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Regional tree line dynamics in response to global change in the Pyrenees

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Summary

1. Many studies in northern Europe, North and South America, describe regional trends of population densification at altitudinal and polar tree lines during the 20th century. The purpose of this study was (1) to ascertain if this regeneration enhancement is present across the alpine ecotones of the Pyrenees, (2) if synchronous recruitment trends are common among the studied populations and (3) to determine the tree limit stability during recent decades.

2. Twelve *Pinus uncinata* tree line populations were studied on the Iberian eastern range of the Pyrenees. Rectangular plots ranging from 940 to 7600 m^2 were set along the forest-alpine grassland transition; more than 3600 *P. uncinata* individuals were mapped. Tree size and age were used to establish the demographic structure at each stand, and to characterize abrupt or smooth transition patterns along the tree line ecotone. A new procedure for estimating missing rings in off-centre cores was developed to ensure a correct interval for the age-classes distribution analysis.

3. Past and recent synchronous recruitment trends (mid 19th century, second half of the 20th century) were apparent at the tree line over the studied area of the Pyrenean range. The ecotone densification since the 1950s occurred in the context of climatic warming and substantial land use abandonment. Both gradual and step-like transition patterns in tree age and size along the ecotone were observed.

4. Regeneration enhancement in the last approximately 30 years appears as an abrupt change in population age structures, which could indicate the importance of feedback mechanisms for tree line recruitment dynamics. In 50% of the surveyed tree lines ecotone densification has been coupled to tree limit shifts in the recent past. This indicates both great tree limit sensitivity to short-term climatic changes and the presence of differential tree line dynamics at a regional scale.

5. *Synthesis.* The observed past and recent synchronous recruitment trends suggest the presence of regional climatic factors modulating tree line structure and dynamics. However, tree line dynamics in the Pyrenees have been widely affected by local anthropogenic activities. We suggest that the presence of step-like tree line transitions in tree age can be considered an evidence of recent human-induced disturbances when no other major natural disturbances affect the tree line dynamics.

Key-words: demographic structure, dendroecology, global change, *Pinus uncinata*, Pyrenees, recruitment, step-like transition, tree line

Introduction

Although the ecotones at alpine (altitudinal) and arctic (latitudinal) tree lines are likely to be sensitive to climate warming (Hansen & di Castri 1992; Kullman 1999; Payette *et al*. 2001), the degree to which tree line response may lag behind climate change and the extent to which sensitivity to the climate may vary among sites remains largely unknown (Lloyd & Fastie 2003). The greater sensitivity of populations at the species' range limit (as is the case at alpine or arctic ecotones) reflects the fact that the climate is expected to be among the main constraints on tree recruitment in these populations (Camarero & Gutiérrez 2007). However, climate change is only one aspect of environmental change that may affect the location of tree lines (Holtmeier & Broll 2005). As in Eurasian mountainous regions, where traditional human use near the tree line is common (Körner 1999), forest-grassland ecotones often appear to be affected by changes in natural or anthropogenic disturbance regimes (League & Veblen 2006). Thus, past and present land use (Hofgaard 1997, 1999; Stöcklin & Körner 1999) and nonlinear responses to climatic change (Arseneault & Payette 1997; Lloyd 2005) are all possible

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factors confounding the effect of climate on tree line populations (Kullman 2000). The complexity of several interacting factors, whose individual degree of impact on tree line dynamics depends on particular local conditions, may explain the great regional and temporal variability in the importance of the various parameters that drive tree lines (Walther *et al.* 2005).

In this paper the term tree line ecotone (or merely tree line) is used in a general sense, and refers to the transition from the uppermost closed forests, or timberline, to the treeless alpine vegetation (Körner 1998, 1999), i.e. the forest-alpine grassland ecotone. Hence, the altitudinal limit of upright tree growth, the tree limit, is included in this transition. Although most would agree with this general definition, many terms and conventions are used to define timberline and tree limit boundaries (Holtmeier 2003). In this study, the timberline position is defined by a coverage threshold of 30–40% (Holtmeier 2003) given by arboreal (at least 5 m height) pines (Smith *et al.* 2003). The tree limit is defined, based on the mean snow cover depth of the study region (Holtmeier 2003), as the uppermost upright tree with a minimum height of 2 m (Kullman 2001, 2003).

Many studies show that the impact of recent warming in forest-grassland ecotones has been on the consolidation of pre-existing tree populations rather than on the position of the tree line (Payette & Filion 1985; Scott *et al.* 1987; Payette & Lavoie 1994; Szeicz & MacDonald 1995; Kullman 1997; MacDonald *et al.* 1998; Stöcklin & Körner 1999; Payette *et al.* 2001; Juntunen *et al.* 2002; Camarero & Gutiérrez 2004; Kullman 2005; Danby & Hik 2007). Such tree line population response has occurred in the context of warmer conditions in arctic and sub-arctic regions since the beginning of the 20th century (Payette & Lavoie 1994) and, since the 1970s, in most European ranges (Diaz & Bradley 1997).

The future position of tree lines is of concern due to the possible loss of alpine species due to upward encroachment of sub-alpine forests (Luckman & Kavanagh 2000). The Pyrenees Mountains may be a paradigmatic example in this sense since they encompass the southernmost distribution range of many European alpine species, including endemic and endangered species (Bolòs & Vigo 1984; Ozenda 1985; Carreras *et al.* 1996a). However, temporal dynamics of tree recruitment at alpine tree line have not been extensively investigated in the Pyrenees. More demographic studies at a regional scale are required to ascertain how current tree line dynamics can affect the alpine flora. Thus, we decided to conduct a dendroecological study to find out if any regional pattern is detectable in the size and age structures of mountain pine populations in the Spanish Pyrenees and Andorra. The major problem for the analysis of tree population age structures is the difficulty of accurately determining the ages of all the trees in a stand (Norton *et al.* 1987; Villalba & Veblen 1997a). When describing age frequency distributions the error in establishment dates can significantly change the shape of age-class distributions if the resolution of analysis is too fine in comparison with the extent of the dating error (Wong & Lertzman 2001). Thus we developed a new procedure to date off-centre cores, which permits us to quantify the error in age determination.

We focused on changes in tree recruitment at several alpine tree line ecotones in the Spanish Pyrenees to assess the tree line dynamics at a regional spatial scale. We developed static age structures of living *Pinus uncinata* individuals to: (1) ascertain if densification processes occurred during the 20th century, (2) detect if synchronous recruitment trends are common among the tree lines studied and (3) assess the stability of tree limit position during recent decades. Limitations of static age distributions are well acknowledged (Johnson *et al.* 1994). Hence, our interpretation of the results simply tests whether, in the global change context, general recruitment trends exist over the alpine ecotones in the Pyrenees and does not make detailed inferences on population dynamics. Due to the lack of data on local changes in land use, the transition pattern in tree ages and sizes (total height and basal diameter) was analysed to ascertain which may be the most plausible driving factor (climate or land use changes) of recent tree line dynamics.

Materials and methods

STUDY AREA

We conducted this study on the eastern half of the Spanish Pyrenees (Catalan Pyrenees) and Andorra (Fig. 1). We combined field visits with aerial photograph interpretation to place 12 rectangular plots at the upper tree line (or alpine ecotone) including the transition from sub-alpine forests to the alpine grasslands (Fig. 1, Table 1). Each plot was placed with its longest side parallel to the altitudinal gradient to include the current timberline and tree limit. We sampled 10 small plots (980–1650 m^2; 10 m width × variable length) and two large plots (6000 m^2 and 7600 m^2; 40 m width × variable length) for inter- and intra-site comparisons of tree line structure. Plot length varied, depending on each site's characteristics, to include the entire forest-grassland transition. This study was mainly restricted to the north-facing tree line ecotones, and the sites selected for sampling covered a wide range of slope steepness, bedrock and plant communities. Past disturbance regimes of the studied ecotones were mainly human induced, and the studied stands were located on homogeneous slopes, away from avalanche paths and major rocky outcrops. Furthermore, in contrast to the northern regions of America, wild fires in the Pyrenees occur rarely and do not affect large areas. Hence, the fires that could have affected the tree line ecotones studied were likely to have been started by humans to increase grasslands for pastoral use. Since none of the sampled trees inside the plots presented fire related scars, we interpret the lack of recent fires as an evidence of declined anthropogenic perturbations at the tree line ecotones studied. Field sampling was conducted between 2003 and 2006 in late spring and summer.

The studied ecotones are dominated by *Pinus uncinata* Ramond ex DC, which reaches its southern and western distribution limit in the Iberian Peninsula. In the Spanish Pyrenees, this species forms most of the alpine tree line ecotones, on any substrate and at any exposure (Ninot *et al.* 2007), and potential tree line elevation has been fixed at approximately 2200–2450 m a.s.l. (Carreras *et al.* 1996b; Bolòs *et al.* 2005). *P. uncinata* is a long-lived, slow-growing and shade-intolerant conifer that shows a large ecological amplitude, since it is a low-demanding species regarding the supply of nutrients

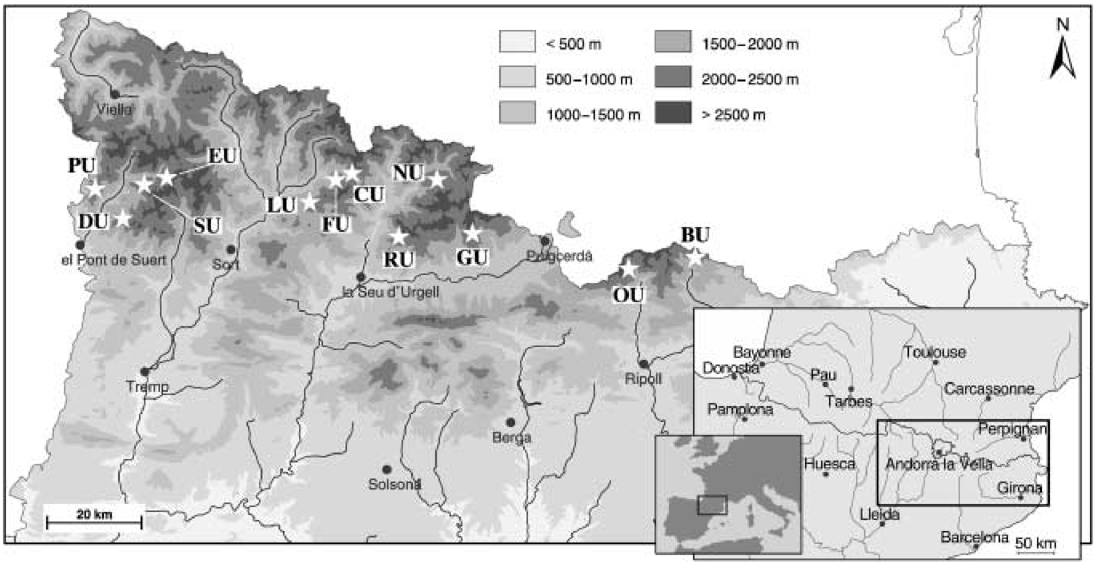

Fig. 1. Map showing the location of study sites in the Catalan Pyrenees (Spain) and Andorra. (see Table 1 for codes).

Table 1. Characteristics of the stands of *Pinus uncinata* sampled at the alpine tree line in the Catalan Pyrenees (Spain) and Andorra

Site	Code	Latitude	Longitude	Plot size (m^2)	Altitude (m a.s.l.)*	Slope (°)	Aspect	Bedrock
Portell	PU	42°31′	0°45′	6000	2199–2268	28	N – 0°	lime
Durro	DU	42°28′	0°49′	1200	2010–2069	30	N – 15°	lime
Serrat del Contador	SU	42°32′	0°53′	1500	2270–2338	27	NW – 320°	lime
Delluí	EU	42°33′	0°56′	940	2299–2339	24	W – 285°	granodiorite
Lo covil	LU	42°31′	1°21′	1180	2363–2405	21	N – 0°	slate
Serrat de Capifonts	FU	42°33′	1°23′	7600	2352–2435	24	NW – 330°	slate
Port de l'Ovella	CU	42°33′	1°25′	1160	2250–2297	26	NW – 295°	lime
La Rabassa	RU	42°26′	1°32′	1650	2236–2271	24	W – 270°	slate
Obac de Canillo	NU	42°34′	1°37′	980	2266–2314	29	N – 10°	lime
Meranges	GU	42°27′	1°44′	1500	2312–2365	16	NE – 65°	slate
Ras de l'Ortigar	OU	42°23′	2°08′	1500	2241–2308	27	N – 20°	slate
Serra de la Balmeta	BU	42°24′	2°19′	1500	2184–2241	22	N – 245°	slate

*Metres above sea level.

and water (Blanco *et al.* 2001). This pine has small (2–6 cm long), asymmetric hanging cones, which mature 2 years after formation, with small-winged seeds dispersed in spring. The radial growth of *P. uncinata* starts in May with cambial re-activation, and the major part of the tree ring develops between June and July (Camarero *et al.* 1998). Latewood development, including formation, later coloration and cell wall apposition, occurs in July–October. In accordance with the traditional tree line paradigm, radial tree growth in high elevation *P. uncinata* forests in the Pyrenees is positively influenced by warm temperatures during the growing period and by high autumn temperatures (Tardif *et al.* 2003).

SAMPLING AND DENDROCHRONOLOGICAL PROCEDURES

Each *P. uncinata* tree inside the plots was tagged and mapped. The position of all dead and living trees was recorded in Cartesian coordinates using 100-m tapes along the shorter (x axis) and longer (y axis) sides of the plot. Point $(x, y) = (0, 0)$ is located in the lower left corner looking upslope. Additional tapes were placed every 5 m to subdivide the plot and measure the coordinates of the centre of each tree to the nearest 0.1 m. We determined the altitude of the lower, middle and upper parts of the plot using a GPS. Basic biometric measurements for each tree were registered (total height, basal and breast height diameters), and the current tree limit position was determined for each site. All individuals big enough (more than 10–12 cm basal diameter) were cored at the base to determine tree age. Each tree was cored repeatedly using an increment borer until a core through the pith (or as near as possible) was obtained. Furthermore, as mineral soil level is not a good indicator of root collar level (Gutsell & Johnson 2002), cores were obtained by excavating a 'coring hole' at the tree base and/or angling the increment borer to approach the root collar as much as possible (Villalba & Veblen 1997a). The mean core extraction height was 0.09 ± 0.04 m. The age determination for the seedling size class (≤ 0.5 m height) and the small sapling class (> 0.5 m height and ≤ 7.5 cm breast height diameter) was done through bud scar counting along the main stem. More than 3600 *P. uncinata* individuals were measured and aged for this study.

Cores were air dried, mounted and sanded following standard procedures (Stokes & Smiley 1968). We used a stereomicroscope to detect light rings, frost-damaged rings and narrow rings of each core

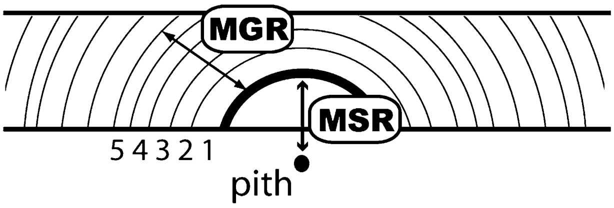

Fig. 2. The bold ring is the one used to calculate the length of the missing radius (MSR) with the pith locator. Left arrow shows the five contiguous rings used to calculate the mean growth rate (MGR) of each off-centre core.

as cross-dating features (Filion *et al.* 1986; Yamaguchi 1991). During the cross-dating process missing rings were rarely encountered, and represented only 0.1% of the analysed rings. Moreover, 60% of the samples that presented absent rings were missing only one. As ageing was the only objective of the cores taken at the base, we tried to get as many cores through the pith as possible (53.3% of extracted cores) to minimise age determination uncertainties. However, trees at the alpine ecotone, growing on steep slopes, commonly present trunk deformities at the base. Hence, off-centre cores were commonly collected.

The only accurate ageing method is by cutting trees at the base and then locating the root collar through consecutive cross-section analysis (Gutsell & Johnson 2002). Obviously, this is a destructive method that was inconvenient in the studied area for many reasons (e.g. some plots are located within protected areas). Cores missing the chronological centre of the tree (or pith) pose a major problem because information about the earliest years of the tree is not known. Different methods have been proposed for calculating missing rings as a function of growth rate of the missing radius of cores (Norton *et al.* 1987; Villalba & Veblen 1997a; Wong & Lertzman 2001; Rozas 2003; Clark & Hallgren 2004). We developed a new procedure to date off-centre cores based on the length of the missing radius and the height of core extraction.

AGE OF OFF-CENTRE INCREMENT CORES

We used a pith locator (concentric circles matched to the curvature of the inner rings) to calculate the missing radius length (MSR) (Norton *et al.* 1987; Fulé *et al.* 1997; Bosch & Gutiérrez 1999). Conversion of MSR into a number of missing rings was done with the mean of the annual growth rate (MGR) of the five outer contiguous rings of the year used as reference to calculate the MSR of each core (Fig. 2).

The accuracy of this method was previously tested with the results of 720 simulated MSRs in cores containing the pith. At each study site 60 simulations were done, 15 simulations at each of the four following MSR categories: 0.25, 0.5, 0.75 and 1 cm. For each category and sampling site, simulations were done with randomly chosen cores of the set of total samples containing the pith. Thus, each core could be used for more than one MSR category. Dating errors of each MSR simulation were calculated as the difference between the true ages of the cores and the ages estimated using the MGR to convert the simulated MSR into a number of missing rings. Mean dating errors in years and standard deviation (SD) for all MSR categories (0.25, 0.5, 0.75 and 1 cm) are presented in Table 2 for each study site. To account for the dating error of each off-centre core depending on its MSR, we used the difference between the mean dating error ± 1 SD at each MSR category.

Table 2. Mean dating error in years (N rings) ± 1standard deviation (SD) of the simulations for different missing radius lengths (MSR) from the pith (0.25 cm, 0.5 cm, 0.75 cm and 1 cm) at each study site

	0.25 cm		0.5 cm		0.75 cm		1 cm	
Site	N rings	SD	N rings	SD	N rings	SD	N rings	SD
PU	3	2.7	6	3.9	6	4.3	9	5.0
DU	3	3.3	4	2.7	5	2.7	8	4.6
SU	3	2.4	5	3.5	8	3.1	9	5.9
EU	3	3.9	6	5.4	6	4.9	9	6.5
LU	3	1.9	5	3.6	8	4.0	8	4.7
FU	3	2.7	4	3.6	7	4.6	9	5.8
CU	3	2.9	6	2.8	7	4.1	8	4.4
RU	4	2.4	6	3.1	7*	4.2*	8*	5.1*
NU	4	1.8	7	3.3	10	6.1	8*	5.1*
GU	5	2.3	7	2.6	9	4.0	10	3.5
BU	2	1.8	5	2.9	6	4.3	8	5.5
OU	3	2.5	5	2.8	7	2.6	7	4.4
Mean dating error	6 years		8 years		8 years		9 years	

*Mean values of the other plots due to unrepresentative sample size.

We restricted the dating process to cores that had a maximum MSR of 1 cm since greater distances were considered too imprecise. Cores that had not reached the centre (mainly due to tree rot) were also rejected. Thus, a small proportion of trees (< 4%) were discarded from the analysis because of rotten piths or excessive ageing uncertainty.

AGE CORRECTIONS FOR CORING HEIGHT

The procedure above gave the age of the tree at coring height. We used annual height growth rate of 270 seedlings and small saplings (individuals < 1.5 m) to account for age-height corrections. We collected these individuals from six representative stands of the 12 study sites. Although it would be preferable to sample each stand because of inter-site differences in initial growth rates (Villalba & Veblen 1997a), we could not do this due to technical problems. Thus, we used initial growth rates of the nearest of the six sampled stands for the age corrections for coring height of the six non-sampled sites. Seedlings and saplings were collected between timberline and tree line zones near the study plots. It was assumed that initial growth rates of the old cored trees of the forests are similar to that of seedlings now located at open areas above timberline (Villalba & Veblen 1997a).

The 270 small pines were removed, along with their roots, and a cross section was cut at the base, containing root and stem tissue. Cross sections were progressively sanded, obtaining thinner disks of 1.5–2 cm. The root collar was detected by noting the shift in the central area, from a vascular cylinder in the root to undifferentiated parenchyma cells in the stem (Telewski 1993; Gutsell & Johnson 2002). Cross sections were dated by ring counting and height growth rate of each individual obtained. Mean height growth rate was then used to estimate the number of missing rings due to coring height.

We used the height growth rate variability among the collected pines at each site to ascertain the dating error due to coring height. Based on the mean height growth rate ± 1 SD, we calculated the age variability in 1-cm height intervals between slow (mean height growth rate – 1 SD) and fast (mean height growth rate + 1 SD)

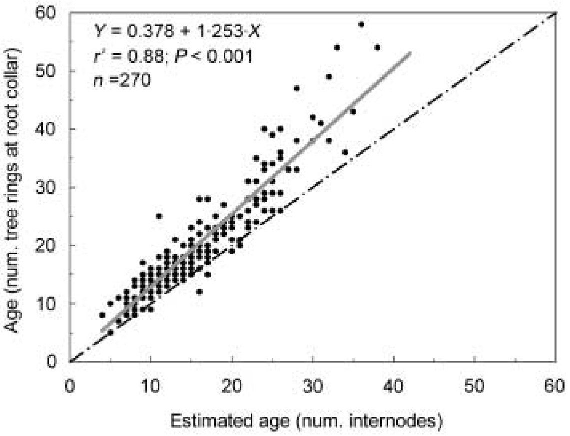

Fig. 3. Mean age correction function (grey bold line) for the 270 small pines (up to 1.5 m high) collected. Dashed line corresponds to the 1 : 1 relation 'age at root collar' = 'estimated age by internode counting'.

growing individuals. We considered these age differences as the dating error for each coring height.

As the age estimation of the small and poorly lignified individuals based on bud scar counting underestimates true age (age at root collar) (Camarero 1999), cross sections of the 270 young pines collected were also used to develop age correction functions to minimise this error. Age correction functions were developed for each of the six stands by means of a linear regression on age at root collar compared with age obtained by counting internodes (Fig. 3). The age correction function of the nearest of the six sampled stands was used for age correction of the seedlings and small saplings of the six non-sampled sites.

In summary, total tree age, or the best estimation of the germination date of each individual when pith was present was: (1) the number of rings in the core plus (2) rings lost due to coring height. While in the off-centre cores, age was the sum of: (1) rings in the core, plus (2) rings missing from the pith, plus (3) rings lost due to coring height. Tree age estimation error depends on MSR and coring height, and with the method used, it can be quantified for each core. Therefore, we determined that the demographic structure of each plot could be presented in 15-year classes, given that the majority (87%) of the individuals were dated with greater precision than this. Given the resolution of the analysis (15 years) and the low frequency of absent rings detected, we considered that missing rings do not add uncertainty to the age estimates in this study. Uncertain tree age estimations, due to greater than 15 years dating error, are presented for each plot separately. Age structures must be interpreted as reasonable estimates for the assessment of recruitment patterns, a trade-off between regeneration and mortality events.

DATA TREATMENT

The temporal patterns of recruitment (age frequency distributions) were compared between the 12 study sites using Kolmogorov-Smirnov tests with Bonferroni adjustment of the significance level ($\alpha = 0.05$/number of comparisons) (Cuevas 2002; Gamache & Payette 2005; Chauchard *et al.* 2007). The same procedure was used to analyse the pattern of recruitment in four sub-plots (10 m width) of the two larger sampled plots (PU and FU) to account for intra-site differences in the age structure. Furthermore, we compared the apparent number and position of pulses of tree recruitment for each stand. We identified pulses as abrupt recruitment increases where the number of trees was at least 50% greater than the preceding age classes (modified from Wells *et al.* 1998; Wong & Lertzman 2001).

The presence of population depletion trends in the age structures was verified by applying both negative exponential and power function models (Hett & Loucks 1976; Ågren & Zackrisson 1990; Szeicz & MacDonald 1995; Gamache & Payette 2005), two models that reliably describe the age structure of tree populations. The major difference between the two models is that the negative exponential assumes a constant mortality rate whereas the power function describes a situation where mortality changes with age. Following Hett & Loucks (1976), age data of each stand were analysed using the appropriate linear regression of log-transformed data. This analysis was confined to the range that excluded the oldest 1% of individuals in each of the populations to avoid the influence of outliers on age models, and a value of 1 was added before log-transformation to permit inclusion of empty age classes (Ågren & Zackrisson 1990; Szeicz & MacDonald 1995).

To characterize abrupt or smooth transition patterns along the ecotone, tree age, total height and basal diameter through the altitudinal gradient were evaluated in all the study plots by fitting linear or smooth spline functions. We used the standardised values of these variables to allow for comparisons among both variables and study sites. Standardisation was done by dividing all the values of each variable by the greatest value in each site. Linear and smooth spline functions were adjusted to the 95th quantile of the variables to describe the general pattern of the transitions since low values were very abundant.

Results

A densification process during the second half of the 20th century was detected at all the tree line ecotones studied. Size demographic structures (Fig. 4) are plotted individually for each stand as frequency distribution of 5-cm d.b.h. (diameter at breast height) classes. The first category (0 d.b.h. class) in each plot represents the abundance of individuals, which do not reach 1.30 m total height, and includes seedlings, small saplings and some stunted individuals. All stands, except BU and CU, have the J-shaped distribution of pine stems expected of uneven-aged forests stands (Hett & Loucks 1976). Although BU is characterized by a bimodal size structure distribution, the abundance of 0 d.b.h. class is clearly greater than the rest. In contrast, the CU population size structure follows a rather bell-shaped distribution, left-skewed, with the 5–10 cm d.b.h. class being the most abundant. Although the J-shaped distribution was by far the most common pattern, 67% of Kolmogorov-Smirnov paired tests showed significant differences (Bonferroni adjusted $P < 0.001$) between the size structures of the populations concerned. The major difference among the studied sites is the range of tree size classes, encompassing maximum d.b.h. values between 35 and 70 cm for various stands.

The age structures of the 12 stands studied were plotted as frequency distributions in time intervals of 15 years (Fig. 4). The approximately 3600 aged mountain pines surviving today range from 1 to nearly 400 years old. Although we intensively examined the area inside each plot, we think that

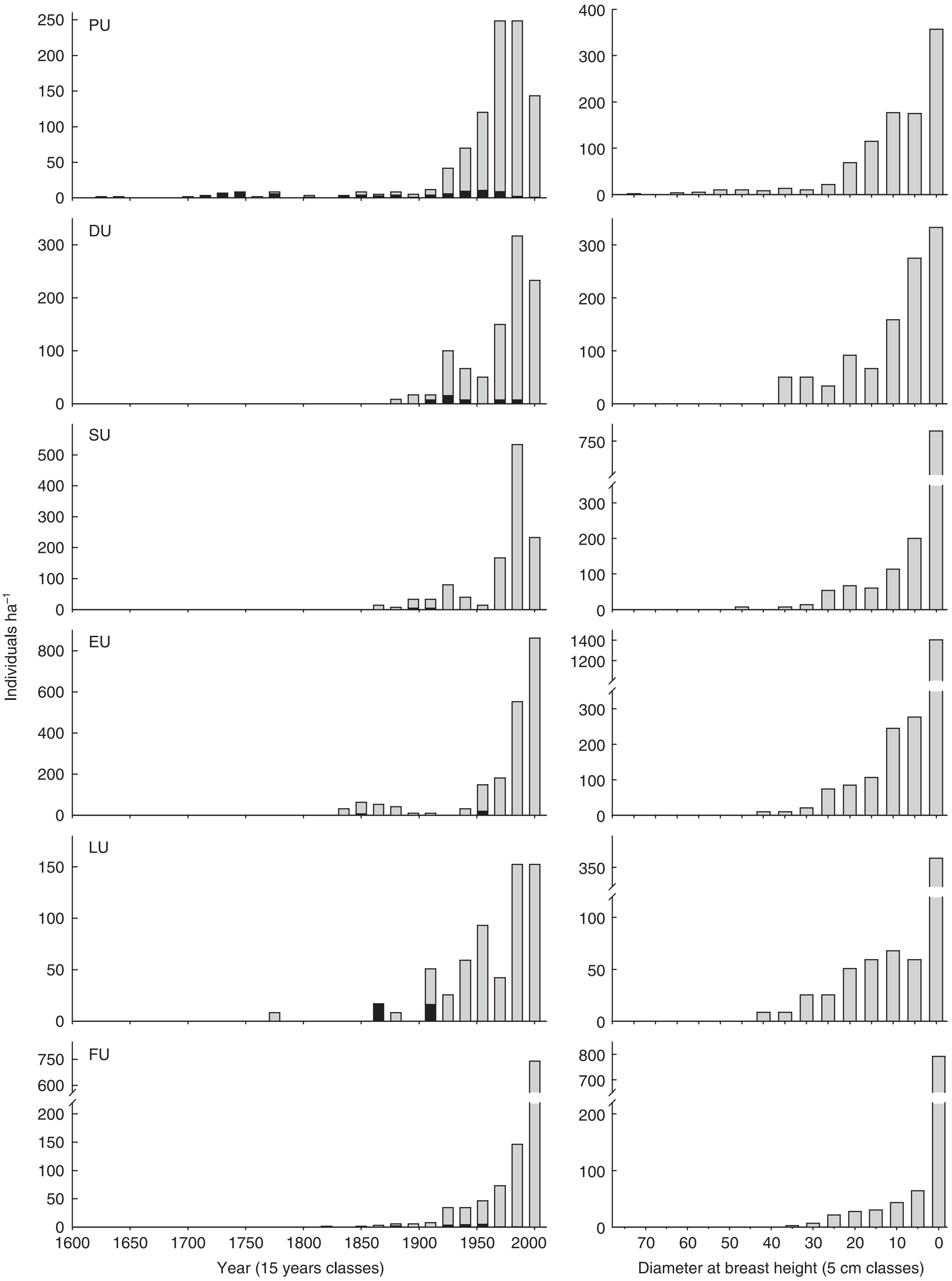

Fig. 4. Age frequency distributions (left) and diameter at breast height (d.b.h.) frequency distributions (right) for all living *Pinus uncinata* individuals at the 12 tree lines studied across the Catalan Pyrenees (Spain) and Andorra. Sites are arranged following the west–east gradient. Light grey bars indicate individuals with a dating error < 15 years; black bars indicate individuals with a greater dating error. Note that vertical scale varies between populations.

the difficulty of detecting very small seedlings (1–3 years) probably led to underestimating the frequency of recently established seedlings. Thus, the age structures presented are confined to pines established prior to the year 2000. Mountain pines older than 200 years were scarce in the stands studied. This finding explains why 8 of the 12 presented age frequency distributions have the older age classes empty. In fact, only 4.5 ± 4% (mean ± 1 SD) of the individuals of all plots were established before 1895. The majority of the sampled pines (79%) were < 50 years old and established between the mid

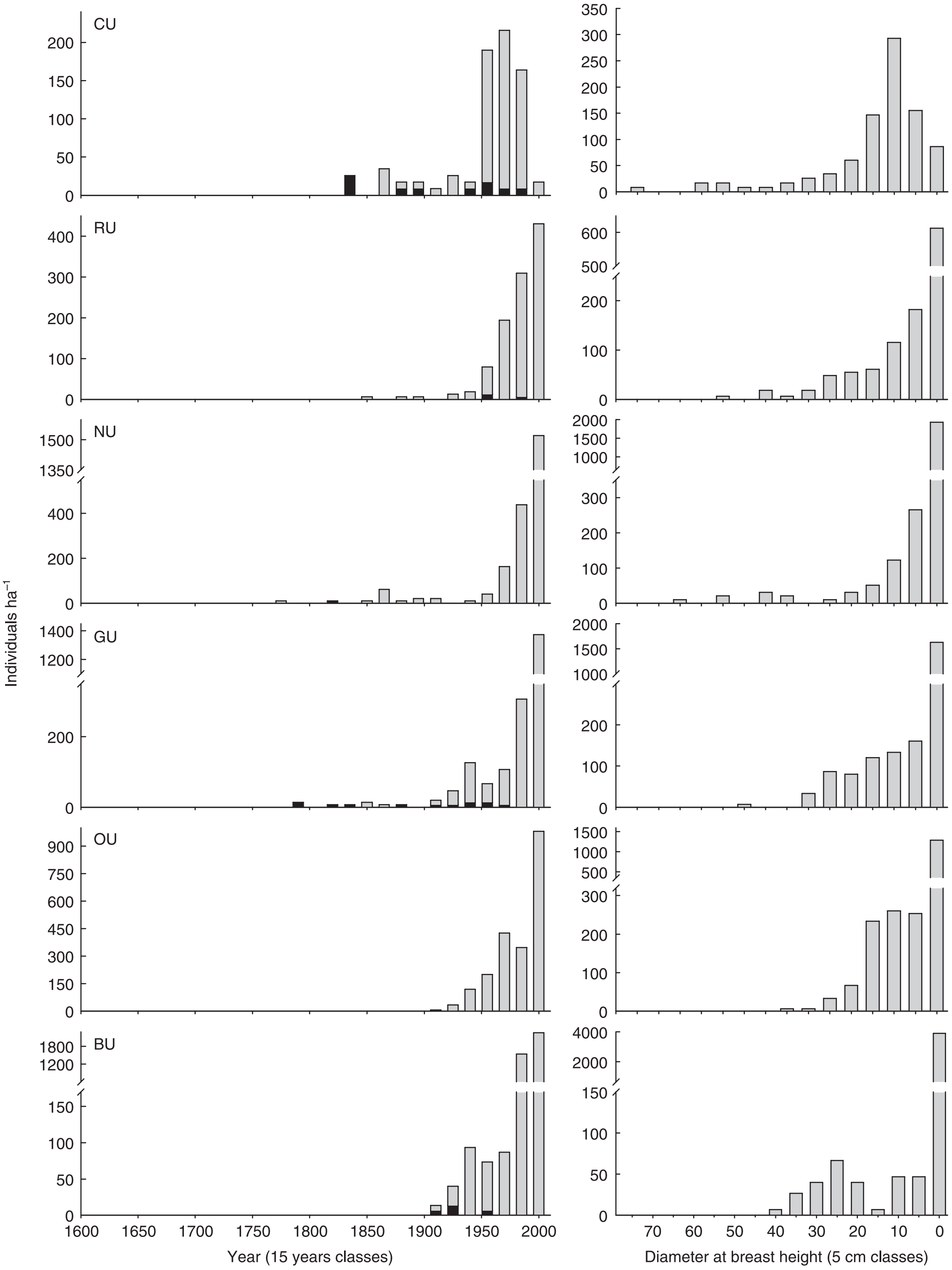

Fig. 4. *Continued.*

1950s and the late 1990s. Individuals < 15 years old (establishment period 1986–2000) represent around 50% (ranging from 40 to 67%) of the total population in 7 of the 12 studied plots. Only in one plot did fewer than 5% of individuals establish in the 1986–2000 period while, in the remaining 4 plots, this age class represents approximately 20% of total population.

The described densification process during the second half of the 20th century has mainly occurred inside the ecotone, and thus below the current tree limit. A total of 88.3 ± 14.3% (mean ± 1 SD) of the individuals recruited since the 1950s have established above the timberline and below the tree limit (Fig. 5). However, the tree limit position in 50% of the tree line ecotones studied has risen during this period, as indicated by

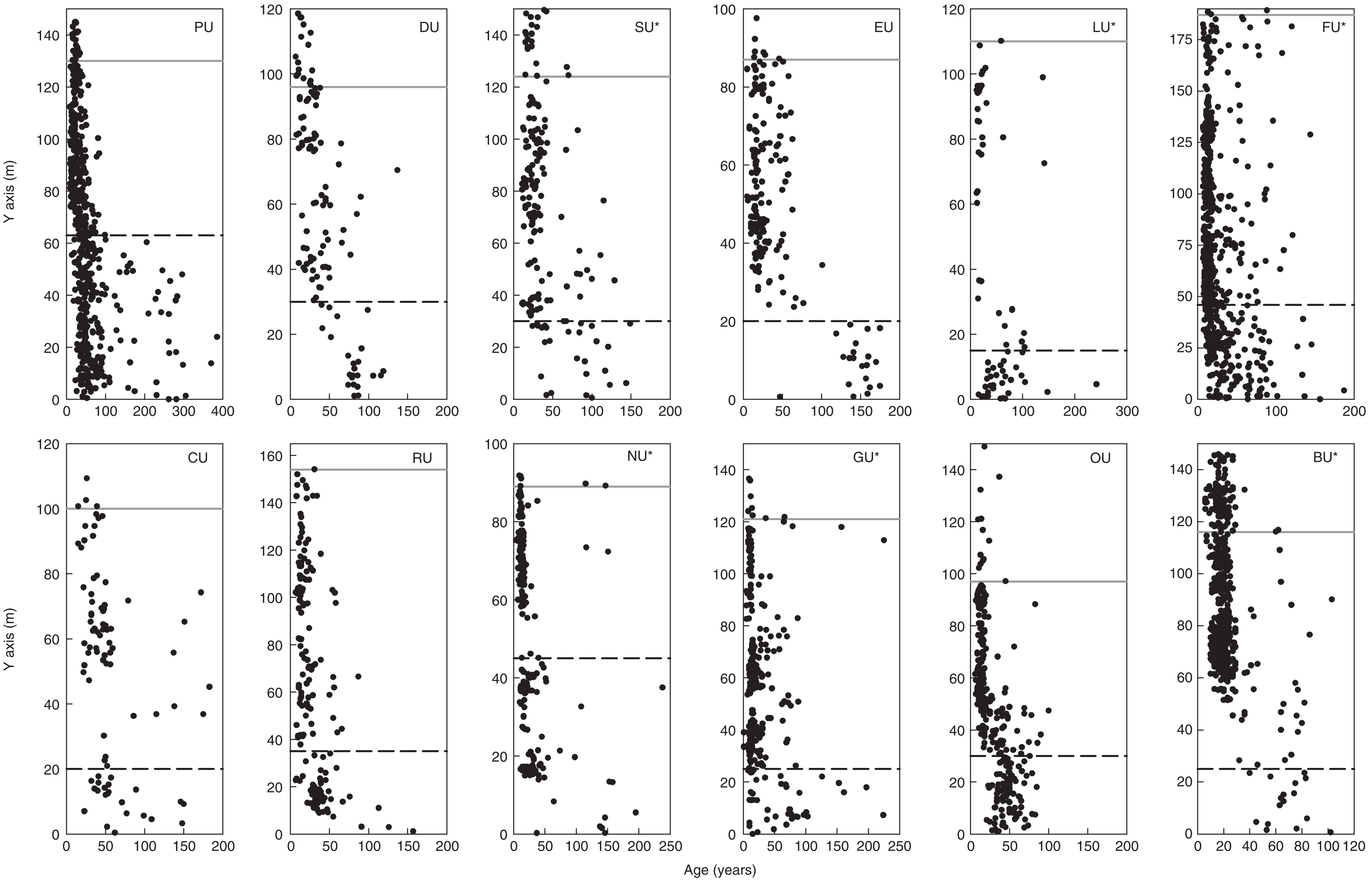

Fig. 5. Age (X axis) and position (Y axis) of all living *Pinus uncinata* individuals of each population. Solid and dashed lines at each plot represent the current tree limit and timberline positions at each site, respectively. The * symbol denotes populations where the tree forming the tree limit was established before 1950.

Table 3. Mortality rate coefficients for the fitted linearized negative exponential and power function models to the age structure data of the 12 tree lines studied. Annual mortality rates derive from the mortality rate coefficients

Site	Negative exponential (r^2)	Mortality rate coefficient	Annual mortality rate	Power function (r^2)	Mortality rate coefficient	Annual mortality rate
PU	0.63†	–0.014	0.09	0.71†	–1.502	1.48
DU	0.86†	–0.028	0.19	0.69*	–1.149	2.11
SU	0.64*	–0.024	0.16	0.61*	–1.177	2.05
EU	0.28	–0.016	0.11	0.43*	–1.314	1.79
LU	0.53*	–0.024	0.16	0.46*	–1.139	2.13
FU	0.93†	–0.035	0.23	0.94†	–1.754	1.15
CU	0.23	–0.012	0.08	0.1	–0.395	4.49
RU	0.80*	–0.045	0.30	0.74*	–1.969	0.93
NU	0.46*	–0.024	0.16	0.63*	–1.817	1.08
GU	0.67†	–0.027	0.18	0.78†	–1.851	1.05
OU	0.91†	–0.049	0.33	0.71*	–1.589	1.36
BU	0.85*	–0.053	0.35	0.86*	–1.987	0.91

Goodness of fit given by r^2; *$P < 0.05$, †$P < 0.001$.

the trees forming the current tree limit of such ecotones (Fig. 5) being < 50 years of age. The youngest individual that marks the tree limit position established in 1988 in the PU plot, while the oldest established in the 19th century (1890) in the NU plot.

The results of negative exponential and power models adjusted to age frequency distributions are presented in Table 3. Negative exponential modelling provided the best fit for five populations, whereas the power function provided the best fit for six populations. Both models explained a high degree of variance in all cases. Annual rates of mortality ranged between 0.09–0.35% and 0.91–2.13% for negative exponential and power function models, respectively. Mortality rates obtained in mature sub-alpine *P. uncinata* forests range between 0.56–0.6% (Bosch & Gutiérrez 1999), while other sub-alpine conifer mortality rates range between 0.6–2.15% (Hett & Loucks 1976; Harcombe 1987; Brang 1988). Only one of the studied plots, CU, presented an age structure that could not be significantly described with either of the adjusted models. This population clearly presents a different age structure from the rest of the stands, with scarce regeneration since the 1970s. There are three other plots (PU, DU and SU) that do not present the youngest age class (1986–2000) as the most abundant, but these populations still show large numbers of recently established recruits.

Whereas two of the stands (FU and RU) present unimodal distributions where the youngest class is the mode, the age structure of the 10 remaining populations presents a multimodal age frequency distribution. Six of the stands studied present a more or less bimodal distribution (BU, DU, EU, NU, OU, SU), and the other four a multimodal distribution (CU, GU, LU, PU). When comparing the temporal pattern of recruitment between plots, significant differences are present between most of the study sites (54 out of 66 paired Kolmogorov-Smirnov tests, Bonferroni-adjusted $P < 0.001$). Intra-site comparisons of the age frequency distributions in PU and FU showed that, in contrast to the differing age structures between plots, 92% of paired Kolmogorov-Smirnov tests show no significant differences (Bonferroni-adjusted $P < 0.01$) between sub-plots of the same population.

Although the age frequency distributions of the 12 plots studied show differing age structures, two apparent trends are shared by the vast majority of them. The most evident and striking is that the age distributions of all tree line ecotones, except CU, present at least one abrupt increase in tree recruitment after 1955. Moreover, in five populations two abrupt increases were detected in their age frequency distributions during this period. However, the recruitment increases were not synchronous between all the stands studied. Three periods of enhanced recruitment were detected: 1956–1970, 1971–1985 and 1986–2000. The most ubiquitous was the recruitment increase in 1971–1985, observed in eight tree line ecotones, while the other periods were detected in four stands. Dead seedlings were scarce in the studied populations, representing only 2.63% of the total sampled seedlings (ranging from 0 to 14% among plots). Finally, the other successful recruitment period, which occurred in the mid 19th century (1836–1865), was observed in six of the nine populations that included old enough individuals.

Standardised age, total height and basal diameter along the altitudinal gradient evidenced gradual and step-like transition patterns. Three of the tree line ecotones, representative of all the stands studied, are presented in Fig. 6. In the PU plot, a differential pattern of altitudinal decrease in tree age, total height and basal diameter can be observed. Whereas tree age showed a step-like distribution, total tree height and basal diameter presented a gradual decrease along the altitudinal gradient. This pattern was also observed in the EU and CU plots. In the FU plot, a gradual decrease of tree age, total height and basal diameter occurred. This was the most common situation, also detected in the DU, SU, LU, RU, NU and GU plots. Finally, in the OU and BU stands, all the analysed variables showed a step-like distribution along the altitudinal gradient.

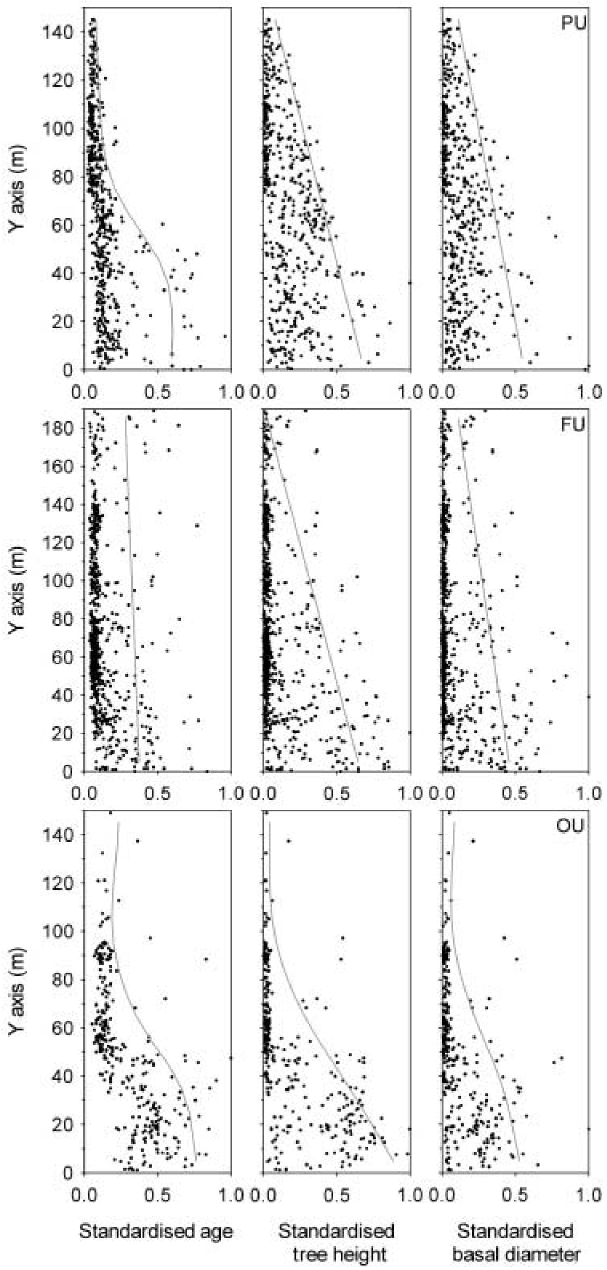

Fig. 6. Transition patterns of tree age and size (height and basal diameter) along the tree line (Y axis) in three of the tree line ecotones representative of all the stands studied (top graphs – PU, middle graphs – FU and bottom graphs – OU). Standardised values of each variable are plotted (X axis), grey lines represent linear or smooth spline fitting (to the 95th quantile of the variables) to highlight gradual and step-like transition patterns along the tree line, respectively.

Discussion

The size structure distributions highlight that all the studied populations, except one, are dominated by small individuals (seedlings and saplings). This suggests that tree establishment was abundant in all the stands in recent decades as Stöcklin & Körner (1999) have also reported. However, trees of the same size can present big differences in age due to distinct tree growing conditions. Hence, suppressed growth of some trees as a result of extreme site conditions and/or competition processes may explain why size distributions are more similar among plots than age distributions are. Besides, this could also explain why some stands present wider age discontinuities than might be expected from their diameter distribution (Lusk & Ogden 1992).

Although the assumptions of stable population size and constant recruitment and mortality rates may seldom be met in natural populations (Johnson *et al.* 1994), fitting negative exponential and power functions to empirical data may still be useful as a means of detecting deviations from these simple models (Hett & Loucks 1976; Ågren & Zackrisson 1990). Deviations of the actual age structure from the modelled or predicted age structures may reflect changing patterns of regeneration and/or survival over time. Such deviations can be identified by an inspection of the residuals, although analysis of the residuals (results not shown) provided no clear patterns, with fluctuations both above and below the values predicted at each site. These departures from the theoretical models may indicate that seedling establishment and survival at tree line varied through time among and within sites (Daniels & Veblen 2004).

In general, the power function, which includes a changing mortality rate, provides a better description of population depletion in stands with older age classes. In two of the stands studied (FU, RU), the marked J-shaped distribution would indicate sustained inputs of individuals. In these two populations, the number of pines drops rapidly from the first class (1986–2000). Although the fitted models also present noticeable deviations between the predicted and observed values, the age structure of these stands are compatible with an assumption of constant recruitment and mortality rates that could be indicative of stable populations in the long term (Payette 2007). However, the age distributions of these two tree lines could only represent a transient state of an ever-changing population structure (Ågren & Zackrisson 1990).

Keeping in mind the limitations of static age structure interpretations, it seems that some observed trends among the 12 studied populations could not be merely a methodological artefact. The plots studied show differing age structures, but several features are shared among them. The dominance of multimodal age distributions (83% of studied populations), also observed in other alpine or forest-tundra ecotones (Szeicz & MacDonald 1995; Camarero 1999; Cuevas 2002), indicates that recruitment in tree line forest ecosystems is episodic rather than gradual (Cullen *et al.* 2001; Walther *et al.* 2005). Based on the differing structure of the age frequency distributions it may seem that the periods of enhanced recruitment are more or less randomly distributed over time, but there are no periods of abundant recruitment that are not periods of abundant recruitment in at least several other plots. This is the case of the increased recruitment in the mid 19th century (mid 1830s to mid 1860s). Nearly 70% of the populations that are sufficiently old present this change in the age frequency distribution. It is important to note that due to cumulative effects of mortality, past periods of enhanced recruitment become increasingly difficult to detect as the cohort ages (Villalba & Veblen 1997b). Thus, we think that the detected presence of enhanced pine recruitment from the mid 1830s to the mid 1860s in several plots distributed over the Pyrenees is a real trend. Furthermore, this enhanced regeneration, also present in other tree line populations studied in the Pyrenees (Camarero 1999), coincides with positive growth trends since 1830 reported in the Pyrenees (Bourquin-Mignot & Girardclos 2001) and Central Italy (Piovesan *et al.* 2003) attributed to the end of the Little Ice Age.

Substantial densification in tree line populations during the 20th century seems to be a common phenomenon in northern and high-elevation environments, and occurs more frequently than actual tree line advance (Payette & Filion 1985; Scott *et al.* 1987; Payette & Lavoie 1994; Szeicz & MacDonald 1995; Kullman 1997; MacDonald *et al.* 1998; Stöcklin & Körner 1999; Payette *et al.* 2001; Juntunen *et al.* 2002; Shiyatov 2003; Camarero & Gutiérrez 2004; Kullman 2005; Danby & Hik 2007). This densification trend is also apparent in all the 12 studied populations over the Pyrenees, but is particularly pronounced during the past 50 years in 92% of the stands studied. Despite the high mortality rates expected at the tree line, the overall annual mortality rates derived from the negative exponential and power function adjusted models are similar to those reported at lower altitude sub-alpine forests (Hett & Loucks 1976; Harcombe 1987; Brang 1988; Bosch & Gutiérrez 1999). Our results indicate that past and present environmental conditions are not causing severe tree mortality at the stands studied. In addition, there was a low presence of dead seedlings in the populations studied (2.63% of total sampled seedlings). Thus, it is reasonable to believe that, under current climate conditions, a large part of the regeneration pool should survive, and that the high seedling density observed in recent decades most likely represents real increases in stand density (Lloyd & Fastie 2003; Gamache & Payette 2005). The latter trend contrasts with the results of other studies in the Pyrenees, and in isolated Spanish *Pinus uncinata* populations (Camarero & Gutiérrez 2004; Camarero & Gutiérrez 2007), as well as other alpine areas (Villalba & Veblen 1997b; Cuevas 2002), where the most evident tree recruitment increase is in the first half and the mid of the 20th century and there is a deficit in seedling establishment after the 1970–1980s.

The observed trend in the age frequency distributions during the second half of the 20th century does not appear as a gradual increase in tree frequency up to a peak over time. Instead, all the populations studied (except CU) show at least one sharp increase in recruitment after 1950, and 83% of them show an abrupt recruitment increase after the 1970s. Recent studies in west-central Sweden (Kullman 2005), reported a clearly discernible process of conspicuous infilling (scattered young trees and saplings are spreading out into previously treeless mires) since the mid 1980s. Gamache & Payette (2005) also describe an important increase in seedling establishment since the late 1970s in the tree lines of the southernmost tundra of Northern Québec. Finally, massive stone pine (*Pinus cembra* L.) regeneration has also been detected in the Western Italian Alps since the 1960s (Motta *et al.* 2006). To some extent, the rapid shifts in recruitment tendencies since the 1950s could be indicative of positive feedback processes. Increasing stand density can modify the distribution pattern of individuals, which can play a role in positive feedback wherein trees are able to modify environmental conditions (Alftine & Malanson 2004). Such modifications (e.g. snow distribution and wind conditions) promote further seedling establishment, growth and survival (Smith *et al.* 2003; Bekker 2005; Kullman 2005). The importance of mechanisms of this kind is suggested to increase with stress conditions (Callaway *et al.* 2002) and to maintain patterning of alpine tree lines (Sveinbjörnsson *et al.* 2002; Alftine & Malanson 2004).

The presence of significant differences in inter-site but not in intra-site comparisons of the demographic age structure at tree line emphasizes the importance of local factors (i.e. climate, natural or anthropogenic disturbance regimes) affecting entire populations. The observed differential tree line responses may result from changes occurring and interacting at different scales (Resler 2006). However, the coincidence of periods of enhanced recruitment in alpine ecotone populations of mountain pine over a large area of the Pyrenees (i.e. mid 19th century, second half of 20th century), suggests that a common external factor, like the climate, has an important role in synchronizing these patterns (League & Veblen 2006; Camarero & Gutiérrez 2007). Other authors relate variation in tree line populations' age structure to climatic variation (Kullman 1987; Payette *et al.* 1989; Gamache & Payette 2005; Kullman 2005). In contrast, several studies conclude that recent establishment of trees in the tree line ecotone results from declined human land use (Hofgaard 1997, 1999; Holtmeier 2003; Cairns & Moen 2004; Motta *et al.* 2006; Gehring-Fasel *et al.* 2007). In the Pyrenees, as in many parts of the world, seasonal farming in high mountain areas has a long tradition, as well as logging to lesser extent. However, important land use abandonment during the 20th century (more pronounced since 1950s) is a general phenomenon across all the Pyrenees (García-Ruiz *et al.* 1996). This occurred in parallel to climatic warming (Diaz & Bradley 1997). Given that local conditions greatly determine tree line responses, it is not feasible to determine the driving factor (climate or land use changes) of the tree line ecotones studied based on the general trends mentioned above. However, we suggest that tree line transition characteristics, gradual decline or step-like transitions in tree age and size along the ecotone, may serve to illustrate different stages concerning time since land use abandonment and its implications for tree line dynamics. Both natural (e.g. topography-induced extreme winds, snow avalanches, rockfall) and anthropogenic disturbances (e.g. fires, grazing pressure) are very important factors in determining local tree line pattern and position (e.g. Mast *et al.* 1998; Holtmeier & Broll 2005; Körner 2007). Furthermore, in the absence of such disturbances, a gradual transition from the sub-alpine forest to the treeless alpine area is expected due to the gradual increase of unfavourable environmental conditions with altitude. Since the study sites are located in homogeneous slopes avoiding major natural disturbances, we propose that step-like distribution patterns in tree age and/or size along the ecotone might derive from recent human-induced perturbations.

The most common pattern in the tree lines studied (7 out of 12) is a progressive decline in tree age and in tree size (total height and basal diameter) through the altitudinal gradient. Populations' dynamics in these ecotones may be mainly influenced by climate and therefore such tree lines may present high sensitivity to climatic change although their position could be lower than the potential tree line altitude (Holtmeier & Broll 2005). In contrast, the cessation of anthropogenic activity at the tree line, in the context of warmer temperatures, might have triggered the described tree line responses in the other five stands studied. The clearest example of this situation may be the two study sites where both tree age and size present step-like transitions along the tree line. Furthermore, the lack of old trees (the oldest individual is < 120 years) and the dominance of recently established pines (1986–2000 period) in these two stands reinforce the idea that recent land use changes may have triggered the observed densification trends. Finally, the remaining three stands studied present step-like patterns in tree age coupled to a progressive reduction in tree size along the tree line. The step-like tree age transitions in these stands suggest that they may have been affected by human-induced perturbations more recently than we initially thought. However, the demographic structure, which evidence the presence of old trees, and the smooth tree size transitions of these three populations may indicate that land use changes are not as recent as in the two plots mentioned above. The scarcity of dead individuals, and the absence of tree remnants in the three populations where only step-like patterns are present in tree age, evidence the great responsiveness of tree growth to short term environmental variation under the current climatic conditions (Payette & Lavoie 1994; Kullman 2002). This is reinforced by the age of trees (< 50 years) forming the current tree limit in these three sites. Overall, our results suggest that gradual transitions in tree size (total height and basal diameter) could mask the effect of recent perturbations, which may, nevertheless, be evident in the tree age transition pattern.

Our results show that tree limit stability since 1950, as reported by previous tree line studies in the Pyrenees (Camarero 1999; Camarero & Gutiérrez 2004), is not ubiquitous at a regional scale and emphasizes once again the presence of differential tree line responses (Dalen & Hofgaard 2005). Tree limit upward shifts have been evidenced in this study by the age of the trees forming the current tree limit (i.e. < 50 years in 50% of studied tree lines). Given the absence of dead tree remnants, these young trees have established and grown to 2 m height during the second half of the 20th century thus raising the tree limit in the recent past. The rate and magnitude of the detected upward shifts in the Pyrenees cannot be assessed accurately with the current data. Detailed studies on tree limit position (e.g. extensive age determination of trees at 2 m height) are needed. But the detected upward shift in some of the populations studied suggests that important changes in alpine vegetation could occur. For example, tree line upward shifts and densification processes may lead to a loss and fragmentation of the habitat of alpine species (Dirnböck *et al.* 2003), which in turn may increase their extinction risk. However, it is not obvious how tree line ecotones will respond to the increased temperatures and decreased precipitation predicted for southern Europe (IPCC 2007), which could lead to increased drought stress limiting tree growth and survival of recruits. Although, based on the traditional tree line paradigm, warm temperature is favourable to both tree radial growth and reproductive success, Camarero & Gutiérrez (2004) state the negative effects of summer drought stress on *P. uncinata* seedling survival whereas, recently, Oberhuber *et al.* (2008) suggest an effect of temporary drought stress during the growing season on radial tree growth at the tree line. Furthermore, the analysis of the climatic influence on the tree line dynamics at the study sites strengthens the idea that the negative effects of drought stress can lead to reduced growth and diminished seedling performance at the Pyrenean tree lines (Batllori 2008). Long-term monitoring of the alpine tree line and interdisciplinary projects (e.g. including ecological and historic documentation research) are required to improve our understanding of tree line responses to global change.

Main conclusions

Despite the differing age structure of populations at alpine tree lines, a regional densification trend in the ecotone has occurred over a large area of the Pyrenees during the 20th century as evidenced by the age and size demographic structures. This occurred in the context of climatic warming and important land use abandonment during the second half of the 20th century. In fact, the observed afforestation process has been particularly important during the past 50 years, and is more apparent in the vast majority of populations since the beginning of the 1970s. Furthermore, the observed recent densification trend has occurred as rapid shifts in recruitment tendencies, which may be indicative of the importance of positive feedback mechanisms in the tree line dynamics. In contrast with previous reports for the Pyrenees, current tree line densification has been coupled to tree limit rise in half of the studied ecotones. This highlights both the presence of differential tree line responses and, to some extent, indicates the great responsiveness of the tree limit to short-term climatic changes. Moreover, the detected upward shifts at tree line could trigger important changes in alpine vegetation if future climatic conditions do not become limiting for tree growth and recruitment (e.g. drought stress). The presence of recent and past synchronous recruitment trends suggests that a common external factor, like climate, probably modulates tree line recruitment at a regional scale. But the differing intensity of anthropogenic disturbances over time and space may have strongly modulated the tree line population trends at local scale. We suggest that, in the absence of major natural perturbations (e.g. snow avalanches, extreme winds), step-like patterns in tree age along the tree line could be reliable records of human-induced perturbations.

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