SEED PRODUCTION AND SIZE OF HEATHS ALONG AN ALTITUDINAL GRADIENT IN NORTH SPAIN

MARÍA LUISA VERA

Departamento de Biología de Organismos y Sistemas. Universidad de Oviedo. 33071 Oviedo. Spain. mlvera@uniovi.es

Disponible en: http://hdl.handle.net/10651/40756

Abstract

The seed production and size of *Calluna vulgaris*, *Erica cinerea* and *Erica vagans* were studied at different altitudes (from coast to high mountain). There were no significant differences in seed production among species, although *E. cinerea* tend to produce more seeds. Seed production of the species varied between localities. A high seed production was not found at the highest altitudes for *E. vagans* and *E. cinerea*. Neither low seed production nor significant annual fluctuations were revealed for *Calluna* at the highest altitudes. Type of substratum seem to influence seed production of *E. vagans*. Its lowest seed production was on quartzite. Altitude did not seem to have an effect on seed size, however, the characteristics of soil could influence on the mean seed size. The smallest seed size of *Calluna* was produced on richer soils. While *E. vagans* showed the highest seed size on this type of soils. Annual variations in mean seed size for two species were also revealed.

Seed production and seed size variations between species and sites could be related with the success of seed regeneration and present distribution patterns of these plants.

Keywords: Elevation effect, Ericaceae species, seeds.

Introduction

The heaths are very common dwarf shrubs in Asturias (Northern Spain), which occur along a wide altitudinal range (Vera 1983a).

The regeneration of heathland plants which can occurs by seeds depends, amongst other factors, on seed production. Furthermore, seed production is one of the main factors which determines the size of the seed bank (Bruggink 1993, Trabaud 2000). The soil seed bank of heathland plants , which is long-term persistent (Mallik & al. 1984; Miller & Cummins 1987) plays an important role in the restoration of heathlands (Hobbs & al. 1984; Gloaguen 1990). The species with a higher seed production may have a greater advantage in the maintenance of existing populations and in the colonization of bare ground, as opposed to those with lower seed production.

However, not only it is necessary to determine the seed production in different species which can occur together, but it must also be estimated in different environments. One way of inferring the significance of particular environment factors on seed production is through altitudinal gradients (Wookey & al. 1993). This can provide a better understanding of factors which affect seed production, and expand our knowledge of natural borders in the distribution of plants. Information on seed regeneration at the geographical limits of species is essential (Pigott 1992). Therefore investigations on seed production along an altitudinal gradient are neccesary in order to know the success of seed regeneration at different altitudes. These studies are essential, particularly in high mountain areas, where poor seed production could be a limiting factor in the reproductive processes. Various investigations have shown variations of seed production with climate and environmental conditions (in McGraw & Vavrek 1989; Crawley 1992; Legg & al. 1992; Thompson 1992; Bruggink 1993; Vera 2007; Vera 2011a, Vera & al. 2013) as well as annual fluctuations (Miller 1979; Miller & Cummins 1987; Bruggink 1993; Holm 1994). Comparative studies on seed production of *Calluna vulgaris* between years for some localities were carried out with the aim of determining if there are such annual fluctuations. This type of study is very important, fundamentally in severe environments, where seed production has rarely been measured, and can vary widely between years.

Several studies have suggested the importance of seed size in the colonization of plants by seedling establishment. In some species, large seeds contribute to a higher germination and seedling survival (Harper 1977; Gross 1984; Tripathi & Khan 1990; Lusk 1995; Vera 1997; Reyes & al. 2000). Therefore, other aim of this study is an estimation of the average seed size of each population of studied heaths at different altitudes.

The contribution of data on seed production and size of studied heaths at different elevations is particularly important, since the estimation of these factors together with those already studied on the germination capacity of seeds and the effect of seed size on germination for the same heathland plants along the same altitudinal gradient (Vera 1997) makes it easier to determine the success of seed regeneration of these heaths at different altitudes.

Investigations on seed production and size which affect seed regeneration along an altitudinal gradient are essential, since such studies can give information on the influence of factors associated with altitudinal gradient on seed production and size. Nowadays this is very important since it could help to understand the potential effects of climatic change on the reprodution and distribution of plants (Vera 2011b).

Material and Methods

Study sites

The study was carried out in Asturias (Northern Spain) along an altitudinal gradient from the coast (Cape Peñas) to the central range of the Cantabrian Mountains (San Isidro Mountain Pass).

The three studied species: *Calluna vulgaris* (L.) Hull (hereafter referred to as *Calluna*), *Erica vagans* L. and *Erica cinerea* L. occur between the coast and the San Isidro mountains, but *Calluna* has a wider altitudinal range than the other two heaths (Vera 1997).

Through altitudinal gradient various types of substrata occur and more than one can be found at the same altitude. On the other hand heaths can grow on soil developed from different rocks (Vera 1983a; Vera 1983b). *Erica vagans* is the heath occurring in a wider range of soil pH growing on all types of substrata. However it is rare to find *E. vagans* on quartzite in the Cantabrian Mountains, but it is less rare on this type of substratum on the coast. Therefore it was not always possible to take samples of the three heaths for each elevation on the same substratum.

Characteristics of the samples site are given in Table 1.

The characterization of climate along altitudinal range is difficult because of the lack or scarcity of data in mountain areas. A thermic altitudinal gradient from the coast to the Cantabrian Mountains is calculated by Muñoz (1982). A decrease of 0’562ºC in the annual average temperature for each 100 m is deduced. The annual average temperature in Cape Peñas (100 m) is 13’93ºC, therefore at 2100 m it would be 2’69ºC (studied altitudinal range). Annual precipitation varies between 942 mm (Cape Peñas) and 1787 mm (Mountain Pass of Leitariegos, 1525 m). Leitariegos is the highest meteorological station above 1500 m with data recorded over several years in the Cantabrian Mountains.

Seed production

Seed capsules were collected in November 1994, from five individuals of each species at each altitude, when most seeds had ripened but before the capsules had dehisced, with the aim of estimating the seed production. The seeds were counted from 20 capsules in each individual. Seed production was obtained by multiplying the mean number of seeds produced per capsule by the total number of flowers collected in each individual in plots of 20x20 cm. The mean seed production in San Isidro at 2090 m was only obtained from three individuals, because the other two individuals don´t have 20 capsules in adequate conditions for its estimation, being several of them open.

Furthermore, the data of 1994 seed production for *Calluna* were compared with seed production estimated in other years for some of the studied sites calculated with the same method, but sometimes it was only possible to estimate the seed production for three individuals. In other cases only the number of seeds per capsule only was indicated (Table 2).

Seed size

30 seeds from each of 5 individuals for each species and from each site were measured, in order to establish the mean seed size for each altitude in 1994. Moreover, seed size for *Calluna* and *E. vagans* was also estimated for two of those studied localities in 1990, with the aim of determining if there were differences in mean seed size between years (Table 4). The lenght and width of each seed was measured with a micrometer under a stereoscopic microscope.

Statiscal analyses

Analysis of varianza (ANOVA) was carried out to examine differences between species, altitudes, years and substrata on seed production and size.

The relationships between the flower number and mean seed number per capsule, the mean seed size and seed production per individual, as well as mean seed size and soil pH per site were established using Pearson correlations.

Results

Seed production

There were no significant differences in seed production among species in 1994, although *Erica cinerea* tend to produce more seeds per area unity (mean 424200 seeds/m^2) than *Erica vagans* (mean 383675 seeds/m^2) and *Calluna* (mean 322825 seeds/m^2). *Erica cinerea* was the species producing more seeds per capsule (mean 8'35) with respect to *E. vagans* (mean 5,16) and *Calluna* (mean 5,59) ($p<0'01$), but this does not imply more significant seed production, as it has already been indicated, since *E. cinerea* developed less flowers (mean:47300 per m^2) compared with *E. vagans* (mean 71375 per m^2) and *Calluna* (mean 58937 per m^2) ($p<0'05$).

Seed production of the studied species varied among localities, being variable both the number of flowers and seeds per capsule (Table 1). Seed production of *Calluna* was variable between sites ($p<0'001$), showing the highest production at 1620 m on siliceous substrate. *Erica vagans* increased its seed production with altitude until 1200 m, but it decreased at highest altitude ($p<0'0001$). *Erica cinerea* had the lowest seed production at highest altitude ($p<0'01$) (Table 1). Number seeds per capsule of *E. cinerea* also decreased with altitude ($p<0'01$).

The type of substratum only seems to have an effect on the seed production and number of flowers for *E. vagans*. The lowest seed production was on quartzite ($p<0'001$), while the highest number of flowers was on shale ($p<0'001$). Type of substratum had no significant effect on the number of flowers, seeds per capsule and seed production for *Calluna*. Although in similar altitudes (range 1500-1700 m), the pH of soil could influence on the seed production. The highest seed production in *Calluna* was in the soil with the lowest soil pH (Table 1).

Table 1. Mean (±SE) of number flowers per m^2 (n=5), seeds per capsule (n=5x20) and seed production per m^2 (n=5) for each species in different localities in 1994, except in San Isidro, 2090 m (n=3).

Calluna vulgaris

Locality and site descriptions	Number flowers/m^2	Seeds per capsule	Number seeds/m^2
Cabo Peñas. 100 m. Quartzite. Soil pH: 3.9	76700 (±10600)	4’07 (±0’43)	279900 (± 16900)
Pto. San Isidro. 800 m. Quartzite. Soil pH: 4.9	91300 (±14900)	4’31 (±0’33)	361800 (± 47800)
Pto. San Isidro. 1200 m. Shale. Soil pH: 4.8	59000 (± 4500)	1’86 (±0’15)	103100 (± 9300)
Pto. San Isidro. 1510 m. Shale. Soil pH : 5.2	59600 (± 8500)	6’24 (±0,37)	382300 (± 85700)
Pto. San Isidro. 1620 m. Shale. Soil pH: 3.7	69400 (± 5300)	9’85 (±0’44)	702800 (±128300)
Pto. San Isidro. 1680 m. Limestone. Soil pH: 5.1	33200 (± 2600)	5’45 (±0’23)	182100 (± 18000)
Pto. San Isidro. 2020 m. Quartzite. Soil pH: 3.6	30000 (± 1600)	6’20 (±0’48)	189600 (± 47600)
Pto. San Isidro. 2090 m. Quartzite. Soil pH: 3.7	52300 (±14900)	6’76 (±0’69)	381000 (±196500)

Erica vagans

Locality and site descriptions	Number flowers/m^2	Seeds per capsule	Number seeds/m^2
Cabo Peñas. 100 m. Quartzite. Soil pH:3.9	60800 (±14900)	1’61 (±0’13)	96200 (±25600)
Pto. San Isidro. 800 m. Limestone. Soil pH: 6.8	50400 (± 3600)	6’38 (±0’46)	323000 (±58900)
Pto. San Isidro. 1200 m. Shale. Soil pH: 4.8	89500 (± 4600)	9’72 (±0’58)	869900 (±91900)
Pto. San Isidro. 1510 m. Shale. Soil pH: 5.2	84800 (± 5600)	2’91 (±0’28)	245600 (±23500)

Erica cinerea

Locality and site descriptions	Number flowers/m^2	Seeds per capsule	Number seeds/m^2
Cabo Peñas. 100 m. Quartzite. Soil pH: 3.9	47400 (±11100)	11’00 (±0’57)	513200 (±109400)
Pto. San Isidro. 800 m. Quartzite. Soil pH: 4.9	66200 (± 8100)	9’37 (±0’56)	617600 (± 98900)
Pto. San Isidro. 1200m. Quartzite. Soil pH: 4.7	28300 (± 3800)	4’70 (±0’47)	141800 (± 39900)

Cabo=Cape; Pto.=Mountain pass

Only Cabo Peñas showed significant annual fluctuations in seed production (p<0’0001). *Calluna* had very low seed production in 1999. The mean number of seeds per capsule in 1999 was very small compared with other years in this locality (Table 2). There were no significant differences in seed production *Calluna* between years in the higher altitudes of Pto. San Isidro, although the number of flowers and seeds per capsule was variable between years. A lower number of flowers was developed in 1999, both in Pto. San Isidro and Cabo Peñas, while more seeds per capsule were produced in that year in both sites of Pto. San Isidro (at 2020 and 2090 m), unlike Cabo Peñas (Table 2).

There was no relationship between number of flowers per individual and mean number of seeds per capsule for any species. There was only a trend in *Calluna* to produce less seeds per capsule in those the years when it produced more flowers in Pto. San Isidro (Table 2).

Table 2. Mean of number flowers, seeds per capsule and seed production of *Calluna vulgaris* in different years and sites on quartzite. Number of samples is given in parentheses.

Locality	Altitude	Year	Number flowers/m^2	Seeds per capsule	Number seeds/m^2
Cabo Peñas	100 m	1990	-	4’31 (n=22)	-
Cabo Peñas	100 m	1991	-	3’00 (n=48)	-
Cabo Peñas	100 m	1993	-	3’36 (n=56)	-
Cabo Peñas	100 m	1994	76700 (n=5)	4’07 (n=5x20)	279900 (n=5)
Cabo Peñas	100 m	1995	-	8’06 (n=5x20)	-
Cabo Peñas	100 m	1999	40760 (n=5)	0’57 (n=5x20)	24857 (n=5)
Pto. San Isidro	2020 m	1994	30000 (n=5)	6’20 (n=5x20)	189600 (n=5)
Pto. San Isidro	2020 m	1998	26733 (n=3)	6’23 (n=3x20)	166056 (n=3)
Pto. San Isidro	2020 m	1999	22860 (n=5)	8’07 (n=5x20)	180378 (n=5)
Pto. San Isidro	2090 m	1994	52300 (n=3)	6’76 (n=3x20)	381000 (n=3)
Pto. San Isidro	2090 m	1998	29933 (n=3)	9’55 (n=3x20)	289333 (n=3)
Pto. San Isidro	2090 m	1999	19940 (n=5)	9’77 (n=5x20)	204310 (n=5)

Cabo=Cape; Pto.=Mountain pass

Seed size

There were significant differences in seed size according to length and width between species for 1994 (P<0’001) (Table 3). *Erica cinerea* had the largest seeds (mean 0’80x0’55 mm) while *Calluna* (mean 0’62x0’46 mm) and *E. vagans* (mean 0’58x0’51 mm) showed smaller seeds.

The shape varied between species, the seeds of *Calluna* and *Erica cinerea* being long, while in *Erica vagans* they were nearly spherical.

There were significant differences in seed size between the different sites in each species (p<0’0001). The altitude did not seem to have an effect on seed size. However the type of substratum and soil pH could influence on the mean seed size. The smallest seed size of *Calluna* was produced on limestone substratum (pH=5’1). Small seed size was also obtained in soil with similar soil pH on shale (pH=5’2). The seed size of *E. vagans* also differed with substrate (p<0’0001), although it was on limestone where it showed the highest seed size. *E. vagans* seed size increased significatly with increasing soil pH (p<0’05). The seeds of *E. cinerea* always collected on quartzite were influenced by soil pH. The largest seed size was found in Cabo Peñas, where the soil pH was lower.

Furthermore, the mean seed size of each individual could be correlated with the number of seeds produced in some of the species. The seed size of *E. cinerea* decreased with increasing seed production (r=-0’52, p<0’05, n=15) and a negative correlation between seed size and number of seeds per capsule was found for *Calluna* (r=-0’34, p<0’05, n=38).

Table 3. Mean seed size (length and windth) in each species in different altitudes in 1994. (See type of substratum in Table 1).

Locality	*Calluna vulgaris* Mean seed size (LxW) (Intervals)	*Erica vagans* Mean seed size (LxW) (Intervals)	*Erica cinerea* Mean seed size (LxW) (Intervals)
Cabo Peñas 100 m	0’64 x 0’46 mm (0’60-0’90) x (0’35-0’65)	0’57 x 0’49 mm (0’45-0’70) x (0’40-0’60)	0’82 x 0’61 mm (0’70-1’00) x (0’55-0’70)
Pto. San Isidro 800 m	0’62 x 0’45 mm (0’50-0’80) x (0’30-0’60)	0’60 x 0’52 mm (0’55-0’70) x (0’45-0’65)	0’77 x 0’52 mm (0’60-1’00) x (0’45-0’65)
Pto. San Isidro 1200 m	0’70 x 0’51 mm (0’60-0’90) x (0’45-0’55)	0’57 x 0’50 mm (0’50-0’70) x (0’40-0’60)	0’81 x 0’50 mm (0’65-1’00) x (0’40-0’60)
Pto. San Isidro 1510 m	0’57 x 0’41 mm (0’40-0’75) x (0’30-0’60)	0’58 x 0’53 mm (0’40-0’80) x (0’40-0’70)	
Pto. San Isidro 1620 m	0’65 x 0’48 mm (0’50-0’80) x (0’40-0’60)		
Pto. San Isidro 1680 m	0’55 x 0’42 mm (0’40-0’95) x (0’30-0’60)		
Pto. San Isidro 2020 m	0’62 x 0’48 mm (0’50-0’80) x (0’35-0’60)		
Pto. San Isidro 2090 m	0’61 x 0’46 mm (0’50-0’90) x (0’35-0’60)		

Cabo=Cape; Pto.=Mountain pass

Variations in mean seed size for *Calluna* and *E. vagans* between years (1990 and 1994) for two studied localities were shown (Table 4). A relationship between number of seeds per capsule and seed size per year in both species and localities was found. A higher mean number of seeds/capsule in 1990 for each species and localities was estimated in 1990 than that in 1994, while the mean seed size was lower in 1990.

Table 4. Mean of number seeds per capsule and seed size (LxW) of *Calluna* and *Erica vagans* in differents years and sites. Number of samples are given in parentheses.

Locality	Year	*Calluna vulgaris* Number seeds per capsule	*Calluna vulgaris* Seed size (mm)	*Erica vagans* Number seeds per capsule	*Erica vagans* Seed size (mm)
Cabo Peñas	1990	4’31 (n=22)	0’58 x 0’39 (n=77)	2’46 (n=50)	0’54 x 0’47 (n=77)
Cabo Peñas	1994	4’07 (n=100)	0’64 x 0’46 (n=150)	1’61 (n=100)	0’57 x 0’49 (n=150)
Pto. San Isidro 800 m	1990	6’30 (n=50)	0’55 x 0’41 (n=146)	6’92 (n=50)	0’57 x 0’50 (n=150)
Pto. San Isidro 800m	1994	4’31 (n=100)	0’62 x 0’45 (n=150)	6’38 (n=100)	0’60 x 0’52 (n=150)

Cabo=Cape; Pto.=Mountain pass

Discussion

Seed production

The three heath species showed a similar overall mean seed production, although the seed production for each species varied between sites. This could have implications on seed regeneration when these species occur together. A higher density of seedlings emerged of *Erica. cinerea* than the two species, *Erica vagans* and *Calluna* was found in Cabo Peñas heathland which had suffered fire damage. *E. cinerea* was the specie with more seed production in this locality (Vera & Obeso 1995).

A higher altitude does not seem to influence seed production for *Calluna*. It could indicate not such great differences in seed production with other latitudes. The seed production of *Calluna* has been studied by a number of authors with varying results, some of the variations being due to the different methods used (Barclay-Estrup & Gimingham 1994). Our estimations of *Calluna* seed production along the altitudinal gradient are included within the limits on seed production indicated by Legg & al. (1992) and Barclay-Estrup & Gimingham (1994) according to their studies and those of other authors, although the mean number of seeds per capsule are usually lower in our studied zone than the other localities of Europa. We rarely found a mean of about 10 seeds per capsule. Only a mean seed per capsule above 11 was estimated between 1400 and 1700 m on siliceous substratum in the Cantabrian mountains in 1990 (unpublished data). A warmer summer in 1990 in the mountain could have had an influence on a good seed production. The highest seed production of *Calluna* about 1600 m on siliceous substratum, where the germinative capacity was high (Vera 1997) could be related to a wide spread of heather in these zones (observ. person.). *Calluna* is less frequent in habitats with soil pH not very acidic (Vera 1983b, Grime & al. 1989; Rameau & al. 1989). The mean number of seeds per capsule produced by the *Calluna* population at the highest altitudes of Asturias was not lower, being even higher than in most lower sites. A high mean number of seeds per capsule in mountain areas of Asturias with its severe climate could explain an usually high number of seeds in other areas of northern Europe which also have a severe climate , where hard environmental conditions when they are not extreme do not seem to affect on average seed production, although annual fluctuations occur. However, these results do not coincide with those obtained by Miller & Cummins (1987) between 300 and 750 m in Scotland, where the average number seeds per capsule declined with increasing altitude, showing wide annual fluctuations. While there were no significant annual fluctuations in seed production of *Calluna* in the higher locality of Pto. San Isidro. But *Calluna* can occurs at more elevated altitudes, above 2400 m (Vera 1983a), since the environmental conditions about 2000 m could be less of a determinant in seed production than at the highest altitudes where *Calluna* can occur. However, there were significant differences between years for Cabo Peñas. The mean seed production for 1999 was extremely low. We do not know the reason for this, because the monthly average temperatures and annual precipitation were similar in the different years, but many plants of *Calluna* are drying up on this site.

Investigations into seed prodution over three years in the high mountain of Pto. San Isidro above 2000 m showed an elevated seed production. Furthermore the seeds from these sites show a good quality because they had a vey high germination in favourable laboratory conditions (Vera 1997). This supports that the view the absence or low densinty of seedlings observed in the high mountain is due neither to seed production nor to the quality of seeds. Probably, the main causes of scarce seedlings are the low temperatures and the usually low moisture content of sandy soils developed on quartzites for germination. The latter even have lower humidity content than the soils on quartzite in lower localities, when there is no snow cover, because they have little organic matter.

Our data for *Erica cinerea* usually show a higher seed production than those recorded by Mallik & al. (1984) and Barclay-Estrup & Gimingham (1994). Although some variation can be expected when different methods are used as was indicated above , other differences could be due to the fact that the studied zones are situated at different latitudes. Our results suggest an effect of altitude on seed production of *E. cinerea*. Therefore, it may also explain a normally lower seed production in Scotland, situated at a higher latitude with hard environmental conditions. Adverse conditions seem to influence seed development of *E. cinerea*. However, a lower seed production in he highest localities studied could not significant a disadvantage in seed regeneration with respect to low populations, since the seed from the highest altitudes had a much higher germination than those from lower altitudes in favourable conditions (Vera 1997).

The seed production for *Erica vagans* has never been estimated. This species shows a different seed production between sites. It is dificult to suggest a pattern of seed production, because both altitude and substratum seem to have an influence on its seed production. A high production was not found at the highest altitude in 1994, although a very higher number seeds per capsule was produced in the same site in 1990 (7’2 seeds, although some them were not very well shaped, but filled) (unpublished date). This may be due to the fact that the highest studied locality of *E. vagans* is near the superior border of its distribution, and the seed production in this situation may be erratic influenced by the weather conditions (Miller & Cummins 1987; Crawley 1992; Legg & al. 1992; Holm 1994).

The type of substratum seems to influence the seed production of *Erica vagans*. The population of *E. vagans* occurring on quartzite had a lower seed production in 1994 than on those other substrates. Other estimations were also carried out for 1990, 1993 and 1995 year in Cabo Peñas (unpublished data) and the mean number seeds per capsule was always low (about 2 seeds), while it was higher in a nearly locality on limestone (7 seeds per capsule). These results suggest that *E. vagans* could have more difficulty than those other heaths in seed regeneration on quartzite, although seeds collected from Cabo Peñas on quartzite did not have a very low germination in controlled chamber conditions (Vera 1997). This is supported by the absence of seedlings of *E. vagans* on this site, while several seedlings of *Calluna* and *E. cinerea* emerged (Vera & Obeso 1995). Furthermore, the sandy soils developed on this type of substrate keep low moisture, which affects on germination. A low humidity seems to influence unfavourably the emergence and establishment of *E. vagans* seedlings (Vera & Obeso 1995; Obeso & Vera 1996). In fact, these data reveal why *E. vagans* usually is less frequent on quartzite.

The characteristics of soil had no significant effect on the number of flowers and seeds per capsule of *Calluna*. However, Macgillivray (1990) showed a lower production of flowers in the poor soils type podsol than in the acidic brown, establishing a negative correlation between flower numbers and seed numbers. However, neither of the species studied by us showed a significant relationship between these variables. Only some tendency have been shown in this study.

Seed size

The results from the mean seed sizes in 1994 for *Erica vagans* and *Erica cinerea* are similar to those obtained in previous studies (Fraga 1984), as well as for *Calluna* (in Gimingham 1960, in Legg & al. 1992). The range of seed size found in this study for these species was generally greater that those shown by Fagúndez 2006 and Fagúndez & Izco 2004, 2011.

There were no significant differences with respect to altitudes in any studied species, although a seed weight increased significantly with increasing altitude was found for other species (Holm 1994).The mean seed size coul be influenced by seed production and characteristics of soil in some of the studied species.

Seed size and seed production has usually been interrelated (Harper 1977; Greene & Johnson 1994; Eriksson & Ehrlen 1998). This could be due to the fact that those individuals which had employed more resources to develop a high number of seeds tend to produce smaller seeds. However, only a negative correlation between seed size and seed production was found for *E. cinerea* and between seed size and number of seeds per capsule for *Calluna*. For this reason, it could be expected that variations in seed size would be found with annual fluctuations in seed production between years. In fact, a smaller mean seed size was estimated for *Calluna* and *E. vagans* both in Cabo Peñas and Pto. San Isidro (800 m) in 1990 than that obtained in 1994, which is related to a higher number of seeds per capsule in 1990, although there is no relationship between number of seeds per capsule and seed size when both localities are considered together. This could be because seed production and size may be influenced by the weather conditions within species and localities, varying with the years while these may be affected by other factors when different localities are compared

The type of substratum and soil pH seem to influence on the mean seed size. *Calluna* produced the smaller seed size on soils with higher pH (above 5), which were developed on limestone and a type of shale. This could be a disadvantage for *Calluna*, growing in soils with not very acidic pH, because the seedlings from smaller seed have a worse survival and growth rate than those from larger seeds (Vera 1997). This may be other reason why *Calluna* is less frequent in habitats with soil pH not very acidic (Vera 1983b, Grime & al. 1989; Rameau & al. 1989). While *Erica vagans* had the largest size on limestone. The seed size of *E. vagans* tends to increase with increasing soil pH. Although this species can occur on all type of substratum (Dupont 1975; Vera 1983a y 1983b; Rameau & al. 1989; Mayor 1999), it is more common on soils which are developed on calcareous substrata, where *E. vagans* produce the largest seeds. Soil pH also seems to influence seed size of *Erica cinerea*, producing the smallest seeds size in habitats with lowest pH. These results suggest that the variation in responses to the effect of soil characteristics on seed size in the species, when they are not always correlated with seed production, could be related to the fact that each species requires different conditions for its optimal developement . Therefore, the species could produce smaller seed size if the conditions are not very favourable for its growth.

Significant differences in seed size among species and within the three species between sites suggest variations on germination and seedling survival related to seed size.

The large seeds within species could germinate earlier and showed better germination (Tripathi & Khan 1990; Arista & al. 1992; Vera 1997). Moreover, a better seedling survival and growth from heavier seeds within species linked with bigger storage reserves of seeds is found by Harper (1977), Tripathi & Khan (1990), Reyes & Casal (1994) and Vera (1997).

Erica cinerea was the species which had the largest seed. This suggests that the seedling survival of *E. cinerea* could be more successful than those other heath species studied, when they occur together. A high correlation between seed weight and initial seedling weight among and within species was found by Gross (1984), although the seedling establishment success depends on the type of ground cover. However, significant differences in seed size of *E. cinerea* and *Calluna* did not show an effect on initial size of their seedlings on a bare soil after a fire in Cabo Peñas (Vera & Obeso 1995), even the survival of seedlings of *E. cinerea* was worse than in *Calluna*, the seedling establishment being independent of seed size, in agreement with Gross (1984) for bare soils.

Aknowledgements

This research was financed in part by the University of Oviedo.

References

Arista, M., Talavera, S. & Herrera, J. 1992. Viabilidad y germinación de las semillas de Abies pinsapo Boiss. *Acta botanica Malacitana* 17:223-228.

Barclay-Estrup, P. & Gimingham, C.H. 1994. Seed-shedding in a Scottish heath community. *Journal of Vegetation Science* 5:197-204.

Bruggink, M. 1993. Seed bank, germination, and establishment of ericaceous and gramineous species in heathlands. In: R. Aerts & G.W. Heil (eds.), *Heathland: Patterns and Processes in a Changing Environment:* 153-180. Kluwer Academic Publishers, Dordrecht.

Crawley, M.J. 1992. Seed predators and plant population dynamics. In: Fenner, M. (ed.), *Seeds. The ecology of regeneration in plant communities*: 157-191. C.A.B. International Wallingford. U.K.

Dupont,P. 1975. Synécologie d' une bruyère atlantique: *Erica vagans* L. *Colloques phytosociologiques* II: 271-299.

Eriksson, O. & Ehrlen, J. 1998. Phenological adaptations fleshy, vertebrate-dispersal fruits of temperate plants. *Oikos* 82 (3): 617-621.

Fagúndez, J. 2006. *Taxonomía del género Erica L. (Ericaceae) en Europa a partir de los caracteres de la cubierta seminal.* Tesis Doctoral. Universidad de Santiago de Compostela.

Fagúndez, J. & Izco, J. 2004. Seed morphology of *Calluna* Salisb. (Ericaceae). Seed description *Calluna vulgaris* (L.) Hull. *Acta Botanica Malacitana* 29: 215-220.

Fagúndez, J. & Izco, J. 2011. Seed morphology and systematics of the european species of *Erica* l. sect. Gypsocallis Salisb.(Ericaceae). *Plant biosystems* 145 (1) : 182-190.

Fraga Vila, M.I. 1984. Valor taxonómico de la morfología de las semillas en las especies del género *Erica* presentes en el NO de España. *Acta botanica Malacitana* 9: 147-152.

Gimingham, C.H. 1960. Biological Flora of the British isles. *Calluna vulgaris* (L.) Hull. *Journal of Ecology* 48: 455-483.

Gloaguen, J.C. 1990. Post-burn succesion on brittany heathlands. *Journal of Vegetation Science* 1: 147-152.

Greene, D.F. & Johnson, E.A. 1994. Estimating the mean annual seed production of trees. *Ecology* 75 (3):642-647.

Grime, J.P., Hodgson, J.G. & Hunt, R. 1989. *Comparative plant ecology. A functional approach to common British species.* Ed. Unwin Hyman, London.

Gross, L.K. 1984. Effects of seed size and growth form on seedling establihment of six monocarpic plants. *Journal of Ecology* 72: 369-387.

Harper, J.L.1977. *Population Biology of Plants*. Academic Press, London.

Hobbs, R.J., Mallik, A.U. & Gimingham, C.H. 1984. Studies on fire in Scottish heathland communities. III. Vital attributes of the species. *Journal of Ecology* 72: 963-976.

Holm, S.O. 1994. Reproductive patterns of *Betula pendula* and *B. pubescens* coll. along a regional altitudinal gradient in northern Sweden. *Ecography* 17: 60-72.

Legg, C.J., Maltby, E. & Proctor , M.C.F. 1992. The ecology of severe moorland fire on the North York Moors: seed distribution and seedling establishment of *Calluna vulgaris*. *Journal of Ecology* 80: 737-752.

Lusk, C.H. 1995. Seed size, establishment sites and species coexistence in a Chilean rain forest. *Journal of Vegetation Science* 6: 249-256.

Macgillivray, C. 1990. *Calluna vulgaris* seed dynamics. *Bulletin British Ecological Society*, vol. XXI (4): 253-257.

McGraw, J.B. & Vavrek, M.C. 1989. The role of buried viable seeds in artic and alpine plant communities. In: Leck, M.A., Parker,V.T. & Simpson, R.L. (eds), *Ecology of soil seed banks*: 91-105. Academic Press, San Diego.

Mallik, A.U., Hobbs, R. J.& Legg, C.J. 1984. Seed dynamics in *Calluna-Arctostaphylos* heath in north-eastern Scotland. *Journal of Ecology* 72:855-871.

Mayor, M. 1999. Ecología de la flora y vegetación del Principado de Asturias. *RIDEA*, Principado de Asturias, Oviedo.

Miller, G.R. 1979. Quantity and quality of the annual production of shoots and flowers by *Calluna vulgaris* in North-East Scotland. *Journal of Ecology* 67:109-129.

Miller, G.R. & Cummins, R.P. 1987. Role of buried viable seeds in the recolonization of disturbed ground by heather (*Calluna vulgaris* (L.) Hull) in the Cairngorm mountains, Scotland, U.K. *Artic and Alpine Research* 19 (4): 396-401.

Muñoz, J. 1982. *Geografía de Asturias.I. Geografía Física*. Ayala, Oviedo.

Obeso, J.R. & Vera, M.L. 1996. Resprouting after experimental fire application and seed germination in *Erica vagans*. *Orsis* 11: 155-163.

Pigott, C.D. 1992. Are the distribution of species determined by failure to set seed?. In: Marshall, C. & Grace, J. (eds), *Fruit and seed production. Aspects of development, environmental physiology and ecology*: 203-216. Cambridge University Press, Cambridge.

Rameau, J.C., Mansio, D., Dumé, G., Timbal, J., Lecointe, A., Dupont, P.& Keller, R. 1989. *Flore forestière française, guide écologique illustré I . Plaines et Collines* . Ministère de l'agriculture et de la forêt, Paris.

Reyes, O. & Casal, M. 1994. Reproductive behaviour of *Quercus robur* related to the size and damage state of the seed. Proc. 2nd. Int. *Conf. Forest fire Research*. Vol. II (21): 1009-1018.

Reyes, O., Basanta, M., Casal, M. & Díaz-Vizcaíno E. 2000. Functioning and dynamics of woody plant ecosystems in Galicia (NW Spain). In: Trabaud L. (ed.), *Life and Environment in the Mediterranean*: 1-41. WITpress, Southampton.

Thompson, K. 1992. The functional ecology of seed banks. In: Fenner, M. (ed.), *The ecology of regeneration in plant communities*: 231-258. C.A.B. International Wallingford,. U.K.

Trabaud, L. 2000. Seeds: their soil bank and their role in post-fire recovery of ecosystems of the Mediterranean basin. In: Trabaud, L. (ed.), *Life and Environment in the Mediterranean*: pp. 229-260. WITpress, Southampton.

Tripathi, R.S. & Khan, M.L. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. *Oikos* 57: 289-296.

Vera, M.L. 1983a. *Estudio de los pastizales de diente, matorrales, y su dinamismo, de la zona comprendida entre el Pto. de Ventana y el Pto. de Ventaniella (Asturias-león).* Memoria Tesis Doctoral. Universidad de Oviedo.

Vera, M.L. 1983b. Rango de variación del pH del suelo de algunos táxones en la Cordillera Cantábrica. *Boletín de Ciencias de la Naturaleza. I.D.E.A.* 31: 169-179.

Vera, M.L..1997. Effects of altitude and seed size on germination and seedling survival of heathland plants in north Spain. *Plant Ecology* 133:101-106.

Vera, M.L. 2007. Reproductive capacity of the heath *Daboecia cantabrica* through seeds along an altitudinal gradient in North Spain. *10th European heathland Workshop*, Noruega. Pág. 152.

Vera, M. L. 2011a. Colonization and demographic structure of *Deschampsia antarctica* and *Colobanthus quitensis* along an altitudinal gradient on Livingston Island, South Shetland Islands, Antarctica. *Polar Research 30*, 7146, DOI:10.3402/polar.v30i0.7146.

Vera, M.L. 2011b. Heathlands in the Cantabrian Mountains (North Spain) under climate change scenario. *12th European heathland workshop*. España-Portugal. Pág.96.

Vera, M.L. & Obeso, J.R. 1995. Regeneración del brezal atlántico de Cabo Peñas después de un incendio severo. *Stvdia Oecologica* 12: 223-236.

Vera, M. L., Fernández-Teruel T. & Quesada A. 2013. Distribution and reproductive capacity of *Deschampsia antarctica* and *Colobanthus quitensis* on Byers peninsula, Livingston Island, South Shetland Islands, Antarctica. *Antarctic Science* 25(2): 292-302. DOI:10.1017/S0954102012000995.

Wookey, P.A., Parsons, A.N., Welker, J.M., Potter, J.A., Callaghan, T.V., Lee, J.A. & Press, M.C. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. *Oikos* 67:490-502.