Forest Ecology and Management 274 (2012) 143–150

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Roles of land-use and climate change on the establishment and regeneration dynamics of Mediterranean semi-deciduous oak forests

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ARTICLE INFO

Article history:
Received 29 September 2011
Received in revised form 13 February 2012
Accepted 26 February 2012

Keywords:
Climate change
Land use changes
Forest dynamics
Pre-Pyrenees
Quercus faginea
Tree recruitment

ABSTRACT

Long-term changes in climate and land use have significant effects on the forest dynamics in formerly managed landscapes. To quantify the relative importance of climatic and land-use factors on tree establishment at regional scales, retrospective analyses are required. In this paper, we provide an historical reconstruction of the establishment of Mediterranean oak (*Quercus faginea*) forests in the 20th century within the context of substantial changes in climate and changes in land use in the Spanish Pre-Pyrenees. Since the late 1930s, *Q. faginea* became established episodically, and the highest peak occurred between 1965 and 1975. Tree establishment was negatively correlated with mean summer maximum temperature, population size of nearby villages, and the amount of livestock, but was positively correlated with annual, winter, and winter–spring precipitation. This study revealed that assessments of the effects of land-use and climate changes on historical forest recruitment are vital in understanding the structure of contemporary forests.

1. Introduction

Changes in land use and climate can have significant influences on tree establishment and on forest structure and dynamics in formerly managed landscapes (Barbero et al., 1990; Améztegui et al., 2010; Chauchard et al., 2010; Gimmi et al., 2010). In the Mediterranean region, the availability of water is the main factor that limits tree growth (Ogaya et al., 2003; Linares et al., 2010) and forest regeneration (Pulido and Díaz, 2005). In addition, inter-annual variability in precipitation significantly affects annual tree recruitment (Urbieta et al., 2008). However, differences in annual rainfall might not be the only climatic factor that influences forest regeneration in inland areas that have a continental Mediterranean climate because in these areas temperature and the amount of precipitation act together to dictate water availability, and low temperatures in winter cause cold stress (Larcher, 2000; Vicente-Serrano et al., 2010). Furthermore, the frequency and intensity of extreme weather events such as severe drought are expected to increase in those inland areas because of global climatic change (IPCC, 2007). In the Mediterranean region, particularly in the southern Pre-Pyrenees, where dry conditions prevail, semi-deciduous oak forests (*Quercus faginea*) occur in areas that are incur variable drought stress and, therefore, they might be especially sensitive to climate warming and increasing aridity (Alla et al., 2011).

Understanding the nature of changes in land use is important for understanding the structure and stand dynamics of contemporary forests (Améztegui et al., 2010; Gimmi et al., 2010). In general, in the mountains of Europe, anthropogenic factors have had a greater influence on the current composition and structure of many forests than have changes in climate (Olano et al., 2008; Tappeiner et al., 2008; Gimmi et al., 2010). Furthermore, the ongoing changes in the policies of the EU for agricultural and rural developmental might lead to even more pronounced changes in the mountain forests (Tappeiner et al., 2008).

In the Central Pre-Pyrenees, changes in land use (i.e., farmland abandonment and grazing cessation) have led to the expansion of forests into formerly cultivated or grazed areas (Lasanta et al., 2006; Améztegui et al., 2010). In particular, *Q. faginea* has colonized some of the abandoned lands in the Central Pre-Pyrenees through natural transitions from abandoned lands to forests (Kouba and Alados, 2012). Acorns dispersed locally by gravity or through short- or long-distance dispersal mediated by rodents (Pulido and Díaz, 2005) and birds (Gómez, 2003), respectively, are the main means by which *Q. faginea* seeds reach abandoned fields (Maltez-Mouro et al., 2008). Encroachment by *Q. faginea* into abandoned lands has led to the formation of two types of forests: (i) *Q. faginea* stands that were harvested intensively for timber and firewood for centuries and that were used as pastures (Sancho et al., 1998), and (ii) new *Q. faginea* stands that became established in the abandoned terraces, mainly during the second half of the 20th century (Kouba and Alados, 2012). Those forests are valued highly because they provide invaluable habitat for maintaining

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http://dx.doi.org/10.1016/j.foreco.2012.02.033

the biodiversity of Mediterranean plant and animal species (Rey Benayas et al., 2005; Kouba et al., 2011; Kouba and Alados, 2012).

To understand how changes in land use and climate influence the dynamics of forest regeneration and how they affect tree establishment, both of these factors should be assessed simultaneously (Abrams and Copenheaver, 1999; Camarero and Gutiérrez, 2007; Chauchard et al., 2007, 2010; Copenheaver and Abrams, 2003); however, identifying the importance of changes in land use and recent climate trends on the regeneration dynamics in forests can be attained only by comparing sites that have contrasting histories and climates.

The main purpose of this study was to assess our understanding of the potential effects of changes in land use and climate on the regeneration and growth dynamics of *Q. faginea* forests. Specifically, we aimed to (i) determine whether tree recruitment in *Q. faginea* forests in the last century was affected by climatic factors (e.g., drought) or changes in land-use (e.g., land abandonment), (ii) assess the importance of specific types of forest habitats (i.e., coppice stands and abandoned terraces) on tree growth and performance in *Q. faginea,* and provide a basis for the development of land-management strategies that can mitigate the effects of global warming and the abandonment of traditional land-use regimes on these sub-Mediterranean forests.

2. Materials and methods

2.1. Study area

The study area was in Huesca Province, within the Central Pre-Pyrenees, Spain, at an elevation of 450–1950 m a.s.l. (Fig. 1). Conglomerate, limestone, marl, and sandstone developed on Eocene flysch sedimentary formations predominate the lithology. The climate is transitional sub-Mediterranean because it is affected by continental effects from the north in the Pyrenees and by milder Mediterranean conditions that prevail from the south; i.e., the Ebro Basin. Based on the weather data collected at the meteorological stations within the study area (see Climate trends section), the mean annual precipitation is 1317 ± 302 mm (1915–2005), but most occurs between October and Jun, and mean annual air temperature is 11.5 ± 2.8° C (1910–2005).

The area has a variety of land covers and uses types including natural forests of several species (*Pinus sylvestris*, *P. nigra* ssp. *salzmannii*, *Fagus sylvatica*, *Quercus ilex* ssp. *ballota,* and *Q. faginea*), shrublands (*Q. coccifera*, *Buxus sempervirens*, *Genista scorpius*, *Juniperus communis*), and plantations (*P. sylvestris* and mostly *P. nigra* ssp. *austriaca*), arable farmland, pastures, abandoned farmland, and urban areas. In the area, *Q. faginea* is one of the most abundant naturally occurring species and the communities in which it occurs constitute a transition zone between Mediterranean forests in which *Q. ilex* ssp. *ballota* or *P. halepensis* are predominant and mountain continental or mesic forests of *P. sylvestris*, *P. nigra* ssp. *salzmannii*, and *F. sylvatica* (Jiménez et al., 1998; Loidi and Herrera, 1990).

2.2. Data collection and analysis

Based on earlier studies (Kouba et al., 2011; Kouba and Alados, 2012), we selected 10 sites throughout the study area that were representative of the most common types of *Q. faginea* forests in the region. A stand dominated by *Q. faginea* was selected at each site (for details of the stands, see Table 1). Within each stand, a 500-m linear transect was established at a randomly chosen location, parallel to elevation contour lines. Each transect had sampling points ($n = 20$) at 25-m intervals. Using the point-quarter method (Cottam and Curtis, 1956) at each point, we identified the closest adult *Q. faginea* tree in each of the four cardinal directions. Adult trees were defined as those >2 m high or that had a stem diameter at breast height (DBH) ⩾4 cm.

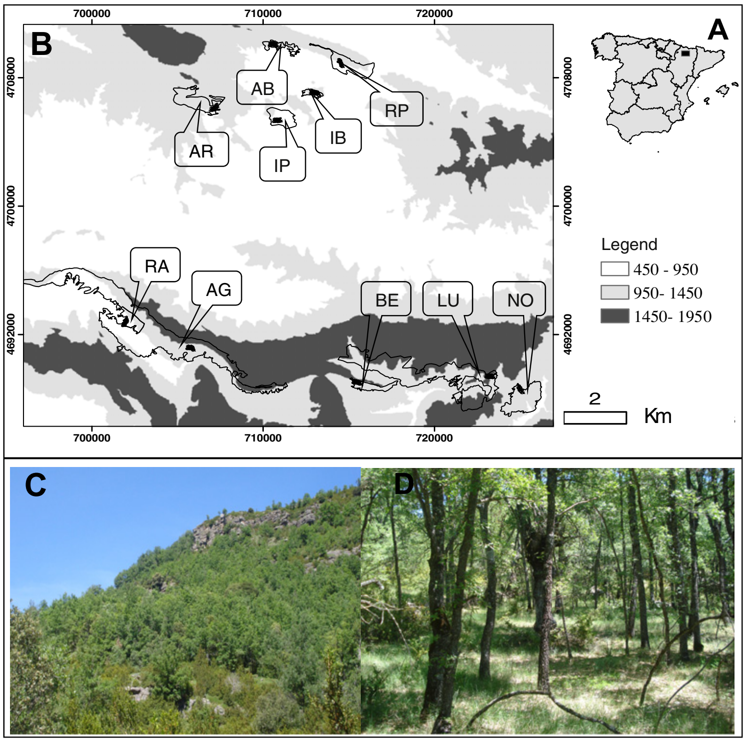

Fig. 1. Location of the study area (A) in the Central Pre-Pyrenees (northeastern Spain), topographical features of the study area (legend shows the elevation classes in meters a.s.l.), and location of the 10 stands sampled (polygons indicated by black lines) (B). The dark points inside each polygon are 500-m linear transects. An example of *Q. faginea* coppice stand (C) and young *Q. faginea* stand on an abandoned terrace (D).

Table 1
Characteristics of 10 *Q. faginea* stands sampled in the Central Pre-Pyrenees, Spain. Values are mean ± standard error.

Stand characteristics	Rasal (RA)	Belsué (BE)	Abena (AB)	Ara (AR)	Lucera (LU)	Ibort (IB)	Ipies (IP)	Nocito (NO)	Arguis (AG)	Rapun (RP)
Area (ha)	114	94	73	244	1115	40	146	294	1847	217
Elevation (m a.s.l.)	868.3 ± 4.8	1158.5 ± 1.2	970.3 ± 1.5	971.1 ± 2.0	1198.0 ± 7.7	950.8 ± 2.6	852.5 ± 2.3	1046.7 ± 2.1	1026.2 ± 1.9	923.31 ± 2.4
Orientation[a]	S	S	S	SE	SE	S	E	SW	S	SW
Slope (°)	9.3 ± 0.5	30.5 ± 0.4	11.7 ± 0.5	19.6 ± 0.5	16.8 ± 1.2	14.8 ± 1.1	7.8 ± 0.6	25.0 ± 0.8	11.0 ± 0.6	17.98 ± 1.4
Density (stems ha^{-1})	607 ± 0.1	1100 ± 0.1	999 ± 0.1	503 ± 0.1	867 ± 0.1	1088 ± 0.1	812 ± 0.1	983 ± 0.1	818 ± 0.1	540 ± 0.1
DBH (cm)	14.0 ± 1.4	9.0 ± 0.7	13.3 ± 1.3	7.2 ± 0.5	12.0 ± 0.8	13.3 ± 0.8	11.4 ± 0.7	12.3 ± 1.7	13.0 ± 1.4	6.8 ± 0.5
Tree height (m)	5.1 ± 0.4	4.8 ± 0.3	5.1 ± 0.3	3.4 ± 0.2	5.5 ± 0.3	6.1 ± 0.2	4.3 ± 0.3	5.5 ± 0.4	4.7 ± 0.3	3..9 ± 0.2
Number of stems per tree[b]	–	4 ± 1	2 ± 0	3 ± 0	3 ± 1	3 ± 1	4 ± 1	2 ± 1	–	3 ± 1
Age (years)	31 ± 3	40 ± 4	50 ± 2	35 ± 1	39 ± 1	63 ± 2	64 ± 2	56 ± 5	50 ± 1	69 ± 2
Radial-growth rate (mm yr^{-1})	2.1 ± 0.1	1.0 ± 0.1	1.3 ± 0.1	0.9 ± 0.0	1.7 ± 0.1	1.0 ± 0.1	0.9 ± 0.0	1.3 ± 0.1	1.2 ± 0.0	0.73 ± 0.1
Height-growth rate (cm yr^{-1})	17.6 ± 2.4	13.6 ± 1.1	11.9 ± 0.6	9.6 ± 0.4	16.3 ± 1.4	11.5 ± 0.7	7.1 ± 0.6	12.9 ± 0.9	10.4 ± 0.8	6.0 ± 0.3

[a] Orientation divided in four classes: S, South; SE, South East; SW, south West; E, East.
[b] Calculated only for multi-stemmed trees.

To estimate tree density in each stand, we measured the distance between each sampling point and each of the four trees. A maximum distance of 5 m was designed between the sampling point and each of the four closest adult trees, and the quadrat was considered empty if there was no adult oak tree within 5 m. Absolute density of the stand was calculated using the equation proposed by Pollard (1971), which was adjusted using a corrector factor based on the number of vacant quadrats (see Warde and Petranka, 1981).

Within each quadrat, the following variables were recorded for each of the four trees: diameter at breast height (DBH) (cm), tree height (m), and habitat (coppice stand or abandoned terrace). Tree-size distributions were examined by plotting the number of trees per class diameter (DBH) or tree height. In each quadrat, the ages of two of the four trees sampled (DBH $\geqslant$ 4 cm) were estimated by taking a core using a Pressler increment borer or by removing a disc using a chain saw (mean ± SE = 29 ± 0.30 trees per stand). Cores were taken or discs were cut from 290 trees at 1.3 m above ground, and another core or disc was taken from 90 of these trees at ground level; i.e., as close to the presumed root collar as possible to obtain an accurate estimate of age (Gutsell and Johnson, 2002). The discs and cores were sanded using progressively finer sandpapers until annual tree rings were clearly visible. Rings were counted under a binocular microscope at 10× magnification. The ring-porous wood of *Q. faginea* is well suited to dendroecological analyses because ring boundaries are clear and false or locally absent rings are rare (Corcuera et al., 2004).

To estimate the ages of the trees that were sampled at 1.3 m, we used the following equation:

$$\text{Age} = \text{Cst} + A \times \text{number of rings at 1.3 m height (DBH)}$$

Cst is the constant of the regression equation and *A* is the coefficient of the regression. Cst and *A* were estimated by applying linear regression analyses to the data from the 90 trees that had cores or discs taken at ground level and at 1.3 m. We assumed that the age estimates had errors lower than 5 yr (Table 1); therefore, the analysis of tree establishment was based on age classes at 5-yr intervals. For those cores that did not contain pith (5%), we estimated the number of missing rings by fitting a geometric pith locator (a transparent plate that has concentric circles matched to the curvature of the innermost rings; Norton et al., 1987). To estimate the year in which each stem became established, we used the estimated age at the time of sampling (2010) and the presumed date of germination. Age estimates were for stems, rather than genetic individuals because, typically, *Q. faginea* produces several shoots per individual, which generally are much younger than the stumps.

To determine whether the recruitment and survival of *Q. faginea* varied significantly over time, the age-structure data were analyzed using a power function (Szeicz and Macdonald, 1995) as follows:

$$y = y_0 x^{-b}$$

where y is the number of individuals in an age class x, y_0 is the initial input into the population at time zero, and b is the mortality rate. Recruitment residuals were calculated by subtracting the predicted from the observed tree frequencies in each 5-yr age-class. The mean annual radial-and height-growth rates of the trees were calculated by dividing the stem radius (i.e., half the DBH, excluding the bark) and the tree height by the age of each stem. The diameter at 1.3 m (DBH), height, age, mean annual radial- and height-growth rates of the trees sampled in coppice stands and those sampled in abandoned terraces were compared statistically using linear mixed-effects models that included site as a random factor and habitat type as a fixed factor (Zuur et al., 2007).

2.3. Climate trends

The analysis of the effects of climate on the establishment of *Q. faginea* was restricted to the periods in which reliable monthly weather data were available. Weather data were obtained from the four meteorological stations that had the longest records and were located within the study area: Canfranc-Los Arañones (42°44′N, 0°31′W, 1160 m a.s.l., 1910–2007), Sabiñánigo (42°31′N, 0°21′W, 790 m, 1941–2007), Botaya (42°30′N, 0°40′W, 790 m, 1927–2007), and Arguis (42°18′N, 0°26′W, 709 m, 1928–2007).

Precipitation data were analyzed for four periods: winter (December–February), winter–spring (December–May), summer (June–August), and the entire year. The following temperature variables were used in the analyses: mean annual temperature, mean summer maximum temperature (average of mean June–August monthly maximum temperatures), mean winter minimum temperature (average of mean December–February monthly minimum temperatures), and absolute monthly maximum and minimum temperatures. All of the climate variables were averaged for each of the 5-yr recruitment-survival age classes.

To assess the effects of climate on *Q. faginea* establishment, we calculated Spearman correlation coefficients (r_s) between the climate variables and both the observed number of trees established (Camarero and Gutiérrez, 2007; Chauchard et al., 2007) and the residuals obtained from the fitted power function (Szeicz and Macdonald, 1995). In addition, we identified significant inflections in the temporal trends in the climate variables that were significantly correlated with either the number of trees established or the residuals of the fitted model (Chauchard et al., 2010). To that end, we used the "turnpoints" function of the "pastecs" package in the R software (Ibanez et al., 2009). The statistical significance of the climate trends in each period was tested using the Mann–Kendall Tau (τ) Test ("Kendall" package in R software, McLeod, 2009).

2.4. Changes in land use

In this study, the temporal changes in the number of inhabitants in villages and the number of livestock: sheep, goats, and cattle (the grazing pressure of one head of cattle was considered equivalent to that of six sheep; see García-González and Marinas, 2008) within the study area were used as indicators for reconstructing past changes in land use and for assessing indirectly changes in grazing intensity.

Demographic data for the four municipalities encompassing the study area (Arguís, Caldearenas, Loarre, and Nueno) were obtained from the Instituto Nacional de Estadística (2011). The data from historical livestock censuses were divided in two periods (1890 until the early 1970s, and the late 1970s until the early 1990s). In the analysis of the data from the first period, we used the livestock numbers for the four villages closest to the 10 stands sampled, which were provided by the Historical Archives of Huesca Province (2011).

Since the early 1970s, exodus from most of the villages in the Central Pyrenees towards cities has led to changes in the boundaries of the municipalities. Several municipalities merged in a large municipality, reducing the total number of municipalities in the study area. In the analysis of the data from the second period, we used the number of livestock in the two municipalities that encompassed the four villages near the 10 sampling sites. Those data were obtained from the Provincial Service of Agriculture of Huesca Province (2011).

Inflections and trends in the land-use variables (number of inhabitants and number of livestock) were assessed in the same way as were climate variables. The effects of changes in human and livestock densities on *Q. faginea* recruitment were evaluated by comparing the number of inhabitants, livestock numbers, and both the observed number of trees established and the residuals of the fitted model for each of the 5-yr age classes by calculating Spearman correlation coefficients.

3. Results

3.1. Tree-size and age strictures explorations

The distribution of the diameters of all of the *Q. faginea* trees fit best a negative exponential distribution, and the most abundant class of trees had DBH between 5 and 10 cm (Fig. 2A). The most abundant class of trees was 4–6 m tall (Fig. 2B). The age distribution of the *Q. faginea* trees (Fig. 3A) indicated episodic recruitment, with highest recruitment in the late 1960s and early 1970s.

Between 1935 and the early 1970s, *Q. faginea* recruitment was greater than the recruitment predicted by a power function, and maximum differences (number of positive residuals) occurred in the late 1960s and early 1970s (Fig. 3A). Furthermore, there were three periods of either reduced recruitment or high mortality (periods in which the predicted tree frequency was much higher than the observed frequency of trees and the residuals were negative): the late 1970s, the late 1980s, and the early 1990s (Fig. 3A). In abandoned terraces, *Q. faginea* recruitment did not occur until the 1940s (Fig. 3B). More than 65% of the individuals sampled on abandoned terraces were established between 1965 and the early 1990s, and most of them recruited in the late 1960s (Fig. 3B). In coppice stands, the first recruitment peak occurred in the late 1930s, and others occurred in the late 1940s and early 1950s, in the early 1970s and early1980s (Fig. 3B).

The *Q. faginea* trees in coppice stands (mean ± SE = 54 ± 4 yr) were significantly ($p < 0.05$) older than the trees in abandoned terraces (mean ± SE = 43 ± 5 yr) (Table 2); however, the trees on abandoned terraces had mean annual radial- and height-growth rates that were significantly ($p < 0.05$) higher than those of the *Q. faginea* trees in coppice stands (Table 2). Although mean annual radial- and height-growth rates are age-dependent, in this study, the difference between the two habitats in the mean age of the trees was not large (overall mean ± SE = 48 ± 5 yr). Thus, a comparison of the rates was a valid means of detecting differences in the vigor and performance of the trees in the two habitats. In addition, the mean DBH of *Q. faginea* trees was significantly ($p < 0.05$) greater on abandoned terraces (13.0 cm) than in coppice stands (10.6 cm) (Table 2).

3.2. Climate trends

In the Central Pre-Pyrenees, mean annual temperatures and mean summer maximum temperatures exhibited moderate interannual variability between 1910 and 1990 (coefficients of variation of 14.3% and 7.2%, respectively). Between 1915 and 1990, mean annual, winter, summer, and winter–spring precipitation exhibited high variability in comparison to temperature variables (coefficients of variation of 40.0%, 54.5%, 32.1%, and 40.0%, respectively).

In the last century, there have been five significant inflections in mean summer maximum temperature trends (Fig. 4A), with low values in 1925 (turn-point test, $p < 0.05$), 1939 ($p < 0.05$), and 1972 ($p < 0.05$), and high values in 1943 ($p < 0.01$) and 1975 ($p < 0.05$). Mean summer maximum temperature anomalies decreased significantly (Mann–Kendall test, $\tau = -0.37$, $p < 0.05$) between 1910 and 1925 (Fig. 4A), increased significantly between 1939 and 1943 ($\tau = 0.70$, $p < 0.05$), and, thereafter, decreased until 1972. Since 1975, mean summer maximum temperatures have increased significantly ($\tau = 0.52$, $p < 0.05$).

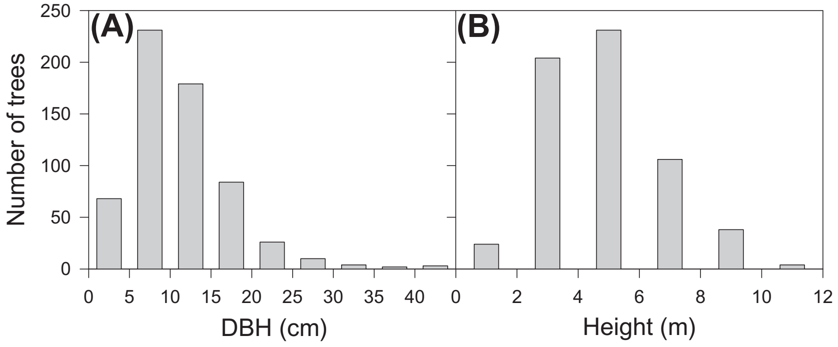

Fig. 2. Diameter at breast height (DBH) (A) and height (B) of *Q. faginea* trees at 10 sampling sites in the Spanish Pre-Pyrenees.

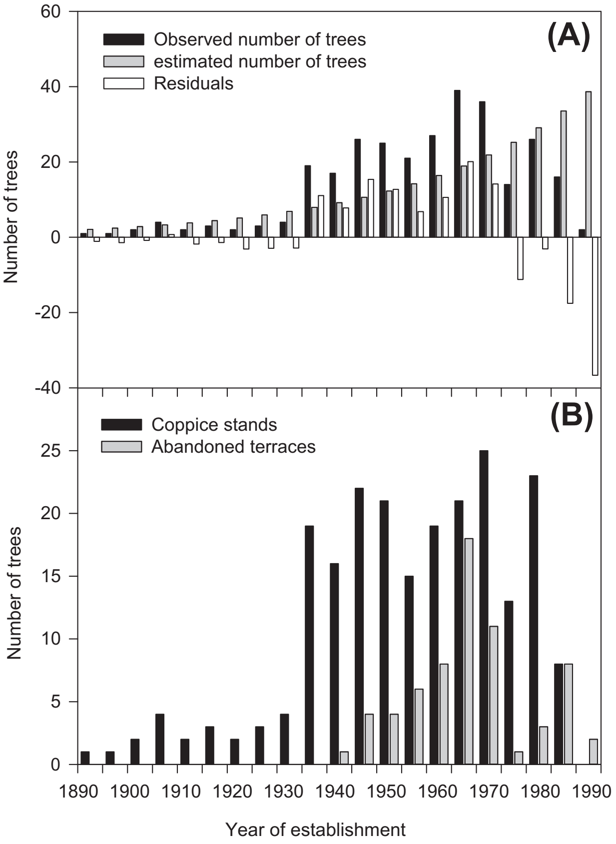

Fig. 3. Observed and estimated numbers of *Q. faginea* trees at 10 sampling sites in the Spanish Pre-Pyrenees, as a function of their year of establishment (A), and the residuals that correspond to the difference between the observed and predicted number of trees. Comparative histograms between abandoned terraces and coppice stands displaying the number of trees against year of establishment (B).

Table 2
Characteristics and related statistics of linear mixed-effects models that compare the *Q. faginea* tree variables of coppice stands (*C*) and abandoned terraces (*T*) with site as a random factor. Significant ($p < 0.05$) differences between forest and terrace are indicated in bold. Values are mean ± standard error.

Variable	Terrace (*T*)	Coppice stands (*C*)	Terrace–coppice stands comparison	*F*	*p*-Value
DBH (cm)	13.0 ± 1.0	10.6 ± 0.5	**T > C**	4.2	0.042
Height (m)	5.4 ± 0.4	4.7 ± 0.2	**T – C**	3.3	0.071
Age (years)	43 ± 5	54 ± 4	**T < C**	11	0.001
Radial-growth rate (mm yr^{-1})	1.5 ± 0.2	1.1 ± 0.1	**T > C**	11	0.001
Height-growth rate (cm yr^{-1})	13.7 ± 1.6	11.9 ± 0.9	**T > C**	5.4	0.020

Between 1915 and 1990, seven inflections were detected in the distributions of either winter–spring or annual precipitation (Fig. 4B). Mean annual precipitation anomalies increased significantly ($p < 0.05$) between 1938 and 1943 ($\tau = 0.61$) and between 1943 and 1960 ($\tau = 0.52$). Between 1960 and 1972, mean annual rainfall was high. From 1973 until 1990, annual rainfall was markedly lower than it was at any other time in the 20th century.

3.3. Changes in land use

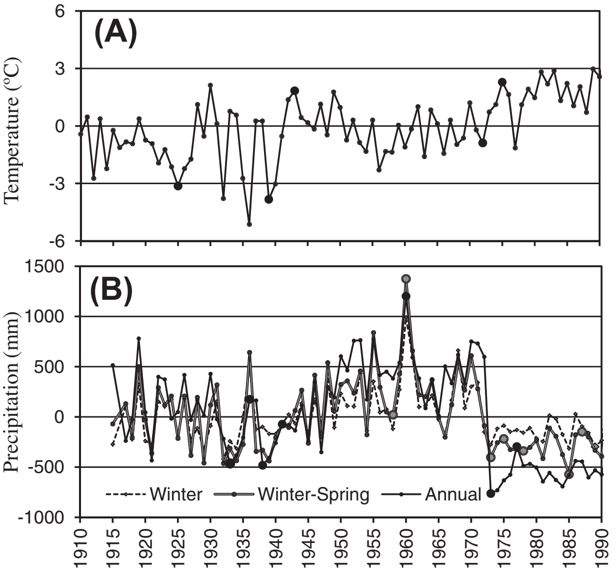

Fig. 4. Mean summer maximum temperature fluctuations and anomalies (with respect to the average) from 1910 to 1990 (A), and winter, winter–spring, and annual precipitation fluctuations and anomalies from 1915 to 1990 (B) within the study area. The marked points indicate significant ($p \leqslant 0.05$) inflections in temperature or precipitation, which were identified using the "turnpoints" function.

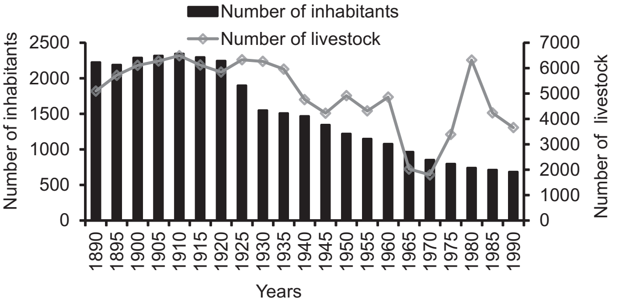

Fig. 5. Changes in the size of the human population and the amount of livestock (cattle, sheep, and goats) in the study area, between 1890 and 1990.

The human population was highest in the early 20th century (Fig. 5), declined sharply between 1920–1930, and continued to decline until 1990 ($\tau = -0.96$, $p < 0.01$). The livestock numbers (Fig. 5) increased significantly ($\tau = 0.98$, $p < 0.05$) between 1890 and 1910, remained high until 1930, and decreased significantly between 1930 and 1970 ($\tau = -0.66$, $p < 0.01$). Between 1970 and 1990, livestock densities have increased substantially and have oscillated in the last 20 yr.

3.4. Factors influencing *Q. faginea* recruitment

All of the climate and land-use variables that were significantly correlated with either the recruitment residuals of the fitted power function or the numbers of trees established were considered to have affected the recruitment history of *Q. faginea* forests. Correlation analyses indicated that the residuals of the power function fitted to the observed number of trees established were significantly negatively correlated with mean summer maximum temperatures and the number of livestock, and significantly positively correlated with annual, winter, and winter–spring precipitation (Table 3). The number of trees established and winter precipitation were significantly positively correlated. In addition, the number of trees established was significantly negatively correlated with the numbers of inhabitants and the amount of livestock within the study area (Table 3).

4. Discussion

4.1. Dynamics of *Q. faginea* forests

The negative exponential distribution of the diameters of the *Q. faginea* trees and the episodic recruitment revealed by this study reflect uneven-aged forests (Smith et al., 1997). The comparison of the age-class distributions of trees in coppice stands and those in young stands established on abandoned terraces can provide insights into the dynamics of forest development on abandoned lands. The colonization of the abandoned terraces by *Q. faginea* began in the 1940s; however, more than 65% of the *Q. faginea* trees present on those abandoned terraces in 2010 became established after 1965. Before *Q. faginea* began colonizing the abandoned terraces, shrubs (e.g., *B. sempervirens*, *G. scorpius*) were occupied them, which indicates that they were abandoned long before 1965 (Montserrat, 1990; Capitanio and Carcaillet, 2008; Kouba and Alados, 2012).

The mean annual radial- and height-growth rates of the *Q. faginea* trees on the abandoned terraces were higher and the stems were thicker than were those of the trees in coppice stands; probably, because the abandoned terraces and farmlands in the study area are on relatively flat lands and some are in valley bottoms where the soils have the highest amounts of nutrients and water, which might have enhanced tree growth (Lasanta et al., 2000). After abandonment, herbaceous plants and shrubs colonized the terraces before becoming forested by *Q. faginea*. The process of secondary succession involves significant changes in habitat and microclimate at local scales, including a reduction in runoff and an improvement in soil infiltration, which enhances soil conservation (Molinillo et al., 1997; Lasanta et al., 2000), an increase in litter accumulation, which generates a large amount of organic-matter because of leaf decomposition (Maltez-Mouro et al., 2005), and the accumulation of minerals in the flatlands, which increases soil nutrient contents (Maltez-Mouro et al., 2005; Garcia et al., 200). Those changes helped to improve soil fertility (Lasanta et al., 2000). In other studies, *Q. faginea* trees had the highest growth rates and stands had the highest densities on the shallowest slopes, which had the highest soil fertility (Maltez-Mouro et al., 2005).

4.2. Effects of climate on *Q. faginea* recruitment

The recent reductions in annual precipitation and increases in summer temperatures in the last 20 yr have had a significant effect on *Q. faginea* recruitment. The positive correlations between *Q. faginea* recruitment and annual, winter, and winter–spring precipitation reflect how inter-annual variability in precipitation has affected *Q. faginea* recruitment. Mean maximum summer temperature and *Q. faginea* recruitment were negatively correlated, which suggests that most of the recruitment occurred in years that had cool summers, and oak seedlings experienced high mortality in years that had hot, dry summers (see also Rey Benayas et al., 2005).

Table 3
Spearman correlation coefficients (r_s) and related probability levels (*p*-value) calculated between weather and land-use variables vs. established trees. Calculations were performed using the observed number of established trees and the residuals of fitted power functions.

Variable	Observed	*p*-Value	Residuals	*p*-Value
Weather variables				
Mean summer maximum temperature	–	–	−0.54	0.025
Annual precipitation	–	–	0.61	0.004
Winter precipitation	0.5	0.048	0.63	0.009
Winter–spring precipitation	–	–	0.62	0.010
Land use variables				
Local population size	−0.72	0.009	–	–
Number of livestock	−0.82	0.000	−0.75	0.001

The establishment of *Q. faginea* was very low in the late 1970s, late 1980s, and early 1990s and high in the late 1960s and early 1970s. Periods of low recruitment coincided with hot summers and low precipitation in winter and spring, which caused the most severe droughts in the region during the 20th century (Vicente-Serrano, 2006) and might have caused high mortality among *Q. faginea* recruits. In the Mediterranean Basin, the weather in summer is one of the main factors that influence recruitment (i.e., seed germination, seedling emergence and survival) in oak species (Pulido and Díaz, 2005; Urbieta et al., 2008). Harsh conditions such as hot and dry summers are major causes of seedling mortality in *Q. faginea* and other Mediterranean oak species (Valladares et al., 2000; Esteso-Martínez et al., 2006; Maltez-Mouro et al., 2008). Sufficient precipitation in winter and spring, and cool summer temperatures in the 1960s and early 1970s, especially between 1970 and 1972, might have produced the recruitment pulses that occurred between 1965 and 1975. The amount of moisture available in the soil has a strong influence on the survival of *Q. faginea* seedlings, which usually germinate in early spring (Esteso-Martínez et al., 2006; Maltez-Mouro et al., 2007). In our study, high precipitation in winter and spring increased soil moisture, which can increase seedling survival if the subsequent summer is not exceptionally hot and dry. Other studies revealed also that low water availability reduces the growth of *Q. faginea* (Rey Benayas et al., 2005).

4.3. Effects of human and livestock populations on *Q. faginea* recruitment

The first expansion of *Q. faginea* into the study area occurred in the late 1930s, when local human populations declined, which might have reduced anthropogenic pressures on the territory in the area. Furthermore, the high *Q. faginea* recruitment in the late 1960s and early 1970s coincided with an increase in the recruitment rate of *Q. faginea* on the abandoned terraces and the decline in the local human population that had begun about 40 yr earlier.

The negative correlation between *Q. faginea* recruitment and the number of livestock suggests that grazing pressure had a significant negative effect on the establishment of *Q. faginea*, particularly between 1890 and 1930. In addition, the first peak in *Q. faginea* recruitment occurred when grazing pressure began to decline, and the highest recruitment peaks occurred in late 1960s and early 1970s, which coincided with the lowest numbers of livestock. Livestock overgrazing constrains the regeneration of tree species (Barbero et al., 1990; Carmel and Kadmon, 1999). Livestock eliminate seedlings, which diminishes recruitment and, consequently, hinders forest regeneration (Cierjacks and Hensen, 2004; Callaway and Davis, 1993; Wahren et al., 1994). The increase in the number of livestock that began in the 1970s was not accompanied by an increase in grazing pressure because of significant changes in livestock husbandry in the Central Pre-Pyrenees (García-Ruiz et al., 1996). Since the 1970s, the number of livestock grazing freely in the mountain grasslands and rangelands of the study area in summer has decreased sharply (Molinillo et al., 1997; Lasanta et al., 2006).

5. Conclusions

In the 20th Century, changes in land use and climate have strongly influenced the dynamics of *Q. faginea* forests in the Central Pre-Pyrenees. The history of recruitment in those forests involved the following stages: (i) before 1935, the establishment of *Q. faginea* was restricted mainly to coppice stands because of extensive farmland cultivation on the mountain terraces and livestock overgrazing; (ii) between 1935 and the early 1960s, reductions in human land use and livestock pressure favored *Q. faginea* recruitment and expansion; (iii) in the late 1960s and early 1970s, the encroachment of abandoned terraces by *Q. faginea* was enhanced by favorable climatic conditions; and (iv) since 1975, *Q. faginea* recruitment has been stressed by drought (insufficient amount of rainfall in winter and spring, and high temperature in summer). high rates of tree growth and recruitment in this species should be maintained by using improved management of the forests based on drought alerts and mitigation adaptive systems (e.g., preventive thinning in very dense forests) and by the enhancement and regulation of *Q. faginea* colonization in formerly cultivated and grazed lands (e.g., selection of vigorous or reproductive trees in encroached abandoned terraces).

Acknowledgements

The Spanish Ministry of Education and Science (projects CICYT CGL2008-00655/BOS and CGL2008-04847-C02-01/BOS) funded this research. A MAEC-AECID grant from the Spanish Agency for International Cooperation and Development supported the first author. J.J. Camarero is grateful for the support of ARAID and the Globimed Network (www.globimed.net). We thank A.Q. Alla, G. Sangüesa-Barreda, and P.N. Galve for assisting in the collecting of field data, and the Agencia Estatal de Meteorología for providing weather data.

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