Structure and spatial variability of *Pinus uncinata* Ram. growth forms at two contrasting treeline ecotones in the Spanish Pyrenees

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SUMMARY

We describe the spatial distribution of *Pinus uncinata* individuals classified according to their growth-form and size at two undisturbed altitudinal treeline ecotones in the Spanish Pyrenees (Ordesa, O; Tessó, T). At each site, a rectangular plot (30   140 m) was located with its longest side along the altitudinal gradient, and encompassing treeline and timberline. At both sites, living individuals were bigger and had a higher number of needle cohorts downslope. The distribution of size and growth-form classes at site O followed a neat sequence of increasing size downslope, from abundant shrubby multi-stemmed krummholz individuals with few needle cohorts (1-3) up to bigger uni-stemmed arborescent trees with several needle cohorts (4-12). In contrast, structural changes through the ecotone at site T were gradual, and they did not follow so neatly this sequence of increasing size downslope.

KEY WORDS: krummholz, needle cohorts, partitioned regression, *Pinus uncinata,* Pyrenees, tree height, timberline.

INTRODUCTION

Recent regional climatic and land-use changes have been described for several mountain areas, including the Pyrenees (García-Ruiz and Lasanta-Martínez, 1990; Bücher and Dessens, 1991). However, we still do not know exactly how will tree populations respond to climate change at their altitudinal limits of distribution (Brubaker, 1986). The altitudinal forest-pasture ecotone (FPE) can be a sensitive monitor of the effects of these

environmental changes on subalpine tree populations (Hansen and di Castri, 1992). The tree populations of these ecotones can respond to global change through changes of: tree size and growth-form, demographic variables (tree density, recruitment rate), and ecotone position. A FPE is here defined as the ecotone that includes treeline (limit of arborescent growth forms, usually at least 2 m high) and timberline (limit of dense forest) separating alpine pasture and subalpine forest (Hustich, 1979). From an ecophysiological point of view, alpine treelines are basically controlled by the decrease of temperature with increasing altitude (Tranquillini, 1979). Nevertheless, current explanations for treeline dynamics at the population level are still unsatisfactory. This is probably due to the longevity and the slow vegetative growth of many tree species (Kullman, 1990). In this study, we will focus on the changes of tree growth-form along the altitudinal gradient. We regard these changes as one of the main responses of treelines to climate variability. The phenotypic plasticity of tree growth can allow treeline populations to withstand unfavourable climatic periods by delaying their response *(treeline inertia;* Kullman, 1990).

Much treeline research has focused on the relationships between regeneration and climate (e.g., Camarero and Gutiérrez, 1999). Several studies have found changes of tree density with minor treeline shifts in response to climate warming (Payette and Filion, 1985; Szeicz and MacDonald, 1995; Weisberg and Baker, 1995). However, the phenotypic change of tree growth form in response to climate has become a key aspect to understand the effects of climate on treeline populations (Kullman, 1986; Scott *et al.,* 1987a; Scott *et al.,* 1987b; Lavoie and Payette, 1992; Hessl and Baker, 1997). It must be taken into account that the effects of climate on tree regeneration in treeline ecotones differ from those on vertical or radial tree growth (Earle, 1993). Climatic variability can increase the vertical stem growth and enhance the death of shrubby stems, what could trigger a change from krummholz (multi-stemmed, crooked and short forms) to uni-stemmed arborescent forms with more symmetrical crowns (Lavoie and Payette, 1994; Pereg and Payette, 1998). This structural change could modify several environmental variables such as the snowpack depth and the wind regime, which in turn affect regeneration within the FPE (Earle, 1993; Scott *et al.,* 1993). This feedback between changes in tree-growth form, environment, and tree regeneration might be triggered by favourable and stable climatic conditions.

The study of the structural and spatial changes of tree-growth form can be a useful tool to infer those processes (regional climate, local environment, biotic interactions) that generated this pattern. Furthermore, this can allow us to distinguish between locally controlled and regionally modulated (by temperature) FPEs (Körner, 1998). Our main objective was to describe the structure in two alpine FPEs, considering the structural and spatial changes of tree-growth form. The two studied sites were selected among a network of treeline sites in the Pyrenees that have not experienced many recent human disturbances, such as logging, overgrazing, or fires (Gil-Pelegrín and Villar-Pérez, 1988). These sites represent a major part of the great variability of Pyrenean FPEs because of their contrasting environmental characteristics.

MATERIAL AND METHODS

Tree species and study area

Pinus uncinata Ram. is the dominant tree species of most of the Pyrenean treelines and timberlines (Cantegrel, 1983). This species reaches its southern limit of distribution in the Iberian Peninsula (Ceballos and Ruiz de la Torre, 1971; Blanco *et al.,* 1997). *Pinus uncinata* is a pioneer and shade-intolerant species whose reproduction is mostly sexual (Bosch *et al.,* 1992). At the end of the glacial period (13000-12000 yr. B.P.), *P. uncinata* timberlines were located up to 800 m lower than today in the Central Pyrenees (Montserrat, 1992). Currently, *P. uncinata* timberlines and treelines in the Pyrenees reach maximum altitudes of ~ 2500 and ~ 2700 m asl, respectively (de Bolós *et al.,* 1993; Carreras *et al.,* 1995). Some of these FPEs follow the typical sequence of growth forms from vertical uni-stemmed trees near the forest limit to shrubby multi-stemmed krummholz forms above the treeline (Gil-Pelegrín and Villar-Pérez, 1988). However, few Pyrenean FPEs have not been affected by local anthropogenic disturbances (fires to expand alpine pastures, and logging). *Pinus uncinata* forests are now reported to be recolonizing many subalpine and alpine pastures in the Pyrenees due to grazing reduction and, possibly, improved climatic conditions (Soutadé *et al.,* 1982).

The study sites are located in the Spanish Central Pyrenees and showed contrasting topographic, climatic, and edaphic characteristics (Fig. 1). The understory vegetation at the Ordesa site (hereafter site O) is dominated by *Festuca rubra* L. and *Calluna vulgaris* (L.) Hull. At the Tessó site (hereafter site T), a dense understory, typical of longer and deeper snow cover sites, was dominated by *Rhododendron ferrugineum* L. and *Vaccinium myrtillus* L. Site O is located on calcareous limestone and acid sandstones, but site T bedrock is mainly composed of calcareous shales (Ríos *et al.,* 1982; Ventura, 1992). Both sites are in the buffer zones of National Parks («Ordesa y Monte Perdido», O; «Aigüestortes i Estany de St. Maurici», T) which we considered a guarantee that recent human activity would diminish further. The present stocking rates at both parks are low. For instance, at site O only 14 (2 % of all living trees) krummholz pines close to treeline pasture showed signs of grazing. Site T has hardly been affected by local human disturbances (grazing, logging) since the end of the XVIIIth century, according to historical data (Bringue, 1995). No evidence of recent fires (fire scars, charcoal) was found at either sites. In addition, no treeline shift could be clearly discerned from a comparison of aerial photographs of the two sites from the last 50 years.

Climate

At site O, the climate is continental with some oromediterranean influence (Góriz meteorological station, 2215 m asl, 42 39' N, 0 01' E; 1981-89 and 1992-95 data). The total annual precipitation is   1600 mm. Snow precipitation may be nil in some winters, and reaches maximum values in spring. The maximum winter snow thickness is within the range 1.0-2.0 m. The mean annual temperature is   5 C. The lowest and highest mean monthly temperatures are –2 C and 13 C, respectively (Balcells and Gil-Pelegrín, 1992).

At site T, the climate is continental with a maritime influence (Esterri 1054 m asl, 42 37' N, 1 07' E, 1970-97; Cavallers 1733 m asl, 42 34' N, 0 51' E, 1955-72). The esti-

Site O   *Site T*

42° 37 56 N   42° 37   N
00° 02 ___ W   01° 02 ___

42° 37 15 N   42° 36   N
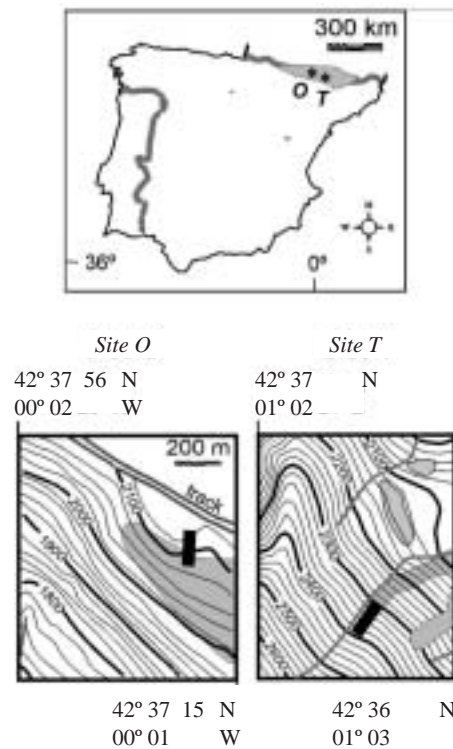00° 01   W   01° 03

Fig. 1.–Geographical location of the study sites (asterisks) in the Pyrenees (Ordesa, O; Tessó, T). The gray area shows the distribution of *P. uncinata* in the Iberian Peninsula. The lower more detailed maps show for both sites, on the same scale, their topographic characteristics and the location of the plots (black rectangles) crossing the timberline (gray areas represent closed forest). Thick gray lines represent streams

mated mean annual precipitation is over   1600 mm. The maximum winter snow thickness is within the range 2.0-3.0 m. The estimated mean annual temperature is   3 C, while the minimum and maximum mean monthly temperatures are   –4 C and   12 C (Plana, 1985). The prevailing winds come from NW-W at both sites. From December 1992 to April 1995, the maximum wind speeds measured near sites O (Góriz station) and T (Tredós-Baqueira, 1880 m, 42 42' N, 0 57' E) were 25.7 m s^{-1} (NW) and 17.0 m s^{-1} (W), respectively. The landscape around site T is composed of forest corridors separated by avalanche paths located in concave surfaces and dominated by pasture. At this site, the risk of avalanches is high mainly because of its steep slopes (Furdada, 1996).

Field sampling

At each site a rectangular plot (140 m   30 m) was placed in topographically uniform parts of the FPE with its longer side along the altitudinal gradient. The plot included current treeline and timberline. The current mean altitude of the timberline was measured in the field (altimeter calibrated against topography map, accuracy of   5 m). For every *P. uncinata* individual within the plot, the following measurements were made: location in the plot (x and y coordinates of the centre of each main stem), diameter at stem base (db), diameter at 1.3 m above the base (dbh), maximum stem height (h), crown projection in four radii along the two directions marked by the plot axes, height of the lowest living branch, number of living needle cohorts retained in the branches (estimated by examining 4 mid-canopy branches), and number and type (arborescent and stunted, living or dead) of stems per individual. All *P. uncinata* individuals were tagged to allow future monitoring. We mapped and measured 692 and 259 *P. uncinata* individuals at sites O and T, respectively. The heights of those individuals higher than 3 m were estimated visually. According to Kullman (1979), the measurement error is ~15 cm for stems 3 m in height.

All individuals in the plot were grouped in five size classes following Bosch *et al.* (1992): adults (A), dbh > 17.5 cm; poles (P), 7.5 < dbh   17.5 cm; saplings (S), dbh   7.5 cm and la > 0.5 m; seedlings (SE), h   0.5 m; and dead individuals (D). Two additional growth-form classes were specified for site O: mat krummholz (K) and flagged multi-stemmed krummholz with arborescent stems (KM). We considered as stems all trunklike woody structures above the ground directly connected with the base of the individual. Flagged krummholz forms develop arborescent shoots above the snowpack and maintain a dense mat-like infranival growth composed of shrubby stems. At site O, we considered krummholz individuals as being those with h   0.5 m that showed asymmetrical growth and multi-stemmed development (Daly and Shankman, 1985). To check for spatial independence, we excavated several tree clumps at site O. At site T, we estimated nondestructively the ages of all P, S and SE by counting the number of branch whorls and bud scars on the main stem. This method yields an age underestimation of 0-5 yr (McCarthy *et al.,* 1991). This procedure was not carried out at site O because of the multi-stemmed character of most of the individuals. Botanical nomenclature follows de Bolós *et al.* (1993) and Sandoz (1987).

Partitioned regression and statistical procedures

To describe the relationships between structural characteristics (height, number of needle cohorts, and number of stems per individual) of krummholz and flagged krummholz individuals, present only at site O, we used partitioned regression (Thomson *et al.,* 1996). This exploratory data analysis is concerned with limits or ceilings of a cloud of points in a scatterplot and not with central average tendency, like the usual bivariate correlation coefficients. First, a main regression line was fitted through all the points (we used nonlinear functions because the scatterplots of the variables suggested this kind of functions). Second, the data set was split into two subsets, those above (positive residuals) and below (negative residuals) the regression line. Different regression lines were fit to the two subsets to partition them similarly. Successive cycles of subdivision may be applied. The analysis finished when the maximum value of explained variance was obtained

and the fit was coherent with the structure of the data cloud. If there is any internal structure inside the cloud, this is revealed by the spray of lines and their correlations coefficients (Thomson *et al.,* 1996). This analysis was applied to the bivariate relationships for maximum height vs. number of living stems per individual (hereafter NLST), and height vs. maximum number of needle cohorts. The total number of stems per individual (NST) is the sum of NLST and the number of dead stems per individual (NDST), i. e. NST = = NLST + NDST. Partitioned regression results were compared with those obtained through regression analyses. The regression was calculated between height and mean values for different discrete classes of needle cohorts or NLST. To summarize the relationships between structural variables, we calculated Spearman's rank correlation coefficients (r_s). To compare the means of variables, the non-parametric Mann-Whitney U-test was used (Sokal and Rohlf, 1995).

Results

Spatial distribution of size and growth-form classes

The most abundant size and growth-form classes were krummholz (n = 404, 58 %) and saplings (n = 75, 29 %) at sites O and T, respectively. The mean coordinates parallel to the slope (y, relative elevation) were significantly (p < 0.001) different among size and growth-form classes at both sites, except those comparisons of mean relative elevation for poles, saplings, and dead individuals at site T, and these classes and flagged krummholz at site O (Fig. 2). No paired comparison between the mean coordinates perpendicular to the slope (x) was significantly different (p < 0.001; Fig. 2). At site O, the timberline was located between the mean coordinates along the altitudinal gradient for adults and poles. At site T, the timberline was near the mean position of adults along the altitudinal gradient.

At site O, the size and growth-form classes appeared across the FPE following a sequence of decreasing size with increasing altitude (Fig. 2). Krummholz and seedlings predominated in the upper areas. However, at site T only seedlings and adults occupied contrasting areas, reaching maximum densities in the upper and lower parts of the FPE, respectively (Fig. 2). There was no clear gradient of decreasing size with altitude. In this site, there were more dead individuals close to the avalanche gully side of the plot. Overall, the distribution of the different size and growth-form classes along the altitudinal gradient was more segregated at site O than at site T.

Structural changes and partitioned regression for K and KM individuals

For site O we applied partitioned regression to the relationship of NLST vs. height, and maximum number of needle cohorts vs. height, for krummholz and flagged krummholz using all the data. We used exponential functions for all regressions between NLST and height because they explained the highest proportion of variance. We obtained the best fit in the third-cycle partitioned regression (i. e. 2^3 = 8 regression lines), which explained 88 % of the variance (a = 10.03, b = –0.09, r_s = –0.75, p < 0.001, n = 36; Fig. 3). These equation parameters differed from those obtained with average values
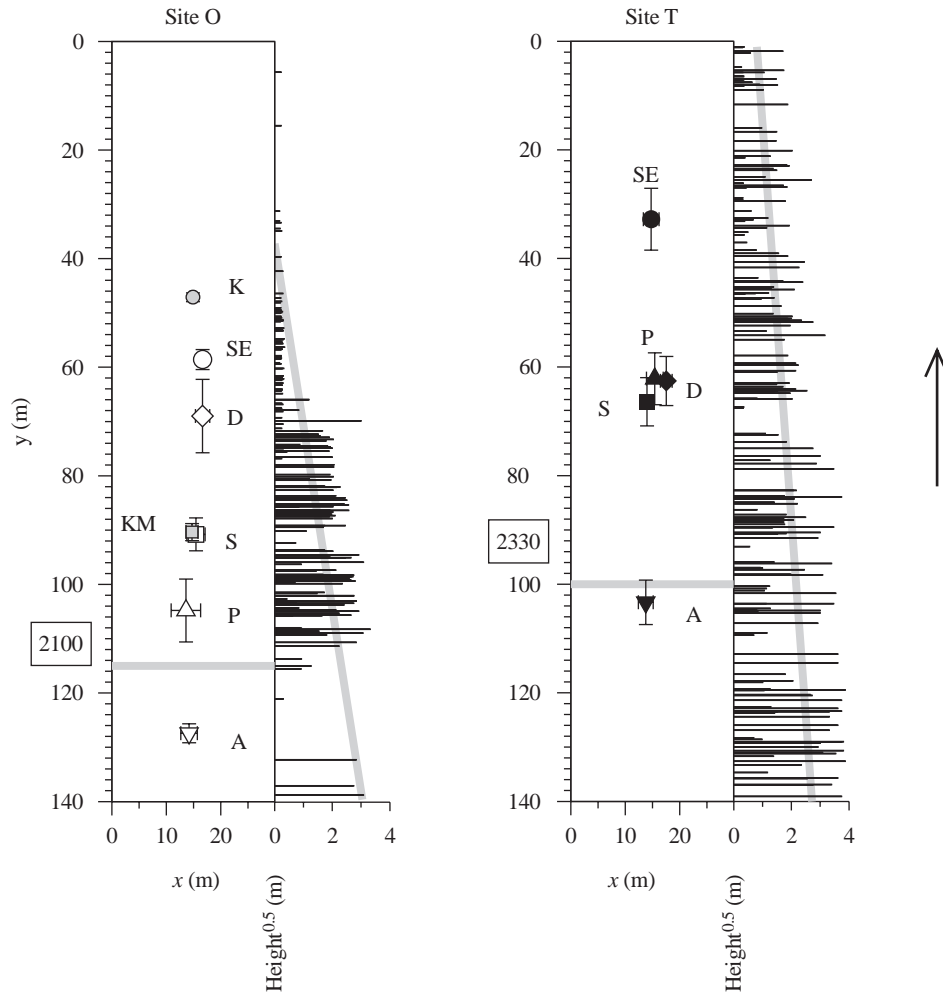
Fig. 2.–Distribution of the different size and growth-form classes across the alpine forest-pasture ecotones (FPEs) at sites O and T. Each symbol is located at the mean value of the coordinates parallel (y; altitudinal gradient) and perpendicular (x; similar elevation) to the maximum slope (the black arrow points upslope), and the error bars are standard errors (SE) of the mean values of the coordinates. The thick horizontal lines show the timberline locations and their current elevations (m asl). At the right side of each graph, the height distribution (height$^{0.5}$) of all living individuals is drawn along the altitudinal gradient (the linear regressions of height *vs.* relative elevation –gray lines– are displayed for visual comparisons). Similar symbols represent the same tree class (white and black symbols for sites O and T, respectively) except the gray symbols for K and KM only present at site O. Abbreviations for size and growth-form classes: adults (A), poles (P), saplings (S), seedlings (SE), krummholz (K), flagged krummholz (KM) and dead individuals (D)

(a = 23.48, b = –0.84, r_s = –0.87, p < 0.001, n = 25; Fig. 4), but showed the same inverse relationship between NLST and height. The same procedure was applied to the relationship between number of needle cohorts and height, using a power model. In this case, the power model explained 99 % of variance in the second-cycle partitioned regression (a = 5.09, b = 0.32, r_s = 0.93, p < 0.001, n = 79). These parameters were similar to those calculated with average values (a = 5.38, b = 0.42, r_s = 0.91, p < 0.001, n = 13; Fig. 4). However, the predictions derived from partitioned regression were more consistent with our data as shown by the higher r_s. Additionally, any separate partitioned regression explained more than 80 % of its data subset variance. Considering all data, height was again significantly and inversely correlated with NLST (r_s = –0.34; p < 0.001, n = 281) and the maximum number of needle cohorts (r_s = –0.40, p < 0.001, n = 246). These results highlight the greater internal structure of the height-needle cohort data cloud compared with the height-NLST data.
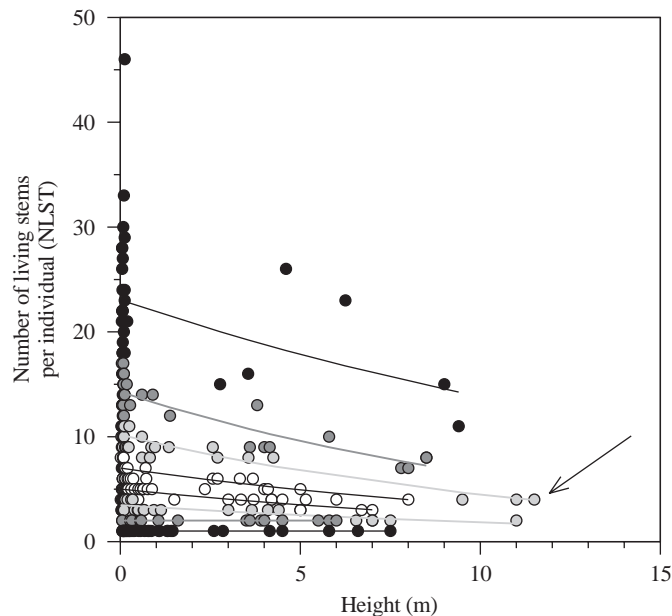

Fig. 3.–Partitioned regression between number of living stems per individual (NLST) and height at site O, considering only krummholz and flagged krummholz individuals. The lines show exponential functions fitted to the data set split into eight subsets (symbols with different colours). These subsets result from successive regressions and subdivisions of the original data set into residuals subsets (those above and below the regression line). We obtained the best fit in the third cycle (2^3 = 8 regression lines shown with different gray intensity and thickness), explaining 88 % of the variance (regression line indicated by the black arrow)

For site O, considering only krummholz and flagged krummholz, the increase in crown radii (r_s = 0.52, p < 0.001), height (r_s = 0.58, p < 0.001), NDST (r_s = 0.15, p < 0.05) and maximum number of needle cohorts (r_s = 0.66, p < 0.001) descending across the
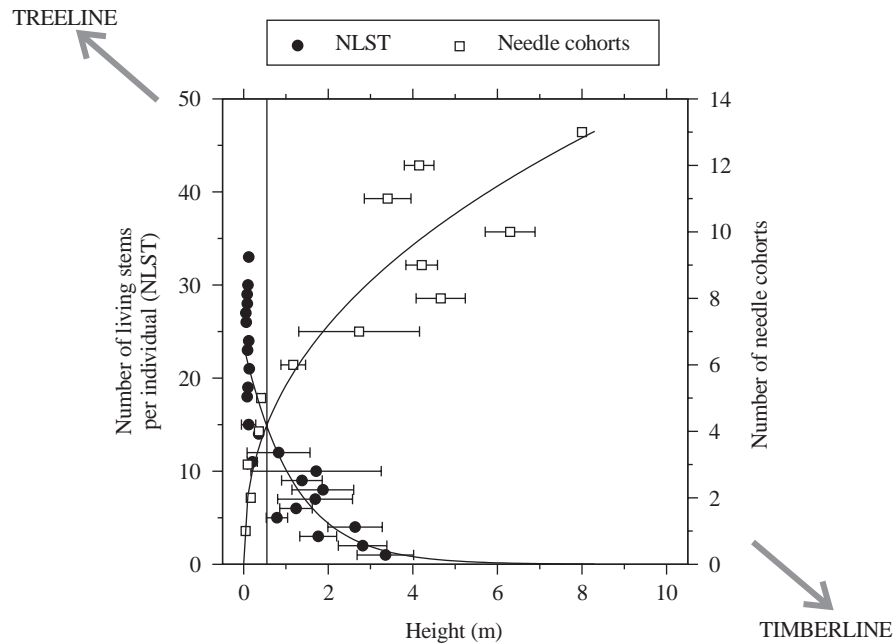
Fig. 4.–Regressions between number of living stems per individual (NLST) and height, and maximum number of needle cohorts in the branches and height. The data correspond to krummholz (K) and flagged krummholz (KM) individuals from site O. The diagonal arrow signals the transition from treeline to timberline across the FPE to emphasize the change from krummholz (shrubby forms with few needle cohorts and many living stems per individual) to flagged krummholz individuals (more needle cohorts, fewer living stems per individual) across the ecotone (the two types of individual are represented at opposite corners of the figure). The symbols are mean values for discrete classes of the dependent variables (NLST or maximum number of needle cohorts) and the horizontal error bars show SE for each dependent variable class. The fitted lines indicate exponential and power functions for the relationships between NLST vs. height (black circles) and maximum number of needle cohorts vs. height (empty squares), respectively. The vertical line indicates the intersection between the two fits

ecotone (higher values of y) was paralleled by a decrease in NST (r_s = –0.22, p < 0.001) and NLST (r_s = –0.34, p < 0.001). The mean (SE) height (h) and basal diameter (db) were significantly (p < 0.001) greater for flagged krummholz (h = 4.97 0.30 m, db = 23.62 1.20 cm) than for krummholz individuals (h = 0.27 0.03 m, db = 2.81 0.27 cm). These trends showed the change from shrubby multi-stemmed forms (krummholz) above the treeline, through intermediate forms with arborescent and shrubby stems (flagged krummholz), to bigger arborescent uni-stemmed individuals (e. g. adults) in the timberline and closed forest (Figs. 4 and 5).

The mean number of stems per individual (NST) at site O (5-6 stems per individual) was significantly (p < 0.001) greater than at site T (1 stem per individual). In fact, most individuals (69 %) at site O were multi-stemmed. The maximum NST, NDST and NLST at site O were 68 (26 live + 42 dead; KM individual), 42 (the same KM) and 46

(46 live + 2 dead; K individual), respectively. We measured the basal diameter of 1881 stems at site O, 202 (11 %) of which were dead. Most of the stems belonged to krummholz (71 %) and flagged krummholz (15 %) classes.

Considering only krummholz, 64 % of the living stems had small basal diameters (db < 0.5 cm), but only 25 % of dead stems belonged to this class of basal diamater. The mean height of the shrubby leafy stem (1 SD) of krummholz and flagged krummholz was 0.74 0.40 cm. The average (1 SD) NST for krummholz and flagged krummholz was 7 6 and 8 9, respectively. These results changed considerably if we considered live (NLST) and dead (NDST) stems per individual separately for krummholz and flagged krummholz growth forms at site O (Fig. 5). The average NLST differed significantly (p < 0.001) among all the classes, reaching the highest values in krummholz and flagged krummholz (Fig. 5). Nevertheless, the average NDST was significantly greater in flagged krummholz and dead individuals compared with the other size and growth-form classes (p < 0.05; Fig. 5).
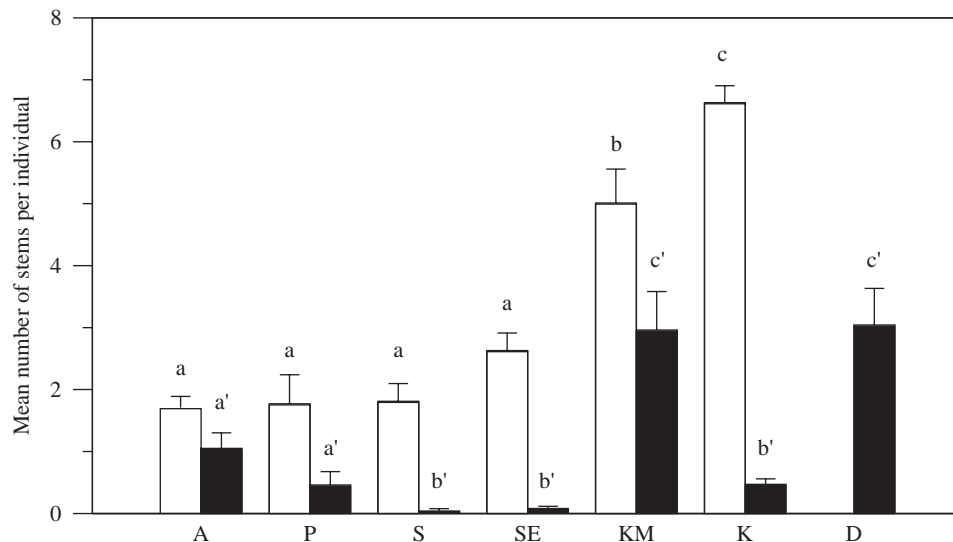

Fig. 5.–Average number of living (white bars) and dead stems (black bars) per individual for the different size and growth-form classes in the alpine FPE at site O. For both variables, different letters show significant differences at p < 0.001 and p < 0.05 for the comparisons within living (a, etc.) and dead (a', etc.) stems per individual, respectively (Mann-Whitney test). Abbreviations for size and growth-form classes as in Fig. 2. Vertical error bars are SE

Changes in structural characteristics of individuals across the FPE

At both sites, living individuals were bigger, had a higher number of needle cohorts downslope, and showed several structural parameters significantly correlated (Table 1, Fig. 4). The best predictors for estimated age at site T were height and basal diameter (Table 1). At site T, the mean estimated age differed significantly among size and

growth-form classes (p < 0.05) following this sequence (mean   1 SD, yrs.): poles (35   7) > saplings (26   9) > seedlings (9   4). At this site, there was a significant trend of increasing age descending across the FPE (Table 1), this being more marked for seedlings (r_s = 0.39, p < 0.05). There was no significant correlation between estimated ages and coordinates perpendicular to the slope (x).

Table 1

Correlation values among structural and spatial (y) variables of individuals from two alpine FPEs, sites O and T (Spearman's rank correlation coefficients, r_s). The diagonal separates values for sites O (up-right half) and T (down-left half), respectively. Only correlations with p < 0.001 are reported. Variable abbreviations: position along the plot axis parallel to the slope or relative elevation (y, this value increases downslope from 0 to 140 m), diameter at the base (db), diameter at breast height (dbh), maximum stem height (h), minimum height of the first living branch (h 1st liv. br.), E radius (eastern crown radius), number of living stems per individual (NLST, only at site O), and age (estimated age as number of internodes in the main stem, only for site T)

Site O / Site T	y	db	dbh	h	h 1st liv.br.	E radius	needle cohorts	NLST
y		0,74	–	0,63	–	–	0,74	–0,50
db	0,47		0,86	0,92	–	0,92	0,88	–
dbh	0,47	0,96		–	–	–	–	–
h	0,51	0,96	0,97		–	–	0,88	–
H 1st liv.br.	0,64	–	–	–		–	–	–
E radius	0,42	–	–	–	–		–	–
Needle cohorts	0,45	–	–	–	–	–		–0,42
age	0,31	0,81	–	0,84	–	–	–	

Changes in tree height

At site O, there was a trend of increasing height descending across the FPE which was characterized by a sharp change halfway through the plot (Fig. 2). At site T, this trend was much more gradual than at site O. The most abundant (krummholz at site O and saplings-seedlings at site T) and smallest (h < 2 m) individuals, located in the upper half of the plot (Fig. 2), produced reverse-J-shaped height distributions for all living individuals for both sites. Power functions explained a high degree of variance for the height distribution of all living individuals at sites O (a = 73.18, b = –1.72, r = 0.94, p < 0.001) and T (a = 50.73., b = –1.02, r = 0.94, p < 0.001). The height distributions did not differ significantly (p = 0.27, n = 8) between the sites.

DISCUSSION

The change from smaller to bigger individuals across the FPE was more gradual at site T than at site O. The sequence of size and growth-form classes descending across the ecotone formed distinct classes of increasing size at site O (Fig. 2), where structural variables were highly correlated with the position along the altitudinal gradient (Table 1). This site was characterized by a gradual change in forms following this spatial sequence: shrubby multi-stemmed krummholz with small stems and few and recent needle cohorts appeared above the treeline   flagged krummholz with more dead stunted stems per individual at intermediate positions   big arborescent uni-stemmed individuals (adults, poles) with more needle cohorts and located at the timberline and the forest (Figs. 2 and 4). This was paralleled by an abrupt reduction of tree height going upslope (Fig. 2).

In fact, it could be defined a quantitative transition of *P. uncinata* growth forms across the ecotone at site O (Fig. 4). In this figure, the left and right sides separated by the crossing point between the fitted curves (height-number of stems and height-needle cohorts) correspond to low multi-stemmed individuals with few needle cohorts (krummholz) and higher individuals with less stems and more needle cohorts (flagged krummholz, arborescent trees), respectively. This transition of forms across the ecotone could be partially explained by the general inverse relationship between canopy architecture (stems per individual) and the size (dbh, height) of woody plants (Stevens and Perkins, 1992). This general relationship should be modified in treeline environments where the survival of above-snow arborescent stems depends on winter climatic variables, such as wind velocity and direction, temperature and snow thickness (Lavoie and Payette, 1992; Pereg and Payette, 1998). The ocurrence of arborescent forms that were previously krummholz forms (they have remains of krummholz characters such as shrubby basal branches), similar to the described flagged krummholz forms, has been previously described for different tree species such as *Nothofagus pumilio* in south-central Chilean timberlines (Veblen *et al.,* 1977), and *Picea mariana* at arctic treelines in NE Canada (Pereg and Payette, 1998). The multi-stemmed character of krummholz forms is typical in alpine timberlines (Tranquillini, 1979; Norton and Schönenberger, 1984). It indicates the response to repeated death and breaking of stems due to snow and wind effects which stimulate epicormic branching by exposure to light, among other factors (Kozlowski and Pallardy, 1997). Krummholz forms can also modify microenvironmental conditions such as microclimate, snow thickness or soil fertility producing positive feedbacks (Daly, 1984; Scott *et al.,* 1993). Dense and compact krummholz mats, mainly composed of young needles (Fig. 4), enhance snow accumulation, thus reducing wind abrasion and needle dehydration (Tranquillini, 1979; Hadley and Smith, 1987).

Overall, the ecotone at the exposed site O seems to be a local phenomenon due to the strong winds and the reduced snowpack. Snow abrasion and wind can generate multi-stemmed forms (krummholz) and flagged krummholz as those observed in this site (Hadley and Smith, 1983; Scott *et al.,* 1987a; Gil-Pelegrín, 1993). In this site, we consider that local factors are more important to control treeline position than the altitudinal gradient (Hansen-Bristow, 1986; Lloyd, 1998). This is confirmed by the lower elevation of timberline at site O compared with site T (Fig. 2) and maximum elevation of timberlines in the Central Pyrenees (~ 2500 m).

Site T showed an overlapping distribution of the size and growth-form classes across the ecotone suggesting a greater spatial heterogeneity (Fig. 2). At this site, tree height de-

creased gradually going upslope. This spatial heterogeneity can partly explained by the importance of snow avalanches at this site (Furdada, 1996). Snow avalanches slice the FPE and create forested strips along the slope increasing the spatial variability of this ecotone (Walsh *et al.,* 1994). The increase in height descending across both ecotones was more abrupt at site O than at site T, where multi-stemmed forms were absent (Fig. 2).

According to van der Maarel (1990), only site O would be a strict ecotone, because structural changes are abrupt. However, site T could be regarded as an ecocline, where transitions are gradual and size and growth-form classes overlap along the altitudinal gradient. For site O, we have shown the structural changes in tree height, number of stems per tree and needle lifespan across the ecotone. These changes could represent an analogue of temporal processes as the different growth forms respond to climatic conditions. In both sites, the altitudinal gradient controls the overall distribution of the different size and growth-form classes, but local factors, such as wind at site O (local treeline) or avalanches at site T (regional treeline), modulate this pattern.

ACKNOWLEDGMENTS

RESUMEN

Estructura y variabilidad espacial de formas de crecimiento de *Pinus uncinata* Ram. en dos ecotonos contrastados del límite del árbol en los Pirineos españoles

Describimos la distribución espacial de individuos de *Pinus uncinata* clasificados según su forma de crecimiento y tamaño en dos ecotonos poco perturbados del límite altitudinal del árbol situados en los Pirineos Centrales españoles (Ordesa, O; Tessó, T). En cada sitio situamos una parcela rectangular (30   140 m), que incluía los límites del árbol y del bosque, y cuyo lado mayor seguía el gradiente altitudinal. En ambos sitios, los individuos vivos eran más grandes y tenían un mayor número de cohortes de acículas pendiente abajo. La distribución de las clases de individuos según su forma de crecimiento y tamaño en el sitio O seguía una secuencia de mayor tamaño pendiente abajo, desde abundantes individuos policórmicos arbustivos (krummholz) con pocas cohortes de acículas (1-3) hasta individuos arbóreos mayores unicórmicos con varias cohortes de acículas (4-12). Por el contrario, los cambios estructurales en el ecotono del sitio T fueron graduales y no siguieron de forma tan clara dicha secuencia.

PALABRAS CLAVE: altura, cohortes de acículas, krummholz, *Pinus uncinata,* Pirineos, regresión con partición, límite del bosque.

REFERENCES

BALCELLS E., GIL-PELEGRÍN, E., 1992. Consideraciones fenológicas de las biocenosis de altitud en el Parque Nacional de Ordesa y Monte Perdido, acompañadas y apoyadas mediante estudio preliminar de los datos meteorológicos obtenidos desde 1981 a 1989 en el observatorio de Góriz. Lucas Mallada 4, 71-162.
BLANCO E., CASADO M.A., COSTA M., ESCRIBANO R., GARCÍA M., GÉNOVA M., GÓMEZ A., GÓMEZ F., MORENO J.C., MORLA C., REGATO P., SAINZ, H., 1997. Los bosques ibéricos: una interpretación geobotánica. Ed. Planeta, pp. 147-163.

BOSCH O., GINÉ L., RAMADORI E.D., BERNAT A., GUTIÉRREZ E., 1992. Disturbance, age and size structure in stands of *Pinus uncinata* Ram. Pirineos 140, 5-14.

BRINGUE G.M., 1995. Comunitats i bens comunals als Pallars Sobirà, segles XV-XVIII. Tesis Doctoral. Universitat Pompeu Fabra, Barcelona.

BRUBAKER L.B., 1986. Responses of tree populations to climatic change. Vegetatio 67, 119-130.

BÜCHER A., DESSENS J., 1991. Secular trend of surface temperature at an elevated observatory in the Pyrenees. J. Clim. 4, 859-868.

CAMARERO J.J., GUTIÉRREZ E., 1999. Structure and recent recruitment at alpine forest-pasture ecotones in the Spanish Central Pyrenees. Écoscience 6, 451-464.

CANTEGREL R., 1983. Le Pin à crochets pyrénéen: biologie, biochimie, sylviculture. Acta Biol. Mont. 2-3, 87-330.

CARRERAS J., CARRILLO E., MASALLES R.M., NINOT J.M., SORIANO I., VIGO J., 1995. Delimitation of the supra-forest zone in the Catalan Pyrenees. Bulletin de la Societé Linnéene de Provence 46, 27-36.

CEBALLOS Y FERNÁNDEZ DE CÓRDOBA L., RUIZ DE LA TORRE J., 1971. Árboles y arbustos de la España Peninsular. Escuela Técnica Superior Ingenieros de Montes, 512 pp.

DALY C., 1984. Snow distribution patterns in the alpine krummholz zone. Prog. Phys.Geogr. 8, 157-175.

DALY C., SHANKMAN D., 1985. Seedling establishment by conifers above tree limit on Niwot Ridge, Front Range, Colorado, U.S.A. Arct. Alp. Res. 17, 389-400.

DE BOLÒS O., VIGO J., MASALLES R.M., NINOT J.M., 1993. Flora manual dels Països Catalans. Pòrtic, 1247 pp.

EARLE C.J., 1993. Forest dynamics in a forest-tundra ecotone, Medicine Bow Mountains, Wyoming. Ph.D. thesis, University of Washington, Seattle.

FURDADA G., 1996. Estudi de les allaus al Pirineu Occidental de Catalunya: predicció espacial i aplicacions de la cartografia. Geoforma, 315 pp.

GARCÍA-RUIZ J.M., LASANTA-MARTÍNEZ T., 1990. Land-use changes in the Spanish Pyrenees. Mt. Res. Dev. 10, 267-279.

GIL-PELEGRÍN E., 1993. Estudios ecofisiológicos sobre *Pinus uncinata* Mill. en el límite superior de la especie. Tesis Doctoral. Universidad Autónoma de Madrid, Madrid.

GIL-PELEGRÍN E., VILLAR-PÉREZ L., 1988. Structure of mountain pine *(Pinus uncinata)* populations at its upper limit in Central Pyrenees. Pirineos 131, 25-42.

HADLEY J.L., SMITH W.K., 1983. Influence of wind exposure on needle dessication and mortality for timberline conifers in Wyoming, U. S. A. Arct. Alp. Res. 15, 127-135.

HADLEY J.L., SMITH W.K., 1987. Influence of krummholz mat microclimate on needle physiology and survival. Oecologia 73, 82-90.

HANSEN A., DI CASTRI F., 1992. Landscape boundaries: consequences for biotic diversity and ecological flows. Springer-Verlag, New York.

HANSEN-BRISTOW K.J., 1986. Influence of increasing elevation on growth characteristics at timberline. Can. J. Bot. 64, 2517-2523.

HESSL A.E., BAKER W.L., 1997. Spruce-fir growth form changes in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, USA. Ecography 20, 356-367.

HUSTICH I., 1979. Ecological concepts and biographical zonation in the North: the need for a generally accepted terminology. Holarct. Ecol. 2, 208-217.

KÖRNER, Ch. 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia 115: 445-459.

KOZLOWSKI T.T., PALLARDY S.G., 1997. Physiology of Woody Plants. Academic Press, 411 pp.

KULLMAN L., 1979. Change and stability in the altitude of the birch tree-limit in the southern Swedish Scandes 1915-1975. Acta Phytogeogr. Suec. 65, 1-121.

KULLMAN L., 1986. Recent tree-limit history of *Picea abies* in the southern Swedish Scandes. Can. J. For. Res. 16, 761-771.

KULLMAN L., 1990. Dynamics of altitudinal tree-limits in Sweden: a review. Norsk Geografisk Tidsskrift 44, 103-116.

LAVOIE C., PAYETTE S., 1992. Black spruce growth forms as a record of a changing winter environment at tree line, Québec, Canada. Arct. Alp. Res. 24, 40-49.

LAVOIE C., PAYETTE S., 1994. Recent fluctuations of the lichen-spruce forest limit in subarctic Québec. J. Ecol. 82, 725-734.

LLOYD A.H., 1998. Growth of foxtail pine seedlings at treeline in the southeastern Sierra Nevada, California, U.S.A. Écoscience 5, 250-257.

MCCARTHY D.P., LUCKMAN B.H., KELLY P.E., 1991. Sampling height-age error correction for spruce seedlings in glacial forefields, Canadian Cordillera. Arct. Alp. Res. 23, 451-455.

MONTSERRAT J.M., 1992. Evolución glaciar y posglaciar del clima y la vegetación en la vertiente Sur del Pirineo: estudio palinológico. C.S.I.C., 152 pp.

NORTON D.A., SCHÖNENBERGER W., 1984. The growth forms and ecology of *Nothofagus solandri* at the alpine timberline, Craigieburn Range, New Zealand. Arct. Alp. Res. 16, 361-370.

PAYETTE S., FILION L., 1985. White spruce expansion at the tree line and recent climatic change. Can. J. For. Res. 15, 241-251.

PEREG D., PAYETTE S., 1998. Development of black spruce growth forms at treeline. Plant Ecol. 138, 137-147.

PLANA J.A., 1985. Estudi Climàtic i Balanç Hídric de la Conca de la Noguera Ribagorçana. Institud d'Estudis Catalans, 265 pp.

RÍOS L.M., LANAJA J.M., FRUTOS E., 1982. Mapa Geológico de España (Hoja 178, Broto). Instituto Geológico y Minero de España, 60 pp.

SANDOZ C.J., 1987. Recherches taxonomiques, biogéographiques et phytoécologiques sur les principaux conifères subalpines des Alpes: Mélèze d'Europe, Pin cembro, Pin à crochets et Pin mugho. These Doctoral, Université d'Aix-Marseille III, Marseille.

SCOTT P.A., BENTLEY C.V., FAYLE D.C.F., HANSELL R.I.C., 1987a. Crown forms and shoot elongation of white spruce at the treeline, Churchill, Manitoba, Canada. Arct. Alp. Res. 19, 175-186.

SCOTT P.A., HANSELL R.I.C., FAYLE D.C.F., 1987b. Establishment of white spruce populations and responses to climatic change at the treeline, Churchill, Manitoba, Canada. Arct. Alp. Res. 19, 45-51.

SCOTT P.A., HANSELL R.I.C., ERICKSON W.R., 1993. Influences of wind and snow on Northern tree-line environments at Churchill, Manitoba, Canada. Arctic 46, 316-323.

SOKAL R.R., ROHLF F.J., 1995. Biometry: the principles and practice of statistics in biological research. Freeman, 887 pp

SOUTADÉ G., BAUDIÉRE A., BÉCAT J., 1982. La limite supérieure de la forêt et sa valeur de seuil. Terra Nostra, 174 pp.

STEVENS G.C, PERKINS A.L., 1992. The branching habits and life history of woody plants. Am. Nat. 139, 267-275.

SZEICZ J.M., MACDONALD G.M., 1995. Recent white spruce dynamics at the subarctic alpine tree line of north-western Canada. J. Ecol. 83, 873-885.

THOMSON J.D., WEIBLEN G., THOMSON B.A., ALFARO S., LEGENDRE P., 1996. Untangling multiple factors in spatial distribution: lilies, gophers, and rocks. Ecology 77, 1698-1715.

TRANQUILLINI W., 1979. Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European Alps. Springer-Verlag, 137 pp.

VAN DER MAAREL E., 1990. Ecotones and ecoclines are different. J. Veg. Sci. 1, 135-138.

VEBLEN T.T., ASHTON D.H., SCHLEGEL F.M., VEBLEN A.T., 1977. Plant succession in a timberline depressed by vulcanism in south-central Chile. J. Biogeogr. 4, 275-294.

VENTURA J., 1992. Geomorfologia glacial de les valls de la Bonaigua, Son i els sectors occidentals de la cubeta d'Esterri d'Àneu. La Investigació al Parc Nacional d'Aigüestortes i Estany de Sant Maurici, II Jornades sobre Recerca, Lleida, pp. 23-41.

WALSH S.J., BUTLER D.R., ALLEN T.R., MALANSON G.P., 1994. Influence of snow patterns and snow avalanches on the alpine treeline ecotone. J. Veg. Sci. 5, 657-672.

WEISBERG P.J., BAKER W.L., 1995. Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky Mountain National Park, Colorado. Can. J. For. Res. 25, 1326-1339.