*'). Pairs of stools comprising group 2 (described in Table S1 [suppl]) were excluded.

Variable	**Stool vigour (Xi)**	**N**	**Mean ± SD**	**Min.**	**Max.**	**Stool vigour effect estimation (β_1)**		
						β_1	**L-ratio**	**Sig.**
SAR/WAP+2 (cm^2/kg)	G	19	15.16 ± 8.95	4.23	42.53			
	B	19	16.7 ± 9.05	6.59	41.18	-1.49	0.99	0.321
	All	38	15.93 ± 8.91	4.23	42.53			
SAR/WAP-2 (cm^2/kg)	G	19	50.15 ± 23.82	14.08	97.3			
	B	19	52.34 ± 19.3	15.3	88.85	-2.26	0.10	0.749
	All	38	51.24 ± 21.41	14.08	97.3			
SAR/LW (cm^2/kg)	G	19	127.02 ± 60.13	34.85	268.57			
	B	19	205.3 ± 157.45	74.52	775.86	-78.27	4.10	**0.050**
	All	38	166.16 ± 124.07	34.85	775.86			
SAR/WAP (cm^2/kg)	G	19	10.93 ± 4.7	3.25	18.06			
	B	19	11.68 ± 4.52	5.05	20.76	-0.75	0.25	0.618
	All	38	11.3 ± 4.56	3.25	20.76			
SAR/TAW (cm^2/kg)	G	19	9.95 ± 4.16	2.98	16.92			
	B	19	10.9 ± 4.13	4.73	19.66	-0.95	0.50	0.482
	All	38	10.42 ± 4.12	2.98	19.66			
SAR/TLA (cm^2/m^2)	G	19	32.38 ± 15.31	8.89	68.36			
	B	19	52.34 ± 40.05	19.00	197.37	-19.96	4.10	**0.050**
	All	38	42.36 ± 31.57	8.89	197.37			

SAR: cross-section of roots leaving pieces Ø>7cm; WAP+2: dry weight of the woody aerial part with Ø>2cm; WAP-2: dry weight of the woody aerial part with Ø<2cm; *LW*: leaf dry weight; WAP: woody aerial part dry weight. TAW: total aerial part dry weight. TLA: total leaf area per stool; G: good vigour stools; B: bad vigour stools; N: sample size for parameters estimation; SD: standard deviation; significant *p* values at 95% confidence level are shown in bold.

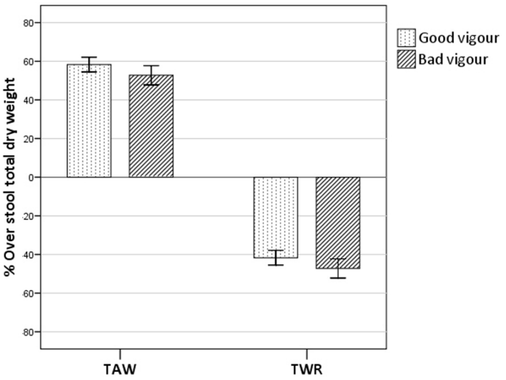

Figure 2. Percentage of total aerial (TAW) and below-ground (TWR) dry weight with respect to the stool total weight by groups according to the factor '*Stool vigour*'. Error bars represent 95% confidence intervals for the mean.

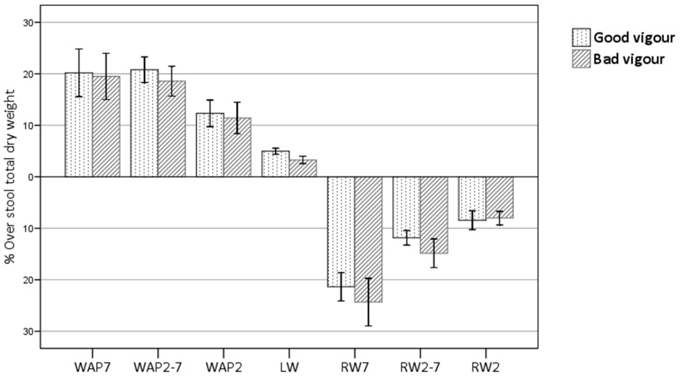

Figure 3. Percentages of dry weight of the different aerial and below-ground size fractions with respect to the stool total dry weight by groups according to '*Stool vigour*'. WAPi: dry weight of the aerial fraction 'i'. RWj: dry weight of the radical fraction 'j'; LW: leaves weight. Error bars represent 95% confidence intervals for the mean

Table 9. Descriptive statistics for the dry weight proportions of the different size fractions of below and above-ground biomass, over stool total dry weight; together with the estimation of the '*Stool vigour*' fixed effect over the means after random effects removal (namely '*Sampling pair*' nested into the '*Sampling region*'). Pairs of stools comprising group 2 (Table S1 [suppl]) were excluded.

Variable	**Stool vigour (Xi)**	**N**	**Mean ± SD**	**Min.**	**Max.**	**Stool vigour effect estimation (β_1)**		
						β_1	**L-ratio**	**Sig.**
WAP2 (%) Dry weight of the woody aerial part with Ø>2 cm	G	19	12.52 ± 7.18	6.26	37.97	0.81	0.76	0.385
	B	19	11.71 ± 7.96	4.54	42.86			
	All	38	12.12 ± 7.49	4.54	42.86			
SWAP2-7 (%) Dry weight of the woody aerial part with 2<Ø<7 cm	G	19	21.89 ± 5.85	10.18	32.01	2.74	**3.17**	0.075
	B	19	19.14 ± 6.85	10.12	33.23			
	All	38	20.51 ± 6.44	10.12	33.23			
WAP7 (%) Dry weight of the woody aerial part with Ø>7 cm	G	19	18.08 ± 10.37	0	38.44	1.28	**0.64**	**0.425**
	B	19	16.8 ± 11.2	0	33.93			
	All	38	17.44 ± 10.66	0	38.44			
LW (%) Dry leaf weight	G	19	4.62 ± 1.21	2.7	7.64	1.32	**9.05**	0.005
	B	19	3.26 ± 1.45	0.89	5.66			
	All	38	3.94 ± 1.49	0.89	7.64			
TAW (%) Total dry weight of the aerial part	G	19	57.1 ± 10.11	37.58	76.31	6.20	**2.91**	0.097
	B	19	50.91 ± 12.18	28.6	75.69			
	All	38	54.01 ± 11.48	28.6	76.31			
RW2 (%) Dry weight of roots with Ø < 2 cm	G	19	8.92 ± 5.1	2.53	21.57	0.76	**0.66**	**0.417**
	B	19	8.17 ± 3.68	3.28	18.1			
	All	38	8.54 ± 4.4	2.53	21.57			
RW2-7 (%) Dry weight of roots with 2 < Ø < 7 cm	G	19	11.65 ± 3.31	7.73	18.53	-3.66	**5.49**	0.019
	B	19	15.32 ± 7.06	5.07	30.51			
	All	38	13.49 ± 5.75	5.07	30.51			
RW7 (%) Dry weight or roots with Ø >7 cm	G	19	22.33 ± 7.17	11.49	35.94	-3.27	**1.47**	**0.226**
	B	19	25.6 ± 11.87	0	46.66			
	All	38	23.96 ± 9.81	0	46.66			
TRW (%) Total dry weight of roots	G	19	42.9 ± 10.11	23.69	62.42	-6.17	**2.88**	0.099
	B	19	49.09 ± 12.18	24.31	71.4			
	All	38	45.99 ± 11.48	23.69	71.4			
TRW / TAW Root to Shoots ratio (R:S)	G	19	0.81 ± 0.34	0.31	1.66	-0.28	3.26	**0.079**
	B	19	1.09 ± 0.59	0.32	2.50			
	All	38	0.95 ± 0.50	0.31	2.50			

G: good vigour stools; B: bad vigour stools; N: sample size for parameters estimation; SD: standard deviation; significant *p*-values at 95% confidence level are shown in bold.

of substances and biomass including the renewal of leaves and fine roots to compensate their turnover and if possible, the production of new ones (Gracia *et al.,* 1999c). Thus, if the below-ground biomass of the stool gets larger and larger, it can be assumed that it will use a progressively greater amount of the available resources to maintain itself, resulting in problems for the renewal of fine roots (Serrada, 2011) and consequently in the possible decline of the stool (Salomón *et al.,* 2016). In the present study, the bad vigour stools neither showed greater absolute total below-ground biomass nor a larger amount of thick roots biomass (Ø>7 cm) as argued above; however, they showed greater percentages of both total and 2-7 cm roots biomass, and largely less absolute fine roots biomass (Ø<2 cm). Since above-ground part of the stools was periodically renewed, the observed results involved that the sampled bad stools, despite displaying total and thick root biomass similar to that of the good stools, have produced a notably smaller amount of aerial biomass since the last coppicing event. The higher R:S biomass ratio measured for bad stools (Table 9) also support this statement. In this regard, Canadell & Rodá (1991) found that the R:S biomass ratio increases significantly with site xericity in the case of single-stemmed holm oak trees, probably as an adaptive mechanism to lack of water. In general terms, the proportion of biomass accumulated in below-ground tissues increases with site limitations in perennial plants (Rundel, 1980). In our study, there were no site disparities which could explain the differences between good and bad stools as they share locations by pairs. However, those differences between the characteristics of the stools might be related to their differing behaviour under similar circumstances; the stools with a poor vigour showing signs of being less efficient on profiting site conditions, therefore displaying features which are typically found in worse site qualities.

Scarcity of fine roots might be relevant to explain the potential lower site-use efficiency of bad stools given that they are responsible of water and nutrient capture (Canadell *et al.,* 1999), and constitute the surface for root hairs insertion which penetrate the pores in the soil noticeably increasing the absorption area (Pardos, 2001). Several studies have already shown the importance of the dynamic of the fine root system in relation to the functioning, growth and response to silvicultural treatments of holm oak stands, especially Mediterranean coppices (López *et al.,* 2003; Gárate & Blanco, 2013).

Concerning root system configuration, bad stools were also found to show slightly worse sap conductivity as measured by SAR. According to Ducrey & Huc (1999) the lower water-use efficiency in coppices may be also associated with problems of conductivity in the stools. The sap and mineral elements should travel from the absorbent roots to the aerial part of the plant via the thick below-ground biomass which resists their passage, and therefore coppices would display transpiration values well below their potential under scenarios of unlimited water availability (Ducrey & Huc, 1999). In this respect, the only physiological variable that showed significant differences depending on the vigour of the stools, was the predawn water potential (WP_P). This variable is highly dependent upon soil water status although it is also affected by other soil and plant characteristics associated with water uptake and flow processes. Hence, WP_P is expected to provide a measure of the real soil water potential experienced by the trees rather than the theoretical one (Hinckley *et al.,* 1978). In the current study the differences in WP_P would imply that the bad stools experience a lower soil water potential despite sharing the same site conditions as the good stools. This fact may therefore confirm, from a physiological perspective, that the bad stools showed a lower capacity to make use of the water resources in the soil previously mentioned.

In short, for the sampled pairs, the differences between good and bad stools as regards the below-ground part do not seem to lie in the overall biomass of the root system, but rather in the less efficient architecture of the root systems within bad stools, which restricts their capacity to exploit site potentiality. A final aspect which should be mentioned concerning root system is that root grafts between roots of different stools have been found, which may partly explain the variability found in the relationship between the apparent root system of the stools and the aerial part. In any case, this finding contradicts results of a study by Canadell & Rodá (1991) and Keeley's (1988) hypothesis, which considers this type of graft to be very unlikely in Mediterranean environments. However, it supports the suspicion expressed in Salomón *et al.* (2016).

The rest of the physiological variables analysed, apart from WP_P, showed no significant differences according to stool vigour. However, since there were far fewer leaves on the bad stools (whether quantified in terms of biomass or leaf area), it is to be expected that, besides their lower root absorption capacity, as a whole, the photosynthetic capacity and ultimate productivity will be lower than that of the good stools. Moreover, under equal conditions for the rest of the factors, this lower ultimate productivity level will result in smaller growth increments, which is in accordance with the lower aerial biomass observed in bad stools group for all the considered fractions, the differences being significant and very pronounced (Table 5). Both good and bad stool percentages of total below-ground biomass (table 9) differed greatly from the reference value reported by different authors for the average tree in high forest of approximately 25 % below-ground biomass (Abrahamson & Caswell, 1982; Agren & Ingestad, 1987; Gower *et al.*, 1993; Alberto & Elvir, 2008). They were also very different from the percentages found for holm oak in high forest by other authors such as Montero *et al.* (2005) in dehesa systems (65 % aerial - 35 % roots) or by Ruiz-Peinado *et al.* (2012) (62% aerial - 38% roots). However, the values obtained in the present study are very similar to those previously found for the species in coppices (Gracia *et al.,* 1997, 1999a, 2005).

Within the analysed sample, the biomass measurements carried out appeared to indicate that the biomass of the smaller size fractions and particularly that of leaves, was the most related to the stool vigour, regardless of size. This fact points again to an adaptation mechanism or response to a situation of increased water stress, which, among other things, leads to the loss of leaves and twigs (Pardos, 2001). In particular, the fact that bad vigour stools have a much lower amount of fine roots, may be closely related to the lower leaf biomass of these stools. As stated by Pardos (2001), the loss of leaves and therefore the reduction in leaf transpiration area could be a defence mechanism, perhaps due to an imbalance between the water lost through transpiration and that absorbed through the roots, leading to effects such as those observed by López *et al.* (2009) following severe drought. In any case, the smaller amount of leaf biomass and roots with a diameter under 2 cm in the bad stools, would seem to be coherent with the idea that fine roots and leaves show parallel dynamics (Gracia *et al.,* 1999c). Moreover, the detailed analysis of the leaf characteristics of the sample confirm that the lower leaf biomass in the stools with poor vigour is due to the fact that although the leaves are of the same size as those on good vigour stools, they have a much smaller number of them. Furthermore, these leaves have a greater weight per unit area (LMA), this increase in single leaf weight being insufficient to offset the decrease in number of leaves as regards total leaf biomass (Table 5). Increasing leaf density and reducing the number of leaves are both strategies described by many authors as a way of adapting to an increase in water stress (Niinemets, 2001; Bussoti *et al.,* 2002; Valladares *et al.*, 2004; Gratani & Varone, 2006, Limousin *et al.*, 2009). In contrast, Ogaya & Peñuelas (2007a) report that, in the case of holm oak, increasing LMA seems to be a protective mechanism against cold winter temperatures rather than to dry conditions. The altitude within the study area ranges from 725 to 1217 m a.s.l., which implies significant variations in the temperature regime. Even so, the ‘location’ of the stools included in the sample, which was included as a random factor in the models for all the variables analysed (‘Data analysis’ section), was not significant in terms of explaining the variability found in the LMA of the sample, whereas the vigour level was found to be significant (Table 4). Therefore, in the case of the sample analysed, the differences observed in leaf morphology would not seem to be due to the range of variation in the site conditions but rather again to the fact that the bad stools are not capable of using site potentiality to the same extent as the good stools, particularly with regard to water resource use.

Among the factors analysed, the poorer root architecture (mainly lower fine root biomass and smaller conductive area, SAR), the greater R:S ratio (lower develop of aerial part for similar root biomass) and particularly the lower leaf biomass, are the main factors identified in the analysed stools influencing predisposition to decay (sensu Manion, 1991). The reason why stools in close proximity displayed these morphological differences remains unknown; it may be related to their genotype, their life history (competition in their immediate surroundings, number and type of cuttings they have undergone etc.) or perhaps their age. With regards to the age of the “never-extracted” below-ground part and therefore of the individual, it is obviously difficult to determine, but in the case of coppices in the Mediterranean basin traditionally used for firewood production the age may reach hundreds of years. Salomón *et al.* (2016), for example, have estimated the age of *Quercus pyrenaica* root systems to be around 550 years through radiocarbon dating.

In any case, in accordance with the theory expressed by Camarero *et al.* (2004), the factors analysed (each of which will have a different weight and probably act in conjunction with other factors not considered in this study) appear to predispose the holm oaks to decay, making them more vulnerable to aggravating factors such as extreme climatic events. Hence, the increase in frequency and intensity of such episodes during recent decades in the Iberian Peninsula (Vericat *et al.,* 2012) has highlighted this vulnerability, leading to the decay and even death of individuals which previously appeared to be viable.

It seems to be a fact that climate change is causing increased aridity in the Mediterranean area of Spain due to lower annual precipitation and more irregular distribution of rainfall (Bravo, 2007; IPCC, 2007; Vericat *et al.,* 2012). If, as argued by some authors, i) forests in the Mediterranean zone are especially vulnerable to these changes (EEA, 2008; Sánchez-Salguero *et al.,* 2017); ii) the most sensitive functional group to this increase in aridity is precisely the sclerophyll group (Valladares *et al.,* 2004), and iii) the holm oak is particularly sensitive to climate change due to its debatable ecophysiological tolerance and low water-use efficiency during episodes of extreme drought (Joffre *et al.,* 2001; Martínez-Vilalta *et al.*, 2002, Reichstein *et al.,* 2002); then the findings of this study suggest that some holm oak stools may already be showing serious problems in this regard. Applying the process model GOTILWA, the following changes were predicted in a holm oak coppice under a scenario of increasing both temperature and atmospheric CO_2 and reducing water availability (Gracia *et al.,* 1999c): increase in the proportion of gross primary production invested in maintenance respiration; increase in leaf shedding and decrease in mean leaf life and as a result of both of these factors, an increase in leaf production, in spite of which, the increase in leaf maintenance costs causes a decrease in LAI; decrease in wood production; tree mortality. The bad stools analysed in this study seem to display many of these changes or at least signs of them, including mortality in some cases.

If this hypothesis is correct (coherent with the abundant and increasing presence of stems with dieback and degraded stools in holm oak coppices in the central region of the Iberian Peninsula) it is likely that the increase in aridity will lead to a rise in the number of individuals being affected, which is why adaptive management strategies must be developed to address the changing situation. In the case of aged holm oak coppices, the best option may be to carry out conversion thinning to high forest, as described by Bravo *et al.* (2008), which it is hoped would have the following positive effects: 1) increased diameter growth (Ducrey, 1992; Aussenac *et al.,* 1995; Gracia *et al.,* 1997; Albeza *et al.,* 1999; Bravo-Fernández *et al.,* 2013) and greater leaf production (Gracia *et al.,* 1997, 1999c; Albeza *et al.,* 1999) in the remaining stems, thereby producing a more balanced structure as regards the relationship between photosynthetic tissue/ respiratory tissue (Pardos, 2001); 2) possible increase in height and crown diameter, as observed in *Quercus faginea* (San Miguel *et al.,* 1984) and *Quercus pyrenaica* (San Miguel, 1985), with the associated increments in all the aerial biomass fractions; 3) increase in the length, biomass and renewal rate of the fine roots (Gracia *et al.,* 1997, 1999a); 4) improved water availability and ecophysiological functioning, especially under drought conditions, hence defoliation is reduced (Aussenac *et al.,* 1995; Cutini & Mascia, 1996; Gracia *et al.,* 1997, 1999a); 5) increase in net photosynthesis (Aussenac *et al.,* 1995; Huc & Ducrey, 1996; Ducrey& Huc, 1999), which would also permit an increase in carbohydrate reserves.

In short, greater resistance to drought would be especially important under future scenarios of greater aridity resulting from current climate change processes (Gracia *et al.,* 1999c).

Conclusions

The worse configuration of the root system of the decayed stools, particularly the lower fine roots biomass (Ø<2cm) and less conductive area, seems to diminish their capacity to fully profit site potentiality. As a result, their productivity decreases too and therefore they develop smaller aerial biomass. This effect is especially strong over the leaf fraction, which undergoes both the accumulated effect of stools size reduction and the punctual effect of increased xericity perception in return for root system inefficiencies. The ultimately generated root to shoot imbalance, together with the lower leaf biomass and worse roots architecture are potential causes to predispose these holm oaks stools to decline, therefore increasing their vulnerability to site conditions worsening.

Acknowledgments

The authors gratefully acknowledge Gregorio Montero his always wise and generous lessons in the field of silviculture, particularly with regard to coppice forests management.

References

Abrahamson W, Caswell H, 1982. On the comparative allocation of biomass, energy and nutrients in plants. Ecology 63: 982-991. https://doi.org/10.2307/1937238

Agren G, Ingestad T, 1987. Root/shoot ratios as a balance between nitrogen productivity and photosynthesis. Plant Cell Environ 10: 579-586.

Alberto DM, Elvir JA, 2008. Acumulación y fijación de carbono en biomasa aérea de *Pinus oocarpa* en bosques naturales en Honduras. Invest Agrar: Sist Recur For 17 (1): 67-78.

Albeza E, Arques E, Bernabé A, Escarré A, Jiménez-Ortiz T, Lledó MJ, Sánchez JR, 1999. Experiencias para la mejora de masas forestales. Programa de investigación y desarrollo en relación con la restauración de la cubierta vegetal: Reunión de Coordinación, Castellón, September 22-24. pp: 21-31.

Aussenac G, Granier A, Bréda N, 1995. Effets des modifications de la structure du couvert forestier sur le bilan hydrique, l'état hydrique des arbres et la croissance. Rev For Fr 47 (1): 55-62. https://doi.org/10.4267/2042/26624

Barbeta A, Ogaya R, Peñuelas J, 2013. Dampening effects of long-term experimental drought on growth and mortality rates of a Holm oak forest. Glob Chang Biol 19: 3133-3144. https://doi.org/10.1111/gcb.12269

Bravo F (coord.), 2007. El papel de los bosques españoles en la mitigación del cambio climático. Fundación Gas Natural, Barcelona, Spain. 315 pp.

Bravo Fernández JA, Roig Gómez S, Serrada Hierro R, 2008. Selvicultura en montes bajos y medios de encina (*Quercus ilex* L.), rebollo (*Q. pyrenaica* Willd.) y quejigo

(*Q. faginea* Lam.): tratamientos tradicionales, situación actual y principales alternativas. In: Compendio de Selvicultura Aplicada en España; Serrada R, Montero G, Reque J (eds,). pp: 657-745. INIA & FUCOVASA, Madrid.

Bravo-Fernández JA, Mutke S, Barrero D, Martinez G, Serrada R, Roig S, 2013. Resalveos de conversión sobre tallares de encina: ¿qué ha pasado 15 años después? 6º Congreso Forestal Español, Vitoria, June 10-14.

Bussotti F, Bettini D, Grossoni P, Mansuino S, Nibbi R, Soda C, Tani C, 2002. Structural and functional traits of *Quercus ilex* in response to water availability. Environ Exp Bot 47: 11-23. https://doi.org/10.1016/S0098-8472(01)00111-3

Camarero JJ, Lloret F, Corcuera L, Pe-uelas J, Gil-Pelegrín E, 2004. Cambio global y decaimiento del bosque. In: Ecología del bosque mediterráneo en un mundo cambiante; Valladares F (ed). pp: 397-423. Ministerio de Medio Ambiente, EGRAF S.A., Madrid.

Canadell J, Roda F, 1991. Root biomass of *Quercus ilex* in a montane Mediterranean forest. Can J For Res 21: 1771-1778. https://doi.org/10.1139/x91-245

Canadell J, Djema A, López B, Lloret F, Sabaté S, Siscart D, Gracia C, 1999. Structure and dynamics of the root system. In: Ecology of Mediterranean evergreen oak forests; Rodà F, Retana J, Gracia C, Bellot J (eds). pp: 47-59. Springer, Berlin. https://doi.org/10.1007/978-3-642-58618-7_4

Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas J, 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proc Natl Acad Sci USA 108: 1474-1478. https://doi.org/10.1073/pnas.1010070108

Cañellas I, San Miguel A, 2000. Biomass of root and shoot systems of *Quercus coccifera* shrublands in Eastern Spain. Ann For Sci 57: 803-810. https://doi.org/10.1051/forest:2000160

Corcuera L, Camarero JJ, Gil-Pelegrín E, 2004. Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy. Trees 18 (1): 83-92. https://doi.org/10.1007/s00468-003-0284-9

Cotillas M, Espelta JM, Sánchez-Costa E, Sabaté S, 2016. Above-ground and below-ground biomass allocation patterns in two Mediterranean oaks with contrasting leaf habit: an insight into carbon stock in young oak coppices. Eur J For Res 135: 243-252. https://doi.org/10.1007/s10342-015-0932-9

Cutini A, Mascia V, 1996. Silvicultural treatment of holm oak (*Quercus ilex* L.) coppices in Southern Sardinia: effects of thinning on water potential, transpiration and stomatal conductance. Ann Ist Sper Selvic 27: 47-53.

de Olazabal L, 1883. Ordenación y valoración de montes. Imprenta de Moreno y Rojas, Madrid. 517 pp.

Ducrey M, 1992. Quelle sylviculture et quel avenir pour les taillis de chêne vert (*Quercus ilex* L.) de la région méditerraneénne française. Rev For Fr 44 (1): 12-33. https://doi.org/10.4267/2042/26291

Ducrey M, Huc R, 1999. Effets de l'éclaircie sur la croissance et le fonctionnement écophysiologique d'un taillis de chêne vert. Rev For Fr 2: 326-340. https://doi.org/10.4267/2042/5440

EEA, 2008. Impacts of Europe's changing climate - 2008. An indicator-based assessment (EEA Report No 4/2008). Office for Official Publications of the European Communities, Luxembourg. 246 pp.

Eichhorn J, Szepesi A, Ferretti M, Durrant D, Roskams P, 2006. Part II: Visual Assessment of Crown Condition. In: Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests. pp: 69. UNECE ICP Forests Programme Coordinating Centre, Hamburg.

Eichhorn J, Roskams P, Ferreti M, Mues V, Szepesi A, Durrant D, 2010. Manual part IV: Visual assessment of crown condition and damaging agents. In: Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests. pp: 49. UNECE ICP Forests Programme Coordinating Centre, Hamburg.

Gárate M, Blanco JA, 2013. Importancia de la caracterización de la biomasa de raíces en la simulación de ecosistemas forestales. Ecosistemas 22 (3): 66-73. https://doi.org/10.7818/ECOS.2013.22-3.10

Gea-Izquierdo G, Martín-Benito D, Cherubini P, Cañellas I, 2009. Climate-growth variability in *Quercus ilex* L. west Iberian open woodlands of different stand density. Ann For Sci 66: 802. https://doi.org/10.1051/forest/2009080

Gower S, Reich B, Son Y, 1993. Canopy dynamics and above-ground production for five tree species with different leaf longevities. Tree Physiol 12 (4): 327-345. https://doi.org/10.1093/treephys/12.4.327

Gracia C, Bellot J, Sabaté S, Albeza E, Djema A, León B, López B, Martínez JM, Ruiz I, Tello E, 1997. Análisis de la respuesta de *Quercus ilex* L. a tratamientos de resalveo selectivo. In: La restauración de la cubierta vegetal de la Comunidad Valenciana. pp: 547-601. Fundación Centro de Estudios Ambientales del Mediterráneo.

Gracia C, Sabaté S, López B, 1999a. Aplicación de la relación funcional entre la biomasa aérea y subterránea para una gestión del encinar encaminada a su conversión en monte alto. Programa de investigación y desarrollo en relación con la restauración de la cubierta vegetal: Reunión de Coordinación, Castellón (Spain), September 22-24. pp: 190-201.

Gracia C, Sabaté S, Martínez J M, Albeza E, 1999b. Functional responses to thinning. In: Ecology of Mediterranean evergreen oak forests; Rodà F *et al.*

(eds). pp: 329-338. Springer, Germany. https://doi.org/10.1007/978-3-642-58618-7_23

Gracia C, Tello E, Sabaté S, Bellot J, 1999c. GOTILWA: an integrated model of water dynamics and forest growth. In: Ecology of Mediterranean evergreen oak forests; Rodà F *et al.* (eds). pp: 163-179. Springler, Germany. https://doi.org/10.1007/978-3-642-58618-7_12

Gracia C, Gil L, Montero G, 2005. Evaluación del impacto climático sobre el sector forestal. In: Evaluación preliminar de los impactos en España por efecto del cambio climático; Moreno JM (ed.). pp: 399-435. Ministerio de Medio Ambiente. Madrid.

Gratani L, Varone L, 2006. Long-time variations in leaf mass and area of Mediterranean evergreen broad-leaf and narrow-leaf maquis species. Photosynthetica 44: 161-168. https://doi.org/10.1007/s11099-006-0001-1

Hinckley T, Lassoie J, Running S, 1978. Temporal and spatial variations in the water status of forest trees. For Sci, Monograph 20: 72 pp.

Huc R, Ducrey M, 1996. Ecophysiological response to thinning in a *Quercus ilex* L. coppice stand. Ann Ist Sper Selvic 27: 39-45.

IPCC, 2007. Fourth Assessment Report of the Intergovernmental Panel in Climate Change. Cambridge University Press.

Joffre R, Rambal S, Winkel T, 2001. Respuestas de las plantas mediterráneas a la limitación de agua: desde la hoja hasta el dosel. In: Aspectos funcionales de los ecosistemas mediterráneos; Zamora R, Pugnaire FI (eds). pp: 37-85. CSIC-AEET, Granada.

Keeley JE, 1988. Population variation in root grafting and a hypotesis. Oikos 52: 364-366. https://doi.org/10.2307/3565212

Larcher W, 1977. Ecofisiología vegetal. Ediciones Omega, S.A. Barcelona, Spain. 305 pp.

Limousin JM, Rambal S, Ourcival JM, Rocheteau A, Joffre R, Rodriguez-Cortina R, 2009. Long-term transpiration change with rainfall decline in a Mediterranean *Quercus ilex* forest. Glob Chang Biol 15: 2163-2175. https://doi.org/10.1111/j.1365-2486.2009.01852.x

López BC, Sabate S, Gracia C, 1998. Fine roots dynamics in a Mediterranean forest: effects of drought and stem density. Tree Physiol 18: 601-606. https://doi.org/10.1093/treephys/18.8-9.601

López BC, Sabaté S, Gracia C, 2003. Thinning effects on carbon allocation to fine roots in a *Quercus ilex* forest. Tree Physiol 23: 1217-1224. https://doi.org/10.1093/treephys/23.17.1217

López BC, Gracia CA, Sabaté S, Keenan T, 2009. Assessing the resilience of Mediterranean holm oaks to disturbances using selective thinning. Acta Oecol 35: 849-854. https://doi.org/10.1016/j.actao.2009.09.001

Manion PD, 1991. Tree disease concepts. Prentice Hall. 402 pp.

Manzano MJ, Sánchez-Peña G, San Pedro S, Torres B, 2013. Vitalidad de *Quercus ilex* durante los últimos 26 años. Dinámica e identificación de áreas críticas desde el punto de vista sanitario. Proc 6º Congreso Forestal Español, Vitoria, June 10-14. 11 pp.

Martinez-Vilalta J, Piñol J, Beven K, 2002. A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. Ecol Model 155: 127-147. https://doi.org/10.1016/S0304-3800(02)00025-X

Mitchell CP, Ford-Robertson JB, Hinckley T, Sennerby-Forss L, 1992. Ecophysiology of short rotation forest crops. Elsevier Sci Publ LTD, Oxford, England. 311 pp.

Montero G, Ortega C, Cañellas I, Bachiller A, 1999. Productividad aérea y dinámica de nutrientes en una repoblación de *Pinus pinaster* Ait. sometida a distintos regímenes de claras. Invest Agrar: Sist Recur For, Fuera de serie: 175-206.

Montero G, Ruiz-Peinado R, Muñoz M, 2005. Producción de biomasa y fijación de CO_2 por los bosques españoles. Monogr INIA: Ser For 13. INIA, Ministerio de Educación y Ciencia, Madrid, España. 270 pp.

Niinemets U, 2001. Global-scale climatic controls of leaf dry mass per area, density and thickness in trees and shrubs. Ecology 82 (2): 453-469. https://doi.org/10.1890/0012-9658(2001)082[0453:GSCCOL]2.0.CO;2

Ogaya R, Peñuelas J, 2007a. Leaf mass per area ratio in *Quercus ilex* leaves under a wide range of climatic conditions. The importance of low temperatures. Acta Oecol 31: 168-173.https://doi.org/10.1016/j.actao.2006.07.004

Ogaya R, Peñuelas J, 2007b. Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five year experimental field drought. Plant Ecol 189: 291-299. https://doi.org/10.1007/s11258-006-9184-6

Ojeda F, 2001. El fuego como factor clave en la evolución de plantas mediterráneas. Ecosistemas Mediterráneos. Análisis Funcional. Simposio de la Sociedad Española de Ecología Terrestre, Granada, February 11-13 (2000). pp: 319-349.

Pardos JA, 2001. Fisiología vegetal aplicada a especies forestales. Fundación Conde del Valle de Salazar, Madrid, Spain. 456 pp.

Pérez-Ramos IM, Rodríguez-Calcerrada J, Ourcival JM, Rambal S, 2013. *Quercus ilex* recruitment in a drier world : a multi-stage demographic approach. Perspec Plant Ecol Evol Syst 15 (2): 106-117. https://doi.org/10.1016/j.ppees.2012.12.005

Pinheiro J, Bates D, DebRoy S, Sakar D, 2016. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-128.

Reichstein M, Tenhunen JD, Roupsard O, Ourcival JM, Rambal S, Miglietta F, Peressotti A, Pecchiari M, Tirone G, Valentini R, 2002. Severe drought effects on ecosystem CO_2 and H_2O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? Global Change Biol 8: 999-1017. https://doi.org/10.1046/j.1365-2486.2002.00530.x

Roda F, Retana J, Gracia CA, Bellot J (eds), 1999. Ecology of mediterranean evergreen oak forests. Springer, Barcelona. 373 pp. https://doi.org/10.1007/978-3-642-58618-7

Rodríguez-Calcerrada J, Pérez-Ramos IM, Ourcival JM, Limousin JM, Joffre R, Rambal S, 2011. Is selective thinning an adequate practice for adapting coppices to climate change? Ann For Sci 68: 575-585. https://doi.org/10.1007/s13595-011-0050-x

Ruiz-Peinado R, del Rio M, Montero G, 2011. New models for estimating the carbon sink capacity of Spanish softwood species. Forest Syst 20 (1):176-188. https://doi.org/10.5424/fs/2011201-11643

Ruiz-Peinado R, Montero G, del Rio M, 2012. Biomass models to estimate carbon stocks for hardwood tree species. Forest Syst 21 (1): 42-52. https://doi.org/10.5424/fs/2112211-02193

Ruiz-Peinado R, Roig S, Serrada R, Bravo-Fernández JA, 2015. ¿Cuánto carbono retienen nuestros antiguos montes leñeros? Ecuaciones de biomasa para tallares de encina (*Quercusilexsubsp. ballota* L.) y quejigo (*Q. faginea* Lam.) en la zona centro de la Península Ibérica. Remedia Workshop. Madrid.

Rundel PW, 1980. Adaptations of Mediterranean-climate oaks to environmental stress. In: Ecology, management and utilization of California oaks. USDA For Serv Gen Tech Rep 44: 43-44.

Sabaté S, Gracia C, Sánchez A, 2002. Likely effects of climate change on growth of , P*inus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. For Ecol Manage 162: 23-37.

Salomón R, Rodríguez-Calcerrada J, Zafra E, Morales-Molino C, Rodríguez-García A, González-Doncel I, Oleksyn J, Zytkowiak R, López R, Miranda JC, *et al.*, 2016. Unearthing the roots of degradation of *Quercus pyrenaica* coppices: A root-to-shoot imbalance caused by historical management? For Ecol Manage 363: 200-211.

San Miguel A, 1985. Variaciones producidas en un pastizal arbolado con rebollos (*Quercus pyrenaica* Willd.) por claras de distinta intensidad. An INIA: Ser For 9: 97-104.

San Miguel A, Montero G, Montoto JL, 1984. Estudios ecológicos y silvopascícolas en un quejigal (*Quercus faginea* Lamk.) de Guadalajara. Primeros resultados. An INIA: Ser For 8: 153-164.

Sánchez-Palomares O, López Senespleda E, Roig Gómez S, Vázquez de la Cueva A, Gandullo Gutiérrez JM, 2012. Las estaciones ecológicas actuales y potenciales de los encinares españoles peninsulares. Monog INIA: Ser For 23. Madrid. 317 pp.

Sánchez-Salguero R, Camarero JJ, Gutiérrez E, González Rouco F, Gazol A, Sangüesa-Barreda G, Andreu-Hayles L, Linares JC, Seftigen K, 2017. Assessing forest vulnerability to climate warming using a process-based model of tree growth: bad prospects for rear-edges. Glob Change Biol 23(7): 2705-2719. https://doi.org/10.1111/gcb.13541

Sanesi G, Lafortezza R, Colangelo G, Marziliano PA, Davies C, 2013. Root system investigation in sclerophyllous vegetation: An overview. Ital J Agron 8: 121-126. https://doi.org/10.4081/ija.2013.e17

Scarascia-Mugnozza G, Oswald H, Piussi P, Radoglou K, 2000. Forests of the Mediterranean region : gaps in knowledge and research needs. For Ecol Manage 132: 97-109.

Serrada R, 2011. Apuntes de Selvicultura. Fundación Conde Valle de Salazar, ETSI Montes, EUIT Forestal, UPM, Madrid. 502 pp.

Serrada R, Allué M, San Miguel A, 1992. The coppice system in Spain. Current situation, state of art and major areas to be investigated. Ann Ist Sper Selvic 23: 266-275.

Serrada Hierro R, Aroca Fernández MJ, Roig Gómez S, Bravo Fernández JA, Gómez Sanz V, 2011. Impactos, vulnerabilidad y adaptación al cambio climático en el sector forestal. Notas sobre gestión adaptativa de las masas forestales ante el cambio climático. Ministerio de Medio Ambiente y Medio Rural y Marino, Madrid. 126 pp.

Serrada Hierro R, Bravo-Fernández JA, Otero De Irizar J, Ruiz-Peinado Gertrudix R, Mutke Regneri S, Roig Gómez S, 2013. El bosque invisible bajo el monte bajo: una mirada al sistema radical de las cepas de encina. Proc 6º Congreso Forestal Español, Vitoria, June 10-14.

SSF-DGDRyPF, 2012. Red de Seguimiento a Gran Escala de Daños en los Montes (Red de Nivel I). Manual de Campo. Ministerio de Agricultura, Alimentación y Medio Ambiente. Madrid. 69 pp.

Terradas J, 1999. Holm oak and holm oak forests: an introduction. In: Ecology of Mediterranean evergreen oak forests; Rodà F, *et al.* (eds). pp: 3-14. Springer Germany. https://doi.org/10.1007/978-3-642-58618-7_1

Tognetti R, Longobucco A, Raschi A, 1998. Vulnerability of xylem to embolism in relation to plant hydraulic resistance in *Quercus pubescens* and co-occurring in a Mediterranean coppice stand in central Italy. New Phytologist 139 (3): 437-447. https://doi.org/10.1046/j.1469-8137.1998.00207.x

Ugarte J, Vélaz de Medrano L, 1921. La encina y su explotación. Catecismos del agricultor y del ganadero. Calpe, Madrid. 32 pp.

Valladares F, Vilagrosa A, Peñuelas J, Ogaya R, Camarero JJ, Corcuera L, Sisó S, Gil-Pelegrín E, 2004. Estrés hídrico: ecofisiología y escalas de la sequía. In: Ecología del bosque mediterráneo en un mundo cambiante, Valladares F (ed). pp: 163-190. Ministerio de Medio Ambiente, EGRAF, Madrid.

Vericat P, Piqué M, Serrada R, 2012. Gestión adaptativa al cambio global en masas de *Quercus* mediterráneos. Centre Tecnològic Forestal de Catalunya, Solsona (Lleida). 172 pp.

Zuur A, Leno EN, Walker N, Saveliev AA, Smith GM, 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, NY. https://doi.org/10.1007/978-0-387-87458-6