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Resprouting after experimental fire application and seed germination in *Erica vagans*

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Abstract

Resprouting after experimental fire treatments and the effect of light and heat on seed germination were studied in the evergreen shrub *Erica vagans*. Experimental fire application consisted of two levels of temperature and two levels of fire duration. The number of resprouts produced were counted after 4, 9 and 12 months. Above-ground plant dry weight influenced plant survival, but not the number of resprouts produced. However, both temperature and duration of fire application showed significant effects on the number of resprouts produced. After low temperature and short application times *E. vagans* produced more resprouts, but did no differ from controls (plants clipped without fire treatment).

Field observations showed that seedling establishment is rare both in control and burned areas. However, the seedlings were frequent in the cleared areas around experimentally burned stumps. To examine the effect of light and heat on seed germination two germination experiments were performed. Both light and heat application largely increased seed germination. Seeds heated from 80 °C to 100 °C increased their germination rates, but temperatures above that range strongly reduced the germination.

Key words: Evergreen shrub, heat treatments, fire duration, germination experiments, regeneration response.

Resumen. *Rebrote después de la aplicación experimental de fuego y germinación en* Erica vagans.

Se estudió la capacidad de rebrote, después de la aplicación experimental de tratamientos de fuego, y la germinación del arbusto perennifolio *Erica vagans*. El fuego experimental consistió en dos niveles de temperatura y en dos niveles de tiempo de duración y se aplicó a tocones de matorrales previamente cortados. El número de rebrotes se contó después de 4, 9 y 12 meses. El peso aéreo del matorral antes del experimento tuvo influencia en la supervivencia de la planta, pero no en el número de rebrotes producidos. No obstante, tanto la temperatura como el tiempo de aplicación del fuego mostraron efectos significativos sobre el número de rebrotes producidos. Los rebrotes producidos tras la aplicación de temperaturas bajas durante períodos breves fue el tratamiento que produjo más rebrotes, pero no se diferenció de plantas control (matorral cortado pero no quemado). A pesar de que la germinación de semillas es rara en condiciones de campo, aparecieron muchas plántulas alrededor de los tocones quemados. Tanto la luz como la aplicación de tratamientos de calor, de 80 a 100 °C, incrementaron las tasas de germinación.

Palabras clave: arbusto perennifolio, duración del fuego, temperatura del fuego, experimentos de germinación, tratamientos de calor, estrategias de regeneración.

Introduction

Resprouting after fire is a common regenerative strategy in communities affected by recurrent fires (James, 1984). Similarly, post-burn seedling production is also a common mechanism in such communities, since germination of many species is controled by fire-related cues (Keeley, 1991).

Plant species may be ranked along a continuum between obligate resprouters and obligate seeders (Moreno & Oechel, 1991), depending on their responses to fire intensity and post-fire conditions (Viro, 1974; Christensen, 1985). Fire characteristics (e.g. temperature and duration) largely determine mortality, resprouting potential and post-fire germination responses, as has been observed in several shrub species after wildfires or experimentation (Trabaud, 1991; Moreno & Oechel, 1991; Canadell et al., 1991; Lloret & López-Soria, 1993).

Recurrent fires are among the most important disturbances of montane shrub vegetation in northern Spain. Fire has been used during centuries in this area to manage pastures and heathlands. Several heath species showing different post-burn regenerating responses occur in this area (e.g. Bannister, 1966, *Erica tetralix;* Hobbs & Gimingham, 1984, *Calluna vulgaris* and *E. cinerea;* Clement & Touffet, 1990, *E. ciliaris;* Mesléard & Lepart, 1991 & Canadell et al., 1991, *E. arborea). Erica vagans* is the dominant heath species on limestone soils. Despite being traditionally managed by prescribed fires, its regenerative potential has not been yet evaluated. This study focuses on the effects of fire intensity on mortality, post-burn regrowth and seedling production in this species.

The goals of this study are (a) to test the effect of experimental fire application at different intensities and (b) to determine the optimum temperature and light conditions for seed germination.

Material and methods

Plant species and study area

Erica vagans L. is a small to medium-sized evergreen shrub that occurs both in calcareous and acid soils of western Europe. It flowers in summer and the seeds ripen from September to November. Unlike most european heath species, this species is abundant on limestone soils, specially in montane pastures. Fires are used to manage montane pastures of northern Spain in order to avoid dominance of shrubs. In calcareous soils of the Cantabrian range *E. vagans* is one of the dominant shrubs and is usually affected by prescribed fires. *E. vagans* produces resprouts from both above- and below-ground stems, but seedling establishment after fire is scarce (pers. observ.).

The study was conducted at Comeya, Covadonga National Park (Asturias province, northern Spain, 43° 16' N, 5° 00' W, 950 m a.s.l). This site is an area of montane pastures with scattered heaths on soils developed over limestones. The dominant heath species is *Erica vagans*. The experimental fire treatments were performed at this site in May 1992 in a north-facing plot of pasture with scattered *E. vagans* shrubs. This area was not pastured during 1992.

Resprouting and germination after experimental fire treatments

The experimental fire treatments consisted of two factors, temperature and fire duration, with two levels per factor . Temperature levels were low (150 °C – 250 °C) and high (350 °C – 450 °C). Fire duration consisted on two levels: 2 and 4 minutes. Values of temperature and time were selected according to Canadell et al. (1991). The treatment were distributed according to a block design to avoid the influence of spatial heterogeneity. We considered five different altitudes on a north-facing slope as blocks. The experiment was carried out in May 1992, coincident with the maximum growth period of the plant.

Fifty individual shrubs were chosen in the plot and their shoots were clipped off at 10 cm of ground level. The age of each shrub was estimated by counting the rings of the main trunk. The above-ground dry weight of the shrubs was determined after oven-drying.

Each treatment was randomly assigned to ten stumps. The ten remaining stumps were employed as controls.

The ground surface around each stump was cleared and the temperature treatments were applied using a butane torch flame. The heat was evenly distributed over the stump in a circle of 25 cm of diameter and the temperature was monitored with a thermocouple placed over the stump. Other thermocouple was placed in the soil (about 2 cm depth). For high temperature treatment soil temperature was 95 ± 51 °C (2 min treatment) and 130 ± 81 °C (4 min treatment). After 4, 9 and 12 months of the experimental manipulation we counted the number of resprouts and seedlings growing around the stumps in a circle of 25 cm of diameter. We could not determine the mass of the resprouts because some died.

Germination experiments: Effect of light and high temperature treatments

To examine the effect of light and temperature on germination rates we performed two laboratory experiments. Heat treatments were performed in an oven and lasted 2 minutes. The levels were: control (no treatment), 60°, 80°, 100°, 120° and 140 °C. Germination rates were estimated by sowing seeds on moist filter paper inside petri dishes. The seeds were examined fortnightly and 3 ml of water were added weekly.

The first experiment began in November 1992 and lasted 9 months. The seeds were kept in the darkness in chambers at 20 °C. We used 14 dishes per heat treatment and 100 seeds per dish. The second experiment began in March 1993 and lasted 6 months. The seeds were maintained in a 12:12 photoperiod in chambers at 20 °C. We used 10 dishes per heat treatment and 50 seeds per dish.

Statistical analyses

Comparisons between germination rates after heat treatments were performed by one-way ANOVAs and «a posteriori» Student-Newman-Keuls tests.

Initially, we intended to use a two-factor analysis of covariance to test the effect of fire on resprouting, including the basal area of the stump as a covariate. However, because resprouting was independent on this variable (type II error was low, $P > 0.25$), we used a two-factor ANOVA. Furthermore there was not significant effect of block and therefore it was ommitted from the tables. To test the influence of plant size on mortality after fire treatments the shrubs were divided into two groups of identical sample size: small plants (< 51 g) and large plants (> 52 g). Differences of mortality among these groups were tested by a G-test by pooling all fire treatments together.

We used the squared root transformation for proportions and the arcsin transformation for percentages.

Results

Resprouting and germination after fire treatments

Our experiment resulted in about 60% mortality after fire treatments, which affected mainly to small shrubs. Large plants (>52 g) exhibited higher ability to resprout than small ones ($G = 3.918, d.f. = 1, p < 0.05$). Nevertheless, neither above-ground plant dry weight nor shrub age showed significant effects on the number of resprouts ($N = 46, r = 0.223, P > 0.05$; and $r = -0.132, p > 0.05$, respectively).

The number of reprouts counted on the stumps after the fire application varied from 4 to 9 and 12 months (Table 1). There was resprout production and morta-

Table 1. Number of resprouts produced by the stumps and number of seedlings growing around the stumps 4, 9 and 12 months after fire treatments (mean ± SD). T1: low temperature; T2: high temperature; t1: 2 min., t2: 4 min. Asterisks indicate the significance of the F-test for comparisons between control and T1-t1 treatment: **, $p < 0.01$; *, $p < 0.05$; n.s., non significant.

	4 mo.	9 mo.	12 mo.
Number of resprouts			
Control	5.17 ± 6.85 n.s.	8.88 ±13.28 n.s.	6.38 ± 9.95 n.s.
T1 - t1	12.80 ±15.94	11.30 ±11.15	10.50 ±10.00
T1 - t2	0.20 ± 0.63	1.30 ± 2.75	2.22 ± 4.18
T2 - t1	1.20 ± 3.16	2.20 ± 3.71	2.70 ± 4.37
T2 - t2	0.90 ± 2.51	0.56 ± 1.67	0.44 ± 1.33
Number of seedlings			
Control	1.10 ± 1.10 *	1.13 ± 0.99 n.s.	0.25 ± 0.46 **
T1 - t1	3.30 ± 1.70	2.50 ± 1.96	3.10 ± 1.97
T1 - t2	5.30 ± 3.56	5.30 ± 6.10	7.67 ± 7.29
T2 - t1	6.10 ± 4.23	10.80 ±10.28	4.00 ± 4.14
T2 - t2	2.80 ± 3.29	4.67 ± 4.03	4.44 ± 5.98

lity and their number significantly varied among treatments (Table 2). The application of low temperature treatment during 2 minutes showed higher number of reprouts (significant interaction term after 4 months, Table 2), but the difference vs. control was not significant (Table 1). Both independent variables, temperature and fire duration exhibited significant effects, being high temperature and long fires more detrimental than the other treatments.

Neither temperature nor fire duration influenced the number of seedlings that colonized areas around burned stumps (Table 2). However, high temperature-2 minutes treatment increased seedling number in the cleared areas (Table 1, and significant interaction term in Table 2). The number of seedlings around burned stumps was greater than around control stumps only 4 and 12 months after treatment (Table 1).

Effect of light and temperature on germination

The percentage of germination in a 12:12 h photoperiod was ten-times the percentage of germination in darkness (Fig. 1). Mean percentage of germination at 12:12 photoperiod was 14.2 ± 15% after 3 months, but there were no significant differences among treatments (Fig. 1, $F_{(3,49)} = 2.482$, $p = 0.076$, treatments at 100 and 140 °C were removed from the analyses because of fungi contamination in the former and 0% germination in the later). After 6 months more seeds germinated at 60 °C heat treatment (60.8 ± 13.6%) and 80 °C (67.2 ± 14.0%). There were significant differences among treatments ($F_{(3,39)} = 9.718$, $p = 0.0001$, Fig. 1).

Six months after darkness treatment the percentage of germination differed among heat treatments ($F_{(5,83)} = 17.419$, $p < 0.0001$). More seeds germinated after treatments at 100 and 120 °C (Fig. 1). Differences among treatments were maintained after 9 months ($F_{(5,83)} = 20.339$, $p < 0.0001$), although the percentage of germination after treatment at 120 °C was lower than 7%.

Table 2. Anova tables of the number of resprouts and seedlings 4, 9 and 12 months after the fire treatment. Block design was omitted from the tables. *, $p < 0.05$; **, $p < 0.01$; n.s., non significant.

Source of variation	d.f.	SS	F	SS	F	SS	F
		No resprouts 4 mo.		No resprouts 9 mo.		No resprouts 12 mo.	
Temperature	1	312.66	4.774 *	257.92	6.593 *	232.31	6.447 *
Time	1	386.70	5.904 *	313.22	8.006 **	262.53	7.285 *
Temperature x time	1	362.86	5.541 *	159.69	4.082 n.s.	85.90	2.381 n.s.
Error	37	2226.75		2060.97		1807.58	
		No seedlings 4 mo.		No seedlings 9 mo.		No seedlings 12 mo.	
Temperature	1	0.421	0.030 n.s.	140.24	3.335 n.s.	10.53	0.397 n.s.
Time	1	0.619	0.057 n.s.	19.31	0.459 n.s.	59.47	2.244 n.s.
Temperature x time	1	70.779	6.514 *	209.77	4.989 *	40.25	1.519 n.s.
Error	37	441.260		1798.97		1011.37	

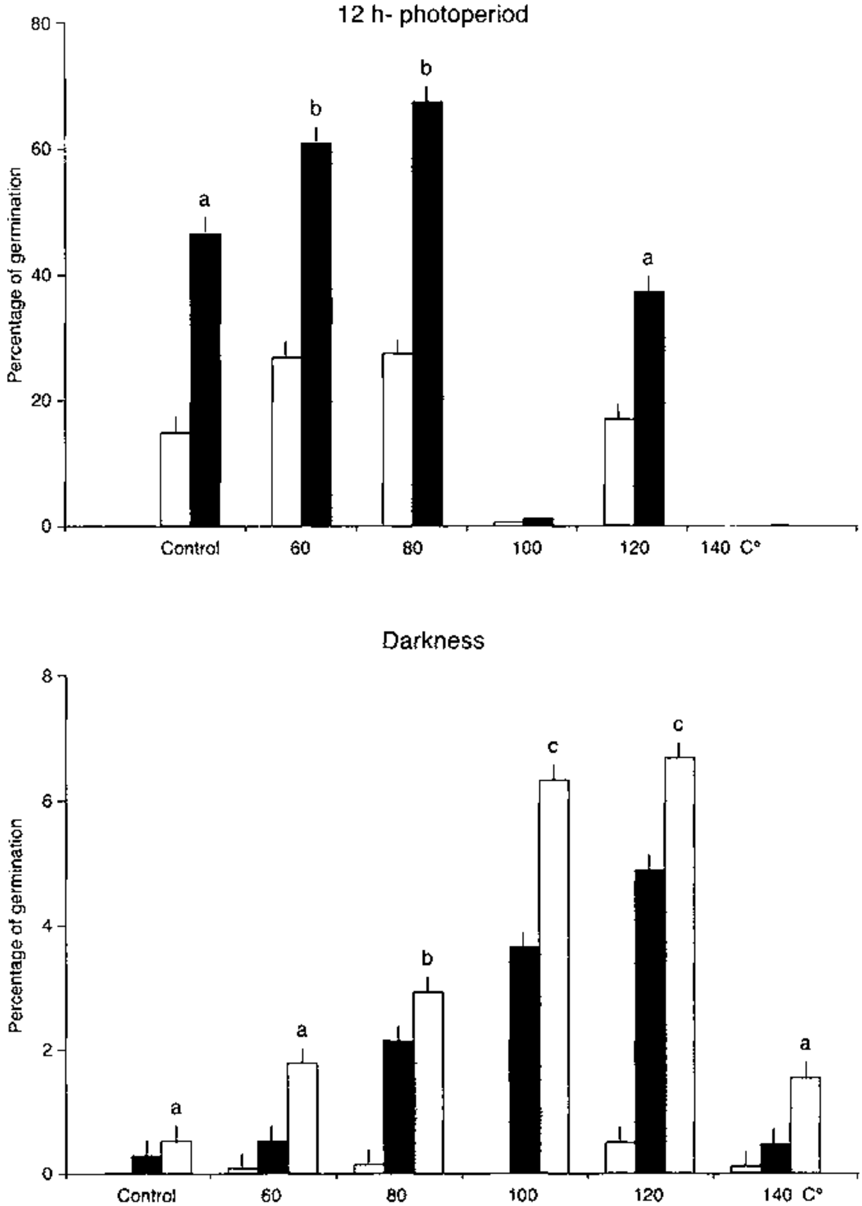

Figure 1. Percentage of germination (mean ± s.e.) after [ ] 3 months, [■] 6 months and [ ] 9 months at 12:12 h photoperiod (the experiment began on 15 march 1993 and lasted 6 months) and darkness (the experiment began on 23 November 1992 and lasted 9 months) for different heat treatments. Differences between means after 6 months are indicated by different letters (S-N-K test).

Discussion

Resprouting after fire

Erica vagans was able to regenerate after fire by both resprouting and seed germination, although seedling recruit appears less frequent after wildfire. Seedling establishment was observed only at some moist places (M.L.V, pers. observ.). Despite mortality after fire application affected mainly to small shrubs, shrub size did not affect the number of resprouts produced. The observed mortality could be produced either by the destruction of the buds on all the meristematic tissues or by lack of resources to support the resprouts (Christensen, 1985). The experiment coincided with maximum growth rates of the plants, which is probably the time of the year with lower below-ground storage of resources and this may result in higher mortality.

Contrarily to our results, Canadell et al. (1991) found that plant size was the most important factor determining the number of resprouts in *Erica arborea;* and Lloret & López-Soria (1993) found that pre-treatment plant size was not important in determining post-fire plant survival in *Erica multiflora*.

There was a decrease in the number of resprouts produced after increased fire intensities, but the effect of low temperature and short time duration did not differ from the control. It may be concluded that the response of *E. vagans* to fire could depend on plant size and temperature reached during wildfires. This species showed high potential to resprout only after low intensity fire application. Nevertheless, the presence of old scars in the growth rings produced by old fires confirms that some plants have resprouted previously. But it is probably that most of these stumps were below the ground while those wildfires passed or fires were light. After wildfires most of the resprouts are produced by below-ground stems (pers. observ.), which were probably less damaged. Therefore, it is likely that mortality mostly affects the above-ground stumps. Our experiment did not produce below-ground resprouting because selected plants had erect trunks.

Seed germination

The establishment of *E. vagans* seedlings after wildfire is rare, however their presence in the cleared areas around the stumps suggests that light might influence seed germination. This was confirmed by our germination experiment in which light greatly enhanced the percentage of germination. Furthermore, cleared control areas produced less seedlings than burned areas, what drives to conclude that heat might affect seed germination. Seed-heating increased the percentage of germination, and seeds under 12:12 h photoperiod treatment produced the largest percentages of germination after heating between 80 and 120 °C. However, in the darkness the highest value was obtained at the 120 °C treatment.

Germination after a short burst of heat (the cue that the fire has passed) is a consequence of the rupture of impermeable seed coats (Christensen, 1985). In our experiments, germination began in late-April, what might suggests either a cyclic change in dormancy or a release from dormancy with time (Fenner, 1985).

However, our previous experiments showed high germination rates with light in November. Other mechanisms might have enhanced germinability in the gaps opened during the experiment, such as wetting-drying cycles or temperature fluctuations (Fenner, 1985).

Germination of ericaceous seeds is stimulated by light (Gimingham, 1972; Pons, 1989; Matter & Williams, 1990), which is important to stablish a persistent seed bank if the seeds are buried (Hill & Stevens, 1981) and explains the absence of emergence of seedlings in a heather vegetation (Miles, 1973). Heat-stimulated germination has been documented for many shrub species, including a large number ericaceous shrubs (e.g. Pons, 1989; Keeley, 1991; Tárrega et al., 1992; Pierce & Moll, 1994; Salvador & Lloret, 1995).

Most of the times, temperatures reached during fires in shrub communities exceed the optimum germination temperatures found in this study (e.g. DeBano & Conrad, 1978; Trabaud, 1979; Muñoz & Fuentes, 1989; Moreno & Oechel, 1989, 1991). Hence, this could partially explain the absence of seedlings in most areas burned by wildfires. Nevertheless, mean temperatures measured during the field experiment at 2 cm depth were adequate for seed germination. These temperatures might slightly increase the percentage of germination, but both soil erosion and subsequent light stimulation may also play an important role. The depth distribution of seeds in the soil should therefore be important in determining seed germination. Seeds dispersed from September to November by shrubs not affected by fire might also germinate in recently burned areas since there is not vegetation cover and the seeds are stimulated by light. However, humidity might also influence the establishment of seedlings (Bruggink, 1993). The presence of seedlings in the cleared area around the stumps could be explained by the moisture of those places surrounded by vegetation and located on a north-facing slope. This issue requires further critical study and field experimentation.

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