



Plant species distribution across two contrasting treeline ecotones in the Spanish Pyrenees

J.J. Camarero* and E. Gutiérrez

Department of Ecology, University of Barcelona, Avda. Diagonal 645, 08028 Barcelona, Catalunya, Spain;

*Author for correspondence (e-mail: chechu@bio.ub.es)

Received 21 August 2000; accepted in revised form 6 March 2001

Key words: Diversity, *Pinus uncinata*, Spatial pattern, Timberline, Understory

Abstract

We describe the structure of two contrasting (elevation, topography, climate, vegetation, soil) alpine forest–pasture ecotones located in the Central Pyrenees (sites Ordesa, O, and Tessó, T). We define ecotone structure as the spatial distribution of trees of different size classes and growth-forms and the relationship between these aspects and the spatial distribution of understory vegetation and substrate. The studied ecotones are dominated by *Pinus uncinata* Ram. and have been little affected by anthropogenic disturbances (logging, grazing) during this century. One rectangular plot (30 × 140 m) was located within each site with its longest side parallel to the slope and encompassing treeline and timberline. The distribution of size and growth-form classes at site O followed a clear sequence of increasing size downslope from shrubby multistemmed krummholz individuals to bigger arborescent trees. At site O, regeneration was concentrated near the krummholz area and over rocky substrates. This suggests that krummholz may modify microenvironment conditions and increase seedling survival. At site T, regeneration was abundant above the treeline where the cover of the dominant understory shrub (*Rhododendron ferrugineum*) decreased. In both ecotones the diversity of plants was higher above the treeline than in the forest and decreased going downslope coinciding with the increase of *P. uncinata* cover. The reduction of plant diversity appeared above the current timberline. At site O, the decrease was steep and spatially heterogeneous what may be due in part to the edaphic heterogeneity. At site T the change was abrupt though smaller. The relationships between the plant community and tree regeneration should be taken into account in future ecological studies of treeline pattern.

Introduction

Several components of global change (Houghton et al. 1996), such as climate change and land-use modifications, are influencing the distribution of tree populations (Brubaker 1986). Both aspects of global change are occurring in the Pyrenees. During this century, an increase in the daily minimum temperature (2.11 °C) accompanied by an increase in cloud cover has been observed at a high-altitude (2862 m a.s.l.) observatory in the Western Pyrenees (Bücher and Dessens 1991). In addition, grazing pressure has fallen continuously in the Pyrenees since the 1950's, which has led to drastic changes in land use (García-Ruiz and Lasanta-Martínez 1990).

Forest ecotones may be sensitive to global change and, therefore, could act as reliable monitors of the effects of global change on tree populations (Hansen and di Castri 1992). An alpine forest–pasture ecotone (FPE) is bounded by a treeline, defined as the maximum elevation of living individuals with stems at least 2 m high and a timberline, defined as the maximum elevation of a closed forest (Hustich 1979; Kullman 1979). Alpine treeline ecotones are dynamic zones whose location is correlated with the isotherm of the mean temperature for the warmest month (Wardle 1971; Tranquillini 1979; Körner 1998). However, we still lack satisfactory mechanistic explanations for treeline dynamics at the population and community levels. This is probably due to the difficulty

of long-term studies and experiments on populations of organisms with great longevities such as trees (Kullman 1990). Furthermore, the longevity, the phenotypic plasticity (changes of growth form; e.g., Scott et al. (1987); Lavoie and Payette (1992)), and the slow vegetative growth of many tree species can allow FPEs to withstand unfavourable climatic periods by delaying their response (treeline inertia, Kullman (1986, 1989)).

Tree regeneration is considered as one of the most sensitive ecological responses of treeline ecotones to climatic warming (Payette and Filion 1985; Weisberg and Baker 1995). In fact, several studies have reported increases in population density but minor treeline shifts following climate warming (Szeicz and MacDonald 1995; Weisberg and Baker 1995). However, the ecotone structure (spatial distribution of trees, plant species and substrate) and its relationship with tree regeneration have been poorly studied in treelines (Hobbie and Chapin 1998; Castro et al. 1999). This interaction can modulate greatly the treeline response to climatic variability. For instance, tree growth-form and associated microenvironmental conditions (snowpack depth, microclimate, soil) influence tree establishment in treeline ecotones (Holtmeier and Broil 1992; Scott et al. 1993; Hattenschwiler and Smith 1999). In this study, we describe and analyse how tree cover and density are related to the plant community at treeline ecotones. In turn, plant structure and composition can also affect tree regeneration.

Our main objective was to describe the FPE structure in two contrasting alpine sites through the quantification of changes of tree (density, size, and growth form) and substrate and understory distribution. The detailed description of the spatial variability across the FPE is necessary to understand how tree regeneration and understory plants interact in treeline ecotones. This is a necessary step towards assessing the sensitivity of FPE to climate change.

Methods

Study area

Two contrasting sites – Ordesa (O) and Tessó (T) – were selected among a network of undisturbed treeline ecotones in the central Pyrenees in Spain (Gil-Pelegrín and Villar 1988). They showed contrasting and extreme characteristics (topography, climate,

Table 1. Geographic, topographic and structural characteristics of the studied ecotones (sites O and T).

Characteristics	Ordesa	Tessó
Latitude	42°37' N	42°36' N
Longitude	00°02' W	01°03' E
Treeline / timberline elevations (m a.s.l.)	2110 / 2100	2360 / 2330
Mean slope (°) / aspect	17 / S	27 / NE
Mean (\pm SE) height (m)	1.56 \pm 0.12	4.00 \pm 0.29
Basal area (m ² · ha ⁻¹)	8.87	12.10

vegetation, soil) within this network (Table 1). The comparison of these FPEs will serve as an approximate description of the spatial structure of the wide spectrum of FPEs in the Pyrenees. Site O is located on calcareous limestone and acid sandstones (Ríos et al. 1982), but site T bedrock is mainly composed of calcareous shales (Ventura 1992).

Both sites are in the buffer zones of two National Parks (Ordesa-Monte Perdido, site O; Aigüestortes-Estany de St. Maurici, site T) which we considered a guarantee that recent human activity would diminish further. The present stocking rates are below 3 LAU · month⁻¹ · ha⁻¹ (1 LAU (Large Animal Unit) = 8 sheep or 1 cow, following Aldezabal et al. (1992) and Bas et al. (1994)). Around site O, there has been a 60 % decrease in the number of livestock during the last 30 years (M. Etxebarria, pers. comm.). In fact, at site O, only 14 (2.18 % 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 eighteenth century, according to local historical documentation (Bringue 1995). No evidence of recent fires (fire scars, charcoal) was found at either sites. No treeline shift could be discerned on comparing aerial photographs of the two sites from the last 50 years. Overall, we consider that the ecotone structure has not been affected by local human disturbances in both sites.

Climate

At site O, the climate is continental (Góriz meteorological station, 2215 m a.s.l., 42°39' N, 00°01' E; 1981–89 and 1992–95 data). The total annual precipitation is \approx 1600 mm, with high interannual variation. The total monthly precipitation has an autumn maximum. The maximum winter snow thickness is within the range 1.0–2.0 m. Snow precipitation may

be nil in some winters and it is higher in spring than in winter. The mean annual temperature is $\approx 5^\circ\text{C}$. The lowest and highest mean monthly temperatures are -1.92°C (February) and 13°C (July), respectively (Balcells and Gil-Peigrín 1992). From December 1992 to April 1995, the maximum wind speed measured at the Góriz station was 25.7 m s^{-1} (NW, March).

At site T, the climate is continental and characteristic of a subalpine area (Estერი station, 1054 m a.s.l., $42^\circ37'$ N, $01^\circ07'$ E, 1970–97 data). The estimated mean annual precipitation is $\approx 1600\text{ mm}$ ($\approx 48\%$ as snow). The maximum snow precipitation is in winter. The maximum winter snow thickness is within the range 1.5–3.0 m. The estimated mean annual temperature is $\approx 3^\circ\text{C}$. The minimum and maximum mean monthly temperatures are $\approx -4^\circ\text{C}$ (January) and $\approx 12^\circ\text{C}$ (July). The prevailing winds come from the NW-W at both sites. 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 probability of avalanches is high (Furdada i Bellavista 1996), mainly because of its very steep slopes (the maximum slope in the plot was 34°).

Vegetation

Pinus uncinata Ram. is the dominant tree species of most of the Pyrenean treelines (Cantegrel 1983). This species reaches its southern limit of distribution in the Iberian Peninsula, where it colonizes all kinds of soils (Ceballos y Fernández de Córdoba and Ruiz de la Torre 1979). *P. uncinata* is a pioneer and shade-intolerant species (Cantegrel 1983). Its seedlings are resistant to winter desiccation and frost even when snow cover is poor (Frey 1983).

At present, *P. uncinata* timberlines and treelines in the Central Pyrenees reach maximum elevations of 2500 and 2700 m a.s.l., respectively (Carreras et al. 1995). Some alpine FPEs in the Pyrenees follow the typical structural sequence of growth forms from vertical unstemmed trees close to the timberline to shrubby multistemmed krummholz forms above the treeline (Gil-Peigrín and Villar-Pérez 1988). In the Pyrenees, few of these ecotones have not been affected by local anthropogenic disturbances (fire, logging). *P. uncinata* forests are now reported to be recolonizing many subalpine pastures in the Pyrenees due to grazing reduction and, possibly, improved climatic conditions (Soutadé et al. 1982).

Table 2. Relative average elevation and cover values (%) of the most abundant understory plant species ($> 3\%$ cover) across the treeline ecotones in sites O and T. The distribution is given as the mean coordinate of the contacts (\pm SE, in m) for a given species along the plot axis parallel to the slope ($y = 0$ –140 m, greater values of y correspond to lower altitudes) and averaged over 6 elevational transects per site.

Species	Cover (%)	Distribution (m)
Site O		
<i>Carex sempervirens</i> Vill.	13.91	35 ± 2
<i>Calluna vulgaris</i> (L.) Hull	23.19	46 ± 2
<i>Festuca rubra</i> L.	27.35	66 ± 2
<i>Nardus stricta</i> L.	3.33	90 ± 6
<i>Vaccinium myrtillus</i> L.	4.28	120 ± 2
Site T		
<i>Dryas octopetala</i> L.	4.88	30 ± 2
<i>Festuca gautieri</i> (Hackel) K. Richt.	12.13	75 ± 2
<i>Rhododendron ferrugineum</i> L.	20.57	77 ± 2
<i>Vaccinium myrtillus</i> L.	15.82	89 ± 2

The understory vegetation at site O is dominated by *Festuca rubra* L. and *Calluna vulgaris* L. A dense understory dominated by *Rhododendron ferrugineum* L. and *Vaccinium myrtillus* L., typical of longer and deeper snow cover sites, is found at site T (Table 2).

Tree distribution and structure

At each site a rectangular plot ($140\text{ m} \times 30\text{ m}$) was placed in topographically uniform parts of the FPE with its longer side parallel to the maximum slope. The plot included current treeline and timberline. The current altitudes of the treeline and timberline were measured in the field (altimeter calibrated against topography map, accuracy of $\pm 1\text{ m}$). At both sites, point $(x, y) = (0, 0)$ is located in the upper right corner looking upslope. At site T, the $(30, y)$ -side is located near an avalanche gully.

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 1.3 m above the base (diameter at breast height, dbh), maximum stem height (h), and total number and type (arborescent or stunted) 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.

All individuals in the plot were grouped in five size classes following Bosch et al. (1992): adults (A), $\text{dbh} > 17.5\text{ cm}$; poles (P), $7.5 < \text{dbh} \leq 17.5\text{ cm}$; sap-

lings (S), $\text{dbh} \leq 7.5$ cm and $h > 0.5$ m; seedlings (SE), $h \leq 0.5$ m; and dead individuals (D). Two additional growth-form classes were specified for site O: krummholz (K) and flagged multistemmed 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 (KM) develop arborescent shoots above the snowpack and maintain a dense mat-like infranival growth composed of shrubby stems. At site O, we considered K individuals as being those with $h \leq 0.5$ m that showed asymmetrical growth and multistemmed development (Daly and Shankman 1985). To check for spatial independence, we excavated several tree clumps at site O. To summarize the spatial diversity of size and growth-form classes across the ecotone, the Shannon-Wiener index (H , $\text{bits} \cdot \text{ind}^{-1}$; Shannon and Weaver (1949)) was computed for all size and growth-form classes and individuals every 2 m along the longest side of the plot (y). At site T, we estimated nondestructively the ages of young individuals (mainly saplings and seedlings) 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 multistemmed character of most of the individuals.

Understory vegetation

To estimate vegetation and substrate cover, we used the point method (Barbour et al. 1987). We laid over the ground a sampling grid formed by 6 transects along the maximum slope (y axis). Transects were located every 6 m perpendicular to the slope (x axis) going downslope from the upper edge of the plot ($y = 0$, above treeline) to the lower edge ($y = 140$, forest). Cover was estimated from the number of contacts of *P. uncinata* individuals (overstory), understory vegetation (shrub and herbaceous species recorded individually) and substrate with a metal rod placed every 1 m along the y axis. At both sites, we recorded all plant species encountered in point sampling. In site O, we grouped all shrub and herbaceous species to obtain a plant cover value for later analyses because of the high diversity and relatively low cover values of the understory species (94 % of the species showed cover values $< 5\%$). At this site, understory and substrate types were grouped into five classes: vegetation (shrubs and herbs), rock (diameter > 1 dm), gravel

(diameter ≤ 1 dm), bare soil, and organic matter. The same classes were used at site T, but considering only those understory species whose cover values were $> 3\%$.

The diversity of shrubs and herbs was characterized using the Shannon-Wiener diversity index (H) as a synthetic measure of community structure, because it reduces the effect of rare species (Margalef 1974; Pielou 1975). Botanical nomenclature follows de Bolós et al. (1993). To summarize the relationships between structural variables, we calculated Spearman's rank correlation coefficients (r_s). To compare the average values of variables, the non-parametric Mann-Whitney U -test was used (Sokal and Rohlf 1995).

Results

Spatial distribution of size and growth-form classes

At site O, krummholz and seedlings predominated in the upper areas of the FPE, while adults were more abundant in the lower parts (Figure 1). The first case produced minimum values of diversity ($\text{bits} \cdot \text{ind}^{-1}$) of size and growth-form classes. Flagged krummholz, saplings and poles occupied intermediate positions (Figure 1). Krummholz and seedlings showed overlapping maximum densities in the upper half of the FPE. The maximum diversity of size and growth-form classes coincided with the end of dominance of flagged krummholz and the beginning of the krummholz forms ($y \approx 75$ m). A second diversity maximum ($y \approx 96$ m) corresponded to the presence of intermediate classes in the lower half of the FPE (Figure 1).

At site T, only seedlings and adults occupied contrasting areas, reaching maximum densities in the upper and lower parts of the FPE, respectively (Figure 2). There were more dead individuals but fewer saplings and seedlings close to the avalanche gully side (30, y) of the plot. Maximum values of diversity of size and growth-form classes appeared in the upper half of this FPE due to the overlap of most size and growth-form classes (Figure 2). The dominance of adults and saplings below the timberline produced several diversity minima. At both sites, dead individuals were present across the ecotone.

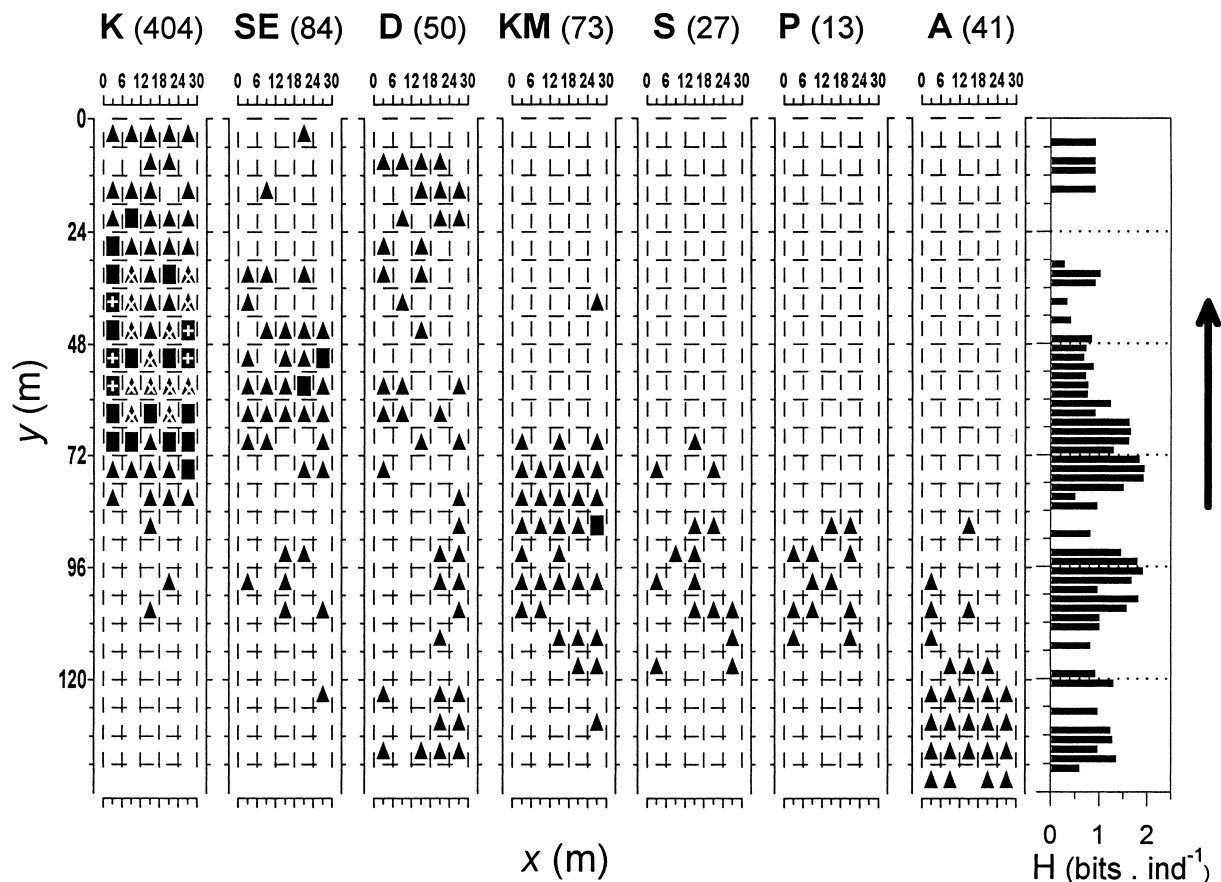


Figure 1. Distribution of *P. uncinata* individuals by different size and growth-form classes along the alpine forest-pasture ecotone at site O. The bars figure shows the diversity of growth-form classes (H) across the ecotone (calculated every 2 m along the y-axis). The arrangement of the different classes from right to left follows increasing density values upslope. Abbreviations for size and growth-form classes: Krummholz (K), seedlings (SE), dead individuals (D), flagged krummholz (KM), saplings (S), poles (P), and adults (A). The numbers in parentheses are the total number of individuals for each class. Densities are expressed as number of individuals in $6\text{ m} \times 6\text{ m}$ quadrats (36 m^2): 0–4 (triangles), 5–9 (squares), 10–14 (triangles with white sails), and 15–25 (squares with white crosses) individuals $\cdot 36\text{ m}^{-2}$. The maximum was reached by K (21 ind. $\cdot 36\text{ m}^{-2}$). The black arrow points upslope.

Substrate, understory and regeneration

At site O, organic matter and *P. uncinata* cover increased going downslope while rocky substrates decreased. At this site, the presence of organic matter was positively related with *P. uncinata* cover. Plant cover and organic matter substrates were weakly and positively related. At site T, the cover of *P. uncinata*, *R. ferrugineum* and *V. myrtillus* were positively related and increased going downslope while that of *Dryas octopetala* L. decreased (Table 3). Seedling frequency was non-significantly related with *P. uncinata* cover in any sites (Ordesa, $r_s = -0.40$, $P = 0.15$; Tessó, $r_s = -0.43$, $P = 0.13$, $n = 14$ in both cases).

The species diversity values decreased going downslope in both sites coinciding with the increase

of *P. uncinata* cover and associated substrates (e.g., organic matter in site O) or plants (e.g., *V. myrtillus* and *R. ferrugineum* in both sites; Tables 2 and 3). At the site O, the decrease was steep and spatially heterogeneous (Figure 3). At site T, the change was abrupt though smaller (Figure 4). The total number of identified shrub and herbaceous species recorded in sites O and T were 40 and 25, respectively (Table 4). Overall, the site O reached higher and lower mean values of diversity for the elevational belts than the site T (Figures 3 and 4), but the mean of all diversity values was not significantly different between sites ($P = 0.52$, $n = 14$). At site O, no significant differences were found for all comparisons among mean values of diversity for the six transects. At this site, the maximum values of diversity were found in the upper area

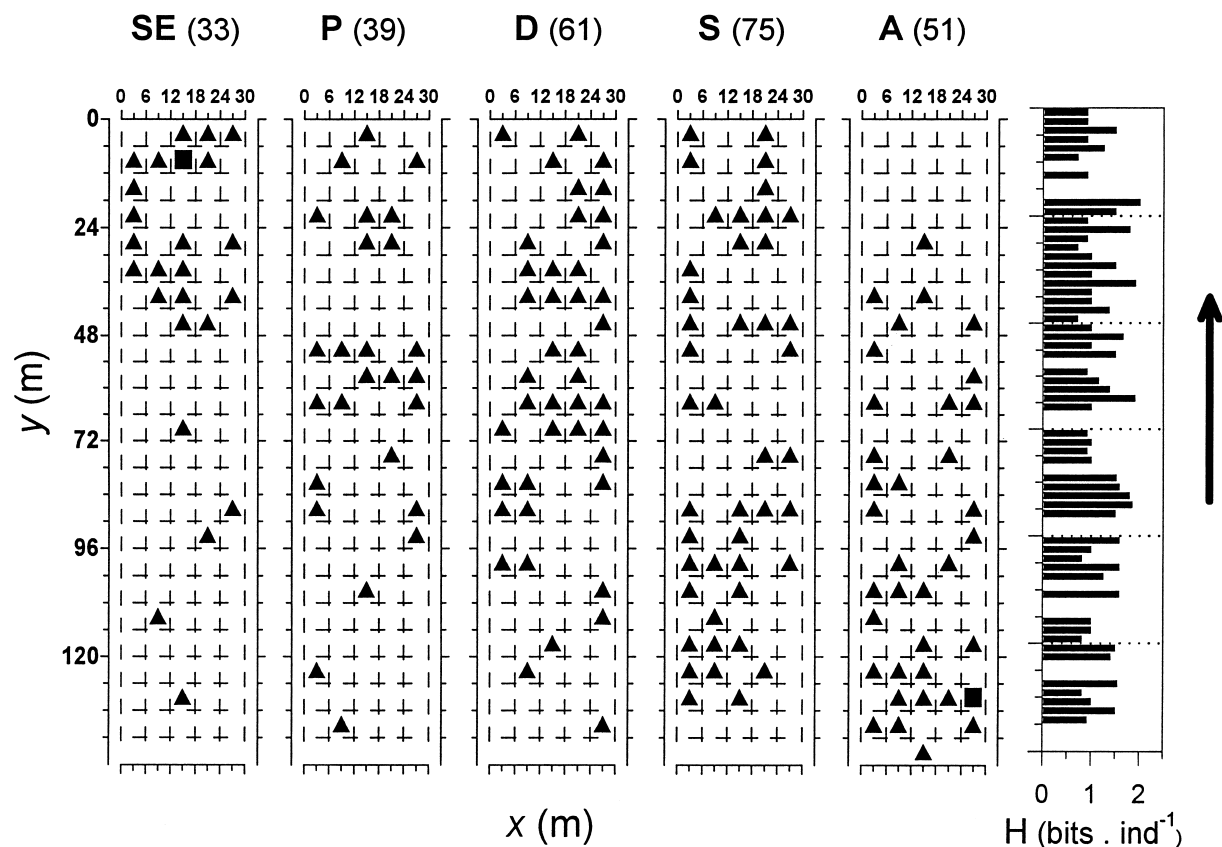


Figure 2. Distribution of *P. uncinata* individuals by different size and growth-form classes along the alpine forest-pasture ecotone at site T. The bars figure shows the diversity of growth-form classes (H) across the ecotone (calculated every 2 m along the y -axis). The arrangement of the different classes from right to left follows increasing density values going upslope. The numbers in parentheses are the total number of individuals for each class. Abbreviations for size and growth-form classes are the same as in Figure 1. Densities are expressed as number of individuals in $6\text{ m} \times 6\text{ m}$ quadrats: 0–4 (triangles), and 5–9 (squares) individuals $\cdot 36\text{ m}^{-2}$. The black arrow points upslope.

($y = 20\text{--}30\text{ m}$) of the central ($x = 18\text{ m}$) transect ($H = 3.12\text{ bits} \cdot \text{ind}^{-1}$). Rocky surfaces were also more abundant in the central parts of the ecotone following the shortest axis ($x = 12\text{--}18\text{ m}$), which had the minimum averages of organic matter, and pine cover. At site T, there was a diversity gradient perpendicular to the slope (x -axis). We found a significantly ($P \leq 0.05$) higher number of plant species in the transects close to an avalanche gully ($x = 18\text{--}30\text{ m}$, 16 species) than those near a rocky stream ($x = 0\text{--}12$, 12 species), these being the maximum and minimum values for all transects, respectively.

Discussion

The change from smaller to bigger individuals along the forest-pasture ecotone was more gradual at site T than at site O. The sequence of size and growth-form

classes descending along the ecotone at site O formed distinct groups following a sequence of decreasing size with increasing elevation (adults \rightarrow poles \rightarrow saplings \rightarrow seedlings; see “diagonal” distribution in Figure 1). This site was characterized by a gradual change in forms from shrubby multistemmed krummholz above the treeline to intermediate forms (flagged krummholz) and, finally, bigger arborescent unstemmed individuals (adults and poles) at timberline and in the forest. However, at site T there was not such a clear gradient because of the overlapping distribution of the size and growth-form classes along the ecotone (Figure 2). This spatial heterogeneity and the elongation of tree groups is explained by the importance of snow avalanches at this site (Furdada i Bellavista 1996). Overall, the distribution of the different size and growth-form classes along the slope was segregated at site O and overlapping at site T (Figures 1 and 2).

Table 3. Relationships among mean position across the ecotone (y , plot axis parallel to the slope; greater values of y correspond to lower altitudes), cover values of the most abundant substrates and understory species and diversity indices for sites O (values above the diagonal) and T (values below the diagonal). All values were calculated every 10 m following the y -axis ($n = 14$ in all cases). Only correlations with $P \leq 0.05$ are reported (Spearman's coefficient of rank correlation, r_s). The correlations among cover values of herbaceous and shrub species or among substrates are not displayed because they are interrelated due to the sampling procedure. Variable abbreviations: R, rocky substrate (only in site O); Om, organic matter substrate; *P. u.*, *P. uncinata* cover; H, diversity (Shannon Wiener index); Plant, cover value of all herbaceous and shrub species taken together (only in site O); Soil, bare soil substrate (only in site O); *D. o.*, *D. octopetala* (only in site T); *R. f.*, *R. ferugineum* (only in site T); *V. m.*, *V. myrtillus* (only in site T).

Site O	y	R	Om	<i>P. u.</i>	H	Plant
Site T						
y	–	–0.65*	0.82***	0.88***	–0.84***	
R		–		–0.61*	0.57*	–0.60*
Om			–	0.88***	–0.73**	
<i>P. u.</i>				–	–0.72**	
H					–	
<i>D. o.</i>					–0.88***	0.83***
<i>R. f.</i>					0.53*	–0.65*
<i>V. m.</i>					0.90***	–0.80***
Soil						0.62*

* $0.01 < P \leq 0.05$, ** $0.001 < P \leq 0.01$, *** $P \leq 0.001$

In treeline environments the survival of supranival arborescent stems depends on winter climatic variables, such as wind velocity and direction, temperature and snow thickness (Lavoie and Payette 1992). The occurrence of arborescent individuals that were previously krummholz forms (they have remains of krummholz characters such as shrubby basal branches), similar to our flagged krummholz forms, has also been described at alpine *Nothofagus* timberlines (Norton and Schönerberger 1984). At site O, the mean height of the shrubby leafy base of stunted individuals is close to that of the mean monthly maximum snowpack (usually April). This structural characteristic and the predominance of shrubby individuals at site O suggest an important interaction between these growth forms and regeneration. Krummholz forms can modify microenvironmental conditions (wind, microclimate, snow thickness, soil temperature; Hadley and Smith (1987); Scott et al. (1993)) and favour the establishment of seedlings.

Krummholz forms are a local phenomenon at site O in comparison with more extensive surveys of treeline ecotones in the Pyrenees (Gil-Pelegrín and Villar-Pérez 1988). This is due to the strong winds

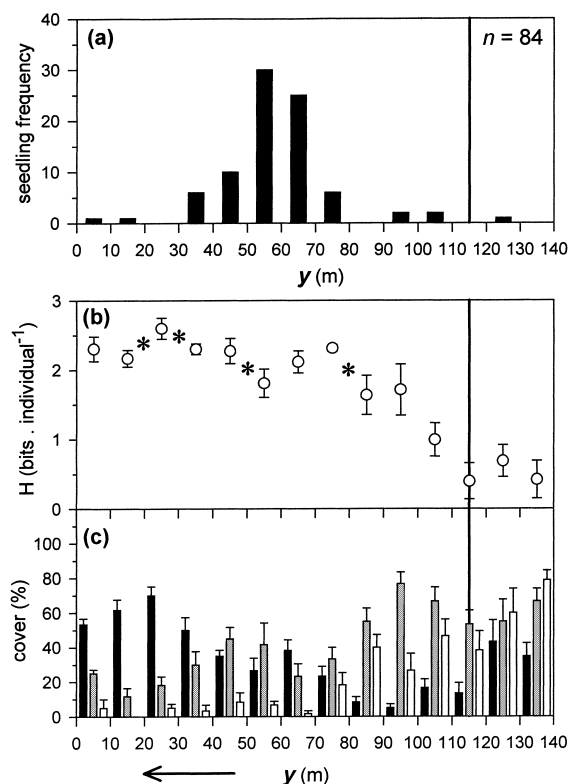


Figure 3. Seedling frequency (a), diversity of plant species (b, Shannon–Wiener's), and percentage cover (c) of rock (black fill) and organic matter (gray fill) substrates, and *P. uncinata* cover (white fill) every 10 m going downslope for the alpine forest–pasture ecotone at site Ordesa. The asterisks correspond to significantly (Mann–Whitney U -test, $P \leq 0.08$, $n = 6$) different comparisons between contiguous mean values of diversity. The vertical line shows the timberline mean location. The black arrow points upslope. The error bars are standard errors.

and topographic conditions in this ecotone. Dense and compact krummholz mats enhance snow accumulation, thus reducing wind abrasion and needle dehydration (Tranquillini 1979; Hadley and Smith 1987; Grace and Norton 1990). Both effects increase survival probability and allow shrubby individuals to reach higher elevations than the arborescent forms.

Rocks were a very abundant substrate at site O and their cover decreased descending along the forest–pasture ecotone (Figure 3). At this site, rocky substrates were associated with the presence of krummholz forms (Figures 1 and 3). The maximum densities of krummholz forms and seedlings at site O coincided. This again suggests that krummholz may modify microenvironment conditions to the benefit of regeneration (“nurse effect”). The positive relationship between *P. uncinata* cover and the presence of organic matter in the substrate (mainly composed of

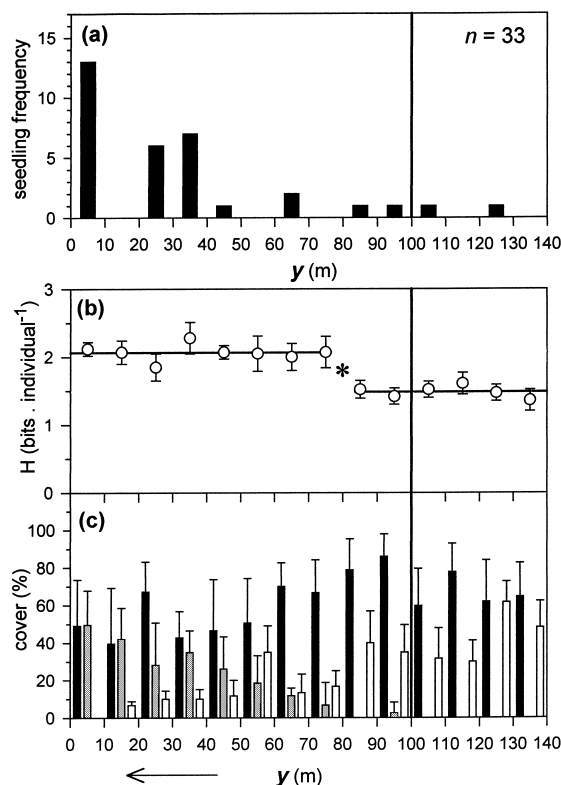


Figure 4. Seedling frequency (a), diversity of plant species (b, Shannon-Wiener's H index), and percentage cover (c) of *R. ferrugineum* (black fill), *D. octopetala* (gray fill), and *P. uncinata* (white fill) every 10 m going downslope for the alpine forest-pasture ecotone at site Tessó. The dark gray lines in the middle plot show the decrease from the mean of diversity values for the upper ($y = 0-80$ m) and lower ($y = 90-140$ m) parts of the ecotone. The breaking point of the gray lines (asterisk) corresponds to the only significantly (Mann-Whitney U -test, $P = 0.06$, $n = 6$) different comparison between contiguous mean values of diversity. The rest of symbols are like in Figure 3.

dead needles), suggested the important role of trees as modifiers of microenvironmental conditions within these ecotones (Table 3).

At site O, plant species characteristic of wind-exposed sites were present (e.g., *Thymelaea nivalis* (Ram.) Meissn. in DC). This site is also characterised by its great edaphic heterogeneity (calcareous limestone and acid sandstone). Both acidophilous (e.g. *Calluna vulgaris*) and basophilous (e.g. *Sideritis hysopifolia*) plants were found above treeline in the ecotone (Tables 2 and 4). The high spatial variability of plant diversity suggests that the spatial distribution of plants may be due in part to edaphic factors (Figure 3). For instance, the plant diversity increased at the upper side of the plot. Botanical studies per-

formed at similar pastures growing on calcareous limestones showed the high diversity of these plant communities (Villar-Pérez and Benito-Alonso 1994). These factors could interact with microclimatic conditions related with the presence of krummholz, tree patches or forest. Future studies should estimate how this edaphic heterogeneity affects the plant community in this treeline ecotone.

Contrastingly, site T had the typical understory of a north-facing subalpine *P. uncinata* community dominated by *R. ferrugineum* (*Rhododendro ferrugini-Pinetum uncinatae*, Rivas Martínez (1968)). The diversity and cover of the understory were related to the spatial distribution of regeneration at site T (Figure 4). At this site, shrub and herb diversity decreased descending across the ecotone. Seedlings were abundant above treeline, where *D. octopetala* dominated and *R. ferrugineum* was locally absent. This decrease and the presence of gaps within the dense mats of *R. ferrugineum* may allow the regeneration of *P. uncinata*, a shade-intolerant species. It has been described how *R. ferrugineum* and other ericaceous shrubs (e.g., *Arctostaphylos uva-ursi* L. (Spreng.)) can form dense mats which prevent the establishment of *P. uncinata* seedlings (Baudière and Fromard 1988; Pornon and Doche 1995). This is supported by previous research by Puig (1982), who found that the main factors favouring *P. uncinata* regeneration in the east Pyrenees were: low to moderate tree densities, low herbaceous cover, non-compacted soils, high soil moisture, and reduced grazing pressure.

The studied ecotones could be compared with the contrasting types of community boundaries proposed by van der Maarel (1990): site O is closer to the ecotone concept, where structural changes are abrupt and produce distinct groups or "belts" of individuals perpendicular to the slope (e.g., krummholz), while site T represents an ecocline, where transitions are gradual (gradient zone) and size and growth-form classes overlap along the ecotone creating greater spatial heterogeneity. For site O, we have shown the structural changes in size and growth form across the forest-pasture ecotone. These changes could represent an analogue of temporal processes as the different growth forms develop in response to climatic conditions. In both ecotones, the elevational gradient affects the distribution of the different size and growth-form classes but local factors, such as wind at site O or avalanches at site T, greatly modify this pattern.

Table 4. List of less abundant (cover \leq 3%) shrubs and herbs species recorded at sites O and T. Plant species are classified according to their presence: mainly above or below timberline (forest), respectively. See also Table 2.

	Site O	Site T
Above timberline (pasture)	<i>Agrostis rupestris</i> All., <i>Alchemilla alpina</i> L., <i>Allium senescens</i> L. subsp. <i>montanum</i> (Fries) Holub, <i>Antennaria dioica</i> (L.) Gaertn., <i>Anthoxanthum odoratum</i> L., <i>Anthyllis montana</i> L., <i>Arabis serpillifolia</i> Vill. subsp. <i>serpillifolia</i> , <i>Aster alpinus</i> L., <i>Bupleurum ranunculoides</i> L. subsp. <i>gramineum</i> (Vill.) Hayek, <i>Campanula rotundifolia</i> L., <i>Danthonia decumbens</i> (L.) DC. in Lam. et DC., <i>Deschampsia flexuosa</i> (L.) Trin., <i>Erigeron uniflorus</i> L., <i>Eryngium bourgatii</i> Gouan, <i>Geranium cinereum</i> Cav. subsp. <i>cinereum</i> , <i>Globularia repens</i> Lam., <i>Oxytropis pyrenaica</i> Godr. et Gren., <i>Phyteuma hemisphaericum</i> L., <i>Plantago maritima</i> L. subsp. <i>alpina</i> (L.) O. Bolòs et J. Vigo, <i>P. monosperma</i> Pourr., <i>Potentilla alchemilloides</i> Lap., <i>Sedum hirsutum</i> All., <i>Sideritis hyssopifolia</i> L., <i>Thymelaea nivalis</i> (Ram.) Meissn. in DC.	<i>Anemone narcissiflora</i> L., <i>A. vernalis</i> L., <i>Botrychium lunaria</i> (L.) Swartz, <i>Carex sempervirens</i> Vill., <i>Daphne cneorum</i> L., <i>Dianthus hyssopifolius</i> L. subsp. <i>hyssopifolius</i> , <i>Galium pumilum</i> Murray, <i>Helianthemum nummularium</i> (L.) Mill., <i>Helictotrichon sedenense</i> (DC.) J. Holub, <i>Hieracium breviscapum</i> DC. in Lam. et DC., <i>H. lactucella</i> Wallr., <i>Iberis sempervirens</i> L., <i>Lotus corniculatus</i> L. subsp. <i>alpinus</i> (Schleich. ex Ser.) Rothm., <i>Primula elatior</i> (L.) L. subsp. <i>intrincata</i> (Godr. et Gren.) Widmer, <i>Pyrola chlorantha</i> Swartz, <i>Saxifraga moschata</i> Wulfen in Jacq., <i>Thymus serpyllum</i> L. subsp. <i>nervosus</i> (Gay ex. Willk.) Nyman, <i>Veronica bellidioides</i> L.
Below timberline (forest)	<i>Carlina acaulis</i> L., <i>Hieracium pilosella</i> L., <i>Hypochoeris radicata</i> L., <i>Jasione crispa</i> (Pourr.) Samp., <i>Juniperus communis</i> L. subsp. <i>communis</i> , <i>Meum athamanticum</i> Jacq. subsp. <i>athamanticum</i> , <i>Rhododendron ferrugineum</i> L., <i>Sedum album</i> L., <i>Seseli montanum</i> L., <i>Thymus serpyllum</i> L. subsp. <i>nervosus</i> (Gay ex. Willk.) Nyman, <i>Trifolium alpinum</i> L.	<i>Cruciata glabra</i> (L.) Ehrend., <i>Galium verum</i> L. subsp. <i>verum</i> , <i>Juncus trifidus</i> L.

Acknowledgements

We thank several anonymous reviewers for comments on earlier versions of this manuscript. We thank many people for their help, specially J.L. Benito, M. Ètxebarria, A. Ferré, E. Muntán, J.M. Ninot, M. Ribas, and M.A. Rodríguez. “Aigüestortes i Estany de Sant Maurici” and “Ordesa y Monte Perdido” National Parks provided logistic help. This research was funded by the Spanish Ministry of Education and Culture (CICyT Project AMB95-0160; F.P.I. grant AP93 72784356).

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