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Influence of Topography on the Colonization of Subalpine Grasslands by the Thorny Cushion Dwarf *Echinospartum horridum*

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Abstract

In this study, we analyzed the effect of topography, particularly slope, on the expansion rates and population dynamics of *Echinospartum horridum* at small spatial and temporal scales in the grassland communities of Ordesa–Monte Perdido National Park (OMPNP) (NE Spain). *E. horridum* is a thorny cushion dwarf, endemic of Spain and south of France, forming dense mono-specific large patches difficult to be penetrated by other plants and large herbivores once it is established. Between 2005 and 2007, we collected demographic parameters from 300 marked plants of *E. horridum* that were distributed in the center and the edge of four patches. At the patch edge, two of the four patches had a high slope ($\geq 10°$) and two had a low slope ($<10°$), whereas at the patch centers the slope was high ($18°$–$30°$). To calculate invasion speed, we use aerial photographs from 1981 and 2003. Plants in the center of patches had lower growth rates, fewer flowers, and higher crown death rates than did the plants at edge of patches. Slope influenced significantly invasion rates: the speed of expansion was lowest on gentle slopes, probably because of competition with grass. The speed of diffusion from 1981 to 2003 varied from 2.09 m yr^{-1} on the steep slopes to 1.93 m yr^{-1} on the shallow slope. Plant dynamics at patch edges suggest that colonization by *E. horridum* will continue in the grasslands of the OMPNP.

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Introduction

The widespread shift in growth form dominance from grasslands to shrublands is one of the most important threats to the conservation of grasslands in many mountainous regions of the world (Grace et al., 2002; Wearne and Morgan, 2001; MacDonald et al., 2000; Olsson et al., 2000; Dullinger et al., 2003) and can have negative effects on livestock production, wildlife, and biodiversity (Schlesinger et al., 1990) by altering facilitative-competitive interactions (Choler et al., 2001; Callaway et al., 2002). The shift involves the impenetrable and irremediable growth of woody species within a matrix of grasslands and differs from the shrub encroachment that occurs in savanna ecosystems (Archer et al., 1988; Brown and Carter, 1988; Aguiar et al., 1996; Roques et al., 2001; Briggs et al., 2005), where water and nutrients limitations constrain woody cover and allow grass to coexist (Sankaran et al., 2005). In Western Europe, shrub expansion into subalpine grasslands is the result of vegetation successional change after anthropomorphic deforestation where the effect of climate change is even limited (Gehrig-Fasel et al., 2007), and disturbance (livestock and fire) is required to maintain grasslands (Sankaran et al., 2005).

Since at least the Middle Ages, alpine and subalpine grasslands in the mountains of Europe have been used for seasonal farming (Montserrat-Recoder and Fillat, 1990; Bätzing, 1991), which has had significant effects on subalpine vegetation (Ellenberg, 1988), giving place to a high biological diversity of these semi-natural grasslands (Eriksson et al., 1995; Pärtel et al., 1999). Typically, high shrub cover is undesirable in grasslands because it has negative effects on livestock production through a reduction in grass production (Scholes and Archer, 1997), or it increases the difficulty of managing livestock (Pyke and Archer, 1991). Repeated physical disturbances of shrubs and trees (Grace, 1999; Cousins and Eriksson, 2001) and management activities such as fire and grazing (Körner, 1999; League and Veblen, 2006; Holtmeier and Broll, 2005; Bartolomé et al., 2005) maintain those grassland communities. As those activities declined over the last century, shrubs colonized alpine grasslands, which has produced a dense shrub cover (Garcia-Ruiz et al., 1996; Austrheim et al., 1999; MacDonald et al., 2000; Tasser and Tappeiner, 2002; Julien et al., 2006; Batllori and Gutiérrez, 2008). The post-abandonment successional displacement has reduced plant species diversity (Jackson et al., 2002; Dullinger et al., 2003). Nevertheless, the patterns, dynamics, and rates of shrub colonization in semi-natural grasslands in response to changes in land use are not well studied (Bartolomé et al., 2005).

Despite numerous studies on the mechanisms of woody plant encroachment and grass-tree interactions (Skarpe, 1990; Wiegand et al., 2006; Sankaran et al., 2005), the underlying mechanisms are not well understood (Sankaran et al., 2004; Ward, 2005). Environmental factors interact with management practices to influence establishment and expansion processes (Rouget and Richardson, 2003; Julien et al., 2006), but the study of responses to climate change at the regional and finer scales requires a more involved approach than is required at the global scale (e.g., Trivedi et al., 2008). Despite the virtues of understanding the patterns and dynamics of shrub colonization in aid of the preservation of biodiversity in protected areas, the subject has received limited study (Bartolomé et al., 2005). After land abandonment, the topography of the area strongly influences the rate of vegetation succession. Plant species richness varies in response to topography

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factors such as solar radiation and slope angle (Pykälä et al., 2005; Bennie et al., 2006). For example, slope can affect shrub-grass interactions because species differ in their root structure. Grass species that have shallow roots are well adapted to shallow slopes or gentle slopes because there is easier access to water in the upper soil layers, whereas species that have deep roots, such as shrubs, can survive on steep slopes (Jackson et al., 1996; Jurena and Archer, 2003). When shrubs expand into grasslands, they can alter many aspects of the environment that lead to a reduction in substrate quality (Polley et al., 1997; Montané et al., 2007, and references therein). In addition, grass can reduce the emergence, growth, and survival of woody seedlings (Gordon et al., 1989; Martinez and Fuentes, 1993; McPherson, 1993; Riginos, 2009), which can influence the size and density of shrub cover (Archer et al., 1995).

In the Central Pyrenees, where the average annual precipitation is >1500 mm (Barrio et al., 1990), human disturbances, such as livestock and fire, are required to maintain grasslands (Sankaran et al., 2005). Thus, traditional land uses practices prevented alpine and subalpine grasslands from shrub encroachment (Lasanta et al., 2006), but a reduction in livestock farming at the end of the 20th century has lead to an irrevocable shrub-colonization process (Pallaruelo, 1993; Manrique et al., 1999; Mottet et al., 2006). In the Central Pyrenees, *Echinospartum horridum* (Vahl) Rothm, a thorny cushion dwarf, is one of the species that plays a significant role in shrub encroachment. *E. horridum* is highly invasive on the southern slopes, where it colonizes subalpine grasslands, one of the important ecosystems for plant diversity (Benito, 2006). Its thorns, which reduce the damage caused by herbivores, and its great colonizing ability contribute to the significant invasive nature of *E. horridum* (Marinas et al., 2004) and its remarkably rapid spread in recent decades (Montserrat-Recoder et al., 1984; Pérez-Cabello and Ibarra, 2004). In addition, as a leguminous plant, *E. horridum* fix more atmospheric nitrogen than grass (Montserrat-Recoder et al., 1984), which increases its competitiveness in colonizing grasslands (Kochy and Wilson, 2000), especially at high elevations, where N is limited (Jacot et al., 2000). *E. horridum* forms large, dense, monospecific patches that can cover several hectares, where only a few other plant species survive within small gaps. It is not well understood, however, how topography can affect grass-shrub interactions community. The aim of this study was to assess the impacts of slope on the growth and reproduction of *E. horridum* in the subalpine grasslands of Ordesa–Monte Perdido National Park (OMPNP), Central Pyrenees, Spain. The study examined the demographic parameters associated with age structure, population density, and ecological conditions (Crawley, 1986), which can provide the best predictions of colonization over time (Prevosto et al., 2004). The following questions were addressed:

1. (1) Does location within a patch (center vs. edge) influence the demography and reproduction of *E. horridum*?
2. (2) Does the slope at the patch periphery affect the demographics of E. horridum?
3. (3) Has slope influenced the expansion rate over the last 25 yrs?

We expected that that plants in the center and those on the edge would differ in their demographics because plants in the interior of a patch experience high population densities and low competition from grass, whereas plants at the periphery are exposed to relatively low *E. horridum* densities and greater competition from grass. Furthermore, we predicted that slope would have differential effects at the center and edge of the patches: higher resistance by grass to encroachment on low slopes because they are better adapted to flat terrain, which leads to a reduction in colonization rates.

Methods

STUDY AREA

The study was conducted in OMPNP, Central Pyrenees, Spain. OMPNP has been a protected area (15,600 ha) since 1918 for the Ordesa Canyon (2100 ha) and, in 1982, it assumed its current limits. More than 75% of the park is alpine and subalpine grassland. In the Pyrenees, the subalpine grasslands are secondary plant communities that replaced native forest and have been grazed continuously for at least 500 yrs (Montserrat-Recoder and Fillat, 1990).

The climatic conditions in the study area are influenced by several factors: the mountain continental climate is modulated by the westward Atlantic winds, whereas the climate farther south is Mediterranean. At the Goriz weather station (42°40′N, 00°02′E; 2215 m a.s.l.), average annual rainfall has been 1735 mm (1981–2006). Snow cover persists from early November to late May. The mean annual temperature is ~5 °C, but with daily temperatures between 25 °C and −21 °C.

The populations of *E. horridum* were in four patches, which were 75.4 ha to 267.5 ha in size, at similar elevations (1765 m to 1980 m), and had southern orientations. At the patch center, the slope ranged from 18° to 30°. The slopes at the edge of patches were classified as either high (12°–13°) or low (5°–8°).

STUDY SPECIES

E. horridum (Vahl.) Rothm. (Fabaceae) is a thorny cushion dwarf that is endemic to the central Spanish Pyrenees and southern France. It is a strictly calcicolous plant (Aparicio et al., 2002) that reproduces sexually and asexually. The inflorescence is apical, with two opposite yellow flowers, and the plant produces sparsely sericeous legumes. The flowering period occurs in mid-July. Sexual reproduction produces persistent seed banks (Aparicio and Guisande, 1997), which confer the capacity for good post-disturbance establishment (Prevosto et al., 2004). Creeping asexual reproduction is through the clonal propagation of decumbent branches, which root at nodes along the stem. Newly rooted stems can break off and become independent clonal fragments. Aged shrubs can split into clonal fragments after a central portion of the plant dies. In this study, we did not differentiate between clonal fragments (originated from nodes) and a genet (originated from seeds). In both cases, individual plants were connected networks of stems and ramets. Clonal fragments allow the plant to maintain and increase its cover, which suppresses the establishment of other species. Because they out-compete neighbors, clonal propagation favors the persistence of the plant in dense coverage where seedling establishment is unusual (Bierzychudek, 1985), which has led to the formation of monospecific patches of *E. horridum* in the study area.

DATA COLLECTION

Age and Crown Size of E. horridum

To detect a relationship between plant age and crown size in *E. horridum*, we measured crown diameter and the number of annual rings. We selected randomly 76 individual plants from the center and the periphery of the four patches. Before we removed the individual by cutting the principal trunk, we measured crown circumference and the largest diameter. Each trunk section was

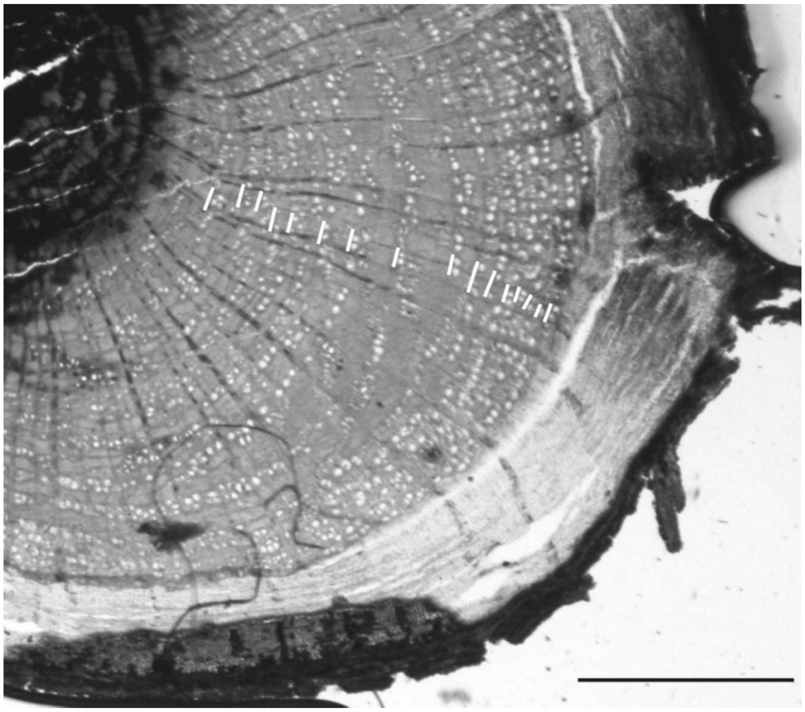

FIGURE 1. Annual growth rings in stem cross sections of *E. horridum* collected in Ordesa–Monte Perdido National Park, Spain. Scale bar = 1 mm.

polished using sandpaper of progressively finer grades until rings were clearly visible. In the laboratory, plant age was estimated by counting the number of annual rings along two radii in each trunk section using at ×3-magnification stereomicroscope (Leica MZ 125, Wetzlar, Germany). As in other species of the genus, the wood of *E. horridum* was semi-ring-porous (Schweingruber, 1990) and, in most of the samples, ring boundaries were distinctive. In addition, the wood had dendritic vessel groups (Fig. 1). When different ring counts were obtained from the same individual, the rounded-up mean of the minimum and maximum counts was used as the estimate of plant age (Dietz and von Arx, 2005). Three size classes were defined based on the relationship between crown diameter and the number of rings: crown diameter <20 cm (Class I), crown diameter 20–50 cm (Class II), and crown diameter >50 cm (Class III). The first size class corresponds with seedlings, the second class is young reproductive plants, and the third class is adult plants.

Vital Rates and Body Condition

In the first week of June 2005, we marked 75 plants in each of the four patches (30 and 45 from the center and from the edge of the patch, respectively. Of the 30 plants marked in the center of each patch, 10 were in Class I, 10 were in Class II, and 10 were in Class III. Of the 45 plants marked at the patch edge, 15 were in Class I, 15 were in Class II, and 15 were in Class III. Between the last week of May and the first week of June in 2005, 2006, and 2007, we measured the largest crown diameter and its perpendicular of all of the plants. In the middle of July in 2005, 2006, and 2007, we recorded the numbers of flowers and estimated the proportion of the standing plant that was dead. To estimate the recruitment of each plant, in June 2005 and June 2007, we recorded the size and the nearest neighbor distance of each juvenile plant around adult plants. Recruitment was estimated based on the plants at the edge of patches because the high density of adult plants in the center of the patches precluded attributing offspring to a specific parent plant.

To estimate population density, we used equal-stratified random sampling. We performed 24 sample plots of 10 × 10 m each, distributed within the four patches of *E. horridum* (6 per patch). Variation in slope was greater at the edge of a patch than in the center of the patch; therefore, we took two samples from the center and four samples from the edge of the four patches. We estimated the number of plants of each class size in each of the 24 sample plots.

We excavated eight *E. horridum* plants complete with their systems of ramets connected by decumbent stems. We identified each ramet (a unit consisting of shoot and root systems) and aged them using the annual growth rings in stem cross sections. We measured decumbent stem length between the apical root and each ramet.

Patch Growth

The patches of *E. horridum* were quantified based on digitized orthorectified aerial photographs taken in 1981 and 2005. To calculate the expansion of *E. horridum* patches, we measured the distance between the front line in 1981 and 2005, along 24 linear transects (6 per patch).

The advances of *E. horridum* along the frontal wave were of interest; therefore, transects were laid out along the slope line. In addition, in June 2005, we recorded *E. horridum* cover using the Line-Intercept Method. We randomly assigned 16 transects along the slope line (four transects per patch) from the base to the top of the patch. Patch width along transects varied between 180 m and 750 m.

DATA ANALYSIS

Estimates of Vital Rates and Body Condition

The probability of surviving one year was calculated for the marked plants using the exponential survival function,

$$S(t) = \exp(-\rho t), \qquad (1)$$

which has a single parameter, ρ, the death rate per unit time, t. The death rate depends on the age of the plant, x, according to this function,

$$\rho(x) = \exp(\alpha + \beta x), \qquad (2)$$

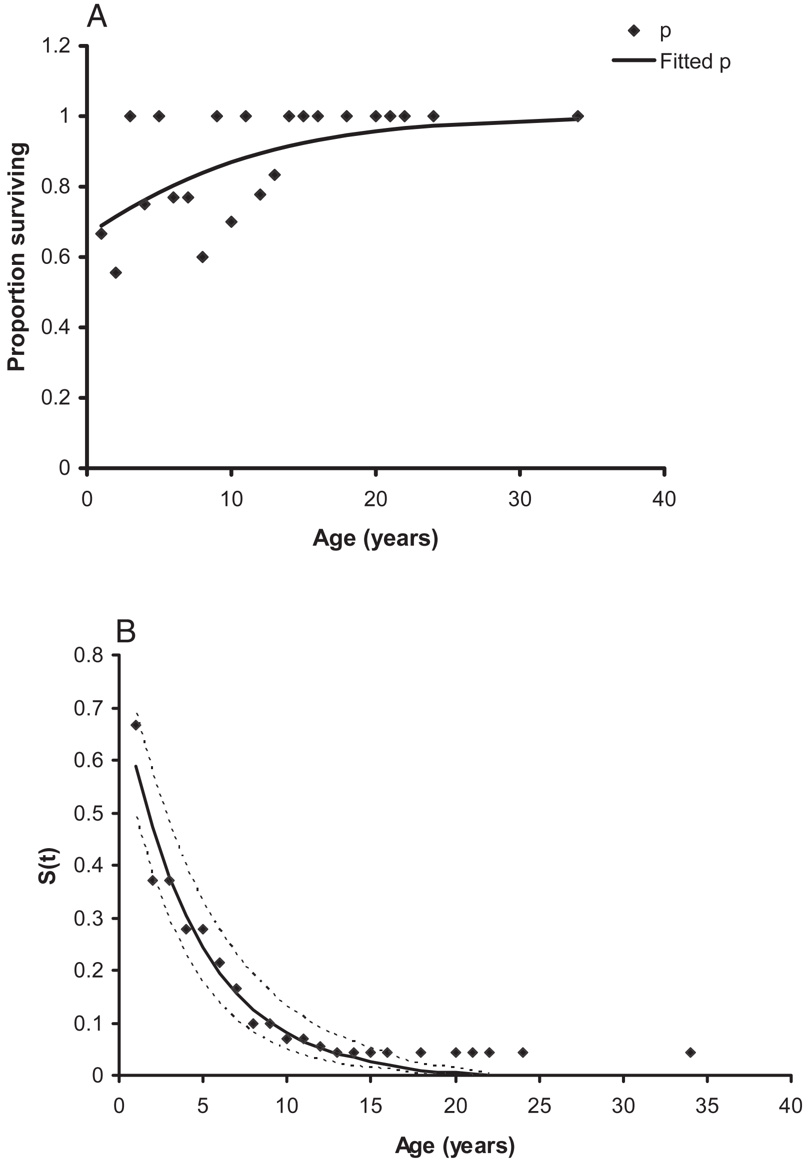

FIGURE 2. (A) Graphical representation of the proportion (p) of *E. horridum* plants that survived and age; (B) the proportion of individuals that survived from birth to a given age from the study area in Ordesa–Monte Perdido National Park, Spain.

where alpha is the natural logarithm of death rate at birth (age equal to zero) and beta is the rate of increase of the logarithm of death rate with age. We calculated the parameters α and β using maximum likelihood estimations from the binomial distribution.

To calculate the proportion of individuals surviving from birth through to a given life history, we estimated the survivorship function by multiplying the proportion of individuals surviving through each previous life-history stage, following the Kaplan-Meier Method (McCallum, 2000). Confidence intervals for the exponential survival function were calculated using Gauss-Newton methods (SAS 9.1; SAS Institute, 2004).

Floral production was calculated as the average number of flowers produced in July 2005, 2006, and 2007 by the marked individuals. The seedling kernel dispersal rate was estimated from the occurrence of seedlings and the distance to the nearest neighbor adult plant at the patch edge. We assumed that the expected number of recruits produced by *E. horridum* is given by the equation

$$u(x) = a\ \exp(-bx) \tag{3}$$

(Ribbens et al., 1994; Clark et al., 1998), where x is the distance from the mother plant.

The crown area, A, was evaluated under the assumption that the plants are ellipsoidal using the Major Diameter, D, and its perpendicular, d:

$$A = \left(\frac{D}{2} \times \frac{d}{2} \times \pi\right). \tag{4}$$

The crown growth rate, G, was calculated as the difference between crown area in 2006 and 2005 divided by the crown area.

$$G = \frac{\left(\frac{D}{2} \times \frac{d}{2} \times \pi\right)_{2006} - \left(\frac{D}{2} \times \frac{d}{2} \times \pi\right)_{2005}}{\left(\frac{D}{2} \times \frac{d}{2} \times \pi\right)_{2005}} \tag{5}$$

The crown death rate was calculated as the average proportion of standing death crown in 2005 and 2006. Dead branches remain standing for at least one year, and can be easily recognized by the yellow color vis-à-vis the green of the living part of the plant. We estimated visually the proportion of death crown following the Daubenmire Method (Daubenmire, 1959).

Clonal propagation was calculated from four plants at the patch edge and four at the patch center. Decumbent stem

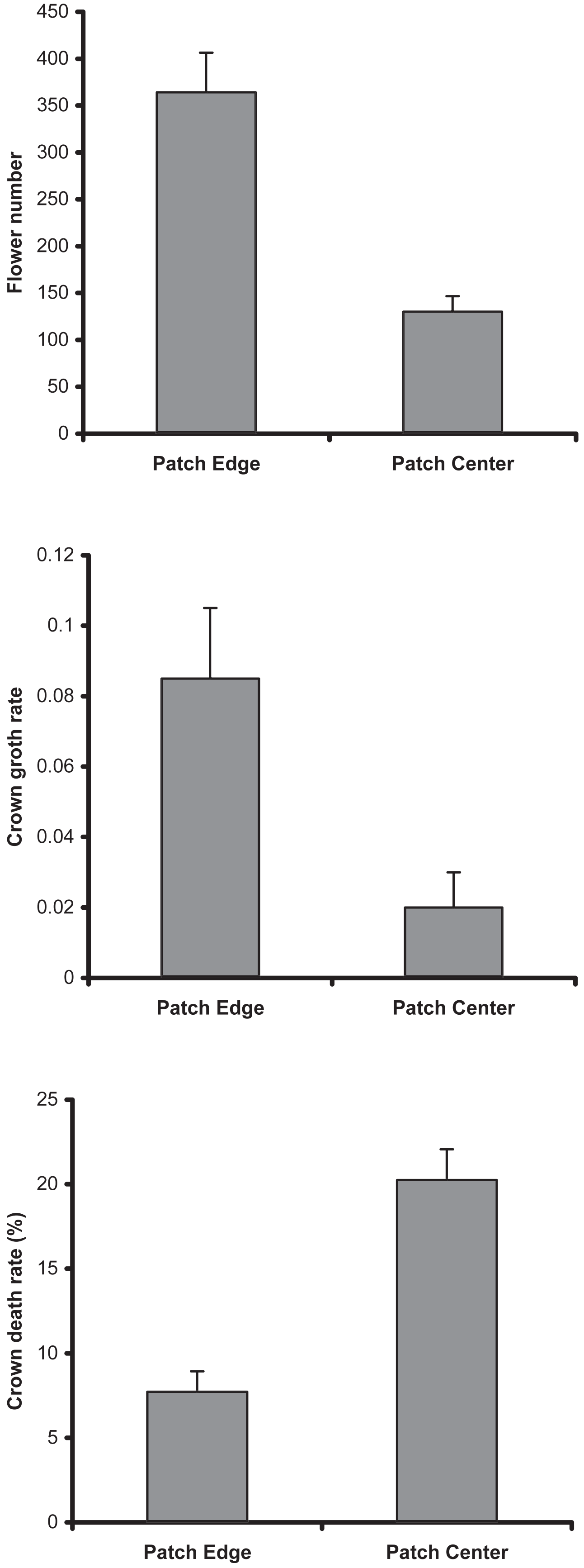

FIGURE 3. Mean (±se) number of flowers, crown growth rate, and the proportion of death crown rate of *E. horridum* plants collected from the edge and the center of patches in Ordesa–Monte Perdido National Park, Spain.

elongation between the main root and the first ramet was calculated assuming exponential growth as

$$dS/dt = rS, \tag{6}$$

where S is decumbent stem, t is time, and r is decumbent stem net growth rate (Cain et al., 1995). We calculated the net growth rate as follows:

$$r = \ln(S_t/S_0)/\Delta t, \tag{7}$$

where S_t and S_0 are the lengths between the initial and final stem length, and Δt is the time elapsed between observations.

Estimates of Patch Growth

For each patch, we analyzed the *E. horridum* density $g(x)$ with distance, x, from the patch center to the external border. The density gradient, α, was estimated from the normalized organism density-distance equation

$$g(x) = \alpha^2 x e^{-\alpha x}, \tag{8}$$

which represents the density of plants with distance x from the starting point of release, and α is the density gradient (Edmonston and Davies, 1978). Non-linear adjustments were performed following the Gauss-Newton Method (SAS 9.1; SAS Institute, 2004).

Assuming exponential growth and the absence of constraints for growth and expansion at the patch edge, patch size at time t (N_t) can be modeled by the following equation:

$$N_t = N_0 \ \exp(rt), \tag{9}$$

where N_t is the patch frontal length in 2005, N_0 is the patch frontal length in 1981, and r is the population growth rate.

Estimates of the diffusion coefficient (D) and velocity of diffusion (c) were calculated under the assumption of no drift and following a Gaussian normal dispersal kernel (Kareiva, 1982, 1983), as

$$\hat{D}(t) = \overline{R}^2(t) \Big/ 4t \tag{10}$$

where $\overline{R}^2(t)$ is the mean squared displacement at time t, and

$$c = 2\sqrt{rD}, \tag{11}$$

where r is the population growth rate.

Results

AGE AND CROWN SIZE OF E. HORRIDUM

To model individual growth, we used the Richards Function (Richards, 1959)

$$y(t) = A\left(1 - be^{-kt}\right)^{-1}, \tag{12}$$

where y is crown diameter, A is asymptotic size, k is intrinsic growth rate, b is the growth constant, and t is age (number of rings). Based on the non-linear adjustment using the Gauss-Newton Method, A = 79.29 ± 9.51; k = 0.238 ± 0.058; b = −19.44 ± 9.47 ($F_{3,\,72}$ = 195.67, $P < 0.0001$). The longest diameter of the crown was used to establish the size-age relationship. Age classes were derived from the equation

$$t = -\ln\left(\frac{A - y}{-by}\right) \Big/ k. \tag{13}$$

Class I corresponded to plants younger than 8 yr and a main crown diameter <20 cm. Class II included plants whose ages

TABLE 1

Observed and expected proportions of three age classes of *E. horridum* at the center and the edge of patches in the grasslands of Ordesa–Monte Perdido National Park, Spain. Class I: <8 years old, Class II: 8–15 years old, and Class III: >15 years). Expected values derived from a bootstrap randomization. Significance values from *t*-test with 23 degrees of freedom are: * $P < 0.05$, ** $P < 0.01$.

	Class I	*t*	Class II	*t*	Class III	*t*
Center	20.41	−3.59**	23.98	−2.07*	55.61	3.74**
Edge	34.89	5.99**	29.04	3.28**	36.07	−6.17**
Expected mean ± SE	29.07 ± 2.41		27.17 ± 1.54		43.75 ± 3.16	

ranged from 8 to 15 yr and their longest crown diameter was 20–50 cm. Class III included plants older than 15 yrs and a crown diameter >50 cm.

Effects of Location within a Patch on E. horridum *Demographics*

To assess whether position in a patch influenced plant performance, we evaluated plants living at the center and plants living at the edge of patches (Table 1). In the twenty-four 10-m × 10-m quadrates, we recorded 3569 individual plants (density = 1.49 ind m^{-2}), with densities in patches ranging from 1.36 ind m^{-2} to 1.78 ind m^{-2}. Age-class structure differed between the center and the edge of a patch. At the center of the patches, 55.6% of the plants were Class III, whereas at the edges, 36.1% were in this age class (Goodness-of-Fit Test: $G = 6.76$, $P < 0.01$). Plants in Age Class I were more common at the edges (34.89%) than in the center (20.41%) of patches ($G = 277.90$, $P < 0.001$), and plants in Class II was more common at the edge (29.04%) than in the center (23.98%) of patches ($G = 129.80$, $P < 0.001$). The results from the 1000 bootstrap randomizations confirmed those differences of patterns.

The survival of *E. horridum* varied as a function of age (x), where the death rate $\rho(x)$ best fit the equation

$$\rho(x) = \exp(0.672 + 0.122x). \qquad (14)$$

The residual deviance of the maximum likelihood estimation was 22.50, which was lower than expected based on the chi-square distribution ($\chi^2_{20,\ 0.05} = 31.41$). *E. horridum* had a high mortality rate in the early years of life, but rates stabilized after age 12 (Fig. 2). Survival probability increased as plants aged.

The proportion of plants that survived p, i.e., number of living individuals at time $t + 1$ divided by the number of individual marked at time t (n_{t+1}/n_t) and the fitted p obtained from the exponential survival function $e^{\rho}/(1 + e^{\rho})$ are present in Figure 2, and it shows that after 12 yrs of age most individuals survive.

The proportion of individuals that survived from birth to a given age declined rapidly during the first years of life and fit the equation,

$$S(t) = 0.7326\ \exp(-0.225x), \qquad (15)$$

$F_{2,\ 20} = 328.62$, $P < 0.0001$, where 0.22 is the death rate (Fig. 2).

Location within a patch (edge or center) had a significant influence on plant demographics. Plants that lived at the edge of the patch produced more flowers ($F_{1,298} = 19.36$, $P < 0.0001$), had higher crown growth rates ($F_{1,298} = 10.68$, $P < 0.001$), and lower mortality (crown death rate) than did those that lived in the center of the patch ($F_{1,298} = 35.49$, $P < 0.0001$) (Fig. 3).

The responses of plants to position within the patch differed among age classes (Table 2), which had an effect on the population dynamics of plants living at the edge or in center of patches. As expected, at the edge of patches, the number of seedlings and plant age were positively correlated. Seedling establishment in the center of patches was not evaluated. The increase in flower production with age was similar at the edges and in the center of patches. Crown growth rate increased most dramatically in plants in the youngest age class and position within a patch had no significant effect on the crown growth rate of plants in the oldest age class. Crown death rate was lowest at the edge of patches and was lowest in Age Class II. Plants in the center of patches had the highest proportions of crown death and the effect was most intense among younger plants.

Seedlings became established close to conspecific neighbors; most of the seedlings <10 yrs of age were established within 50 cm of the adult plant. The number of seedlings decreased with an increase in the distance from the plant and their frequency distribution fit significantly a negative exponential function ($F_{2,59} = 66.57$, $P < 0.001$) (Fig. 4).

Decumbent stem elongation between the main root and the first-generation ramets ($n = 39$) was 65.05 ± 5.66 mm. The time elapsed for the production of the first ramet was 11 ± 2 yrs ($n = 38$). Plants at the edge and those in the center of patches did not differ significantly in their stem elongation rates and the generation times for the first-generation ramets ($F_{1,37} = 1.18$, NS, for stem elongation; $F_{1,36} = 0.01$, NS for first-generation time elapsed). Second-generation ramets were produced after 5 ± 1 yrs ($n = 34$) and an average stem elongation of 100.53 ± 9.30 mm ($n = 30$), but stem elongation rates ($F_{1,32} = 1.06$, NS) and generation times for second-generation ramets ($F_{1,28} = 2.33$, NS) did not differ significantly between plants at the edge and those in the center of patches. Plants at the edge produced significantly ($\chi^2 = 10.8$, $P < 0.001$) more second-order ramets (24) than did plants in the center (6) of patches.

Clonal growth rate of first-order ramets (S_{01}) fit the equation

$$S_1 = S_0 e^{0.125} \qquad (16)$$

($F_{1,\ 36} = 7.50$, $P < 0.01$), whereas the growth rate of second-order ramets fit the equation

$$S_2 = S_1 e^{0.037} \qquad (17)$$

($F_{1,\ 28} = 74.54$, $P < 0.0001$).

Effect of Slope on E. horridum *Demographics*

To confirm whether slope had a significant effect on plant demographics, we evaluated separately plants that lived in the center and plants that lived at the edge of patches, where steep and shallow slopes occurred. At the edge of patches, plants on steep slopes had significantly higher crown growth rates ($F_{1,178} = 5.95$, $P < 0.05$) and lower crown death rate ($F_{1,178} = 3.90$, $P < 0.05$) than did the plants on shallow slopes (Fig. 5), but slope did not have a significant effect on flower production or seedling establishment. Among the youngest plants only, crown growth rate was significantly ($F_{1,62} = 5.48$, $P < 0.05$) higher among plants on steep slopes (0.158 ± 0.024) than among plants on shallow slopes (0.047 ± 0.040). Among the plants in Age Class II, crown death rate was significantly higher ($F_{1,58} = 6.01$, $P < 0.05$) for the plants on shallow slopes (1.81 ± 0.97) than for plants on steep slopes (7.86 ± 2.33). Among the plants in the oldest age class,

TABLE 2

Means ± SE values of number of flowers per plant, annual crown growth rate, proportion of crown death, and the one-way ANOVA test of the effects of location within a patch for three age classes of *E. horridum* in Ordesa–Monte Perdido National Park, Spain. Significance values from *t*-test are: *** $P < 0.001$ ** $P < 0.01$, * $P < 0.05$, no asterisks indicate $P > 0.05$.

Variables		Location within a patch	
		Edge	Center
Age Class I	F(1, 103)	Means ± SE (n=180)	Means ± SE (n=120)
No. flowers	5.81*	39.63 ± 8.85	12.26 ± 3.12
Crown growth rate	6.50*	0.101± 0.024	−0.033 ± 0.053
Crown death rate	8.72**	9.07± 2.76	23.16 ± 4.12
		Edge	Center
Age Class II	F(1,103)	Means ± SE (n=89)	Means ± SE (n=91)
No. flowers	10.06**	195.96 ± 22.45	103.27 ± 15.39
Crown growth rate	5.11**	0.092 ± 0.011	0.053 ± 0.014
Crown death rate	36.29***	4.74 ± 1.28	20.74 ± 2.55
		Edge	Center
Age Class III	F(1,88)	Means ± SE (n=60)	Means ± SE (n=60)
No. flowers	22.16***	915.59 ± 97.40	307.79 ± 40.19
Crown growth rate	2.15	0.058 ± 0.009	0.040 ± 0.006
Crown death rate	5.29*	9.37 ± 1.86	16.12 ± 2.19

slope did not have a significant effect on crown growth rate or crown death rate.

Patch Growth

The change in patch density with an increase in the distance from a patch edge fit significantly the normalized density function

$$g(x) = \alpha^2 x e^{-\alpha x} \tag{18}$$

(Table 3). The steeper the slope, S, the higher the density gradient (α). Thus, the distribution of *E. horridum* was most dispersed on the shallowest slopes and the data fit significantly ($F_{2,4} = 26.33$, $P < 0.05$) a Holling Type III functional response (Holling, 1959)

$$\alpha = \frac{aS^2}{h^2 + S^2} \tag{19}$$

(Fig. 6), where parameter a (mean = 0.038 ± 0.021) is the maximum density gradient, and parameter h (mean = 9.49 ± 5.51)

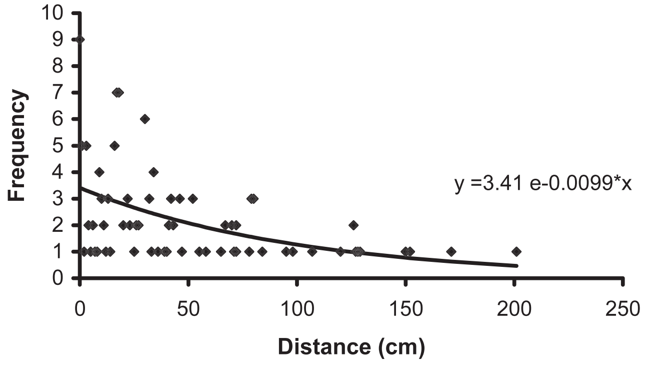

FIGURE 4. Graphical representation of the frequency of *E. horridum* seedlings established as a function of the distance (cm) from the adult plant in Ordesa–Monte Perdido National Park, Spain.

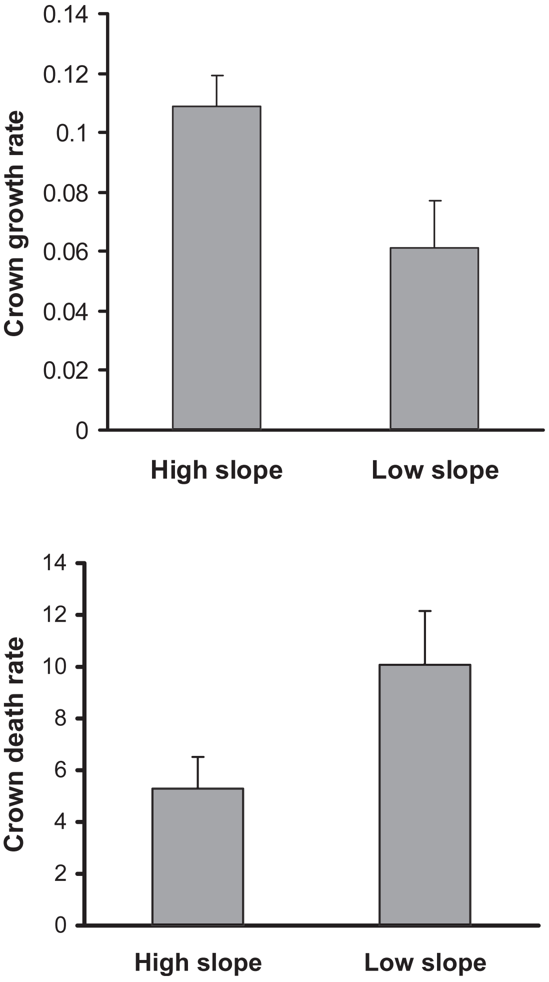

FIGURE 5. Mean (±se) number of crown growth rate and proportion of death crown rate of *E. horridum* plants collected from the edge of the patch in high- or low-slope sites in Ordesa–Monte Perdido National Park, Spain.

TABLE 3

Variation in *E. horridum* density $g(x)$ with distance from the patch edge (x) after normalization, for the four patches analyzed in Ordesa–Monte Perdido National Park, Spain, based on the equation $g(x) = \alpha^2 x e^{-\alpha x}$, where α is the density gradient (Edmonston and Davies, 1978). F statistic, n_1 and n_2 degrees of freedom, and significance P values are obtained from the non-linear adjustment (Gauss–Newton method) between density $g(x)$ and distance (x). Patch size is shown as width (direction perpendicular to the maximum slope) by length (direction along the slope).

Site	Size (ha)	Slope (°)	α	F	n1, n2	P
Patch 1	26.7	5	0.003	5.34	2, 69	0.007
Patch 2	75.2	8	0.019	43.89	2, 71	0.0001
Patch 3	7.5	10	0.022	9.96	2, 64	0.0002
Patch 4	10.2	13	0.022	29.30	2, 71	0.0001

is the saturation constant; i.e., the slope at which the density gradient is half of its maximum.

Average annual growth rate of the four *E. horridum* patches was 0.008 ± 0.001 yr^{-1}, and attained 0.20 ± 0.04 over a 24-yr period. Slope of the terrain favored the *E. horridum* growth rate ($F_{1,22} = 8.87$, $P < 0.01$). Plants on steep slopes had a mean (± SE) annual growth rate (0.013 ± 0.003) that was significantly higher than the rate for plants on shallow slopes (0.004 ± 0.0006). The mean (± SE) growth rate over 24 yr was 0.31 ± 0.07 and 0.09 ± 0.01 on the high and low slopes, respectively.

On the steep-sloped sites, the diffusion coefficient $D_{(24)}$ was 83.9 $\text{m}^2\ \text{yr}^{-1}$, with upper and lower 1-SE limits of 79.5 and 87.3, respectively. On the shallow-sloped sites, $D_{(24)}$ was 234.0 $\text{m}^2\ \text{yr}^{-1}$ (286.9, 186.4, 1-SE upper and lower limits, respectively). The velocities of diffusion (c) were 2.09 m yr^{-1} and 1.93 m yr^{-1} at steep-sloped and shallow-sloped sites, respectively.

Discussion

EFFECTS OF LOCATION WITHIN A PATCH ON E. HORRIDUM *DEMOGRAPHICS*

In the subalpine grasslands of OMPNP, location within a patch had a significant effect on the age distribution of *E. horridum* plants. In the center of patches, the majority (55.6%) of plants were older than 15 yrs and a small proportion (20.4%) were young plants, whereas at the edge of patches, the proportions of the three were similar. Eriksson (1993) suggested that intraspecific competition might be responsible for the smaller proportion of young plants in the center of a patch. At the edge of patches, the relatively high proportion of seedlings and plants aged 8 to 15 yrs (despite the high potential for competition with grasses) reflected the colonization dynamics of this species.

In our study, plants at the edge of patches were in better general condition, produced more flowers, and had higher growth and lower mortality than did the plants in the center of patches. Other studies also reported high seed production in colonizing species (Williamson, 1996; Julien et al., 2006).

In *E. horridum* flower production increased with the age of the plants, which led to a greater production of seedlings associated with the older plants at the edge of patches. Seedling was the stage most susceptible to death but, if they survive, they were the plants that had the highest growth rates. The mortality rate was highest among the plants younger than 12 yrs. Similarly, Weppler et al. (2006) found that seedlings and young plants experienced the highest mortality because the survival probability is influenced by plant size (Riba et al., 2002). Seedling recruitment is an important component of a shrub invasion and this stage can be the most critical, particularly where a thick grass cover surrounds seedlings because grasses are superior competitors to shrub seedlings (Kochy and Wilson, 2000).

E. horridum produced first-generation ramets after ~10–12 yrs of age and at a distance of 60–70 cm from the main root, and second-generation ramets appeared 4–5 yrs later and 90–100 cm away from the main root. Decumbent stem elongation and the time elapsed for the production of first- and second-generation ramets did vary significantly with location in a patch. Others have found that clonal propagation can be highly variable and habitat does influence significantly ramet production (Damman and Cain, 1998). In our study, the presence of grass did not appear to affect ramet production. In *E. horridum*, clonal reproduction is associated with shrub persistence, rather than with an increase in cover. Plants at the edge had more second-order ramets than did the plants in the center of patches. Plants in areas that have abundant resources produce more ramets than do plants in less favorable areas (Cain, 1994; Van Kleunen and Fischer, 2001;

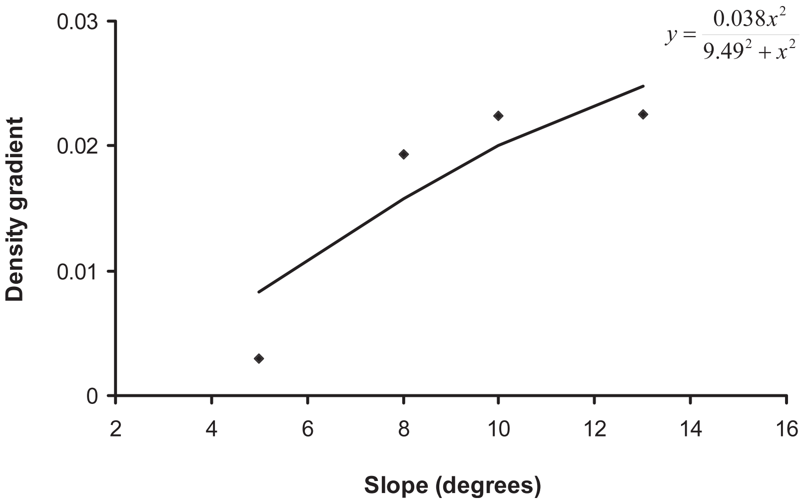

FIGURE 6. Graphical representation of the variation in the density gradient of the patch as a function of the slope at the patch edge in Ordesa–Monte Perdido National Park, Spain.

Nesmith et al., 2006). We found that intra-species competition had a more important effect on the performance of *E. horridum* than did grass-shrub competition. Flower production and clonal growth were higher among the plants at the edge than among plants in the center of patches. Those parameters were affected similarly because the factors that influenced sexual reproduction (intraspecific competition and location) seemed to affect asexual reproduction in the same way: growth rates were highest at the edge where intraspecific competition is lower than it is in the center of a patch (see also Damman and Cain, 1998).

EFFECT OF SLOPE ON E. HORRIDUM *DEMOGRAPHICS*

As we predicted, the slope of the terrain appeared to influence significantly the colonization by *E. horridum* plants in the OMPNP. Colonization was fastest on the steepest slopes, where the plants appeared in better condition than did the plants from sites that had shallow slopes. The plants on steep slopes had higher growth rates and lower death rates than did the plants on shallow slopes, and seedlings and young plants (Age Class I) were more strongly affected than were adult plants. Plants in Class I had the highest growth rates and plants in Class II had lower death rates on the steepest slopes. Competition between *E. horridum* and grasses probably is most intense in areas that have shallow slopes (Alados et al., 2006; Dalaka and Sgardelis, 2006) and, in our study, younger plants seemed to be the age class most strongly affected, and seedling establishment was not significantly affected by slope. In our study and that of Riba et al., (2002), growth and death rates were affected by site characteristics, but flower production and seedling establishment were not influenced by site.

PATCH GROWTH

Slope influenced the growth of the patch over a 24-yr period: at shallow-sloped sites, the expansion rate (1.93 m^2 yr^{-1}) was lower than it was at steep-sloped sites (2.09 m^2 yr^{-1}). We suspect that competition with grasses at sites where the slope is shallow might have limited the rate of expansion. The roots of grasses are better adapted to flat areas than are those of shrubs (Polley et al., 1997; Guerrero-Campo et al., 1999; Alados et al., 2006), which might give grass a competitive advantage, improving its resistance to shrub invasion, and moderating the expansion rate of *E. horridum*.

In summary, although in our study area, with high average rainfall, livestock pressure and fire are needed to maintain grasslands (Sankaran et al., 2005), the higher competitive ability of grasses in low-slope areas play an important role in the persistence of subalpine grasslands. The slope of the terrain had a significant effect on the invasion of grasslands by the shrub *E. horridum* which may be due to the intense competition between shrubs and grass at low-slope areas retarded the expansion of *E. horridum*, and invasion rates were highest on the steepest sites. Indeed, plants at the edge had higher productivity, growth rates, flower production, and seedling production than did plants in the center of patches. Clonal reproduction, a means of persistence, produced dense, monospecific patches of *E. horridum*, which did not vary with slope.

At the time of our study, there were recent reductions in livestock farming and the controlled burning by shepherds, and colonization by *E. horridum* was in the initial stage. In time, however, the rate of invasion probably will decrease when shrubs reach the forest line. In terms of management, the most appropriate practice might be a grazing of the seedlings by, for instance, reintroduced goats, which have a larger preference than sheep for woody species, being able to forage on spiny legumes such as *E. horridum* (Papachristou et al., 2005).

As others (Crawley, 1986; Sheppard et al., 2002) have suggested, demographic analyses at the early stage of colonization should allow a comparison of the invasion rates across a range of habitats, which would provide an estimate of the invasion dynamic and of the life cycle stage more sensitive to management directives.

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