



Does the persistence of sweet chestnut depend on cultural inputs? Regeneration, recruitment, and mortality in *Quercus*- and *Castanea*-dominated forests

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Abstract

- **Key message** *Quercus* secondary forests show a gradual transition toward mixed forests, with sweet chestnut (*Castanea sativa*) becoming increasingly abundant in the western Spanish Central System. Additionally, in chestnut-dominated stands, it shows a certain resistance to competitive displacement by *Quercus pyrenaica*. Our results partially refute the traditional view that *C. sativa* is unable to recruit in the absence of cultural inputs.
- **Context** Sweet chestnut, *Castanea sativa*, is a component of European broadleaf forests and is one of the most managed trees. Due to a reduction in cultural inputs, chestnut-dominated stands tend to be invaded by other species, and it is unclear how chestnut is able to persist in natural mixed forests.
- **Aims** Our work aimed to identify the main factors that limit the establishment of *C. sativa* and to analyze the recruitment and mortality processes of *C. sativa* trees.
- **Methods** The age, growth ring patterns, regeneration density, and the spatial structure of trees and saplings in 11 plots in the Spanish Central System were analyzed.
- **Results** Chestnut seedling density increased with *C. sativa* basal area, but transition toward the sapling stage appeared limited owing to light availability. In *Quercus pyrenaica* secondary forests, sparse canopies did not constrain chestnut regeneration, and in old chestnut stands, *C. sativa* showed a certain resistance to competitive displacement. By contrast, mixed young coppices showed a high mortality, most likely due to competition with other vigorous resprouters.
- **Conclusion** *Quercus* secondary forests showed a gradual transition toward mixed forests with sweet chestnut becoming increasingly more abundant. In old stands, *C. sativa* is likely to persist under a gap-phase mode of regeneration. Our results partially refute the traditional view that *C. sativa* is unable to recruit in the absence of cultural inputs.

Keywords Chestnut recruitment · *Quercus pyrenaica* · Secondary forest · Tree mortality · Forest succession

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1 Introduction

The sweet chestnut (*Castanea sativa* Mill.) is one of the most managed trees in Europe and covers more than 2.5 million ha (Amorini et al. 2000; Scarascia-Mugnozza et al. 2000; Conedera et al. 2004, 2016; San Roman Sanz et al. 2013). Palynological, anthracological, and macrofossil evidence indicates that *C. sativa* survived the main glacial events that occurred in favorable refuges, ranging from the west of the Iberian Peninsula to the east coast of the Black Sea-Caucasus region (Fineschi et al. 2000; Conedera et al. 2004; Krebs et al. 2004), and it is considered a component of European temperate broadleaf forests (Conedera et al. 2016). The cultivation of *C. sativa* has expanded its natural range, and sweet chestnut has become a widespread element of the landscape in most of the Mediterranean basin and southern parts of Central Europe (Scarascia-Mugnozza et al. 2000; Conedera and Krebs 2008; Morales-Molino et al. 2015). Socioeconomic factors and the spread of diseases, such as chestnut blight (*Cryphonectria parasitica*) and ink disease (*Phytophthora* spp.), has reduced the interest in the management of these forests (Amorini et al. 2000; Gallardo 2001; Conedera and Krebs 2008; San Roman Sanz et al. 2013; Seijo et al. 2015). As a result, chestnut stands tend to become invaded by other species and to evolve toward mixed deciduous forests (Conedera et al. 2000, 2001, 2016; Zlatanov et al. 2013). However, in recent decades, naturally occurring hypovirulent strains of *C. parasitica* with attenuated pathogenesis has allowed *C. sativa* to become again a viable species for timber and nut production (Milgroom and Cortesi 2004; Waldböth and Oberhuber 2009; Zlatanov et al. 2015). Also, a large amount of naturally occurring genetic variation resistant to ink disease has been detected, suggesting the potential of breeding programs to improve the health status of *C. sativa* populations (Robin et al. 2006).

The regeneration dynamics of *C. sativa* has not been studied in depth, and it is unclear how *C. sativa* recruitment occurs within natural forests. Most of the recruitment dynamics have been inferred from studies carried out on managed forests, where *C. sativa* trees exhibit vigorous sprouting after being cut (Cutini 2001; Giudici and Zingg 2005). The few studies that have addressed *C. sativa* seedling dynamics found that low shade tolerance limits successful recruitment under close canopies, where the low level of regeneration of *C. sativa* seedlings is outcompeted by more shade-tolerant species (Pridnya et al. 1996; Sevilla 2008; Pividori et al. 2005; Zlatanov et al. 2013). Furthermore, the lack of pristine mixed temperate forests in the Mediterranean basin, due to centuries of human intervention, is a relevant limitation in the study of *C. sativa* regeneration dynamics (Scarascia-Mugnozza et al. 2000; Conedera et al. 2016). Despite the various limitations and owing to the need for knowledge regarding ecological forestry, we established the following hypothesis. (1) Seedling recruitment of *C. sativa* is mainly limited by seed

production, and therefore, we expect to find a positive relationship between seedling abundance and basal area and/or tree density of *C. sativa*. (2) Transition from seedling to sapling stage and sapling growth are a light-limited process, and we expect a higher *C. sativa* sapling/seedling ratio and sapling-growth rate in the forest stands with higher light availability in the understory. (3) Tree establishment is also light-limited and linked to canopy opening. This time, we establish that *C. sativa* dominance in forests is mainly linked to recruitment after disturbance, and in the absence of cultural inputs, reaching into the main canopy is limited by light availability and competition with other tree species. (4) Tree mortality is a non-random-spatial process mainly influenced by competition, and we expect to find *C. sativa* dead trees more frequently closer to other trees than what could be expected if they came from a completely randomized spatial distribution. To test these hypotheses, age structure, growth ring patterns, regeneration density, and spatial structure of trees and saplings were analyzed in *Quercus*- and *Castanea*-dominated forests in the Spanish Central System.

2 Material and methods

2.1 Study area

The study region is located in the mountain range of the Sierra de Francia-Quilamas, in the west subdivision of the Central System, Spain. Within this region, two areas were selected: the Quilamas range (900–1423 m a.s.l.) and the slopes of the Alagón river basin (500–900 m a.s.l.). Annual precipitation varies between 1000 and 1400 mm in the Quilamas range and between 1100 and 1300 mm in the Alagón river basin. Both have a typical Mediterranean period of low precipitation during July and August. The mean annual temperature is between 10 and 12.5 °C for the Quilamas range and around 14–15 °C for the Alagón river basin.

Chestnut blight was first time detected in the early 2000s and still remains isolated within a small area in the Sierra de Francia-Quilamas range (García and Monte 2005; Zamora et al. 2012). Ink disease has also been reported in the region (García and Monte 2005).

2.2 Sampling design and data collection

We selected six stands dominated by *C. sativa* (CDF: *Castanea*-dominated forests), encompassing three young abandoned coppices (CDF1–3) and three old coppices converted by thinning to high forests (CDF4–6), as well as five nearby *Q. pyrenaica* secondary forests (QSFs). Abandoned coppices were not managed after last clear-cutting (1983, 1954 and 1954 in CDF1, CDF2 and CDF3, respectively; Dirección General de Montes, Caza y Pesca Fluvial 1967),

showing between 7 and 12 shoots (> 2 m height) per chestnut stool. The *C. sativa* trees in one abandoned coppice (CDF2) had scars in their bark, which was the result of a previous undated fire. One plot was established in each stand. Plot size was variable in the areas, ranging between 400 and 1200 m², because of differences in tree density between stands (Table 1). An initial 400 m² plot was located and was sequentially expanded to 900 or 1200 m² until at least 35–40 trees were available for tree coring and subsequent dendrochronological and forest disturbance analysis (Veblen 1992). All plots were square-shaped and their sides were oriented in the directions of the cardinal points. All data were collected between October 2011 and June 2016.

All trees (live and dead) and saplings in each plot were recorded. Seedling regeneration was estimated using 20 randomly located sampling units of 4 m long and 0.25 m wide in each plot. We used these long, narrow sampling units in order to reduce some of the variance due to the clumped seedling distribution of *Q. pyrenaica* observed at many plots (Krebs 1999). Trees were defined as individuals with a diameter at breast height (dbh) ≥ 5 cm; saplings as individuals with a dbh < 5 cm and height > 200 cm, and seedlings as individuals < 200 cm in height. Additionally, positions of trees and saplings were located to the nearest centimeter using measuring tapes that were aligned with the sides of the plots, providing X and Y coordinates for them.

2.2.1 Photosynthetic photon lux measurements

A pair of QSO-S photon flux sensors (Decagon Devices, Inc., USA) was positioned randomly at a height of 30 cm above-ground in each stand to measure the photosynthetic photon flux (PPF) in μmol m⁻² s⁻¹. The PPF was recorded each minute using an EM50 digital data logger (Decagon Devices, Inc., USA). PPF data were taken per stand on clear-sky days during 2 days (in a different position each day) from June to September; however, only the data taken between 11:00 and 16:00 solar time were used. To calculate the percentage of light that reached the understory, the PPF was measured in a nearby sun-exposed site on consecutive days.

2.2.2 Sapling primary growth rate

In order to obtain information about the primary growth rates of advanced regeneration, 7 and 10 *C. sativa* saplings (2–3 per plot) of seed origin from the CDF and QSF stands, respectively, were randomly selected. Saplings were cut at ground level and taken to the laboratory. Sapling stems were dissected each 20 cm from the base to the tip into stem-cross sections. Next, cross sections were manually sanded until annual rings were clearly visible for counting. Primary growth rates were estimated through the relationship between the age of the sapling

Table 1 Summary of plot characteristics

Plot	Geographic coordinates	Plot size (m ²)	Elevation (m a.s.l.)	Orientation	Plot density (living trees/ha)	Cs dead trees (%)	Maximum/mean tree age (years)
QSF1	40°34'33"N 05°57'24"W	400	1177	N	1550.0	0.0	54/41
QSF2	40°34'40"N 05°56'19"W	400	1000	N	1475.0	0.0	53/48
QSF3	40°33'54"N 05°54'48"W	900	998	N	666.7	0.0	65/53
QSF4	40°34'01"N 05°56'56"W	400	1136	N	950.0	0.0	68/53
QSF5	40°34'00"N 05°54'55"W	400	1005	N-NW	2050.0	0.0	73/57
CDF1	40°34'42"N 05°56'21"W	400	1006	NW	2300.0	16.0	31/26
CDF2	40°29'30"N 05°55'21"W	900	640	N	2166.7	31.6	60/29
CDF3	40°29'26"N 05°55'06"W	900	625	N	1833.3	75.4	63/44
CDF4	40°34'01"N 05°54'56"W	900	1000	N-NW	766.7	6.8	119/57
CDF5	40°34'25"N 05°56'53"W	900	1090	N	688.9	6.3	115/53
CDF6	40°34'24"N 05°57'17"W	1200	1150	NE	708.3	10.5	124/64

C. sativa (Cs) dead trees are shown as a percentage in relation to all *C. sativa* trees
QSF *Quercus* secondary forest, CDF *Castanea*-dominated forest

(number of tree-rings at the base) and the number of tree-rings in each 20-cm-distant cross section.

2.2.3 Dendrochronological analysis

Increment cores from all trees were extracted with Pressler increment borers (Häglof, Sweden) at 0.3–0.4 m above-ground level to obtain the most accurate age for each tree (Veblen 1992) and at 0.6 m when the tree centers were rotten. A total of 972 cores were collected (one core per tree). Increment cores were mounted and sanded following the procedure established by Stokes and Smiley (1968), and the annual rings were counted using a stereomicroscope (SMZ800, Nikon, Japan). When the cores did not reach the pith, the number of rings to the center was estimated using the geometric procedure described by Duncan (1989). If the center was rotten, the rings counted in the non-rotten section of the core were considered as the minimum age for that tree. Cores were scanned at 2000 dpi resolution (Perfection V550, Epson, Japan), and tree-ring widths were measured with a 0.01-mm resolution on the scanned JPG images using the software CooRecorder 7.6 (Cybis, Sweden). The visual and statistical cross-dating of the tree-ring width series was done and checked using the software CDendro 7.6 (Cybis, Sweden) and Cofecha (Holmes 1983), respectively.

2.2.4 Forest disturbance

Forest disturbances were inferred by radial-growth release detection methods. Specifically, the radial-growth averaging criteria (Nowacki and Abrams 1997) were applied by comparing the medians of a consecutive 10-year period. The threshold for considering a release was set up to a 50% relative growth change over 5 years.

2.3 Statistical analysis

We modeled relationships between forest variables (tree density, basal area, and percentage of incident light) and between age and height of *C. sativa* saplings using the most suitable simple regression model (linear, exponential, power and/or logarithmic functions). Relationships between seedling abundance and forest variables were modeled using the binomial negative regression of generalized linear models (GLMs). In QSF stands, we also tested the relationship between *C. sativa* tree abundance and the maximum age of *Q. pyrenaica* trees (as a substitute of stand initiation age) using the same GLM model. Owing to the lack of normality of the non-transformed and transformed data, we used the non-parametric Wilcoxon/Kruskal-Wallis tests to evaluate statistical differences in seedling abundance between tree species and in percentage of light that reached the understory between QSF and CDF stands. These analyses were performed using vegan package under

R environment (R Development Core Team 2013). The R software package TRADER (Altman et al. 2014) was used to infer forest disturbances through radial-growth releases.

For each plot, the spatial relationship between saplings and trees of *C. sativa* was analyzed using the bivariate O-ring statistic using the toroidal shift model (Wiegand and Moloney 2014). In the case of two different age cohorts of *C. sativa* trees, the spatial distribution of the youngest in relation to the oldest cohort was also determined. O-ring statistic was derived from the pair correlation function, which was defined as the expected number of points of one variable (e.g., saplings) between the larger and smaller radius of a ring of fixed width, at increasing distances from an arbitrary point of the other variable (e.g., trees), divided by the intensity λ of the pattern (Diggle 2003; Wiegand and Moloney 2014). In addition, *C. sativa* mortality was analyzed using the random labeling model, where locations of all *C. sativa* trees were maintained, and the alive/dead condition was randomly assigned (Wiegand and Moloney 2014). Lastly, we performed a trivariate analysis with the mark correlation function to test if *C. sativa* mortality was influenced by the presence of other species, and at what spatial scales (de la Cruz et al. 2008; Wiegand and Moloney 2014). To evaluate the significance of the spatial statistics under the considered null model, 95% simulated envelopes were generated using 199 MonteCarlo simulations. The fifth highest and lowest values of the 199 iterated functions were chosen to obtain the upper and lower values of the envelopes, respectively (Wiegand and Moloney 2014). Also, the goodness-of-fit (GoF) test was used to provide expected type I error rates, selecting a distance interval of 0–10 m to assess departures from the null model (Diggle 2003; Loosmore and Ford 2006). All spatial analyses were performed using the 2014 version of the Programita software (Wiegand and Moloney 2014).

3 Results

3.1 Light conditions

The percentage of incident light that reached the understory was significantly higher in QSF than in CDF (18.6 ± 2.8 and 5.1 ± 2.5 , mean \pm se for QSF and CDF, respectively; $p = 0.0025$, $n = 11$). The percentage of incident light was significantly inversely related to the basal area of *C. sativa* trees ($\log(y) = 2.54 - 0.03x$, $n = 11$, $p = 0.020$), but not with the total basal area of all tree species ($\log(y) = 3.28 - 0.04x$, $n = 11$, $p = 0.161$).

3.2 Regeneration abundance and sapling age-height models

The abundance of *C. sativa* and *Q. pyrenaica* seedlings were positively correlated with *C. sativa* and *Q. pyrenaica* tree basal areas across the stands, respectively (Table 2). But only *Q. pyrenaica* seedling abundance was significantly correlated

with tree density and percentage of incident light that reached the understory (Table 2). However, there was a positive linear relationship between the *C. sativa* ratio of saplings per seedling with the percentage of incident light across stands, but not for the *Quercus* species (Table 2). In QSF stands, although *C. sativa* seedling regeneration was significantly lower than *Q. pyrenaica* ($p < 0.001$, $n = 5$, Table 3), there were no significant differences in sapling abundance ($p = 0.1991$, $n = 5$, Table 3). In the older CDF4-6 stands, *C. sativa* showed higher abundance of seedlings ($p = 0.0463$, $n = 3$, Table 3) and saplings ($p = 0.0369$, $n = 3$, Table 3) than *Q. pyrenaica*. By contrast, in younger CDF1-3 stands, there were no significant differences in seedling ($p = 0.4029$, $n = 3$, Table 3) or sapling abundance ($p = 0.1051$, $n = 3$, Table 3) between *C. sativa* and *Quercus* species.

In relation to age-height growth models for *C. sativa* saplings from seed origin (Fig. 1), the best adjustment for QSF followed an exponential model ($R^2 = 0.81$; $p < 0.0001$; $n = 11$), whereas CDF followed a linear model ($R^2 = 0.88$; $p < 0.0001$; $n = 7$).

3.3 Age structures and radial-growth releases

QSF plots were characterized by a single cohort of trees with no recruitment of *Q. pyrenaica* young trees during the last few decades (Fig. 2a-e). Only *C. sativa* was recruited in small numbers, and the number of *C. sativa* trees was positively and significantly related with the age of the oldest *Q. pyrenaica* tree (negative binomial GLM, $p = 0.004$, $n = 5$, AIC = 21.7) in the QSF plots.

Except for CDF1, broad and multiage age structures dominated by *C. sativa* characterized together with other tree species the CDF plots (Fig. 3). These stands showed complex structures which varied from distinct age cohorts to continuous tree recruitment patterns. CDF2, CDF4, and CDF6 showed multiage structures where recruitment waves in *C. sativa* trees was produced just after synchronous

radial-growth releases of the older trees in the 54%, 50%, and 76.9%, respectively (Fig. 4g, j, k). Although CDF5 showed a complex multiage pattern, tree recruitment was not associated to any previous synchronous release in tree growth. However, 38.5% of the trees in CDF5 showed asynchronous individual radial-growth releases between 1924 and 1997. CDF3 showed continuous recruitment after stand initiation with a broad and left-skewed age structure dominated by *Quercus* spp. (Fig. 3c). No synchronous release in the radial-growth pattern was evident in CDF3 (Fig. 4h), but 19% of all trees showed individual growth releases between 1966 and 2000. The youngest CDF1 showed a narrow and left-skewed age distribution, and no release in the radial-growth pattern was found.

C. sativa mortality was low in the older stands but was from moderate to high in the younger coppices, especially in the CDF3 plot where 75.4% of all *C. sativa* trees were dead (Table 1).

3.4 Bivariate and trivariate spatial patterns and tree mortality

In the CDF stands, *C. sativa* saplings were independently distributed from trees at most of the distances analyzed, as confirmed by the GoF tests (Table 4). In the CDF stands, when two age cohorts were clearly distinguished, the young cohort was independently distributed from the old cohort (Table 4). *C. sativa* tree mortality was nil in the QSF stands, low in the old CDF stands, and from moderate to high in the young CDF stands (Table 1). When the distribution of dead *C. sativa* trees in relation to live trees in the overstory was analyzed in the young CDF stands, using the random labeling null model, the segregation of dead trees from live trees was found at short distances in CDF1, but up to 12-13 m in the plots with the highest mortality (Table 4). Trivariate analysis in CDF1 did not show that the proximity of *Q. pyrenaica* trees influenced the

Table 2 Regression models for seedling abundance (binomial negative models) and sapling/seedling ratio (linear models)

Species	Model	Explained deviance (%)	R ²	AIC	p
<i>C. sativa</i>	$\ln(\text{seedling.abun}) = 0.71 + 0.05*(\text{BA.Cs})$	47.8		64.21	< 0.001
	$\ln(\text{seedling.abun}) = 1.45 + 0.01*(\text{TD.Cs})$	4.4		71.20	0.181
	$\ln(\text{seedling.abun}) = 2.69 - 0.09*(\% \text{light})$	19.3		69.15	0.076
	$\text{sapling:seedling.ratio} = 0.018 + 0.007*(\% \text{light})$		37.6		0.045
<i>Q. pyrenaica</i>	$\ln(\text{seedling.abun}) = 1.23 + 0.15*(\text{BA.Qp})$	43.2		98.56	< 0.001
	$\ln(\text{seedling.abun}) = 2.11 + 0.04*(\text{TD.Qp})$	26.9		101.69	0.004
	$\ln(\text{seedling.abun}) = 1.99 + 0.13*(\% \text{light})$	27.3		101.50	0.009
	$\text{sapling:seedling.ratio} = 0.0006 + 0.00007*(\% \text{light})$		7.38		0.419

Basal area (BA) and tree density (TD) of each species, and the percentage of understory light (% light) used as independent variables

Cs *C. sativa*; Qp *Q. pyrenaica*

Table 3 Regeneration density per hectare (mean ± standard error) of the main tree and tree-like species at each plot: *C. sativa*

Plot	Seedlings/ ha							Saplings/ha					
	Cs	Qp	Qf	Qi	Pa	Ia	Au	Cs	Qp	Qf	Pa	Ia	Au
QSF1	2070 ± 544	36,739 ± 7722	–	–	637 ± 382	637 ± 382	–	375	–	–	–	–	–
QFS2	637 ± 334	22,341 ± 3775	–	–	–	–	–	75	25	–	–	–	–
QFS3	1134 ± 852	39,600 ± 8380	–	–	–	–	–	44	178	–	–	–	–
QFS4	2000 ± 941	89,000 ± 10,471	–	–	–	–	–	225	200	–	–	–	–
QFS5	1500 ± 819	39,000 ± 8010	–	–	–	–	–	225	25	–	–	–	–
CDF1	1274 ± 358	3662 ± 1748	–	–	637 ± 292	–	–	425	25	–	–	–	–
CDF2	–	–	3333 ± 1594	–	1333 ± 909	–	10,667 ± 2754	444	–	78	22	–	78
CDF3	–	3500 ± 2436	6500 ± 1957	500 ± 500	–	–	–	33	–	67	–	–	–
CDF4	1756 ± 425	–	–	–	267 ± 157	–	–	155	–	–	–	–	–
CDF5	13,500 ± 3719	–	–	–	1000 ± 1000	11,500 ± 4309	–	322	–	–	122	11	–
CDF6	16,500 ± 2927	500 ± 500	–	–	–	5000 ± 1701	–	275	–	–	–	133	–

Qp *Q. pyrenaica*, *Qf* *Q. faginea*, *Qi* *Q. ilex*, *Pa* *Prunus avium*, *Ia* *Ilex aquifolium*, *Au* *Arbutus unedo*

mortality of *C. sativa* overstory trees. However, in the CDF2 plot, trivariate analysis showed that dead *C. sativa* trees were less frequent than expected under a random process at distances beyond 10 m from another tree species (Table 4). In the CDF3 stand, trivariate analysis showed that dead *C. sativa* trees were more frequent at distances between 2 and 6 m from other trees species and less frequent at 11 and 14 m (Table 4).

4 Discussion

4.1 Seedling and sapling dynamics

Seedling regeneration is not related to light availability, but it increases with *C. sativa* basal area due to the greater availability

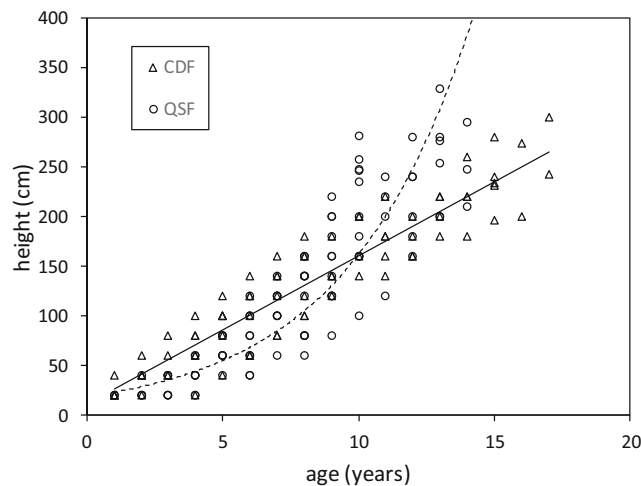
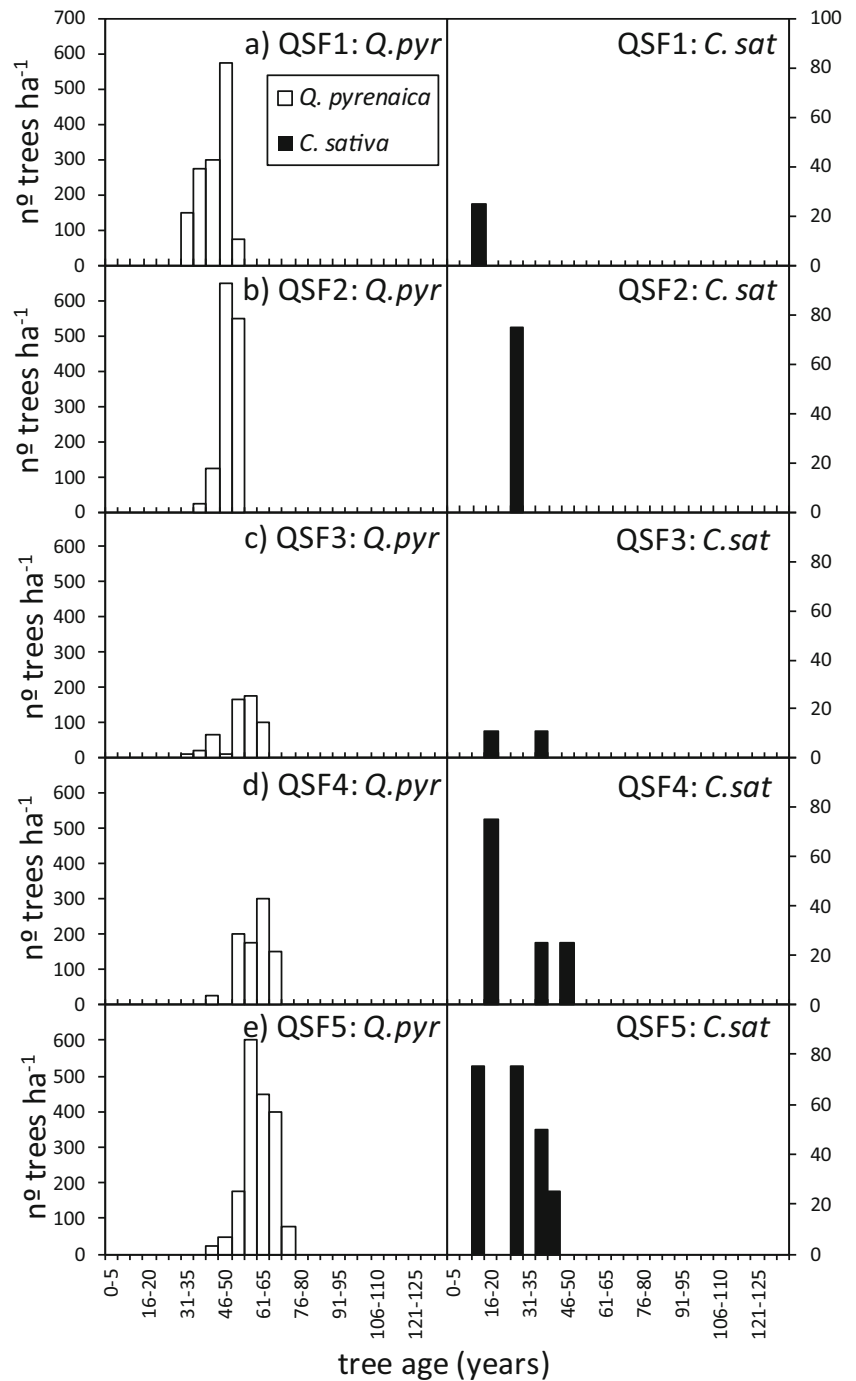


Fig. 1 Age-height growth models for *C. sativa* saplings from seed origin for QSF (circles, dashed line) and CDF (triangles, continuous line) stands

of chestnuts produced and dispersed by barochory, with the mature CDF stands showing the highest densities of *C. sativa* seedlings (Pridnya et al. 1996; Gilland et al. 2012; Zlatanov et al. 2013). In the QSF stands, low seedling density appears mainly limited by seed dispersal, due to the heavy weight of chestnuts (Mujic et al. 2010). Although *C. sativa* is likely sciophilous at the very early seedling stage, canopy cover of QSF stands still intercepts 80% of the incident light. Besides, most of the plots are N or NW oriented, so the excess of light is not a limiting factor in seedling recruitment in the QSF plots. Potential *C. sativa* mother trees are commonly close to QSF sites (100–300 m away) but are always downhill, as chestnut stands are usually placed at the bottom of the slopes or small valleys. Although the dispersion syndrome of the *Castanea* genus has been minimally addressed (Vander Wall 2001), the Eurasian jay, *Garrulus glandarius* L., a common corvid in our study area, harvests small quantities of chestnuts, hiding them in the same manner as acorns (Holyoak 1968). Furthermore, this practice is likely the main dispersion vector for *C. sativa* in our study areas, where chestnuts are spread across several hundreds of meters away from the mother trees, as shown in other sites (Urbisz and Urbisz 2007). Despite seed limitation in QSF stands, *C. sativa* has higher sapling/seedling ratio than in CDF stands suggesting greater seedling survival and probability to promote to the sapling stage due to better light conditions, as shadowed understories are linked to high mortality at the seedling stage (Pridnya et al. 1996; Pividori et al. 2005; Zlatanov et al. 2013). Additionally, the thin canopies of QSF stands allowed increasing height growth with age in *C. sativa* saplings during the first years of establishment, whereas in the closed CDF, canopies surviving *C. sativa* saplings showed a constant but slower height-growth rate. In the CDF stands, sapling distribution is independent of trees, as treefall gaps are still not common in these developing forests. However, sunflecks, brief

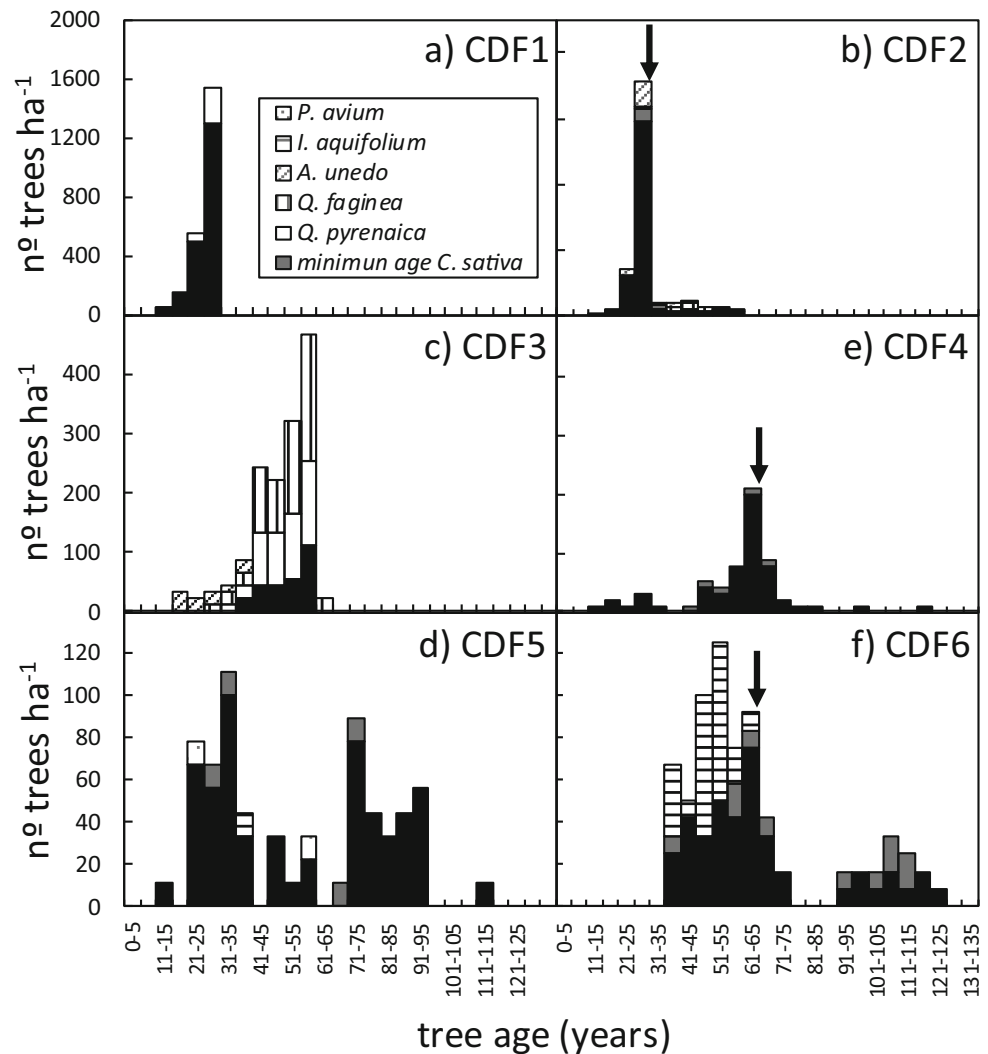
Fig. 2 Age distributions in 5-year establishment classes of the QSF stands. Left panels and open bars: *Q. pyrenaica*; right panels and black solid bars: *C. sativa*. Note that the y-axis in the left and right panels has different scales



intermittent periods of high photon flux density that significantly improve carbon gain and hold a small positive carbon balance (Chazdon 1988; Way and Pearcy 2012), were occasionally recorded at CDF stands as short intervals (3–8 min) of photon fluxes of $150\text{--}700\text{ mol m}^{-2}\text{ s}^{-1}$ (data not shown). Thus, our data suggest that *C. sativa* can persist as advanced regeneration in the understory and can attain the main canopy layer throughout the gap regeneration phase of typical mature forests (Veblen 1992; Oliver and Larson 1996; Franklin et al. 2007).

By contrast, *Q. pyrenaica*, the main tree species in the study area, shows higher seedling regeneration than *C. sativa* in the QSF stands, but similar sapling density. This finding suggests lower shade tolerance than *C. sativa* and/or strong competition for water and nutrients between clones, as sprouting from lateral roots dominates *Q. pyrenaica* regeneration (Salomón et al. 2013; Camisón et al. 2015). However, the CDF stands show very little or no regeneration of *Q. pyrenaica*. Sexual reproduction is likely limited in

Fig. 3 Age distributions in 5-year establishment classes of the CDF stands. Black solid bars: *C. sativa* total age; gray solid bars: *C. sativa* minimum ages; open bars: *Q. pyrenaica*; vertically hatched bars: *Q. faginea*; horizontally hatched bars: *I. aquifolium*; diagonally hatched bars: *A. unedo*; dotted bars: *P. avium*. Black arrows show the time of the synchronic radial-growth releases of Fig. 4



Q. pyrenaica due to a combination of factors such as low acorn production (Jiménez et al. 1998), high rates of acorn predation (Gómez et al. 2003), and low shade tolerance of the seedlings (Rodríguez-Calcerrada et al. 2007).

4.2 *C. sativa* tree recruitment and mortality

One of the more interesting findings of our study is the ability of *C. sativa* to recruit in QSF stands. Low tree density, a significant relationship between forest age and the number of *C. sativa* trees, nil chestnut mortality and the vigorous radial-growth of *C. sativa* trees indicate the potential for steadily increasing recruitment in our QSF stands. Although *C. sativa* is considered an intermediate shade-intolerant species at seedling/sapling stage (Pridnya et al. 1996; Pividori et al. 2005; Sevilla 2008; Zlatanov et al. 2013), light availability under the thin canopy of *Q. pyrenaica* allowed tree recruitment and a gradual transition to more natural mixed forests.

On the contrary, in CDF stands, *C. sativa* shows more complex tree dynamics that reflect past and diverse human

intervention. The old forests, CDF4 and CDF6, show multi-age stands and synchronic radial-growth release events that undoubtedly show signs of clear-cutting, and subsequent recruitment mainly because of sprouting (Cabanettes and Pagès 1992; Giudici and Zingg 2005). Old CDF5 shows asynchronous release patterns in *C. sativa* trees, which is consistent with minor-scale wood extraction and the small recruitment peaks of *C. sativa* and light-demanding *Prunus avium* (Stojecová and Kupka 2009). Low *C. sativa* mortality and the absence of effective recruitment of *Q. pyrenaica* is an indication of the resistance of *C. sativa* to competitive displacement during a short-medium successional time. As in the older stands, young coppices of *C. sativa* show strong recruitment (Giudici and Zingg 2005), as they sprout from stools after disturbances such as cutting (CDF1 and CDF3) or fire (CDF2). However, young mixed coppices show high non-random *C. sativa* mortality which highlights the importance of intra- and interspecific competition for limited resources. Departure from the random labeling model at short scales shows that stem mortality was not randomly

Fig. 4 Annual radial-growth (mm) of the main trees species in the study plots. Thick lines represent the mean ring growth and the thin lines indicate upper and lower standard error. Blue lines: *Q. pyrenaica*; red lines: *C. sativa* old cohort; dark red lines: *C. sativa* young cohort; green lines: *Q. faginea*. Black arrows indicate synchronic radial-growth liberations in the older trees

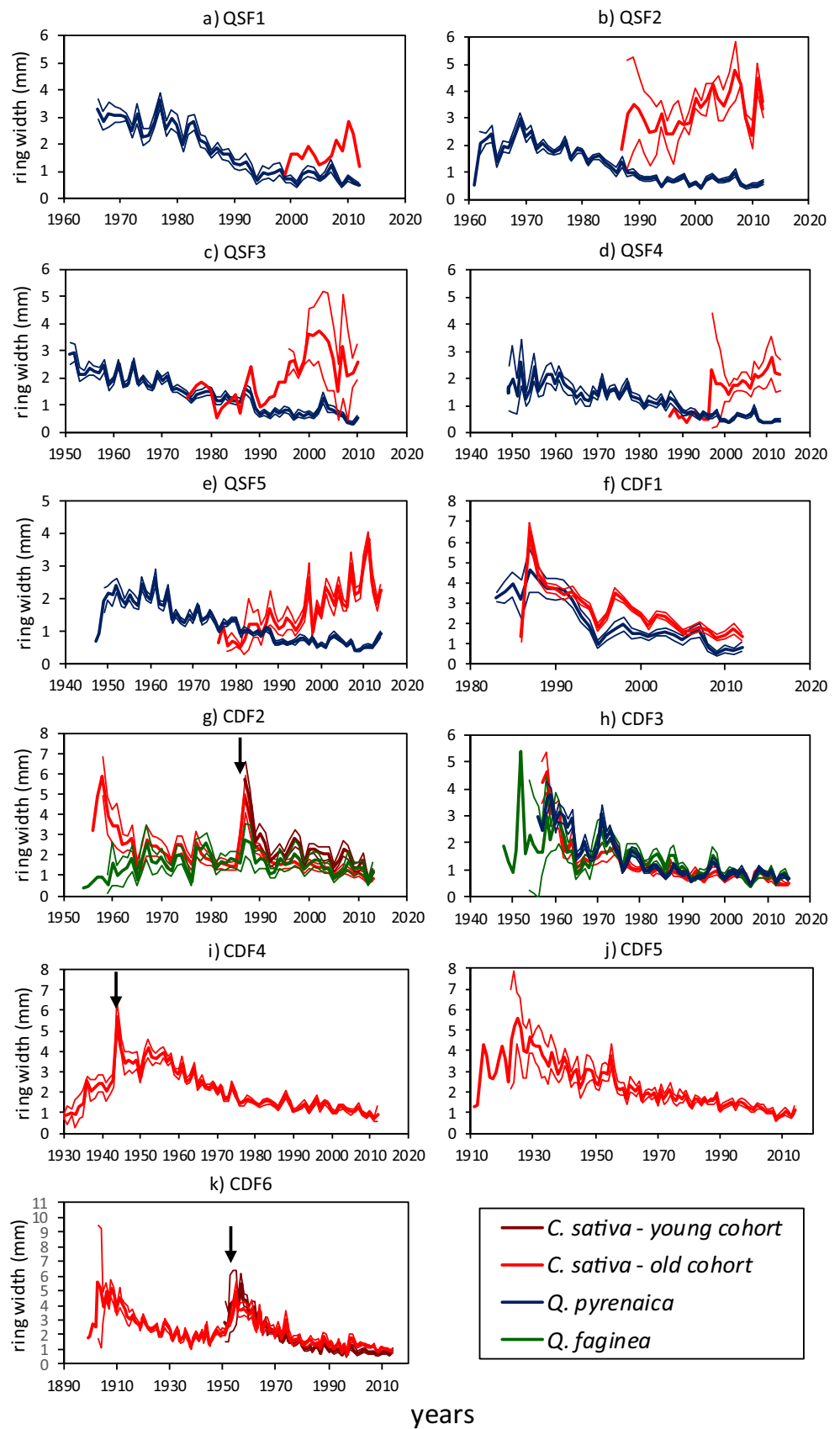


Table 4 Results of the bivariate O-ring statistic for bivariate analysis

Sites	Point pattern	Model	P (0–10 m)	Rank	Distance (m)															
					1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
CDF1	Cs saplings vs trees	Toroidal shift	0.155	170	r	R	r	r	r	r	r	r	r	r	r	r	r	r	r	r
CDF2	Cs saplings vs trees	Toroidal shift	0.135	174	r	R	+	r	+	r	r	r	r	r	r	r	r	r	r	r
CDF4	Cs saplings vs trees	Toroidal shift	0.670	66	r	R	r	r	r	r	r	r	r	r	r	r	r	r	r	r
CDF5	Cs saplings vs trees	Toroidal shift	0.120	170	r	R	r	r	r	r	r	r	r	-	r	r	r	r	r	r
CDF6	Cs saplings vs trees	Toroidal shift	0.220	157	r	R	r	-	r	r	r	r	r	r	r	r	r	r	r	r
CDF5	Cs young vs old cohorts	Toroidal shift	0.795	42	r	R	r	r	r	r	r	r	r	r	r	r	r	r	r	r
CDF6	Cs young vs old cohorts	Toroidal shift	0.035	194	r	R	-	r	r	-	r	r	r	r	r	r	r	r	r	r
CDF1	Cs alive vs dead trees	Random labeling	0.005	200	-	-	r	r	r	r	r	r	r	r	r	r	r	r	r	r
CDF2	Cs alive vs dead trees	Random labeling	0.005	200	-	-	-	-	-	-	-	-	-	-	-	-	-	-	r	r
CDF3	Cs alive vs dead trees	Random labeling	0.010	199	-	R	r	-	r	r	-	-	-	r	r	-	r	r	r	r
CDF1	Cs alive and dead trees vs other trees	Trivariate			r	R	r	r	r	r	r	r	r	r	r	r	r	r	r	r
CDF2	Cs alive and dead trees vs other trees	Trivariate			r	R	r	r	r	r	r	-	r	-	-	-	-	-	-	-
CDF3	Cs alive and dead trees vs other trees	Trivariate			r	+	+	+	+	+	r	r	r	r	-	r	r	-	r	

P value of the goodness-of-fit (GoF) tests at distances of up to 10 m and rank of the pair correlation function after 199 iterations are shown. Statistical significance at 95% simulated envelopes: (r) independent pattern; (+) association pattern; (-) repulsion pattern

distributed between stools, with some stools showing low mortality and others almost or completely dead, as found in other coppices undisturbed by human activities (Giudici and Zingg 2005). In addition, the trivariate analyses of the two coppices with the highest mortality show that *C. sativa* dead trees are less frequently far away from each other than what could be expected if they were randomly distributed. Also, they are more frequently closer to the live trees of other species. Hence, intraspecific competition at the stool level and interspecific competition with *Quercus* spp. and *A. unedo* sprouts play a role in the spatial pattern of *C. sativa* mortality. Although the trees did not show any sign of the characteristic signs of chestnut blight, such as pustules and cankers (Waldboth and Oberhuber 2009), we cannot discard the possibility that poor health conditions weaken chestnut trees pushing them toward mortality by tree competition. Chestnut trees with small leaves and dieback signs in the plot with the highest mortality provide some circumstantial evidence of ink disease, but more direct evidence through the pathogen isolation is needed (Vannini and Vettraino 2001; Juhássová and Bernadovicová 2001).

4.3 Conclusions

Our work clearly shows that *C. sativa* is able to recruit in secondary forests in the absence of forest management and cultural inputs. In the older chestnut-dominated stands, *C. sativa* shows certain resistance to competitive displacement, as the dominant species in the area, *Q. pyrenaica*, is unable to successfully become established. *C. sativa* seedling density is limited due to fruit production, but transition toward

the sapling stage appears limited due to low light availability. By contrast, mixed young coppices of *C. sativa* show a high level of mortality and dieback, owing to competition with other vigorous resprouters.

Additionally, our results suggest that although *C. sativa* recolonizes after disturbances through sprouting, it maintains an advanced regeneration in mature forests and can also persist through a gap-phase mode of regeneration (sensu Veblen 1992). The replication of gap-forming processes through silvicultural management in closed forests could help to develop the horizontal and vertical structural heterogeneity typical of old-growth forests and facilitate the recruitment and self-replacement of this iconic species of the European landscape (Zlatanov et al. 2015).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Altman J, Fibich P, Dolezal J, Aakala T (2014) TRADER: a package for tree ring analysis of disturbance events in R. *Dendrochronologia* 32: 107–112
- Amorini E, Chatziphilippidis G, Cianci O, Di Castri F, Giudici F, Leonardi S, Manetti MC, Nocentiin S, Pividori M, Rapp M, Romane F, Sevrin E, Zingg A (2000) Sustainability of chestnut forest ecosystems: is it possible? *Ecol Mediterr* 26:3–14
- Cabanettes A, Pagès L (1992) Effet des techniques de coupe et des variations du milieu sur la croissance en hauteur des cèpées dans un taillis de châtaignier (*Castanea sativa*). *Can J For Res* 22:1694–1700
- Camisón A, Miguel R, Marcos JL, Revilla J, Tardáguila M, Hernández D, Lakicevic M, Jovellar L, Silla F (2015) Regeneration dynamics of *Quercus pyrenaica* Willd. in the central system (Spain). *For Ecol Manag* 343:42–52
- Chazdon R (1988) Sunflecks and their importance to forest understory plants. *Adv Ecol Res* 18:1–63
- Conedera M, Krebs P (2008) History, present situation and perspective of chestnut cultivation in Europe. *Acta Hort* 784:23–27
- Conedera M, Stanga P, Lischer C, Stöckli V (2000) Competition and dynamics in abandoned chestnut orchards in southern Switzerland. *Ecol Mediterr* 26:101–112
- Conedera M, Stanga P, Oester B, Bachmann P (2001) Different post-culture dynamics in abandoned chestnut orchards and coppices. *For Snow Landsc Res* 76:487–492
- Conedera M, Krebs P, Tinner W, Pradella M, Torriani D (2004) The cultivation of *Castanea sativa* (mill.) in Europe, from its origin to its diffusion on a continental scale. *Veget Hist Archaeobot* 13:161–169
- Conedera M, Tinner W, Krebs P, de Rigo D, Caudullo G (2016) *Castanea sativa* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (eds) *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, p e0125e0+
- Cutini A (2001) New management options in chestnut coppices: an evaluation on ecological bases. *For Ecol Manag* 141:165–174
- De la Cruz M, Romao RL, Escudero A, Maestre FT (2008) Where do seedlings go? A spatio-temporal analysis of seedling mortality in a semi-arid gypsophyte. *Ecography* 31:1–11
- Diggle PJ (2003) *Statistical analysis of spatial point patterns*. Arnold, London
- Dirección General de Montes, Caza y Pesca Fluvial (1967) Proyecto de Ordenación definitiva del monte n° 80 del Catálogo de UP de esta provincia, denominado “Dehesa, Sierra Mayor, Honfrías, Coquilla, Mata Corcera y Majada Llana” sito en el término municipal de Linares de Riofrío (Salamanca). Ministerio de Agricultura, Distrito Forestal de Salamanca
- Duncan RP (1989) An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). *NZ Nat Sci* 16:31–37
- Fineschi S, Turchini D, Villani F, Vendramin GG (2000) Chloroplast DNA polymorphism reveals little geographical structure in *Castanea sativa* mill. (Fagaceae) throughout southern European countries. *Mol Ecol* 9:1495–1503
- Franklin JF, Mitchell R, Palik B (2007) Natural disturbance and stand development principles for ecological forestry. General Technical Report NRS-19, USDA Forest Service
- Gallardo JF (2001) Distribution of chestnut (*Castanea sativa* Mill.) forests in Spain: possible ecological criteria for quality and management (focusing on timber coppices). *For Snow Landsc Res* 76:477–481
- García P, Monte E (2005) Fitopatología del Castaño. El Chancro y la Tinta en la Provincia de Salamanca. AGRO Interreg IIIB. Espacio Atlántico. DPS - OAEDR - FEDER
- Gilland KE, Keiffer CH, McCarthy BC (2012) Seed production of mature forest-grown American chestnut (*Castanea dentata* (Marsh.) Borkh.). *J Torrey Bot Soc* 139:283–289
- Giudici F, Zingg A (2005) Sprouting ability and mortality of chestnut (*Castanea sativa* mill.) after coppicing. A case study. *Ann For Sci* 62:513–523
- Gómez JM, García D, Zamora R (2003) Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. *For Ecol Manag* 180:125–134
- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull* 43:69–78
- Holyoak D (1968) A comparative study of the food of some British corvidae. *Bird Study* 15:147–153
- Jiménez MPS, Fernández PMD, Albertos SM, Sánchez LG (1998) Regiones de procedencia de *Quercus pyrenaica* Willd. *Quercus faginea* Lam, *Quercus canariensis* Willd. OAPN, Madrid
- Juhásová G, Bernadovicová S (2001) *Cryphonectria parasitica* (Murr.) Barr and *Phytophthora* spp. in chestnut (*Castanea sativa* mill.) in Slovakia. *For Snow Landsc Res* 76:373–377
- Krebs CJ (1999) *Ecological methodology*, second ed. Addison-Wesley Educational Publishers, Inc
- Krebs P, Conedera M, Pradella M, Torriani D, Felber M, Tinner W (2004) Quaternary refugia of the sweet chestnut (*Castanea sativa* mill.): an extended palynological approach. *Veget Hist Archaeobot* 13:145–160
- Loosmore NB, Ford ED (2006) Statistical inference using the G or K point pattern spatial statistics. *Ecology* 87:1925–1931
- Milgroom MG, Cortesi P (2004) Biological control of chestnut blight with hypovirulence: a critical analysis. *Annu Rev Phytopathol* 42: 311–338
- Morales-Molino C, Vescovi E, Krebs P, Carlevaro E, Kaltenrieder P, Conedera M, Tinner W, Colombaroli D (2015) The role of human-induced fire and sweet chestnut (*Castanea sativa* mill.) cultivation on the long-term landscape dynamics of the southern Swiss Alps. *Holocene* 25:482–494
- Mujic I, Alibabic V, Zivkovic J, Jahic S, Jokic S, Prgommet Z, Tuzlak Z (2010) Morphological characteristics of chestnut *Castanea sativa* from the area of Una- Sana canton. *J Cent Eur Agric* 11:185–190
- Nowacki GJ, Abrams MD (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol Monogr* 67:225–249
- Oliver CD, Larson BC (1996) *Forest stand dynamics*, updated ed. McGraw Hill, New York
- Pividori M, Armando F, Conedera M (2005) Post cultural dynamics in a mixed chestnut coppice at its ecological border. *Acta Hort: Proc III Intl Chestnut Congress* 693:219–224
- Pridnya M, Cherpakov V, Paillet F (1996) Ecology and pathology of European chestnut (*Castanea sativa*) in the deciduous forests of the Caucasus mountains in southern Russia. *Bull Torrey Bot Club* 123:213–222
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>. Accessed date: 25 July 2018
- Robin C, Morel O, Vettraino AM, Perlerou C, Diamandis S, Vannini A (2006) Genetic variation in susceptibility to *Phytophthora*

- cambivora* in European chestnut (*Castanea sativa*). For Ecol Manag 226:199–207
- Rodríguez-Calcerrada J, Pardos JA, Gil L, Aranda I (2007) Acclimation to light in seedlings of *Quercus petraea* (Mattuschka) Liebl. and *Quercus pyrenaica* Willd. planted along a forest-edge gradient. Trees 21:45–54
- Salomón R, Valbuena-Carabaña M, Gil L, González-Doncel I (2013) Clonal structure influences stem growth in *Quercus pyrenaica* Willd. coppices: bigger is less vigorous. For Ecol Manag 296:108–118
- San Roman Sanz A, Fernandez C, Mouillot F, Ferrat L, Istria D, Pasqualini V (2013) Long-term forest dynamics and land-use abandonment in the Mediterranean mountains, Corsica, France. Ecol Soc 18:38
- Scarascia-Mugnozza G, Oswald H, Piussi P, Radoglou K (2000) Forest of the Mediterranean region: gaps in knowledge and research needs. For Ecol Manag 132:97–109
- Seijo F, Millington J, Gray R, Sanz V, Lozano J, García-Serrano F, Sangüesa-Barreda G, Camarero JJ (2015) Forgetting fire: traditional fire knowledge in two chestnut forest ecosystems of the Iberian Peninsula and its implications for European fire management policy. Land Use Policy 47:130–144
- Sevilla F (2008) Una teoría ecológica para los bosques ibéricos. Junta de Castilla y León. In: León
- Silla (2018) Dynamics and Regeneration of Chestnut forests [Dataset]. Version 31 Aug 2018. Open Science Framework. <https://doi.org/10.17605/OSF.IO/JRCFD>. Accessed date: 25 July 2018
- Stojecová R, Kupka I (2009) Growth of wild cherry (*Prunus avium* L.) in a mixture with other species in a demonstration forest. J For Sci 55: 264–269
- Stokes MA, Smiley TL (1968) An introduction to tree-ring dating. The University of Chicago Press, Chicago
- Urbisz A, Urbisz A (2007) European chestnut (*Castanea sativa* Mill.)—a tree naturalized on the Baltic Sea coast? Pol J Ecol 55:175–179
- Vander Wall SB (2001) The evolutionary ecology of nut dispersal. Bot Rev 67:74–118
- Vannini A, Vettrano AM (2001) Ink disease in chestnuts: impact on the European chestnut. For Snow Landsc Res 76:345–350
- Veblen TT (1992) Regeneration dynamics. In: Glenn-Lewin DC, Peet RK, Veblen TT (eds) Plant succession: theory and prediction. Chapman and Hall, London, pp 152–187
- Waldboth M, Oberhuber W (2009) Synergistic effect of drought and chestnut blight (*Cryphonectria parasitica*) on growth decline of European chestnut (*Castanea sativa*). For Path 39:43–55
- Way DA, Pearcy RW (2012) Sunflecks in trees and forests: from photosynthetic physiology to global change biology. Tree Physiol 32: 1066–1081
- Wiegand T, Moloney KA (2014) Handbook of spatial point-pattern analysis in ecology. CRC Press, Boca Raton
- Zamora P, Martín AB, Rigling D, Diez JJ (2012) Diversity of *Cryphonectria parasitica* in western Spain and identification of hypovirus-infected isolates. For Pathol 42:412–419
- Zlatanov T, Schleppe P, Velichkov I, Hinkov G, Georgieva M, Eggertsson O, Zlatanova M, Vacik H (2013) Structural diversity of abandoned chestnut (*Castanea sativa* Mill.) dominated forests: implications for forest management. For Ecol Manag 291:326–335
- Zlatanov T, Velichkov I, Georgieva M, Hinkov G, Zlatanova M, Gogusev G, Eastaugh CS (2015) Does management improve the state of chestnut (*Castanea sativa* L.) on Belasitsa Mountain, southwest Bulgaria? iForest 8:860–865