



ELSEVIER

Forest Ecology and Management 134 (2000) 1–16

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees

J. Julio Camarero^{a,*}, Emilia Gutiérrez^a, Marie-Josée Fortin^{b,1}

^aFaculty of Biology, Department of Ecology, University of Barcelona, Avda. Diagonal 645, 08028 Barcelona, Catalunya, Spain

^bDépartement de Biologie, Université de Sherbrooke, Québec, Canada J1K 2R1

Received 28 December 1998; received in revised form 12 July 1999; accepted 16 August 1999

Abstract

We describe the spatial structure of two contrasting subalpine *Pinus uncinata* forest-alpine grassland ecotones located in the Central Pyrenees (Ordesa and Tessó sites) as a preliminary step to infer the processes that produced their spatial patterns. All trees were mapped and measured within 4200 m² rectangular plots parallel to the maximum slope and encompassing timberline and treeline. The spatial description of the ecotones was accomplished using several methodologies. Point pattern analysis (Ripley's *K*) was first used to quantify the spatial pattern of trees using each stem *x*–*y* coordinates. Then, surface pattern analyses (Moran and Mantel spatial correlograms) were used to quantify the spatial pattern of tree characteristics across the ecotone (size, growth-form, estimated age). In the Ordesa site, krummholz individuals showed significant and positive spatial interaction with seedlings. In this site, *P. uncinata* individuals evolved from shrubby to vertical growth-forms abruptly, producing a steep spatial gradient. In the Tessó site, regeneration was concentrated near the treeline and the spatial gradient was gradual. Both ecotones formed ~45 m long zones of influence along the slope based on different variables. Wind and snow avalanches seem to be the main controlling factors of the spatial pattern of trees in the sites Ordesa and Tessó, respectively. Our results point out potential different responses of treeline populations to environmental changes according to the spatial pattern. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Ecotone; Treeline; *Pinus uncinata* Ram.; Ripley's *K*; Moran and Mantel correlograms; Spatial pattern

1. Introduction

Altitudinal treelines are part of the subalpine forest-alpine grassland ecotones which are considered dynamic zones potentially sensitive to monitor climate change effects (Brubaker, 1986; Kullman, 1990;

Hansen and di Castri, 1992). However, there is a great uncertainty about the suitability of treeline shifts to monitor the response of tree populations to climate change (Noble, 1993). The complex responses of forest–grassland ecotones to climate change are described by the numerous works in treeline dynamics. These include: examples of tree invasion of tundra or alpine meadows (Wardle and Coleman, 1992; Rochefort et al., 1994), changes in tree growth-form as the increase in height from krummholz to vertical tree (Lavoie and Payette, 1994; Lescop-Sinclair and Payette, 1995; Weisberg and Baker, 1995a), and variations of the density or

* Corresponding author. Tel.: +34-93-4021508; fax: +34-93-4111438.

E-mail address: chechu@porthos.bio.ub.es (J.J. Camarero)

¹Present address: Département de Géographie, Université de Montréal, C P 6128, Succ. Centre-Ville, Montréal, Québec, Canada H3C 3J7.

of the latitudinal or altitudinal position of the ecotone (Gorchakovskiy and Shiyatov, 1978; Kullman, 1979, 1990; Morin and Payette, 1984; Payette and Filion, 1985; Weisberg and Baker, 1995b; Lloyd, 1997; Lloyd and Graumlich, 1997). The growth and density changes in the forest-alpine grassland ecotones seem to be more suitable variables for monitoring climate change than treeline shifts (Noble, 1993).

Nevertheless, while some of the mentioned studies of treeline dynamics have analyzed spatial variation at different spatial scales, none of them have considered space as a main controlling factor (Veblen, 1979; Légère and Payette, 1981; Payette and Filion, 1985; Kullman, 1991; Arseneault and Payette, 1992, 1997; Lavoie and Payette, 1992; Earle, 1993; Weisberg and Baker, 1995a, 1995b; Lloyd, 1996). In addition, there is a lack of information on the spatial structure of forest limits in the Pyrenees (Cantegrel, 1987).

The description of the spatial pattern of the plant community is a necessary step to understand its dynamics (Watt, 1947). In this study, the structure of the subalpine forest-alpine grassland ecotone will be described quantifying the spatial autocorrelation of several tree characteristics like density, size, and age (Fortin et al., 1989; Duncan and Stewart, 1991; Brodie et al., 1995; Kuuluvainen et al., 1998). Spatial autocorrelation may result from beneficial regeneration near parents (positive autocorrelation, aggregation) or from competition (negative autocorrelation, avoidance) (Sokal and Thomson, 1987; Legendre, 1993). In spite of the possibility of different processes producing the same pattern, spatial autocorrelation analysis can generate hypotheses as to causative processes (Legendre and Fortin, 1989; Legendre, 1993; Thomson et al., 1996).

The objectives of this study are: (i) to describe the point pattern of *P. uncinata* tree-classes grouped according to their size and growth-form, using each tree stem x - y coordinates (Ripley, 1981; Duncan and Stewart, 1991), and (ii) to quantify the surface pattern of several variables (size, growth-form, age) of these tree-classes across two contrasting subalpine forest-alpine grassland ecotones. The description of the spatial patterns can generate hypotheses about the environmental variables that influence more the spatial structure of these ecotones.

2. Material and methods

2.1. Tree species

P. uncinata Ram. forms most of the Pyrenees treelines. During the late-glacial, *P. uncinata* timberlines were below 1700 m asl in the Central meridional Pyrenees because of cooler climatic conditions (Montserrat, 1992). In the Central Pyrenees, current *P. uncinata* treelines and timberlines reach up to 2700 m and 2350–2500 m asl, respectively (Bolós et al., 1993; Carreras et al., 1995). The structure of some forest–grassland ecotones in the Pyrenees follows the typical sequence of growth-forms from vertical trees close to the timberline (limit of closed forest) to krummholz growth-forms above the treeline (a tree is defined as a vertical individual with a stem at least 2 m high) (Hustich, 1979). In a few places, the upper timberline in the Pyrenees has remained relatively undisturbed by local anthropogenic disturbances such as logging and fires (Gil-Pelegrín and Villar-Pérez, 1988). In many sites the forest is now recolonizing subalpine grasslands (Soutadé et al., 1982).

P. uncinata is a pioneer, evergreen and shade-intolerant conifer, as is shown by its dependence on disturbances for regeneration (Bosch et al., 1992). This species regenerates mostly sexually and its light seeds (8–9 mg) are mainly dispersed by the wind (Cantegrel, 1983). *P. uncinata* colonizes all kind of soils including those more eroded soils because of the adaptability of its mycorrhizal associations (Ceballos and Ruiz de la Torre, 1971; Cantegrel, 1983).

2.2. Study sites

The Ordesa site is an oromediterranean pine community mostly developed on sandstones and calcareous limestones. Tessó site bedrocks are mainly composed of intrusions of shales and calcopelites under strong decalcification processes due to high precipitation.

Both sites are situated in the Spanish Central Pyrenees that form the western main distribution area for *P. uncinata* (Sandoz, 1987). The Ordesa site is dominated by *P. uncinata* and *Juniperus communis* L. (Villar Pérez and Benito Alonso, 1994). The Tessó site is a subalpine forest developing a closed

0.50–0.75 m high understory composed of *Rhododendron ferrugineum* L. and *Vaccinium myrtillus* L., typical of sites with longer and deeper snow cover.

2.3. Field sampling

We placed a rectangular plot (140 m × 30 m) in each site across the forest–grassland ecotone with its longer side parallel to the maximum slope and where topography was uniform. The upper and lower edges of the plots include and abut on the treeline and the timberline, respectively. The position of all dead and living trees was recorded in Cartesian coordinates to the nearest 0.1 m. Point $(x, y) = (0, 0)$ is located in the upper right corner looking downslope. Current elevations of treeline, timberline, and the lower and upper parts of the plot were measured in the field (accuracy of ±1 m).

We measured for every tree inside the plot: position of the center of the tree (x and y coordinates), maximum diameter at stem base (db) and at 1.3 m above the base (diameter at breast height, dbh), maximum stem height, four radii of the vertical crown projection along the two directions marked by the plot axes, height of the lowest living branch, maximum number of needle cohorts retained in the branches (estimated leaf longevity), and number and type — vertical and stunted, living or dead — of stems in every tree (stem is any woody structure emerging directly from the base of the trunk and whose db ≥ 0.5 cm). We measured the height of all individuals except of those higher than 3 m whose heights were estimated visually (the measurement uncertainty for this estimation is around 15 cm for stems 3 m in height; Kullman, 1979). Basal area was calculated including bark.

We grouped trees in size and growth-form classes (Bosch et al., 1992): adults, dbh > 17.5 cm; poles, 7.5 < dbh ≤ 17.5 cm; saplings, dbh ≤ 7.5 cm and height > 0.5 m; seedlings, height ≤ 0.5 m; dead trees; krummholz; and flagged multistemmed krummholz that show a combination of prostrate and vertical stems. Flagged krummholz have several vertical shoots and a dense mat developed above and below the snowpack, respectively. In Ordesa site, trees with height less than 0.5 m that showed asymmetrical growth and multistemmed development were considered krummholz (Daly and Shankman, 1985).

Krummholz and flagged krummholz classes were not present in the Tessó site.

Many of the sampled trees are multistemmed in the Ordesa site, so we consider the center of these shrubby individuals to be the spatial center of the tree clump for practical reasons. We excavated superficially many tree clumps in this site to check for spatial independence among tree clumps. We estimated non-destructively the ages of seedlings, saplings and poles in Tessó site by counting the number of branch whorls and scars in the main stem. This procedure was not carried out in Ordesa site because of the multistemmed character of most of the trees that showed less evident scars and greater errors for age estimation. This methodology yields an underestimate of 0–5 years (McCarthy et al., 1991).

In both sites, we used a systematic sampling with six altitudinal transects parallel to the slope placed every 6 m in the direction perpendicular to the slope (x -axis). Points were sampled every 1 m, for a total of 846 sampling points. We recorded types of understory vegetation and substrate in the Ordesa site, grouping them in five qualitative classes: rocks, organic matter, bare soil, pine, and vegetation. We described and classified the substrate of every seedling to find out possible regeneration preferences. Botanical nomenclature follows Bolós et al. (1993) for vascular plants and Sandoz (1987) and Ceballos and Ruiz de la Torre (1971) for trees, respectively.

2.4. Substrate and understory

Both sites showed typical subalpine communities with *P. uncinata* as the dominant tree, but density of living individuals was much higher in the Ordesa site due to the abundance of shrubby and multistemmed krummholz forms (Table 1). The Tessó site contained understory species typically found in north-facing *P. uncinata* communities like: *R. ferrugineum*, *V. myrtillus*, and *Festuca gautieri* (Hackel) K. Richt. The subalpine and alpine grasslands species (e.g., *Dryas octopetala* L.) appeared predominantly in the upper part of Tessó site.

The Ordesa site was a south-facing *P. uncinata* community. We found similar subalpine plants (e.g., *R. ferrugineum*) but combined with oromediterranean species (*Leontopodium alpinum* Cass., *Thymelaea tinctoria* subsp. *nivalis* (Ramond) Nyman, *Astragalus*

Table 1

Geographic, topographic and structural characteristics of the studied forest–grassland ecotones in the Central Pyrenees (Ordesa and Tessó sites) where K represents krummholz and S for saplings

Characteristics	Ordesa	Tessó
Latitude	42°37'N	42°36'N
Longitude	00°02'W	01°03'E
Range of plot elevations (m asl)	2124–2084	2359–2295
Mean slope (°)	16.6	27.2
Aspect (°)	186	42
Maximum treeline/timberline elevations (m asl)	2110/2100	2360/2330
Density of living/dead trees (no. per hectare)	1529/119	471/145
Mean (\pm SE) height (m)	1.56 \pm 0.12	4.00 \pm 0.29
Mean (\pm SE) number of stems per tree	5.00 \pm 0.25	1.00 \pm 0.06
Number of individuals of the most abundant tree-class (percentage respect total number in plot)	K-404 (58.38%)	S-75 (28.96%)
Basal area (m ² ha ⁻¹)	8.87	12.10

sempervirens Lam. and *F. gautieri*). Rocks and organic matter, mainly derived from pine needles, formed most of Ordesa site substrate. A more detailed description of the plots and their substrate and understorey can be found elsewhere (Camarero and Gutiérrez, 1998b).

2.5. Climate

Climatic records from the Góriz station (2215 m asl, 42°40'N, 00°02'E; 1981–1989 and 1992–1995 data) describe the Ordesa site climatology. This climate could be described as continental with mediterranean influence. The mean annual temperature in Góriz is \approx 5.0°C. The lowest and highest mean monthly temperatures are -1.9°C (February) and 13.0°C (July), respectively (Balcells and Gil-Pelegrín, 1992). The mean annual precipitation is \approx 1600 mm with a seasonal distribution characterized by fall (32%) and spring (30%) maxima, winter (16%) and summer (22%) minima, and showing a high interannual variability. Snow precipitation is higher in spring than in winter and may be very low some winters. During the snow period (November–April), mean snow depth (\pm 1 SD) was only 36.6 ± 21.7 cm for the period 1980–1989. Monthly average maximum snowpack is \approx 125 cm (April). Prevailing dominant winds are from the northwest and west and can clear the snow present in many places in late winter and early spring. During the period 1993–1995, wind speed reached maximum values of 90 km h^{-1} (March 1995).

The Tessó site is under more oceanic influence than the Ordesa site. The estimation from several stations close to the study area (Estერი 1054 m asl, 42°38'N, 01°07'E, 1970–1997 data; Cavallers 1733 m asl, 42°35'N, 00°51'E, 1955–1972 data) gives a mean annual temperature of \approx 2.0°C at this site. Prevailing dominant winds are from the northwest and west. Estimated minimum and maximum mean monthly temperatures are \approx -4.0°C (January) and \approx 11.9°C (July), respectively. Estimated mean annual precipitation is over \approx 1500 mm, with \approx 48% falling as snow. Estimated monthly average maximum snowpack is \approx 180 cm (March or April). Dominant winds are from the northwest. The Tessó site shows a high risk of avalanches due to its great slope and NE aspect (Furdada Bellavista, 1996).

2.6. Disturbances

The selection of both sites considered their proximity to Ordesa y Monte Perdido (created in 1916; Ordesa site) and Aigüestortes i Estany de St. Maurici (created in 1955; Tessó site) National Parks as a prior guarantee of reduced recent human disturbances (Gil-Pelegrín and Villar-Pérez, 1988). Both sites are part of the respective park buffer zones. The present livestock in nearby areas are not high (8–24 and 2–6 sheep month ha⁻¹ in Ordesa and Aigüestortes parks, respectively; Aldezabal et al., 1992; Bas et al., 1994). The available historical documentation show relatively few local anthropogenic disturbances at either site

during the last 200 years. Some dead individuals in the lower edge of Ordesa site showed burnt wood due to a fire during the 1930s that affected the lower subalpine forest. However, a trend of increasing density is discernible in the Ordesa site. The Tessó site is not appropriate for logging because of poor access and has not been subject to local human disturbances like grazing since at least the 1790s (Bringue, 1995). No treeline/timberline shift was observed comparing 1946 (scale 1:43 000), 1957 (scale 1:32 000), 1986–1988 (scale 1:5000) aerial photographs for both sites.

3. Spatial analyses

3.1. Univariate point pattern analysis: Ripley's K -function

When the data resolution is at the x - y coordinate level, the presence of spatial autocorrelation can be tested using point pattern methods such as the $K(t)$ statistics (Ripley, 1981). The purpose of point pattern analysis is to establish if a spatial distribution of points is random or not, and to describe the type of pattern. To describe the spatial distribution patterns of *P. uncinata* tree-classes we used Ripley's $K(t)$ function which is based on the variance (second-order analysis) of all point-to-point (tree-to-tree) distances in a two-dimensional space (Ripley, 1977). This kind of analysis can identify different scales of spatial pattern and the distances where clustering or heterogeneity are significant (Duncan, 1991). Details for the calculation of an unbiased estimator of $K(t)$, modifications of this function and edge effects can be found elsewhere (Besag, 1977; Ripley, 1981, 1987; Diggle, 1983; Upton and Fingleton, 1985; Haase, 1995). In this study, we used the toroidal edge correction. The function $\lambda K(t)$, where λ is the intensity or density (mean number of trees per unit area), is defined as the expected number of trees within a distance t of a randomly chosen tree. In a random distribution, $K(t) = \pi t^2$. The function $K(t)$ uses all tree-to-tree distances to calculate a measure of spatial pattern at various distances t . Monte Carlo methods simulate randomly generated plots of the same dimensions as the empirical plot. We produced 99 simulations to compare the value of the function $K(t)$ with that expected from a randomly distributed group of points

and assess its significance ($P < 0.01$). The spatial pattern can then be described as clumped, random, or regular at any distance t up to half the length of the shortest rectangular plot side if the calculated $K(t)$ function is greater, equal or lower than the 99% confidence envelopes, respectively.

The statistical assumption of any spatial statistics is the stationarity (Legendre and Fortin, 1989). Therefore, the variable of interest must have a probability to occur over the entire area. To minimize the impact of lack of stationarity over the entire area, that crosses an ecotone where a high degree of variability is present, we limit our radius search to small distances.

3.2. Bivariate point pattern analysis: Ripley's K_{12} -function

To get information on the spatial relationships between tree-classes we examined bivariate spatial interactions using $K_{12}(t)$ function. This function is a generalization of $K(t)$ for a bivariate point process (Diggle, 1983; Upton and Fingleton, 1985). We calculated the 99% confidence intervals from 99 toroidal shifts of one class of trees with respect to the other. Values of $K_{12}(t)$ greater, equal or lower than the 99% confidence envelopes indicated positive association (attraction), spatial independence and significant negative association (repulsion) between the two tree-classes analyzed, respectively (Duncan, 1991). All possible combinations between two types of trees-classes were analyzed in both sites (21 and 10 comparisons for sites Ordesa and Tessó, respectively). Only those bivariate comparisons that showed some significant spatial interaction are presented.

3.3. Univariate surface pattern analysis: Moran's I

To quantify the surface pattern of several variables (size, growth-form, age) of the tree-classes, surface pattern methods can be used such as Moran's I (Legendre and Fortin, 1989). In this case, each variable (z) is attached to the coordinates of the tree (x, y) and each tree is considered to represent its surrounding portion of space. Moran's I spatial autocorrelation coefficient ranges from -1 to $+1$, with zero being the expected value for no spatial autocorrelation (Cliff and Ord, 1981; Upton and Fingleton, 1985). A graph showing how autocorrelation changes as a function of

distance, regardless of direction, is an all-directional spatial correlogram and it assumes isotropy for the variable analyzed. We used several equal distance classes to study the spatial distribution of the variables. Each correlogram has to be tested for global significance at the 5% level using Bonferroni procedures to correct for the dependence among the autocorrelation coefficients calculated for each distance class (Legendre and Fortin, 1989). In addition, each autocorrelation coefficient of the correlogram has to be tested to show that its value is significantly different from zero. Different shapes of all-directional spatial correlograms describe different spatial structures (Sokal and Oden, 1978; Legendre and Fortin, 1989). A spatial gradient produces a correlogram that starts with positive values at short distances (positive autocorrelation), crosses the abscissa axis at the expected value of null significant autocorrelation (average all-directional patch size), and ends with negative values for larger distance classes (negative autocorrelation). For globally significant correlograms, we interpret the shape of the curve only for the distance classes with 20 or more point pairs. Point pattern analysis and all-directional Moran correlograms were computed using R.P. Duncan's programs (1995, Spatial Analysis Programs, Dept. of Plant Science, Lincoln University, Canterbury, New Zealand).

3.4. Multivariate surface pattern analysis: Mantel correlogram

To quantify the surface pattern of a multivariate set of quantitative tree variables we used the normalized Mantel statistic. This statistic is based on Mantel tests (Legendre and Fortin, 1989). A graph of the Mantel statistic against distance classes gives a multivariate correlogram where each value has to be tested for significance (Legendre and Fortin, 1989). All-directional Mantel correlograms were computed using structural variables of trees (db, dbh, height, height of the lowest living branch, crown radii, number of stems, number of stem nodes and maximum number of needle cohorts) to identify the spatial structure for multivariate data in each ecotone. To compare spatial structures among tree-classes in the Ordesa site, the all-directional Mantel correlograms were calculated for different tree-classes (krummholz, flagged krumm-

holz and vertical trees — adults, poles, saplings, seedlings) because of the predominance of shrubby forms. To study the presence of spatial heterogeneity of size variables in the Tessó site, we computed an all-directional and directional Mantel correlograms for all living trees following directions parallel and perpendicular to the slope, respectively. Like univariate correlograms, the Mantel correlogram must be tested for overall significance using the Bonferroni method. We calculated the Mantel statistic at equal distance classes with the selected groups of variables using the R-Package for multi-dimensional and spatial analyses (Legendre and Vaudor, 1991). The interpretation of shapes of Mantel correlograms is similar to that for univariate correlograms and can be confirmed by maps and close inspection of the data.

4. Results

4.1. Univariate point pattern analysis

All tree-classes were significantly ($P < 0.01$) clumped in both sites but at different distances (Table 2). Only seedlings in the Tessó site and seedlings and krummholz in the Ordesa site were clumped at all distances up to 15 m (Table 2, Figs. 1 and 2). Overall, bigger trees showed clumped distributions at greater distances (Table 2). In the Tessó site, seedlings appeared predominantly above the treeline, in the upper part of the ecotone (Figs. 1 and 2), where the cover of *D. octopetala* and *R. ferrugineum* were maximum and minimum, respectively. In this site, the cover of *D. octopetala* was positively related with the number of *P. uncinata* seedlings every 10 m along the slope (Spearman's rank correlation coefficient, $r_s = 0.42$, $P < 0.15$, $n = 14$). In fact, 71% of all *P. uncinata* seedlings grew on a *D. octopetala* substrate. In the Ordesa site, no significant correlation was found between seedling density and any kind of substrate.

4.2. Bivariate point pattern analysis

In the Ordesa site, positive spatial association (attraction) was found for krummholz and seedlings at all distances but was significant ($P < 0.01$) only at 2 m (Table 3). Seedlings were abundant in the area where krummholz reached very high densities (3917

Table 2

Patterns of spatial dispersion for tree-classes in two Pyrenean forest–grassland ecotones: Ordesa (O) and Tessó (T) sites, where the symbols (+) indicate significant ($P < 0.01$) clumped distribution at distance t based on $K(t)$ function values distribution and (●) correspond to a random distribution (all analyzed classes have more than 15 individuals (n))

Site	Classes	n	t (m)														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
O	A	44	●	+	+	+	+	+	+	+	+	+	+	+	+	+	
	P	17	●	●	●	●	+	+	+	+	+	+	+	+	+	+	
	S	21	●	+	+	●	+	+	+	+	+	+	+	+	+	+	
	SE	80	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
	K	414	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
	KM	64	●	●	+	+	+	+	+	+	+	+	+	+	+	+	
	D	54	+	●	●	●	●	+	●	●	+	+	●	●	●	●	
T	A	56	●	●	●	+	+	+	+	+	+	+	+	+	+	+	
	P	36	●	+	+	+	+	+	+	●	●	●	●	●	●	+	
	S	66	+	+	+	+	+	+	+	●	●	●	●	●	●	●	
	SE	40	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
	D	59	●	●	●	+	+	+	+	+	+	+	+	+	+	+	

individuals ha^{-1}) forming a krummholz-belt ($y \approx 40–60$ m in Fig. 1). We obtained significant spatial attraction ($P < 0.05$) between krummholz and seedlings at 0.25 m and 1.75–3 m considering 0.25 m distance steps (data not shown).

We found different and significant ($P < 0.01$) spatial interactions between tree-classes in both sites (Table 3). Adults and seedlings were significantly segregated (repulsion) at distances 9–11 m and 14 m in the Ordesa site (Table 3; Fig. 1). A similar

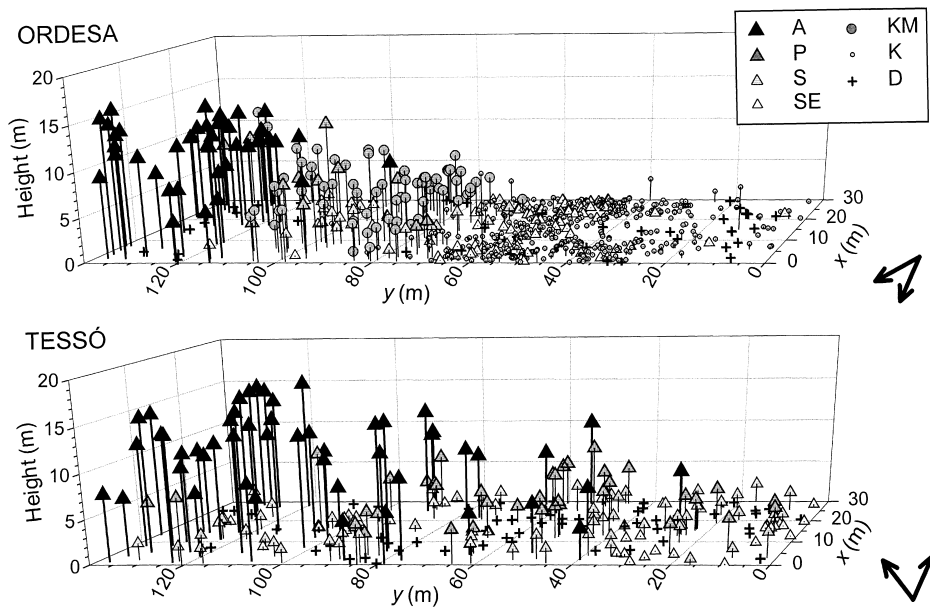


Fig. 1. Spatial location and height of all individuals in the sites Ordesa and Tessó. Abbreviations of the size and growth-form tree-classes: adults (A), poles (P), saplings (S), seedlings (SE), dead trees (D), krummholz (K) and flagged krummholz (KM). The black arrows show the directions of the dominant winds.

In the Tessó site, the correlograms for all living trees showed spatial gradients for the variables basal diameter, height and number of needle cohorts, but patchiness for estimated age. The distances of high positive autocorrelation values were 18–24 m for basal diameter; 6–12 m for height; 0–6, 24–30, 60–66 and 78–84 m for estimated age; and 0–6 and 24–30 m for number of needle cohorts. The patch sizes were: 48 m for basal diameter, ≈ 67 m for height, and ≈ 47 m for number of needle cohorts. The needle cohorts correlogram showed some patchiness superimposed over the spatial gradient. Estimated age showed a correlogram where positive and negative autocorrelation values alternate suggesting the existence of patches with a mean radius of 15–18 m.

4.4. Mantel correlograms

In the Ordesa site, the all-directional multivariate Mantel correlograms for structural variables of living trees (basal diameter, height, eastward and southward crown radii, needle cohorts and number of stems) were significant overall ($P \leq 0.05$). For any of the three subtransects of krummholz (0–10 m, 10–20 m and 20–30 m wide), the Mantel correlograms indicated the existence of steep gradients with a mean influence area of ≈ 23 m, where the positive autocorrelation finished (Fig. 3). The first significant negative autocorrelation values were reached at ≈ 33 , ≈ 24 and ≈ 42 m for krummholz trees located at 0–10 m, 10–20 m and 20–30 m subtransects, respectively (Fig. 3). This last result suggested the existence of spatial heterogeneity perpendicular to the slope for the structural variables of krummholz. Both flagged krummholz and the rest of tree-classes (adults, poles, saplings and seedlings), produced correlograms representing “sharp steps”, but not so steep as the correlograms of krummholz, and with mean influence areas of ≈ 37 m and ≈ 46 m, respectively. The heterogeneous structure perpendicular to the slope is confirmed by the histogram of all living trees distributed along this direction (most of them are krummholz; Table 1, which forms a central minimum flanked by lateral maxima (Figs. 1 and 3).

In the Tessó site, the all-directional Mantel correlogram for structure variables of living trees (basal diameter, dbh, height, height of the lowest living branch, westward and northward crown radii, number of stem nodes and maximum number of needle

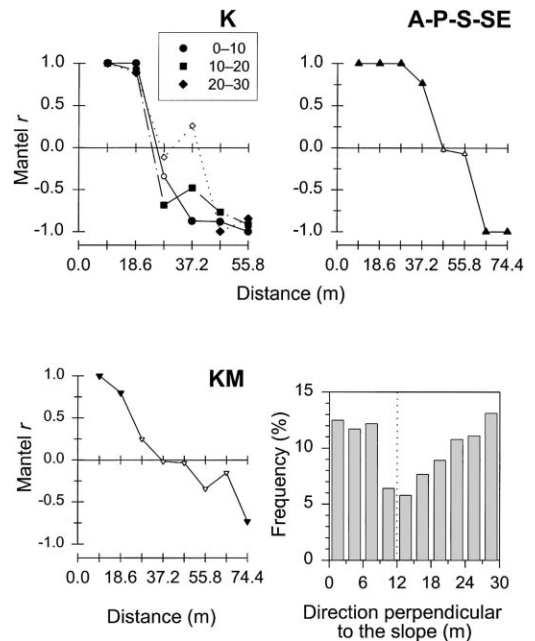


Fig. 3. Mantel correlograms for the structural variables of living trees in the Ordesa site. The correlograms were obtained using six variables for flagged krummholz and adults–poles–saplings–seedlings and five variables for krummholz (see Section 4.4). The upper correlograms show three correlograms for krummholz (located in subtransects along the slope at coordinates 0–10 m, $n = 161$ trees; 10–20 m, $n = 94$; and 20–30 m, $n = 149$) and the all-directional correlogram for individuals with vertical stems (adults–poles–saplings–seedlings, $n = 162$), respectively. The lower left figure is the all-directional correlogram for flagged krummholz ($n = 72$). The histogram shows the frequency (%) of all living trees ($n = 641$) along the axis perpendicular to the slope, indicating the end of positive autocorrelation (dotted line), observed up to 20 m for flagged krummholz in the Mantel correlogram. Abbreviations of the size and growth-form tree-classes as in Fig. 1. Black symbols are significant ($P \leq 0.05$) values of the normalized Mantel statistic r and white symbols are non-significant values.

cohorts) was overall significant ($P \leq 0.05$) and showed significant positive and negative autocorrelation in the small and large distances, respectively (Fig. 4). The global shape of this correlogram reflected a gradient with steps. The positive autocorrelation appeared up to ≈ 39 m, considering all coordinates or only those parallel to the slope. The average size of the influence area for structural variables was ≈ 45 m in both cases. The non-significant positive autocorrelation value at ≈ 18 m, present in the all coordinates

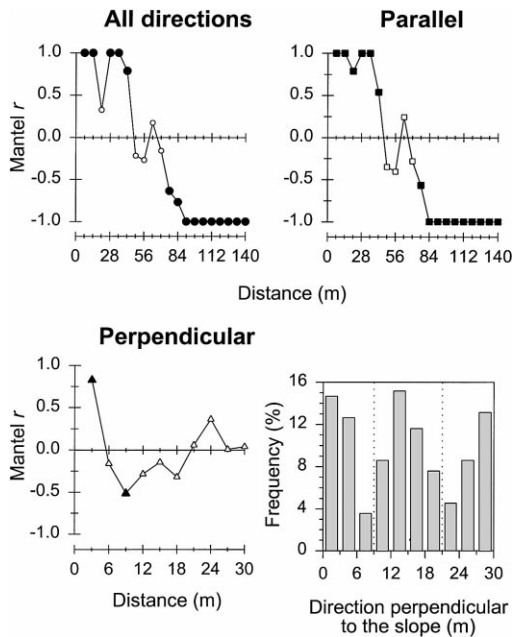


Fig. 4. Mantel correlograms for the structural variables of living trees in the Tessó site. These multivariate correlograms were calculated using 198 objects (trees) and eight structural variables (see Section 4.4). The upper correlograms consider all coordinates and only coordinates parallel to the slope. The lower left correlogram considers only coordinates perpendicular to the slope and the histogram shows the frequency (%) of all living trees ($n = 198$) along the axis perpendicular to the slope indicating the significant negative autocorrelation observed at 6–9 m (dotted lines) in the directional correlogram with coordinates perpendicular to the slope. All correlograms were globally significant using the Bonferroni correction for multiple tests. Black symbols are significant ($P \leq 0.05$) values of the normalized Mantel statistic r and white symbols are non-significant values.

Mantel correlogram, became significant ($P \leq 0.05$) when we computed the correlogram only for locations parallel to the slope (Fig. 4). This result revealed the presence of subtle negative autocorrelation for the short distances of the all-directional correlogram. This was confirmed by the appearance of significant ($P \leq 0.05$) negative autocorrelation in the direction perpendicular to the slope at 6–9 m but lasting from 6 m up to 18 m (Fig. 4). This can be observed in the histogram of living trees along this direction (Fig. 4). The distribution of trees along the direction perpendicular to the slope in the Tessó site is characterized by a central maximum (Fig. 4).

5. Discussion

5.1. Point pattern analyses

We found more indications of spatial segregation for the different tree-classes in the Ordesa site than in the Tessó site where middle-sized trees overlapped each other in the lower zones of the forest–grassland ecotone. The dense krummholz-belt in the Ordesa site comprised most of the upper part of the ecotone. The most striking feature in the Ordesa site was the close location of krummholz and seedlings (Fig. 1). The abundance of seedlings in the krummholz-belt is consistent with previous ideas based on the “seedling bank” concept because rapid germination of these limited treeline populations could decrease seed mortality and produce a seedling bank as an establishment source instead of a seed bank (Payette et al., 1982). We found spatial attraction between krummholz and seedlings at a distance consistent with mean horizontal canopy radius (0.25 m). In addition, these point pattern analyses agree with similar results calculated computing simple correlations between densities of tree-classes and corrected taking into account the spatial autocorrelation (Camarero and Gutiérrez, 1998b).

Holtmeier and Broll (1992) found a maximum length for the leeward snowdrift equal to 4–5 times the height of *Picea engelmannii* islands in a forest-alpine tundra ecotone in the Colorado Front Range. Unfortunately, there are no similar data of snowdrift size for the studied Pyrenees treelines. Nevertheless, the snow precipitation in the Ordesa site does not produce so deep snowpacks, as suggested by the estimated snow depth based in the mean height ± 1 SD of the krummholz mats (0.74 ± 0.40 cm; see Pereg and Payette, 1998). In fact, the snow cover may be absent some winters, leading to water stress, desiccation damage and death of *P. uncinata* seedlings (Frey, 1983). Considering the local snow and wind conditions and the relationship between mat height and snowdrift size described by Holtmeier and Broll (1992), the mean krummholz mat height would correspond to a maximum leeward snowdrift size of ~ 2 –3 m. This “influence size” is quite close to the inferred spatial attraction between krummholz patches and seedlings at longer distances (1.75–3 m). In addition, this distance of attraction between seedlings and

krummholz is consistent with the mean patch size for krummholz crown radii according to the correlograms (2.5–3.5 m). The extended spatial effects of krummholz patches on regeneration through snow accumulation could explain spatial attraction at longer distances. The spatial attraction was not found at very short distances (1 m), what confirmed the shade-intolerant condition of this species (Bosch et al., 1992). Most krummholz did not bear cones in the Ordesa site and wind is the main dispersal agent of *P. uncinata* seeds. No preferential dispersal could have caused the observed spatial pattern, excepting the seed “trapping” in the leeward side of krummholz. There is no indication in the literature that selective predation of seedlings or other factor could explain this pattern (Cantegrel, 1983).

Krummholz can favor *P. uncinata* establishment through enhanced snow deposition, providing shelter against abrasion by windblown snow and ice and adequate soil moisture during the start of the growing season. Other treeline studies showed that a too deep snow cover can limit establishment, but they considered different species and climatological conditions than those described here (Billings and Bliss, 1959; Earle, 1993). Under more similar environmental conditions, Minnich (1984) suggested that *Pinus contorta*–*P. flexilis* establishment in Mt. S. Gorgonio (California) timberline was dependent on habitat amelioration by close parent trees by reducing wind or capturing snow. The ability of tree and krummholz patches to modify microenvironmental conditions in the forest–grassland ecotone (snow cover, soil moisture and temperature, microclimate, etc.) is well known (Hadley and Smith, 1987; Holtmeier and Broll, 1992; Scott et al., 1993). Snow cover affects tree form and establishment (Earle, 1993; Schaefer and Messier, 1995; Hessel and Baker, 1997; Pereg and Payette, 1998). For example, Earle (1993) found that intermediate snow depths (1–1.5 m) were adequate for successful seedling establishment of *P. engelmannii* and *Abies lasiocarpa* in SE Wyoming. Tree establishment and growth can change the depth and density of snow and modify the pattern of snowdrift (Payette et al., 1973; Minnich, 1984; Holtmeier and Broll, 1992). The endogenous feedback between trees and snow affects population changes through microenvironmental changes that affect the regeneration niche (Grubb, 1977; Earle, 1993).

Positive plant interactions have been studied in harsh environments like arctic tundra and alpine communities (Carlsson and Callaghan, 1991; Bertness and Callaway, 1994; Kikvidze and Nakhutsrishvili, 1998). The presence of intraspecific positive interactions buffering seedlings from extreme conditions at tree-line has been inferred by studies revealing preferential establishment in the periphery of adult trees, contagious dispersion and spatial heterogeneity of mortality (Kullman, 1983; Payette and Filion, 1985; Taylor, 1995). The “nurse effect” should be taken into account to understand the potential response of tree-line populations to climatic change. This positive interaction can explain why large changes in treeline position due to the death of isolated individuals are not related to major density fluctuations in non-marginal populations (Lloyd, 1997).

A greater sample of plots taking into account the spatial variability between sites and experimental manipulations should address the suggested protective influence of krummholz on seedlings. There are at least two possibilities to explain this association. If wind is the main limiting factor, then the seedlings should be more abundant in the protected leeward side of neighbor krummholz. If snowdepth is the main issue, it should limit establishment to the windward side of krummholz where snow is not too deep (Earle, 1993). Given the very high density of the krummholz-belt in the Ordesa site, it is not possible to discern which of the two suggested directional krummholz–seedling distributions exists and which environmental variable affects more establishment. It is also possible that several environmental variables, like wind and snowpack, work simultaneously. Other microenvironmental factors such as changes of soil conditions (moisture, temperature, nutrients) should also be taken into account (Holtmeier and Broll, 1992). We hypothesize that the wind–snow interaction is the main factor controlling *P. uncinata* establishment in the Ordesa site because snowpack is not so deep to prevent establishment. The abundant krummholz forms with foliage damages due to wind abrasion and insufficient snow protection are additional factors suggesting this hypothesis (Grace, 1977; Tranquillini, 1979; Camarero and Gutiérrez, 1998a).

Positive interspecific interactions between tussock grass (*Poa* spp.) and *Eucalyptus pauciflora* at intermediate distances have been described in other tree-

line ecotones (Noble, 1980). Noble (1980) found that *E. pauciflora* seedlings more distant from grass clumps tend to be shorter, larger and multistemmed. He suggested that this change of seedling habit could be explained by a reduced competition with tussock grass (hence the larger size) and a greater exposure of growing tips to harsh microenvironmental conditions such as frost damage (hence the shorter and multistemmed habit). We have found negative but not significant relationships between two variables of seedling size and the seedling–krummholz distance (north–south crown diameter, $r_s = -0.20$, $P = 0.11$, $n = 64$, considering separation distances ≤ 2 m; and height, $r_s = -0.29$, $P = 0.31$, $n = 14$, considering separation distances ≤ 0.5 m). Therefore, we cannot confirm our hypothesis with the available data. However, we are only considering hypothetical processes generated by the spatial pattern, such as the nurse effect by krummholz forms (intraspecific positive interaction). These hypothetical causative processes should be confirmed in the future by experiments considering growth and survivorship of seedlings near krummholz and the trade-off between above-ground shelter and below-ground competition (e.g., Carlsson and Callaghan, 1991). The trade-off between facilitation and competition should produce a turning point in a graph of seedlings–krummholz minimum distances and any variable expressing seedling performance.

In the Ordesa site, microclimate and the spatial position of seedlings with respect to krummholz become decisive for establishment. The spatial location of trees in the forest–grassland ecotone might modify external climatic constraints and become a new source of inertia (Lloyd, 1996; Arseneault and Payette, 1997). In addition, the change from krummholz patches to patch forest in response to improved climatic conditions positively affects regeneration (Weisberg and Baker, 1995b). In contrast with this, the regeneration in the Tessó site is concentrated in upper areas of the forest–grassland ecotone without any positive association between seedlings and other tree-classes. This regeneration located near treeline is probably related to the presence of *D. octopetala* and the absence of a dense *R. ferrugineum* understory. The closed mats of *R. ferrugineum* can prevent the establishment of *P. uncinata* seedlings through direct competition (Pornon and Doche, 1995) or retaining snow

and shortening the snow-free period and the growing season (Tranquillini, 1979). More empirical studies are needed to determine the below-ground competition for water or nutrients between tree seedlings and herbaceous species, such as those developed to study tree establishment in arctic tundra (Black and Bliss, 1980; Hobbie and Chapin, 1998).

All tree-classes in both sites showed clumped distributions (Table 2). The smallest trees (seedlings and krummholz) were clumped at all distances in both sites but bigger trees (adults and poles) were clumped at greater distances according to their greater mean size. Clumps of trees can create more favorable microenvironments than those available for isolated trees (Tranquillini, 1979). The clumping process can produce very high tree densities such as those described for the krummholz-belt. The spatial overlap along the ecotone in the Tessó site is illustrated by the spatial interaction between saplings and seedlings. This seems to describe a more gradual size gradient than in the Ordesa site without any clear positive interaction between tree-classes. The trend towards random distribution for the tree-classes with the largest size is more evident in the Tessó site (Table 2). This trend suggests a more marked limitation for space and resources (e.g., light and soil nutrients) for bigger trees. Contrastingly, the clumped distribution of adults in the Ordesa site at small distances could indicate their possible origin from krummholz (Lavoie and Payette, 1992).

5.2. Surface pattern analyses

Different variables, functional or statistically related, as well as different tree-classes have their own spatial pattern in each site. The spatial pattern revealed by the surface analyses is very related with the distribution of the most abundant tree-class in each site (e.g., krummholz in the Ordesa site). Overall, the spatial gradient of the structural variables is more step-like in the Ordesa site than in the Tessó site. In the Ordesa site, the drastic size changes follow the morphological sequence from multistemmed shrubby krummholz in the upper areas of the forest–grassland ecotone to intermediate flagged krummholz forms with many less shrubby stems and, finally, unstemmed vertical trees in the lower area of the ecotone (adults, poles and saplings). Most structural variables

follow a gradient in the Tessó site except the estimated age of young trees, which forms patches with a mean radius of 15–18 m.

The complementary analysis of the spatial variation of height of living individuals using directional semi-variograms has showed that the Ordesa site is a “false” gradient. In this case, the spatial structure should be mainly caused by local interactions and processes such as the dominance of krummholz forms due to wind effects, predominating the autocorrelation at small-scales (Dutilleul and Legendre, 1993; Legendre, 1993). However, the Tessó site formed a “true” gradient (large-scale trend). In this case, the monotonic variation of height across the ecotone is mainly explained by environmental variables, such as the altitudinal decrease of temperature.

The mean zones of influence for structural variables in both sites occupied ≈ 45 m (Figs. 3 and 4) along the maximum slope but showed finer heterogeneity along the direction perpendicular to the slope. In the Ordesa site, the krummholz-belt formed dense groups at both lateral sides of the plot, which suggests a wave-like variation of density of krummholz perpendicular to the slope. This variation is perpendicular to the prevailing wind direction (NW–W). Taking into account the level slope of this site and the absence of snow avalanche, this suggests a similar dynamic process that those described for wave-regenerated *Abies balsamea* subalpine forests (Sprugel, 1976). In these stands, prevailing wind blows perpendicular to the stripes of trees and they move slowly downwind. The mortality is higher in the most exposed wave-edge trees because the prevailing wind may cause winter dessication, summer cooling, rime deposition, and branch breakage (Sprugel, 1976). Similarly, it is likely that wind is one of the environmental variables responsible for this wave-like variation of density of krummholz. This hypothesis should be tested in a larger sample of wind-exposed forest–grassland ecotones across the Pyrenees.

The sinuous distribution perpendicular to the slope is more evident as well in the Tessó site, thus giving place to a central and two lateral maxima. The spatial pattern of structural variables follows a gradient along the slope, but forming zones of influence of ≈ 45 m. This forest–grassland ecotone is formed by long forest strips ~ 15 – 18 m wide along the direction perpendicular to the slope, structurally similar, producing a

greater spatial heterogeneity in finer spatial scales. In the Tessó site, the similar size of forest strip width and mean radius of patches with similar estimated age for young individuals suggests that establishment is occurring parallel to avalanche paths occupied by grassland. The avalanches can create long non-forested corridors down the main slope separated by forested strips whose upper limits are not located at the same elevations (Furdada Bellavista, 1996; Walsh et al., 1994). It is well established that snow avalanches and snow patterns influence treeline dynamics in mid- and high-latitude mountains (Minnich, 1984; Earle, 1993; Walsh et al., 1994).

6. Conclusions

Two different patterns of regeneration arise: most seedlings in the Ordesa site appeared near krummholz but seedlings in the Tessó site occupied locations above the treeline, where the cover of subalpine shrubs decreased (*R. ferrugineum*). We found positive spatial interaction between krummholz and seedlings in the Ordesa site for two different spatial scales: tree and patch. The spatial gradient of the structural variables was more step-like (threshold-like) in the Ordesa site than in the Tessó site (gradual change of size and overlap of tree-classes). These contrasting patterns reflected the different influence of the most limiting environmental variables in each site. These were wind and snowpack in the Ordesa and the Tessó sites, respectively. The spatial structure of the Tessó site forming long forest strips reflects the effect of snow avalanches. The Ordesa site shows a potentially greater inertia to harsher climatic conditions due to positive spatial interactions between krummholz and seedlings what can reduce the possibility of declines in treeline. However, this interaction can also show the reverse effect increasing the sensitivity to positive changes because krummholz can create favorable microsites in which the seedling bank may establish. In both cases, this inertia should be assessed taking into account possible growth-form changes in response to climate variations, as well as their consequences on the establishment in the ecotone. The effects on inertia will depend on the type of interaction between individuals or species and the direction of environmental change.

Acknowledgements

Earlier drafts of this manuscript were greatly improved by comments from Lloyd, A., Sheppard, P., Tardif, J. and several anonymous reviewers. Rodríguez, M.A. helped with statistical analyses. The logistic help from “Aigüestortes i Estany de Sant Maurici” and “Ordesa y Monte Perdido” National Parks is gratefully acknowledged. We are grateful to Duncan, R.P. for allowing to use his software. Snow data were kindly provided by García, C. (Service for Protection against Snow Avalanches, Generalitat de Catalunya). Historical data were kindly provided by Bas, J., Bringue, G.M. and Etxebarria, M. We thank many people for field assistance and encouragement. We are grateful for the financial support of the CICYT (Ref. AMB95-0160) and a FPI grant to the first author (AP93 72784356).

References

- Aldezabal, A., Bas, J., Fillat, F., García-González, R., Garin, I., Gómez, D., Sanz, J.L., 1992. Utilización ganadera de los pastos supraforestales en el Parque Nacional de Ordesa y Monte Perdido. Report. Instituto Pirenaico de Ecología (CSIC)-ICONA, Jaca, Spain.
- Arseneault, D., Payette, S., 1992. A postfire shift from lichen-spruce to lichen-tundra vegetation at tree line. *Ecology* 73, 1067–1081.
- Arseneault, D., Payette, S., 1997. Reconstruction of millennial forest dynamics from tree remains in a subarctic tree line peatland. *Ecology* 78, 1873–1883.
- 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 (Huesca, Spain)* 4, 71–162.
- Bas, J., Moreno, A., Luna, A., Martínez, J., Sanuy, D., Fanlo, R., 1994. L'explotació ramadera a les pastures del Parc Nacional: dades preliminars. In: *La Investigació al Parc Nacional d'Aigüestortes i Estany de Sant Maurici, III Jornades sobre Recerca*. Generalitat de Catalunya, Espot, Spain, pp. 237–247.
- Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193.
- Besag, J., 1977. Contribution to the discussion of Dr. Ripley's paper. *J. R. Stat. Soc. B* 39, 193–195.
- Billings, W.D., Bliss, L.C., 1959. An alpine snowbank environment and its effects on vegetation, plant development and productivity. *Ecology* 40, 388–397.
- Black, R.A., Bliss, L.C., 1980. Reproductive ecology of *Picea mariana* (Mill.) Bsp. at tree line near Inuvik, Northwest Territories, Canada. *Ecol. Monogr.* 50, 331–354.
- Bolós, O. de, Vigo, J., Masalles, R.M., Ninot, J.M., 1993. *Flora manual dels Països Catalans*. Ed. Pòrtic, Barcelona, 1247 pp.
- 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*. Ph.D. Thesis. Dept. of History, University Pompeu Fabra, Barcelona.
- Brodie, C., Houle, G., Fortin, M.-J., 1995. Development of a *Populus balsamifera* clone in subarctic Québec reconstructed from spatial analyses. *J. Ecol.* 83, 309–320.
- Brubaker, L.B., 1986. Responses of tree populations to climatic change. *Vegetatio* 67, 119–130.
- Camarero, J.J., Gutiérrez, E., 1998a. Estructura y patrón espacial del ecotono bosque subalpino–pastos alpinos (Las Cutas, Ordesa). Report. Ordesa y Monte Perdido National Park, Huesca, Spain.
- Camarero, J.J., Gutiérrez, E., 1998b. Structure and recent recruitment at alpine forest–pasture ecotones in the Spanish Central Pyrenees. *Écoscience*, in press.
- Cantegrel, R., 1983. Le Pin à crochets pyrénéen: biologie, biochimie sylviculture. *Acta Biol. Montana* 2-3, 87–330 (in French).
- Cantegrel, R., 1987. Productivité ligneuse et organisation des marges forestières a *Pinus uncinata* Ram. en Pyrénées Occidentales. *Pirineos* 130, 3–27.
- Carlsson, B.A., Callaghan, T.V., 1991. Positive plant interactions in tundra vegetation and the importance of shelter. *J. Ecol.* 79, 973–983.
- 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. *Bull. Soc. Linnéenne de Provence* 46, 27–36.
- Ceballos y Fernández de Córdoba, L., Ruiz de la Torre, J., 1971. *Árboles y Arbustos de la España Peninsular*. Madrid: Ed. IFIE-ET Sup. Ingenieros de Montes, Madrid, 512 pp.
- Cliff, A.D., Ord, J.K., 1981. *Spatial Processes: Models and Applications*. Pion, London, 266 pp.
- Daly, C., Shankman, D., 1985. Seedling establishment by conifers above tree limit on Niwot Ridge, Front Range, Colorado, USA. *Arct. Alp. Res.* 17, 389–400.
- Diggle, P.J., 1983. *Statistical Analysis of Spatial Point Patterns*. Academic Press, London, 148 pp.
- Duncan, R.P., 1991. Competition and the coexistence of species in a mixed podocarp stand. *J. Ecol.* 79, 1073–1084.
- Duncan, R.P., Stewart, G.H., 1991. The temporal and spatial analysis of tree age distributions. *Can. J. For. Res.* 21, 1703–1710.
- Dutilleul, P., Legendre, P., 1993. Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept. *Oikos* 66, 152–171.
- Earle, C.J., 1993. *Forest dynamics in a forest-tundra ecotone, Medicine Bow Mountains, Wyoming*. Ph.D. Thesis. University of Washington, Seattle.
- Fortin, M.-J., Drapeau, P., Legendre, P., 1989. Spatial autocorrelation and sampling design in plant ecology. *Vegetatio* 83, 209–222.
- Frey, W., 1983. The influence of snow on growth and survival of planted trees. *Arct. Alp. Res.* 15, 241–251.

- Furdada Bellavista, G., 1996. Les allaus al Pirineu Occidental de Catalunya: Predicció Espacial i Aplicacions de la Cartografia. Geofoma, Logroño, Spain, 315 pp.
- Gil-Pelegrín, E., Villar-Pérez, L., 1988. Structure of mountain pine (*Pinus uncinata*) populations at its upper limit in Central Pyrenees. *Pyreneos* 131, 25–42.
- Gorchakovskiy, P.L., Shiyatov, S.G., 1978. The upper forest limit in the mountains of the boreal zone of the USSR. *Arct. Alp. Res.* 10, 349–363.
- Grace, J., 1977. *Plant Responses to Wind*. Academic Press, London, 190 pp.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52, 107–145.
- Haase, P., 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: introduction and methods of edge correction. *J. Veg. Sci.* 6, 575–582.
- 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. (Eds.), 1992. *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer, New York, 452 pp.
- Hessl, A.E., Baker, W.L., 1997. Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, USA. *Arct. Alp. Res.* 29, 173–183.
- Hobbie, S.E., Chapin, F.S.III., 1998. An experimental test of limits to tree establishment in Arctic tundra. *J. Ecol.* 86, 449–461.
- Holtmeier, F.-K., Broll, G., 1992. The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, USA. *Arct. Alp. Res.* 24, 216–228.
- Hustich, I., 1979. Ecological concepts and biographical zonation in the North: the need for a generally accepted terminology. *Holarct. Ecol.* 2, 208–217.
- Kikvidze, Z., Nakhutsrishvili, G., 1998. Facilitation in subnival vegetation patches. *J. Veg. Sci.* 9, 261–264.
- Kullman, L., 1979. Change and stability in the altitude of the birch tree-limit in the southern Swedish Scandes 1915–1975. *Acta Phytogeographica Suecica* 65, 1–121.
- Kullman, L., 1983. Short-term population trends of isolated tree-limit stands of *Pinus sylvestris* L. in central Sweden. *Arct. Alp. Res.* 15, 369–382.
- Kullman, L., 1990. Dynamics of altitudinal tree-limits in Sweden: a review. *Norsk Geografisk Tidsskrift* 44, 103–116.
- Kullman, L., 1991. Structural change in a subalpine birch woodland in North Sweden during the past century. *J. Biogeogr.* 18, 53–62.
- Kuuluvainen, T., Järvinen, E., Hokkanen, T.J., Rouvinen, S., Heikkinen, K., 1998. Structural heterogeneity and spatial autocorrelation in a natural mature *Pinus sylvestris* dominated forest. *Ecography* 21, 159–174.
- 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.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm. *Ecology* 74, 1659–1673.
- Legendre, P., Fortin, M.-J., 1989. Spatial pattern and ecological analysis. *Vegetatio* 80, 107–138.
- Legendre, P., Vaudor, A., 1991. *Le Progiciel R — Analyse Multidimensionnelle, Analyse Spatiale, versions CMS (IBM), VMS (VAX) et Macintosh*. Université de Montréal, Montréal, Québec, Canada.
- Légère, A., Payette, S., 1981. Ecology of a black spruce (*Picea mariana*) clonal population in the hemiarctic zone, northern Québec: population dynamics and spatial development. *Arct. Alp. Res.* 13, 261–276.
- Lescop-Sinclair, K., Payette, S., 1995. Recent advance of the arctic tree line along the eastern coast of Hudson Bay. *J. Ecol.* 83, 929–936.
- Lloyd, A.H., 1996. Patterns and processes of tree line response to late Holocene climate change in the Sierra Nevada, California. Ph.D. Thesis. The University of Arizona, Tucson.
- Lloyd, A.H., 1997. Response of tree-line populations of foxtail pine (*Pinus balfouriana*) to climate variation over the last 1000 years. *Can. J. For. Res.* 27, 936–942.
- Lloyd, A.H., Graumlich, L.J., 1997. Holocene dynamics of tree line forests in the Sierra Nevada. *Ecology* 78, 1199–1210.
- 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.
- Minnich, R.A., 1984. Snow drifting and timberline dynamics on Mount San Geronio, California, USA. *Arct. Alp. Res.* 16, 395–412.
- Montserrat, J.M., 1992. Evolución Glaciar y Postglaciar del Clima y la Vegetación en la Vertiente Sur del Pirineo: Estudio Palinológico. CSIC, Zaragoza, Spain, 152 pp.
- Morin, A., Payette, S., 1984. Expansion récente du mélèze à la limite des forêts (Québec nordique). *Can. J. Bot.* 62, 1404–1408.
- Noble, I.R., 1980. Interactions between tussock grass (*Poa* spp.) and *Eucalyptus pauciflora* seedlings near treeline in south-eastern Australia. *Oecologia* 45, 350–353.
- Noble, I.R., 1993. A model of the responses of ecotones to climate change. *Ecol. Appl.* 3, 396–403.
- Payette, S., Deshayé, J., Gilbert, H., 1982. Tree seed populations at the tree line in Rivière aux Feuilles area, Northern Quebec, Canada. *Arct. Alp. Res.* 14, 215–221.
- Payette, S., Filion, L., 1985. White spruce expansion at the tree line and recent climatic change. *Can. J. For. Res.* 15, 241–251.
- Payette, S., Filion, L., Ouzilleau, J., 1973. Relations neige-végétation dans la toundra forestière du Nouveau-Québec, Baie d'Hudson. *Naturaliste Canadienne* 100, 493–508.
- Pereg, D., Payette, S., 1998. Development of black spruce growth-forms at treeline. *Plant Ecol.* 138, 137–147.
- Pornon, A., Doche, B., 1995. Age structure and dynamics of *Rhododendron ferrugineum* L. populations in the northwestern French Alps. *J. Veg. Sci.* 6, 265–272.
- Ripley, B.D., 1977. Modelling spatial patterns. *J.R. Stat. Soc. B* 39, 172–212.
- Ripley, B.D., 1981. *Spatial Statistics*. Wiley, New York, 252 pp.

- Ripley, B.D., 1987. Spatial point pattern analysis in ecology. In: Legendre, P., Legendre, L. (Eds.), *Developments in Numerical Ecology*, NATO ASI Series vol. G14. Springer, Berlin, pp. 407–429.
- Rochefort, R.M., Little, R.L., Woodward, A., Peterson, D.L., 1994. Changes in sub-alpine tree distribution in western North America: a review of climatic and other causal factors. *The Holocene* 4, 89–100.
- Sandoz, H., 1987. Recherches taxonomiques, biogéographiques et phytocécologiques sur les principaux conifères subalpines des Alpes: Mélèze d'Europe, Pin cembro, Pin à crochets et Pin mugho. These. Université d'Aix-Marseille III, Marseille.
- Schaefer, J.A., Messier, F., 1995. Scale-dependent correlations of arctic vegetation and snow cover. *Arct. Alp. Res.* 27, 38–43.
- Scott, P.A., Hansell, R.I.C., Erickson, W.R., 1993. Influences of wind and snow on treeline environments at Churchill, Manitoba, Canada. *Arctic* 46, 316–323.
- Sokal, R.R., Oden, N.L., 1978. Spatial autocorrelation in biology. 2. Some biological implications and four applications of evolutionary and ecological interest. *Biol. J. Linn. Soc.* 10, 229–249.
- Sokal, R.R., Thomson, J.D., 1987. Applications of spatial autocorrelation in ecology. In: Legendre, P., Legendre, L. (Eds.), *Developments in Numerical Ecology*, NATO ASI Series, vol. G14. Springer, Berlin, pp. 431–466.
- Soutadé, G., Baudiere, A., Bécat, J. (Eds.), 1982. *La Limite Supérieure de la Forêt et sa Valeur de Seuil*. Ed. Terra Nostra-Institut d'Estudis Andorrans, Perpignan, France, 174 pp.
- Sprugel, D.G., 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. *J. Ecol.* 64, 889–911.
- Taylor, A.H., 1995. Forest expansion and climate change in the Mountain Hemlock (*Tsuga mertensiana*) Zone, Lassen National Park, California, USA. *Arct. Alp. Res.* 27, 207–216.
- Thomson, J.D., Weiblen, G., Thomson, B.A., Alfaro, S., Legendre, P., 1996. Untangling multiple factors in spatial distributions: 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, Berlin, 137 pp.
- Upton, G.J.G., Fingleton, B., 1985. *Spatial data analysis by example. Point Pattern and Quantitative Data*, vol. 1. Wiley, Chichester, 410 pp.
- Veblen, T.T., 1979. Structure and dynamics of *Nothofagus* forests near timberline in south-central Chile. *Ecology* 60, 937–945.
- Villar Pérez, L., Benito Alonso, J.L., 1994. Esquema de la vegetación del Parque Nacional de Ordesa y Monte Perdido, más su zona periférica. *Lucas Mallada (Huesca, Spain)* 6, 235–273.
- 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.
- Wardle, P., Coleman, M.C., 1992. Evidence for rising upper limits of four native New Zealand forest trees. *New Zealand J. Bot.* 30, 303–314.
- Watt, A.S., 1947. Pattern and process in the plant community. *J. Ecol.* 35, 1–22.
- Weisberg, P.J., Baker, W.L., 1995a. Spatial variation in tree seedling and krummholz growth in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, USA. *Arct. Alp. Res.* 27, 116–129.
- Weisberg, P.J., Baker, W.L., 1995b. Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky Mountain National Park, Colorado. *Can. J. For. Res.* 25, 1326–1339.