

Drought-Induced Multifactor Decline of Scots Pine in the Pyrenees and Potential Vegetation Change by the Expansion of Co-occurring Oak Species

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ABSTRACT

Episodes of drought-induced tree dieback have been recently observed in many forest areas of the world, particularly at the dry edge of species distributions. Under climate change, those effects could signal potential vegetation shifts occurring over large geographical areas, with major impacts on ecosystem form and function. In this article, we studied the effect of a single drought episode, which occurred in summer 2005, on a Scots pine population in central Pyrenees (NE Spain). Our main objective was to study the environmental correlates of forest decline and vegetation change at the plot level. General and generalized linear models were used to study the relationship between canopy defoliation, mortality and recruitment, and plot characteristics. A drought-driven multifactor dieback was observed in the study forest. Defoliation and mortality were associated with the local level of drought stress estimated at each plot. In addition, stand structure, soil

properties, and mistletoe infection were also associated with the observed pattern of defoliation, presumably acting as long-term predisposing factors. Recruitment of Scots pine was low in all plots. In contrast, we observed abundant recruitment of other tree species, mostly *Quercus ilex* and *Q. humilis*, particularly in plots where Scots pine showed high defoliation and mortality. These results suggest that an altitudinal upwards migration of *Quercus* species, mediated by the dieback of the currently dominant species, may take place in the studied slopes. Many rear-edge populations of Scots pine sheltered in the mountain environments of the Iberian Peninsula could be at risk under future climate scenarios.

Key words: drought; scots pine (*Pinus sylvestris* L.); canopy defoliation; mortality; recruitment; summer water availability; stand structure; soil properties; mistletoe.

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INTRODUCTION

Climate-related forest dieback is a recurrent phenomenon that has already been reported in a variety of woodland and forest communities in many parts of the world (Auclair 1993; Williamson and others 2000; Rice and others 2004; Allen and others 2010; van Mantgem and others 2009).

Climate change may increase physiological stress on long-lived woody vegetation, occasionally leading to increased mortality rates and episodes of forest dieback (Allen and others 2010). This dieback is characterized by rapid defoliation and progressive increase in mortality of overstory trees (Bréda and others 2006). Such widespread mortality events have the capacity to transform regional landscapes on a sub-decadal timescale, with significant implications for stand structure and dynamics and ecosystem function (McDowell and others 2008).

Our current understanding of the mechanisms underlying tree dieback is still limited (Bréda and others 2006; McDowell and others 2008). Tree death is a complex process that has been attributed to a wide range of potential causes, often involving prior droughts that initiate a growth decline (Pedersen 1998; Oberhuber 2001; Camarero and others 2002; Das and others 2007) and a lengthy chain of interacting events (Waring 1987; Franklin and others 1987). Thus, many studies have assumed a slow-decline hypothesis (Manion 1991) that considers a three-stage decline: (1) predisposing factors expose plants to long-term stress, for instance, poor soil conditions and/or high stand density; these predisposing factors increase the susceptibility of trees to (2) severe short-term stresses known as inciting factors, for instance an extreme drought; and (3) eventually the contributing factors (for instance parasites and/or additional climatic events) can kill the trees. Despite the robust theoretical background of this hypothesis, the empirical support is relatively weak because the studies documenting drought-induced dieback rarely analyze the relative importance of all the factors that are potentially involved.

The large-scale control of climate on water availability in the soil may also be influenced by topography and soil properties at the local scale (Stephenson 1990; Western and others 2002). In Mediterranean regions, especially in summer, when evapotranspiration continuously exceeds precipitation, topographic characteristics such as altitude, slope, aspect, and texture and depth of soil influence soil water availability as local controls (Grayson and others 1997). Despite the importance of these factors on the spatial patterns of tree mortality, few studies have evaluated their effects, with the exception of the effect of altitude (Allen and Breshears 1998; Guarín and Taylor 2005).

Parasite outbreaks may be enhanced by climate change (Mattson and Haack 1987; Breshears and others 2005). In addition to modifications in the parasite life cycle, climate-induced changes in plant

carbon allocation may diminish the production of defense compounds (Waring 1987; Dunn and others 1990; Croisé and Lieutier 1993), reducing the ability of trees to withstand, for instance, the attack of cambium-eating insects (Mattson and Haack 1987; Negrón and others 2009). Hemiparasitic plants may also impact on host–water relations as a result of their high rates of transpiration, needed to take up water, nutrients, and carbohydrates from host trees (Ehleringer and Marshall 1995). Therefore, increased vulnerability of trees to parasite attacks under water stress conditions can lead to episodes of high tree mortality (Williams and Liebholt 2002; Breshears and others 2005; Dobbertin and others 2007; Negrón and others 2009).

In recent decades, changes in human use of many temperate forests have resulted in denser stands due to abandonment of agropastoral activities (Barbéro and others 1998; Poyatos and others 2003), to artificial afforestation (Martínez-García 1999) and to decreases in logging practices (Linares and others 2009). Denser stands normally result in stronger plant competition (Linares and others 2009) and “natural” self-thinning processes (Peet and Christensen 1987; Kenkel 1988; Chen and others 2008), because of the corresponding reduction in soil water availability per unit of basal area. Therefore, trees in dense stands may be more predisposed to die under water stress conditions (Guarín and Taylor 2005; Bigler and others 2006).

Forest communities are dynamic and changes occur continuously at the individual and population levels, due to a balance among growth, recruitment, and mortality. Light-gaps are created when trees die in closed-canopy forests, initiating a micro-successional sequence that culminates in the replacement of the original canopy tree by one or more new trees (Hubbell and Foster 1986). Because altered conditions of light and soil moisture are expected in the gaps compared with conditions under the canopy (Suarez and Kitzberger 2008), recruitment of new species with different resource requirements could occur, with major implications for community dynamics (Connell 1978). Consistent with this, changes in the recruitment pattern associated with high mortality rates may promote shifts in species composition and in distribution areas in response to drought episodes. Nevertheless, research on the changes in recruitment patterns associated with drought-induced mortality in the overstory vegetation is still scarce (but see Condit 1998; Slik 2004; Kelly and Goulden 2008).

Scots pine (*Pinus sylvestris* L.) is one of the most widely distributed trees on Earth. Although the

largest populations of this species occur in boreal regions, Scots pine also occupies large areas in relatively dry regions within the Mediterranean basin, from the Iberian Peninsula to Turkey (Barbéro and others 1998). The south-western limit of Scots pine is in the Iberian Peninsula, with important populations in the Pyrenees and several populations scattered in southern, more arid localities (Castroviejo and others 1986). These populations, located at the low-latitude, rear-edge of the species distribution area, are likely to be particularly sensitive to the effects of increased aridity (Hampe and Petit 2005). In fact, drought-related Scots pine dieback has already been reported in the Iberian Peninsula (Martínez-Vilalta and Piñol 2002; Hódar and others 2003) and in the Alps (Hódar and others 2003; Bigler and others 2006). As the Mediterranean basin climate is becoming warmer and drier (IPCC 2007), an increase in drought-induced mortality of Scots pine has been predicted (Martínez-Vilalta and Piñol 2002).

The main objective of this study is to evaluate drought as the potential inciting factor of the dieback observed in southern Scots pine forests. Although several studies have analyzed drought-related dieback episodes in many regions of the world (Rice and others 2004; Mueller and others 2005; Bigler and others 2006; van Mantgem and Stephenson 2007), the many factors potentially associated with forest decline have been rarely examined exhaustively. We emphasize here the role of the forest intrinsic factors such as stand structure and soil properties, and extrinsic factors such as mistletoe infection. We study the stand demographic trends in response to a recent drought episode, accounting for the patterns of defoliation and mortality, as well as recruitment at the level of a single valley in the Central Pyrenees (NE Spain). Three main questions are addressed. (a) Are mortality and defoliation associated with the local level of drought stress estimated for each plot? (b) Does the effect of drought stress depend on other factors such as soil properties or stand-level competition? (c) Is the recruitment of other species related to the drought effects on the Scots pine tree canopy?

MATERIALS AND METHODS

Experimental Site

The study was carried out in a Scots pine forest located in Central Pyrenees (Soriguera, Pallars Sobirà, 42° 22' 43"N, 1° 6' 29"E, ca. 16 km²). Most of the Scots pine forests in the area have

traditionally been under agropastoral pressures up until the early twentieth century, and some forest patches were completely removed. Regarding the management practices at the study stands, selective activities on species establishment have never taken place in the area and logging activities on Scots pine stands have not been practiced since the 1980s (pers. com. by Carles Fañanàs, Catalan Forest Service). Although both natural and artificial afforestation have been taking place in the area during the twentieth century, the study site appears absolutely within the distribution area of Scots pine and this species has naturally been present in the area since the Catalan Forest Service began keeping records. Accordingly, the studied Scots pine population exhibits natural regeneration and an uneven age and size structure (Supplemental Materials, Figure s1). This is further corroborated by dendrochronological analyses of tree-rings showing that Scots pines with a diameter between 20 and 40 cm have ages ranging between 30 and 100 years (Ana Heres, unpublished data). These forests are mainly on northern slopes and are continuously distributed in altitudes from 600 to 1500 m a.s.l. The shrub layer is predominantly occupied by *Buxus sempervirens*, *Amelanchier ovalis*, and *Lonicera xylosteum*. Other species of trees, *Quercus humilis*, *Quercus ilex*, and *Betula pendula*, occasionally appear in the understory, mostly at lower (*Quercus* species) and higher altitudes, respectively. Some younger *Pinus nigra* plantations interrupt the Scots pine forest. A well-established mistletoe population, with individuals up to 30 years old, infects most Scots pine trees in the area.

The climate of the region is characterized by an annual mean temperature of 9.6°C and an annual mean rainfall around 643 mm (climate data for the period 1951–1999 from the Climatic Digital Atlas of Catalonia (CDAC) (Pons 1996; Ninyerola and others 2000)), corresponding to the temperate oceanic submediterranean bioclimatic region (Worldwide Bioclimatic Classification System 1996–2000). In 2005, the Iberian Peninsula experienced a severe drought episode preceded by several dry periods during the last years (EEA 2008). This drought affected our study area (Figure 1), and was associated with the observation of evident damage on Scots pine stands (pers. com. by Carles Fañanàs, Catalan Forest Service). This observation was supported by dendroecological analyses that showed lower growth and higher mortality in 2005 and subsequent years, although minor mortality episodes were also detected prior to 2005 (Ana Heres, unpublished data).

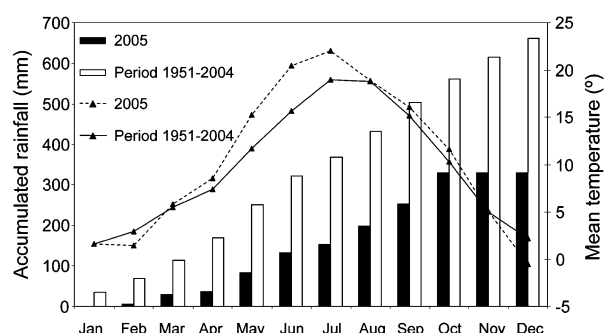


Figure 1. Monthly meteorological data for the studied area (data obtained from the Spanish meteorological station network (Agencia Estatal de Meteorología)). Accumulated rainfall (*bars*) and mean temperature (*lines*), from January to December, are shown for year 2005 and for the average conditions during the 1951–2004 period.

Field Sampling Methods

In August 2007, 30 circular plots (314 m² each) were sampled along a steep altitudinal gradient from 645 to 1383 m a.s.l. in two nearby slopes within the same valley. To avoid excessive environmental heterogeneity, plot selection used the following criteria: (a) slopes from 10° to 40° and North aspect; (b) no signs of recent disturbance or management; (c) distance between plots greater than 50 m.

Plots were defined around a central Scots pine tree. In each plot, trees, shrubs, and the presence of parasites, that is, the epiphyte mistletoe (*Viscum album* L.), were recorded (see below). All trees and shrubs were identified to species. Two size classes were considered for all woody species including Scots pine.

- Seedlings (< 50 cm height and < 1.5 cm diameter at breast height (DBH)) were recorded at the least disturbed 1 m width side of the 20 m central transect of the plot that was perpendicular to the slope. Seedling sprouts and seedlings may look quite similar when their height is close to 50 cm. We felt the root collar zone to detect possible important lignifications which would have evidenced that sprouts emerged from the roots.
- Adult trees (> 50 cm height and > 1.5 cm DBH) were recorded all over the plot. DBH was measured on all adult trees.

For all adult Scots pine individuals, additional information was recorded: state (dead or alive), visual estimation of the percentage of crown defoliation (%), presence/absence of bark beetles, and

mistletoe occurrence (0 = no mistletoe, 1 = low mistletoe infestation with few mistletoe plants, 2 = medium mistletoe infestation with several large mistletoe bushes or many small plants found in the crown, 3 = heavy mistletoe infestation with many large mistletoes on at least one-third of the branches in the tree crown; Dobbertin and Rigling 2006). In each plot, a mistletoe index was calculated by averaging mistletoe occurrence across trees.

Response Variables

Canopy defoliation and standing mortality were the response variables used to assess forest decline in this study. At the plot level, canopy defoliation (%) was calculated by averaging the percentage of crown defoliation for all living individuals, weighted by the basal area of each tree. Total canopy defoliation including dead trees was also calculated and used as predictor variable in the recruitment analysis (see below). Mortality was measured as the count of dead individuals relative to the total number of individuals (see “Statistical analyses” section). Patterns of recruitment for *Quercus ilex* and *Quercus humilis* were also studied at the plot level, on the basis that these species could potentially replace Scots pine under future climatic conditions. Seedling abundance of *Quercus ilex* and *Quercus humilis* were pooled together because of their relatively similar characteristics and abundance pattern along the altitudinal gradient (see Figure 4A).

Forest Structural Variables and Competition

Forest structural variables were recorded on the basis that competition could be affecting Scots pine defoliation and mortality patterns. At the plot level, intra-specific (Scots pine) competition was assessed using stand density, mean DBH, and an aggregation index (z value) based on distances to the nearest neighbor recorded for all Scots pine trees (Clark and Evans 1954). Large values of this index ($z > 1.96$) imply a regular distribution of trees and small values ($z < -1.96$) imply a clumped pattern, whereas values of z greater than -1.96 or less than 1.96 indicate a random distribution. At the individual level, we computed the Hegyi index of competition (Hegyi 1974) in a 5-m radius around each individual. This index takes into account the distance of the competitor to the focal tree as well as the size of the trees. Competition indexes were corrected for edge effects by assuming that the distribution of individuals inside and outside plots was similar.

Water Availability

Water availability in the soil is mainly determined by soil properties at small scales and by the balance between net rainfall and evapotranspiration as well as topography at larger spatial scales (Western and others 2002). Three sets of variables were thus used to characterize local water availability at the plot level. Note that these variables are not a precise record of conditions occurring during the 2005 drought episode and should be considered only as relative indicators of water availability among plots.

Summer Water Availability Index

Summer water availability (SWA) was assessed as: $SWA = P/PET$, where P is the average (1951–1999) precipitation from June to August and PET is the average potential evapotranspiration for the same period. Given that there was no weather station within the sampled altitude gradient, the monthly values of temperature and precipitation, as well as their altitudinal lapse rates, were obtained from the CDAC (Pons 1996; Ninyerola and others 2000), at a resolution of 180 m. The Hargreaves equation (Hargreaves and Samani 1985) was used to compute PET , accounting for the extraterrestrial solar radiation (Allen and others 1998). Summer water availability ranged from 0.44 to 0.66.

Topographic Wetness Index

Topographic wetness indices developed by different authors (Beven and Kirkby 1979; O'Loughlin 1986) have long been used to characterize spatial soil moisture conditions at within-catchment scales. They assume that, from a simplified but realistic physical approach, topography is dominant in controlling and modifying the hydrologic processes operating at the hillslope scale (Grayson and others 1999). We used the topographic index developed by Beven and Kirkby (1979), which accounts for the contributing area in the catchment that drains into a given point, and for the slope of the terrain. As the plots were distributed only on northern slopes, the aspect was not relevant in our case. The topographic index was computed from a digital elevation model (DEM) with a resolution of 30 m, together with topographic information recorded at the plots. The topographic wetness index ranged from 7.62 to 11.60, with higher values representing wetter conditions.

Soil Texture Measurements

The studied soils are calcareous and belong predominantly to the clayey-loam texture class. We

excavated one profile per plot and extracted a soil sample from 20 cm depth using a metal core (height = 7 cm, diameter = 5.6 cm) to determine the bulk density and the soil texture. The measurements were performed in the laboratory using mechanical methods. Soils were separated into the following size fractions (%): coarse sand (2–0.2 mm), fine sand (0.2–0.02 mm), silt (0.02–0.002 mm), and clay (<0.002 mm). We computed the B coefficient from the Saxton equation (Saxton and others 1986) with the purpose of obtaining a representative value of the water retention capacity from the texture of the soil. Large values of this index are characteristic of sandy soils, and imply a low water retention capacity. The fact that the studied soils were fairly rocky (44% of large stones on average) made it difficult to excavate the C horizon. Thus, we used the depth of the upper (A and B) horizons as a measure of soil depth.

Statistical Analyses

Statistical analyses were conducted at the individual tree and at the plot levels. At the plot level, most variables were normally distributed or normalizable using standard transformations (see Table 1). Stand density, dead individuals (%), and seedling abundance of *Quercus* species, however, remained non-normal. General and generalized linear models were thus used to study the relationship between plot characteristics and defoliation, mortality and recruitment. For the defoliation model, an identity link function was used because the canopy defoliation variable was normally distributed. In the mortality model, the number of standing dead Scots pines in each plot was considered a count response variable; the logarithm of the total number of Scots pine was introduced into the model as an explanatory variable. We used this approach because this response variable was not normalizable after standard transformations and it is effectively very similar to modeling the proportion of dead individuals (Faraway 2006). For the mortality and recruitment models, preliminary analyses using a Poisson distribution of errors for count variables showed overdispersion, and thus a negative binomial distribution was used in the final models (White and Bennetts 1996). All models (defoliation, mortality, and recruitment) were as similar as possible in terms of explanatory variables (see Table 1). The occurrence of bark beetles was not introduced in the models because bark beetles appeared basically on dead trees, and thus were likely a consequence, not a cause, of tree mortality.

Table 1. Explanatory Variables Introduced into the Defoliation, Mortality, and Recruitment Models at the Individual and Plot Levels

Description of the explanatory variables	Units	Model
Plot level ($N = 30$)		
Summer water availability index (arcsin transformation)	Adimensional	All
Stand density	Individuals/m ²	All
Mean DBH	cm	All
Aggregation index	Adimensional	All
Topographic wetness index	Adimensional	All
Saxton B coefficient (inverse transformation)	%	All
Depth of the soil	cm	All
Mistletoe index (log transformation)	Adimensional	Defoliation and mortality
Weighted percentage of total canopy defoliation including dead trees	%	Recruitment
Total individuals (log transformation)	Individuals/plot	Mortality
Individual level ($N = 1002$)		
DBH	cm	All
Hegyi competition index (log transformation)	Adimensional	All
Mistletoe occurrence	Adimensional	All

See text for details.

At the individual level, general and generalized mixed linear models were used to study the relationship between individual characteristics and defoliation (normally distributed) and mortality (binomially distributed). Among the explanatory variables, solely the Hegyi competition index was normalizable using standard transformations (see Table 1). DBH and mistletoe occurrence remained non-normal. Mistletoe occurrence was observed essentially on living trees and was tested as a fixed factor with four abundance classes in the defoliation model. Plot effects were modeled as a random factor in both individual-level models to account for the spatial autocorrelation among individuals within a plot.

Parameters (β) of all fitted models were estimated using maximum likelihood methods. Model selection was based on a stepwise selection

procedure using the Aikake information criterion (AIC). Some additional analyses were conducted using Pearson and Spearman correlation coefficients as a measure of association between pairs of variables. Analysis of variance (One-Way ANOVA using Post Hoc Multiple Comparisons) was used to compare means between more than two groups. All statistical analyses were carried out with R version 2.9.0. (2009 The R Foundation for Statistical Computing).

RESULTS

Determinants of Defoliation and Mortality Patterns

At the plot level, average defoliation and standing mortality of Scots pine were 45.18 and 14.3%,

Table 2. Structural Attributes of the Studied Stands

	Living individuals	Dead individuals	Total stand
Number of individuals	856	146	1002
Mean dbh (cm)	18.24 (0.36)	11.95 (0.84)	17.32 (0.34)
Stand density (individuals/ha)	—	—	1071 (81)
Basal area (m ² /ha)	—	—	35.90 (2.7)
Canopy defoliation (weighted %)	—	—	45.18 (2.89)
Canopy defoliation (%)	—	—	51.05 (2.65)
Dead individuals (%)	—	—	14.3 (2.65)
Dead basal area (%)	—	—	9.13 (2.32)

Standard errors are in brackets.

Table 3. General and Generalized Linear Models for Defoliation and Mortality, Respectively, at the Plot Level

Model terms	β	SE	P-value
Defoliation plot-level model			
Summer water availability index	-133.569	27.850	<0.001
Stand density	252.394	50.963	<0.001
Mean DBH	1.438	0.408	0.002
Mistletoe index	8.952	3.645	0.022
Saxton <i>B</i> coefficient	-298.505	122.384	0.023
Soil depth	-0.250	0.125	0.057
Mortality plot-level model			
Summer water availability index	-6.251	2.073	0.003
Total individuals (log)	2.907	1.014	0.004

A stepwise model selection was used in both cases starting from the same initial set of explanatory variables. Only the final models are shown. $N = 30$ plots; $AIC_{\text{defoliation model}} = 142.62$; $AIC_{\text{mortality model}} = 155.20$.

respectively (Table 2). In contrast, no mortality was found in *Quercus* species. The final models fitted using stepwise model selection from the same initial set of explanatory variables differed notably for defoliation and mortality (Table 3). Both defoliation and mortality were mostly affected by summer water availability and stand density, but canopy defoliation was associated with additional explanatory variables (Table 3). Increases in defoliation and mortality were associated with lower summer water availability and higher stand density (as shown by the $\beta > 1$ for the total number of individuals in the mortality model). Indeed, defoliation and mortality of Scots pine tended to be higher at low and intermediate altitudes coinciding with lower climatic water availability (Figure 2). Mean DBH and, to a lesser extent, mistletoe index were also significant in the defoliation model; larger values of those variables were associated with higher canopy defoliation. In contrast, soil properties such as the Saxton *B* coefficient and soil depth were negatively correlated with canopy defoliation, although the relationship was only marginally significant in the case of soil depth. Interactions among explanatory variables were not significant for either defoliation or mortality. There was a positive relationship between canopy defoliation and mortality ($r = 0.620$, $P < 0.001$) indicating that the most affected plots in terms of mortality were still highly defoliated 2 years after the drought event.

At the individual level, the stepwise model selection used to fit both defoliation and mortality models did not remove any explanatory variable. All the variables tested were significantly associated with defoliation and mortality (Table 4). Canopy defoliation and mortality were higher in smaller

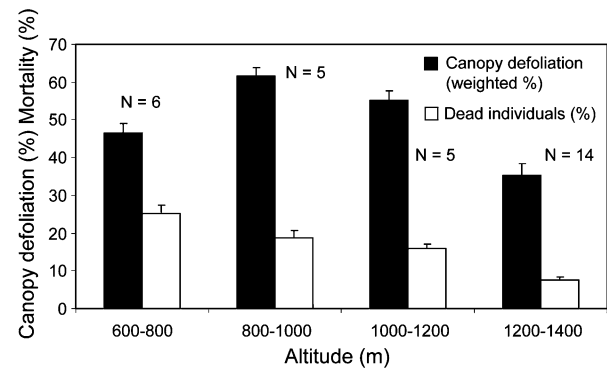


Figure 2. Percentage of canopy defoliation of living individuals and standing mortality (plot level) along the altitudinal gradient. Error bars show standard errors. The number of plots (N) at each altitude level is shown on top of the bars.

trees (lower DBH; see Figure 3) and with high intra-specific competition (larger values of Hegyi competition index; see Figure 3). Defoliation was also associated with mistletoe occurrence, with defoliation progressively increasing on more heavily infested trees (Table 4). High intensity of mistletoe infection tended to occur on larger trees (one-way ANOVA, $F = 51.927$, $P < 0.001$; see also Figure 3), but within a given mistletoe occurrence class small trees were more defoliated than large ones (Figure 3).

Community Dynamics

At the plot level, a high recruitment of the shrub *Buxus sempervirens* was found in all plots (10,250 seedlings/ha on average; Supplemental materials, Figure s2). *Quercus humilis* and *Quercus ilex* were the trees with higher recruitment in the

Table 4. General and Generalized Linear Mixed Models for Defoliation and Mortality, Respectively, at the Individual level

Model terms	β	SE	P-value
Defoliation individual-level model			
DBH	-0.009	0.001	<0.001
Hegyi competition index	0.002	0.001	0.006
Mistletoe index—low occurrence	0.048	0.023	0.038
Mistletoe index—medium occurrence	0.110	0.035	0.002
Mistletoe index—high occurrence	0.130	0.039	0.001
Mortality individual-level model			
DBH	-0.058	0.014	<0.001
Hegyi competition index	0.036	0.009	<0.001

A stepwise model selection was used in both cases starting from the same initial set of explanatory variables. Only the final models are shown. $AIC_{\text{defoliation model}} = -151.414$, $N = 856$; $AIC_{\text{mortality model}} = 688.7$, $N = 1002$.

study area, with 2483 and 1700 seedlings/ha on average, respectively. In contrast, we found an average abundance of 766 seedlings/ha for Scots pine, mostly concentrated in one single plot with a density of 13,500 seedlings/ha (see also Figure 4A). Average Scots pine seedling abundance excluding this plot was 327 seedlings/ha.

Quercus humilis and *Quercus ilex* abundance were correlated to each other (Figure 4A; $r = 0.755$, $P < 0.001$). Overall seedling abundance of *Quercus* species tended to be higher at low altitudes (Figure 4A), in agreement with higher density of adults of these species toward the valley bottom (Figure 4B). Nevertheless, *Quercus* recruitment was

also high at intermediate altitudes; despite that mature trees of *Quercus* species were almost absent (Figure 4B).

The stepwise model selection used to fit the recruitment model removed two explanatory variables: stand density and the Saxton B coefficient. Total canopy defoliation was the most significant variable in the recruitment model, with higher *Quercus* recruitment where defoliation was higher (Table 5). With regard to the variables linked to competition, mean Scots pine DBH was the most important in the model. Large values of DBH were related to lower seedling abundance of *Quercus* species. The aggregation index was marginally (and

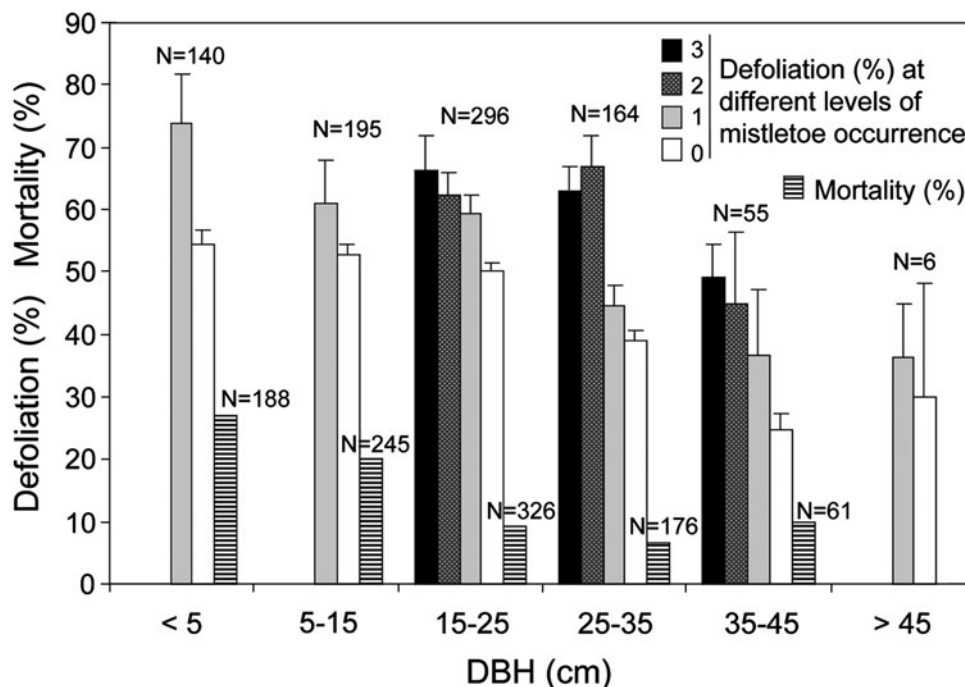


Figure 3. Distribution of defoliation and mortality across diameter classes in the studied Scots pine stands. Defoliation effects are split by mistletoe occurrence levels (0 = no, 1 = low, 2 = medium, 3 = heavy) for each diameter class. Error bars show standard errors. The number of individuals (N) in each diameter class (including all mistletoe classes) for defoliation is shown on top of the defoliation bars. The number of individuals (N) used for mortality estimates is shown on top of the mortality bars.

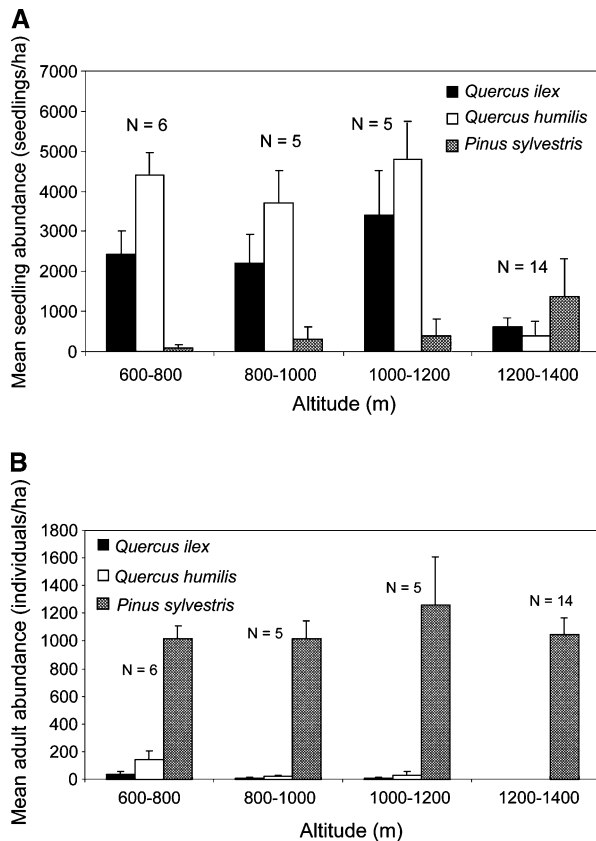


Figure 4. Seedling (A) and adult (B) abundance distribution of *Quercus ilex*, *Quercus humilis*, and *Pinus sylvestris* along the altitudinal gradient (bars). Error bars show standard errors. The number of plots (N) at each altitude level is shown on top of the bars.

positively) related to seedling abundance, indicating that recruitment of *Quercus* species was higher where the adult trees of Scots pine were more uniformly distributed. The topographic wetness index and the depth of the soil were negatively associated with the seedling abundance of *Quercus* species. Finally, summer water availability was also negatively associated with the recruitment of *Quercus*, probably influenced by the absence of severe defoliation under relatively moist conditions (see Table 3).

DISCUSSION

Determinants of Defoliation and Mortality

In addition to the expected association between forest decline (defoliation and mortality) and local level of drought stress, our results showed that such a relationship is complex and may involve a wide range of other contributing causes (Waring 1987; Franklin and others 1987; Manion 1991). This is one of the few studies that have examined the many factors potentially associated with tree death, revealing the multifactor nature of drought-driven forest decline. The involved factors act differently on the dieback parameters: summer water availability and stand density were the most important driving factors of both mortality and defoliation, presumably acting during the 2005 drought episode as inciting and long-term predisposing factors, respectively; whereas canopy defoliation was associated with additional predisposing factors such as soil properties and mistletoe infection. Thus, biotic as well as abiotic factors seemed to induce the first decline-symptoms of defoliation, but local drought conditions and stand structure were probably the factors that determined the mortality pattern.

Previous drought events surely initiated a lengthy chain of memory effects on trees (Bréda and Badeau 2008) that led to defoliation and mortality at the drier and lower altitudes within the studied valley during the severe 2005 drought. During drought episodes, leaf-shedding could initially occur as an avoidance mechanism to maintain a favorable water balance by reducing transpiring needle area (Bréda and others 2006). Nevertheless, leaf-shedding also signals the early stages of a sequence leading to tree death (Dobbertin 1999; Dobbertin and Brang 2001). In our case, stand-level mortality was positively correlated with defoliation recorded 2 years after the 2005 drought event. This result suggests that the remaining trees did not take advantage of a release

Table 5. Generalized Linear Model for Recruitment at the Plot level

Model terms	0	SE	P-value
Summer water availability index	-4.640	2.325	0.046
Mean DBH	-0.097	0.036	0.007
Aggregation index	0.147	0.087	0.091
Topographic wetness index	-0.426	0.143	0.003
Soil depth	-0.021	0.009	0.023
Total canopy defoliation	0.049	0.009	<0.001

A stepwise model selection criterion was used. Only the final model is shown. N = 30 plots; $AIC_{recruitment} = 165.82$.

of competition for resources, probably because some sort of long-term drought effect occurred on the surviving trees (Bréda and Badeau 2008) and/or the inherently drier conditions impaired the recovery of trees in those plots.

Water availability per unit of basal area is likely to be lower in plots with higher basal area (compare Callaway and Walker 1997; Briones and others 1998). The relatively high tree density in the studied valley is likely the result of management abandonment during the last decades, as has been observed in other areas (Barbéro and others 1998; Poyatos and others 2003; Linares and others 2009), and particularly of the reduction of logging practices in our Scots pine forests since the 1980s (Catalan Forest Service, pers. com. by Carles Fañanàs). The effect of increased aridity due to climate change occurs therefore on top of an ongoing process of “natural” self-thinning triggered by changes in forest management. Nevertheless, the absence of a significant interaction between the effects of drought stress and stand density for either defoliation or mortality suggests that competition and plot-level water availability have exerted additive effects on the studied Scots pine forest.

Soil properties, particularly soil texture and depth, were also associated with defoliation rates. Our results demonstrated that the least affected plots are distributed on deeper soils with more abundant clay. Clayey soils retain more water at a given water potential and cause a more gradual decrease in wetness as soil water content declines (Sperry and others 1998). Other studies have associated fine-textured soils with milder effects of drought on plants (Hacke and others 2000; Sperry and Hacke 2002; Hultine and others 2005). The topographic wetness index did not improve the models explaining defoliation or mortality, possibly due to the relatively narrow range of topographic conditions occupied by Scots pine in the studied valley, which are constrained to steep slopes that remained unused by traditional agriculture (García-Ruiz and others 1996; Poyatos and others 2003).

Our results showed that defoliation was associated with mistletoe occurrence, with defoliation progressively increasing on more heavily infested trees. This is consistent with previous studies (Dobbertin and Rigling 2006), and with the fact that during a drought episode, when the tree reduces its transpiration rates by stomatal closure, the mistletoe continues to transpire increasing the water stress experienced by host trees (Fischer 1983; Press and others 1988; Strong and Bannister 2002). Although we cannot rule out the possibility that

defoliated trees are more prone to new mistletoe infections, the old age of most mistletoe individuals clearly suggests that infection occurred before 2005 in most cases, and likely acted as a predisposing factor during the 2005 drought episode. High occurrence of mistletoe tended to appear on larger trees, probably because these trees contain large branches that provide perching and feeding sites for birds dispersing mistletoe seeds (Aukema and Martínez del Río 2002). However, under the same mistletoe occurrence conditions, defoliation was observed preferentially on small trees, probably due to their lower rooting depth, and the corresponding disadvantage for belowground water competition (Pugnaire and others 2000). Other studies have also documented major effects of drought on small trees (Martínez-Vilalta and Piñol 2002; Lloret and others 2004; Smith and others 2005; Bravo-Oviedo and others 2005; Chen and others 2008).

Community Dynamics

Mortality of overstory trees has the capacity to alter the structure of the forest, including the regeneration environment. Light intensity and soil moisture conditions are key regulators of regeneration success (Pigott and Pigott 1993; Sack and Grubb 2002; Castro and others 2004). In closed-canopy forests, gaps created when trees die promote high light intensity and a more xeric environment in the already drier stands (Suarez and Kitzberger 2008). In this study, the recruitment of Scots pine was very low in almost all plots, including those with high defoliation. This low recruitment contrasts with the high regeneration of pines in general and Scots pine in particular observed under open canopies (Keeley and Zedler 1998; Castro and others 2004). Despite the shade-intolerant nature of Scots pine (Ceballos and Ruiz de la Torre 1971), seedlings require moderate shade to ensure certain soil moisture and air humidity (Schultz and Gatherum 1971; Karlsson and Nordell 1987; Broadmeadow and Jackson 2000; Castro and others 2004).

Recent drought episodes may also have impaired directly the reproductive success of Scots pine in the study area. Some studies have reported lower cone production under drought (compare Zlotin and Parmenter 2008, for *Pinus edulis*; Mutke and others 2005, for *Pinus pinea*) and under other stressful conditions that also entail defoliation (Hódar and others 2003). Mistletoe infection has been also related to lower cone production and seed quantity and quality in pines (Schaffer and others 1983; Singh and Carew 1989; Mathiasen

and others 2008). Loss of seed quality is likely to eventually limit the performance of Scots pine seedlings (Reich and others 1994; Castro 1999).

Quercus humilis and *Quercus ilex* were the trees with higher recruitment in the studied area. Interestingly, we found that the density of *Quercus* seedlings was higher in patches with increasing canopy defoliation, in agreement with the fact that seedlings of *Quercus* species are known to have a competitive advantage over Scots pine under drought stress conditions (Marañón and others 2004). Unfortunately, we could not demonstrate that the 2005 drought increased the emergence of new *Quercus* seedlings, because we do not know their age distribution in the study plots, and some seedlings may have been there before the drought event. Regardless of when the seedlings emerged, their current density was apparently increased by canopy defoliation, initiating the process of an eventual replacement of Scots pine. In the mid-term, this trend could result in a vegetation shift in the study area, from pine-dominated to broadleaf-dominated forests.

Few studies have addressed the changes in recruitment patterns related to drought-induced mortality of the overstory vegetation. Van Mantgem and Stephenson (2007) analyzed mid-term changes in demographic rates of species growing in forests from southern USA. They found increased mortality rates in *Pinus* and *Abies* but no change in recruitment. We observed a differential pattern of seedling establishment favoring species that are not dominant under the current conditions. In general, the abundance of *Quercus* adult trees was very low in the studied area, and although they were mainly concentrated at low altitudes, the recruitment of *Quercus* species was also high at intermediate altitudes. Therefore, our results suggest that an altitudinal upwards migration of hardwood forests may take place in the studied area, as reported in other mountains of the region (Peñuelas and Boada 2003); noticeably, in our case this migration would be mediated by the drought-induced dieback of the dominant canopy species.

CONCLUSIONS

In conclusion, our study documents an episode of multifactor forest decline at the level of a single valley. At that scale, defoliation and mortality were mostly associated with the local water availability at each plot and to stand structure. The high mortality rates found in this study, together with the differential recruitment favoring species that are not dominant under the current conditions, have

the capacity to transform the stand structure, composition, and dynamics of the studied forests in the mid term. This trend observed at the local scale supports biogeographical approaches revealing that many rear-edge populations of Scots pine sheltered in the mountain environments of the Iberian Peninsula could be at risk under future climate scenarios. At the same time, the relevance of stand structure in the observed pattern has important implications for forest management, as thinning treatments and sustainable harvest activities could potentially be used to mitigate the effects of climate change on high-density stands (Millar and others 2007).

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