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Response of Pinus uncinata Recruitment to Climate Warming and Changes in Grazing Pressure in an Isolated Population of the Iberian System (NE Spain)

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Abstract

To infer future changes in the distribution of tree species in response to climatic variability, we need an understanding of the recruitment dynamics and their climatic controls at the species' distribution limit. We studied the recruitment processes in an isolated population of Pinus uncinata Ram. located at the southwestern limit of the species' distribution in Europe (Iberian System, NE Spain). We assessed (1) the temporal patterns of pine recruitment, and (2) how climate influenced recruitment. To reconstruct the recent recruitment episodes and to assess the climatic influence on recruitment and radial growth we employed dendrochronological methods. We mapped, measured the size, and estimated the age of all P. uncinata individuals located within a 50 m × 40 m plot. Additional age data were obtained from individuals located in four nearby 20 m × 20 m plots. The main episodes of tree establishment (early 1960s, late 1980s) coincided with low radial growth during a period with reduced grazing pressure. Grazing pressure and tree recruitment were not related at the spatiotemporal scale of this study. High May, August, and September minimum temperatures and high April precipitation were positively associated with recruitment, whereas high maximum April and June temperatures were negatively associated with recruitment. The studied population was in equilibrium with climate until the late 1990s, one of the warmest decades in the 20th century, when recruitment decreased despite the availability of suitable sites for establishment and the presence of reproductive individuals. We suggest that late-summer temperatures might have a non-linear negative threshold effect on recruitment rather than a linear effect. Despite increasing evidence of climate-induced recruitment episodes in isolated cold mountain forests, threshold effects of temperature on recruitment may imply limited range shifts of these populations in response to climate warming.
might be affected by their isolation history and genetic differentiation. In addition, the greater sensitivity of stands at the species’ range limit may be a result of the fact that climate is expected to be among the main constraints on tree recruitment in these populations. Recruitment is among the most critical determinants of the rate of forest shift to climatic change. Tree recruitment has been shown to be more sensitive to climate than adult mortality in harsh environments, where competition is low, because recruitment has lower climatic thresholds than adult mortality (Lloyd, 1997). However, the temporal dynamics of recruitment have not been carefully investigated in most tree species, and specifically in isolated stands (Veblen, 1992). In addition, tree recruitment in harsh environments might be also modulated by positive feedbacks at small spatial scales (Camarero et al., 2000; Smith et al., 2003; Bekker, 2005).

In most European ranges instrumental records have shown a sharp temperature rise since the 1940s (Diaz and Bradley, 1997), especially in SW Europe, where several Pinus species have been present in the Iberian Peninsula at least since the early Holocene (Peñalba, 1994). Hence, current climate change might affect the recruitment ability of these mountain pine stands in SW Europe. Currently, an isolated population of Pinus uncinata Ram. forms the SW distribution limit of the species, and it is located in the northern Iberian System, NE Spain (Fig. 1). The distribution area of P. uncinata encompasses the E Alps, the Pyrenees, and the Iberian System (Fig. 2). In Spain, subalpine forests in the Pyrenees form its main distribution area. The studied population currently occupies 115 ha, and it is located 150 km from the nearest P. uncinata forests in the Pyrenees. This forest is formed by sparse old P. uncinata individuals intermingled with Pinus sylvestris L. However, recent P. uncinata colonization of non-forested areas has been observed (Fig. 1). Ceballos (1968) noted a natural expansion of P. uncinata in the study area during the 1930s, which was confirmed by aerial photographs (years 1946, 1957, 1984, 1990) of the study area showing an increase of tree cover.

P. uncinata is a shade-intolerant species that colonizes all kinds of soils (Ceballos and Ruiz de la Torre, 1979). Its small-winged seeds are primarily dispersed by wind in late winter, and seedling emergence occurs in April–May. Two features make this species a good invader: (1) a short pre-reproductive period, and (2) frequent large crops every 2–4 years. The age of the oldest individuals is ca. 850 years in the Pyrenees and ca. 500 years in the study area. In this paper, we aimed at describing the temporal dynamics of an isolated population of P. uncinata at its southwestern distribution limit in the Iberian Peninsula. Specifically, we assessed: (1) the temporal patterns of recent recruitment, and (2) how climate influenced recruitment.

Study Area

The stand studied (42°01’N, 02°44’W, 2040 m a.s.l.) is located on moraine sediments. The moraine deposits are mostly vegetated and located near lakes of glacial origin. The substratum consists of Lower Cretaceous sandstones and quartzitic conglomerates. The study site was selected because it was a recently colonized area according to the maximum age of pine recruits where no signs of recent disturbances (fire, grazing, logging) were observed. The effect of topographical factors on tree recruitment through their influence on the abiotic environment may be regarded as minimal because the study area was relatively flat (mean slope 5°). The climate is continental (meteorological data were supplied from the Vinuesa station situated 12 km from the study site, 41°55’N, 02°46’W, 1107 m a.s.l., temperature data, 1961–1983, and precipitation data, 1961–1986). The annual precipitation is 1400 mm with July–August minima (Ortega Villazán, 1992). The annual mean temperature is 2 °C, with the highest and lowest mean temperatures in July (12 °C) and January (0 °C), respectively. In December 1998, mean snow depth (±SD) in the study site was 11.3 ± 8.1 cm. Dominant winds are from W, N, and NW. The soils are acidic and shallow. Most forests in the
area are dominated by *P. sylvestris* and *Calluna vulgaris* (L.) Hull in the understory.

Palynological studies in the Northwest Iberian System have shown an increase in pine cover during the 20th century due to a decrease in grazing pressure and to climate warming (Gil García et al., 1996). However, the relevance at small spatiotemporal scales of these factors in the recent expansion of pines in this area has not yet been quantified. Historical data show that the current livestock number in the study area is ca.15% of that recorded in the 18th century (Catastro del Marqués de Ensenada, 1752).

**Methods**

**SAMPLING PROCEDURES**

We mapped and measured the size (diameter at 1.3 m, dbh; height, *h*), of all individuals located within a 50 m × 40 m rectangular plot (Fig. 2). The plot was subjectively placed at the margin of the expanding *P. uncinata* population where intense recruitment has taken place during the past 50 years. The x and y plot axes were arranged along NW–SE and SW–NE directions, respectively. We also estimated the age of all *P. uncinata* individuals located within the plot. Additional age data were estimated for individuals located in four 20 m × 20 m plots located at 5 m from the corners of the 50 m × 40 m plot. No stumps were found within the plots. All browsing traces were recorded on a categorical scale (presence/absence). *P. uncinata* individuals were classified as mature (dbh > 17.5 cm), poles (7.5 < dbh < 17.5 cm), saplings (dbh < 7.5 cm, *h* > 0.5 m), seedlings (*h* < 0.5 m), dead trees, or krummholz. To sample and find small seedlings (*h* < 0.2 m), the plots were subdivided into 1-m² quadrats. We also recorded if each stem was bearing or had produced cones, and related age (5-yr classes), and the frequency of trees per age class with cones. In December 1998, the maximum snow thickness was noted in every point within the 50 m × 40 m plot using a 1 m × 1 m grid (*n* = 2000 sample points). A contour map of snow thickness in December 1998 was built using kriging.

**RELATIONSHIPS BETWEEN RECRUITMENT, RADIAL GROWTH, AND CLIMATE**

To reconstruct recent recruitment dynamics and quantify the climatic influence on recruitment and radial growth, we employed dendrochronological procedures. We built a chronology using the
oldest trees within the plots (ca. 50 yrs old), and mature trees from
the same population located 200 m apart. Two cores per tree were
taken from perpendicular directions at 1.3 m. They were prepared
and cross-dated following standard dendrochronological pro-
dures (Fritts, 1976). Tree-ring widths were measured to the nearest
0.01 mm. Cross-dating and measurement quality were validated
using COFECHA (Holmes, 1983). All ring-width series were
filtered with a cubic smoothing spline function with 32-yr stiffness
and a 50% frequency cutoff. Sample size was constant throughout
the second half of the 20th century (n = 20 mature trees, 65% of
them were located inside the plots). Autoregressive modeling was
then performed on detrended series, which mostly showed
autocorrelation of order 1. The final residual chronology was
obtained using ARSTAN (Cook, 1985).
To estimate the age of seedlings we tagged them and counted
their annual internodes to allow their future monitoring. The age
of the remaining trees was estimated taking cores at 1.3 m with
pith and cross-dating them. Their final ages were estimated as the
sum of the number of cross-dated rings from 1.3-m cores plus the
number of internodes up to the base. To calibrate the estimated
age based on the number of annual whorls, we cut basal sections
from the root collar of saplings and poles growing outside the
plots (n = 20). The sections were sanded and the tree-rings were
counted. Both age estimates were positively correlated (R^2 = 0.22,
P = 0.03) with a mean 4 yrs underestimate for the internode
counts. Kullman (1983) reported a similar underestimate (–5 yrs)
for P. sylvestris recruits. Following Lloyd (1997), the temporal
resolution on the estimates of the germination dates was checked
calculating the 95% confidence interval (±1.3 yrs) of the age-basal
diameter power regression (age = 11.8 diameter0.3, R^2 = 0.82, P <
0.0001, n = 434). We used 5-yr time classes as the finest resolution
to take into account uncertainties in age estimates. The age
distribution of trees located inside the 50 m × 40 m plot did not
differ significantly from that of trees placed in the four 20 m ×
20 m plots (P > 0.05, Kolmogorov-Smirnov test). Therefore, both
data sets were combined in a single age distribution.
Any inference based on age structures must be done with
care because they are produced by changes in recruitment and
mortality (Veblen, 1992). We used recruitment residuals instead of
raw age data to account for temporal patterns of sapling
mortality, and because the relationships between climate and
residuals were stronger than those based on raw data. Recruitment
residuals were obtained using an exponential function for the
period 1950–1999, excluding the oldest trees to remove the effect
of outliers (age = 1.8 10^{-7} exp(0.08 time), R^2 = 0.18, P = 0.0025).
Residuals were converted into 5-yr time classes. The exponential
model explained the variance better than a power function (R^2 =
0.17). The exponential model assumes constant recruitment and
mortality. Other studies have used a similar approach to account
for recruitment underestimates due to the disappearance of dead
seedlings not detected in later censuses (Hett and Loucks, 1976;
Bergeron and Gagnon, 1987; Sziecz and MacDonald, 1995).

To describe the climate-recruitment relationships we used
monthly climatic data (maximum and minimum temperatures,
total precipitation) from “Embalse de Cuerda del Pozo” station,
located 16 km from the study site (41°53’N, 02°42’W, 1150 m
a.s.l., 1963–1996 data), because of its long and complete series
(missing data: temperature: 2.2%; precipitation: 0.2%). Climate
data and missing values were estimated for the 1950–1997 period
using data from “Soria” station, located 36 km from the study site
(41°46’N, 02°29’W, 1080 m a.s.l.), because data from both
stations were highly related (R^2 = 0.32–0.86, P < 0.05). They
were transformed into 5-yr classes using means for temperature or
totals for precipitation. The relationships between grazing,
monthly climatic variables, and recruitment were quantified with
the Spearman rank correlation coefficient (r_s) for 5-yr classes.
Finally, to compare P. uncinata recruitment and grazing pressure
we used a 5-yr grazing series for the 20th century. The grazing
series was built summing for 5-yr classes the number of grazing
cattle (including sheep and goats) recorded in the historical
archives from Villoslada de Cameros, a nearby village located
12 km from the study site. This rural community has experienced
the same decrease in livestock number during the 20th century as
most similar areas in the Iberian System (Lasanta Martinez et al.,
1996).

Results and Discussion

STRUCTURE AND RECRUITMENT

Both bimodal dbh and height (h) distributions were observed,
with maximum frequencies for dbh < 1 cm and h < 1 m, and
minor peaks for dbh = 15–20 cm and h = 4–5 m. The distributions
of dbh and h suggested the existence of two cohorts, corresponding
to seedlings and poles and mature individuals. Seedlings domi-
nated the recently colonized area at the spatiotemporal scale of
this study because they were 83% (n = 362) of all living individuals
(n = 436). Such abundance of recruits is a typical feature of a stand
initiation stage (Oliver and Larson, 1990). We also found 34
saplings, 14 krummholz individuals, 13 poles, and 13 mature trees.
However, we located only 3 stems of mature dead individuals,
which were well preserved and did not show signs of logging or fire
scars. The age of the dead trees corresponded to the time of stand
initiation, i.e. the early 1950s. Browsing signals were rare and
restricted to saplings. No pine younger than 15 yrs bore cones,
whereas at least 50% of pines older than 25 yrs did produce cones.
Comparatively, 50% of pines older than 55 yrs produced cones in
alpine treelines (Camarero, 1999).

GRAZING IMPACTS ON PINE RECRUITMENT

The oldest individuals in the study site were established in
the early 1950s, when grazing pressure was still high (Fig. 3).
However, we cored trees at least 350 yrs old in the nearby stands
which form a continuous forest located 100–500 m from the
isolated population. Thus, P. uncinata has colonized a new area
where it had not been established during the first half of the 20th
century. Our findings concur that the first P. uncinata expansion
in the study area was during the 1930s, which was related to a
decrease in grazing pressure (Ceballos, 1968). If P. uncinata
individuals take 15–20 yrs to become reproductive in the study
site, the trees recruited in the study site during the 1950s might
come from seeds produced by trees established in the 1930s
expansion. Since 1950, no significant relationship was found
between recruitment and grazing (r_s = –0.46, P = 0.15), despite
the oldest pines being within the plots recruited when grazing
started a declining trend. The recruitment–grazing negative
relationship became stronger, but still not significant, when
comparing grazing data of the previous 5-yr period with recruits
number of the following period (r_s = –0.56, P = 0.09). Grazing
and climate were uncorrelated at the spatiotemporal scale of this
study. In summary, the absence of browsing signals in most pine
recruits and the lack of significant relationships between grazing
and recruitment or climate strengthens the case that recent
recruitment may be mainly controlled by climate. Grazing was
not impacting tree recruitment at the small spatial scale of the
study during past decades. However, the regional reduction in
grazing pressure during the late 20th century probably facilitated

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the current reforestation in formerly grazed mountain areas. The relevance of land-use changes as a stronger driver on forest increase at regional scales compared to climate warming has been illustrated for treeline ecotones in the Scandes Mountains (Hofgaard, 1997). Therefore, future studies should encompass several spatiotemporal scales to assess the relative importance of changes in grazing pressure and climate on forest expansion.

**CLIMATE INFLUENCES ON PINE RECRUITMENT**

The decrease in grazing pressure coincided with the start of the pine colonization during the 20th century, which suggests that climate became the main factor controlling forest expansion in the study area once grazing pressure dropped below a certain threshold (Motta and Nola, 2001). The recruitment increase in the late 1950s and early 1960s observed in the study site was also detected in Pyrenean alpine treeline ecotones dominated by *P. uncinata* in response to increasing May temperatures but before any major decrease in grazing pressure (Camarero and Gutiérrez, 1999, 2004). Therefore, climate seems to be the main driving factor of forest expansion in this isolated stand and in high-elevation alpine treelines under moderate to low grazing pressures. Similar results have been observed in boreal and subalpine forests in northern Europe (Kullman, 1983; Zackrisson et al., 1995; Stöcklin and Körner, 1999; Shiyatov, 2003). Furthermore, the recruitment drop in the early 1970s was observed both in the study sites and in the Pyrenees, and coincided with cold summers and falls due to intense cyclonic conditions in NE Spain (Camarero, 1999). Seedlings recruited in the late 1980s dominated the population, but tree recruitment has decreased since this decade. The recruitment pulses in the late 1980s corresponded to low values of radial growth because both variables were not significantly related. Climate conditions that facilitated *P. uncinata* establishment were different from those that enhanced radial growth as has been found in other tree species (Earle, 1993; Daniels and Veblen, 2004).

We have found a strong recruitment response in the studied isolated population, which suggests that its recruitment history has been very sensitive to the past decrease in grazing pressure and the recent climate warming. Further research is needed to determine if...
this response is due to the contrasting structure and dynamics between expanding isolated populations at the limit of the species’ geographical range and forest stands at the core of the range. Historical isolation in “mountain islands” may also produce genetic differentiation (Oline et al., 2000), including a greater sensitivity to climate.

Temperature was the main climatic factor controlling *P. uncinata* recruitment in the study site at decadal scales. High May, August, and September minimum temperatures and high April precipitation were positively associated with recruitment, whereas high maximum April and June temperatures were negatively associated with recruitment (Fig. 3). In continental systems, winter frosts and warm summer temperatures are important mortality factors of pine seedlings (Frey, 1983). Both factors affected *P. uncinata* recruitment, especially high minimum temperatures in spring and late summer which enhanced recruitment. This might be explained by an elongation of the growing season in late summer or because of lower cold-induced damage in spring when seedlings establish. The positive effect of April precipitation may also be related to an enhancement of seedling survival and establishment.

The overwhelming role of minimum temperatures for successful recruitment in this stand might be due to the much colder temperatures registered in the study area as compared with Pyrenean sites located at similar elevation (Ortega Villazán, 1992). Despite the similar climate-recruitment relationships found at the isolated stand and in alpine *P. uncinata* treeline ecotones (Camarero and Gutiérrez, 1999), we did not detect any positive effect of summer rainfall on recruitment in the study site. Therefore, water stress may be a greater constraint on *P. uncinata* recruitment in alpine treelines under Mediterranean influence than in this isolated high-elevation stand under continental influence. Further studies are needed to separate the effects of climate on the two main processes determining tree recruitment, i.e. seed production (e.g., masting) and seedling establishment.

The recruitment of new individuals into openings occurred almost continuously. The expanding pine population has colonized open microsites within or near *C. vulgaris* mats which reduce understory light and may prevent pine recruitment (Camarero et al., 2005). Doche (1984) observed a similar colonization pattern for *P. sylvestris* seedlings. In the eastern Pyrenees, Puig (1982) found the following factors favoring *P. uncinata* regeneration: low herbaceous cover, and reduced grazing pressure. Thus, recruitment may have responded to climate variability in the study site because the understory was relatively “invasive.” Prévosto et al. (2003) reached a similar conclusion studying *P. sylvestris* invasion of grasslands. Zackrisson et al. (1995) also emphasized that an adequate regeneration niche (Grubb, 1977) was necessary for successful recruitment of *P. sylvestris* in boreal forests. They suggested that the interference of the understory on *P. sylvestris* recruitment might explain the temporal lags (20–30 yrs) that they found between warm periods and recruitment peaks. We did not find long climate-recruitment lags for *P. uncinata* which indicates that the interference of the forest floor vegetation on recruitment was much stronger for *P. sylvestris* in boreal forests than for *P. uncinata* in the studied mountain stand (Camarero et al., 2005). In addition, these two pine species might show different responses of seed production and germination to climate. Other indirect interactions between *P. uncinata* seedlings and *C. vulgaris* might have affected the observed recruitment patterns. For instance, Scots pine recruits suffered fewer snow blight attacks thus showing lower mortality inside *C. vulgaris* patches than on lichens (Burdon et al., 1994). Finally, trees may facilitate leeward seedling establishment by depositing wind-blown snow thus allowing forest encroachment as has been observed in similar harsh environments such as alpine treelines (Smith et al., 2003; Bekker, 2005). In the study site, snow-accumulation patterns were not related to seedling density, but more data are needed to account for the year-to-year variability in snow depth and its relationship with forest structure.

We noted reduced rates of recruitment in the late 1990s despite the availability of suitable sites for establishment, and the presence of reproductive individuals. Therefore, the studied population was in equilibrium until the 1990s, one of the warmest periods during the past century, when warming may have exerted a negative non-linear effect on recruitment if a threshold in the temperature-recruitment relationship was surpassed. In species with long life spans such as *P. uncinata*, it is critical to preserve reproductive adults in order to “store” recruitment potential (Warner and Chesson, 1985). Such a storage effect allows a high population growth during favorable climatic periods in sites with low adult population density (Dovciak et al., 2005). *Pinus uncinata* is restricted to mountains in SW Europe, and it reaches its southernmost limit of distribution in the Iberian System, NE Spain. Managers should try to “store” the recruitment potential of these stands, protecting reproductive individuals and providing suitable sites for regeneration.

**Conclusions**

Grazing pressure and tree recruitment were not related at the spatiotemporal scale of this study, and the oldest individuals in the study site established under moderate to high grazing pressure in a nearby village. Thus, the decrease in grazing pressure since the mid-1900s did not explain the recent regeneration pulses. Nevertheless, the decline in grazing pressure coincided with the start of the pine colonization during the past 20th century, which suggests that climate became the main triggering force of the recent tree colonization once grazing pressure dropped below a certain threshold. Climate was then the main driving force of the recent pine expansion at small spatial scales, but this process may have been facilitated by the reduction in the number of grazing cattle. The presence of a relatively “invasive” understory and the grazing decline may be prerequisites for further expansion of pine populations.

Our findings emphasize the need for care in making predictions implying an increase of tree recruitment in cold mountain areas in response to climate warming. Non-linear relationships between climate and recruitment and interactions of tree seedlings with the understory species might explain why *P. uncinata* and other tree species restricted to cold mountain areas show moderate range shifts in response to climate warming. Both aspects merit additional investigation if we aim to forecast future range shifts of tree species. Threshold responses of recent pine recruitment to current climate warming in isolated high-elevation populations should not be discarded despite the remaining uncertainties of climate vs. grazing as past triggers.

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