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Effect of seed shape and size on their distribution in the soil seed bank

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Abstract

Endemic to the NW part of the Iberian Peninsula, *Cytisus multiflorus* has various reproductive and germinative strategies. Its seeds show a high degree of polymorphism, which can affect their location at different depth in a persistent soil seed bank. This paper puts forward a hypothesis that the dimensions and weight (shape and size) of *Cytisus multiflorus* seeds may be responsible for their vertical distribution in the soil seed bank. This hypothesis was tested and several anomalies and deviations were found that could be explained when considering the history of land use, such as tilling, grazing, or the activity of seed predators.

Introduction

Cytisus multiflorus (L'Her) Sweet is a shrubby leguminous species endemic to the NW part of the Iberian Penninsula (López González 1995). It grows in monospecific stands or in plurispecific formations with other genisteae (*Cytisus scoparius*, *Cystisus balansae*, *Genista hystrix* etc.) in dry soils of basal and montane strata, constituting the undergrowth of *Quercus ilex* and *Q. pyrenaica* canopy. It forms persistent seed banks in the soil (Grime et al. 1981; Keeley 1991; Russi *et al.* 1992a; Legg *et al.* 1992; Moreno Marcos *et al.* 1992; Pérez Fernández 1996). It shows a marked hard-seed dormancy (Harper 1977) typical of many members of the Fabaceae family. This dormancy is related to species survival under Mediterranean-climate conditions (Russi *et al.* 1992b). Seed viability can extend up to 10 years when seeds are stored under laboratory conditions (Pérez-Fernández and Gómez-Gutiérrez 2000). Moreover, the present work provides evidence that seeds of *C. multiflorus* can remain viable for at least 25 years when stored in the soil seed bank. Some seeds germinate immediately provided environmental conditions are appropriate (Vleeshouwers *et al.* 1995), while other seeds remain apparently inactive for prolonged periods of time irrespective of the suitability of environmental conditions. The intrinsic latency of such seeds allows for prolonged storage in the soil as an adaptation to climatic variability.

Pérez Fernández (1996) showed that adult plants of *C. multiflorus* produce various seed morphotypes, and that the physiological behaviour of these morphotypes (in response to environmental variables) could be correlated with both gravimetric and dimensional differences in seed morphology. Such differences, in seed mass and size, could affect the vertical distribution of seeds in a persistent soil seed bank, and may also be responsible for the differential reproductive success in the face of changing environmental conditions such as ambient temperature and light intensity (Harper 1977; Foster 1986;

Leishman and Westoby 1994b; Westoby et al. 1992; Seiwa & Kikuzawa 1996).

Thompson *et al.* (1993) proposed a method to predict the capacity of a seed to persist in the soil according to its shape and size. These authors suggest that there is a relationship between the shape and size or weight of seeds and the capacity of a species to form persistent soil seed banks. From the perspective of the probability of burial, persistent seeds tend to be small and compact, while short-lived ones tend to be larger, and either flat or elongated. Thompson's predictive method is based on this assumption. In it, seed size is given as the average weight of a high number of samples.

The predictive model requires a quantitative expression for the diaspore shape. This morphological variable can be numerically expressed as the variance of the ratios of seed width and depth to seed length. Minimum variance value is zero in a perfectly spherical seed and maximum values would be attained by very elongated or flat seeds (Thompson *et al.* 1993).

Heavy and spherical seeds are more likely to penetrate and persist in the soil by, for example, running into cracks in soil, being washed into soil by rain or being transported by insects into nests (Thompson *et al.* 1993; Setterfield 1997). Spherical form diminishes friction, thereby favouring both vertical and horizontal displacement caused by either physical phenomena or biological activity.

In this study we adopt the Thompson's predictive model and further propose, that for *C. multiflorus*, the vertical distribution of seed within the soil, can be predicted according to the dimensional morphology. We will estimate seed size as its weight and seed shape as the variance of its dimensions as explained above. Seeds of lower weight and higher dimensional variance will not show high propensity to penetrate soil whereas seeds of higher weight and lower variance will be deeply buried. We can thus assume *a priori* that at the four depths that we have selected (D1 = 0 - 2.5 cm; D2 =2.5 - 5; D3 = 5 - 10 cm and D4 = 10 - 15 cm) the vertical distribution of seeds as should approach the criteria given in Table 1.

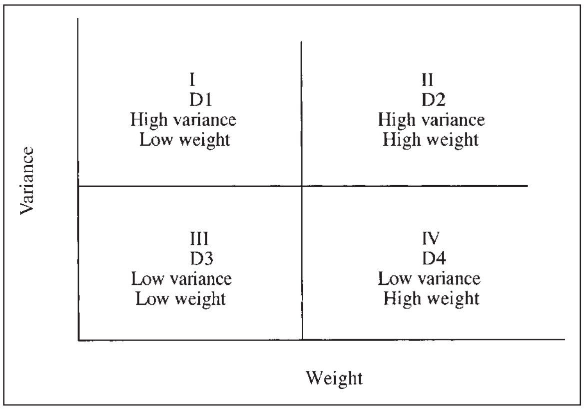

Fig. 1: Expected seed distribution in relation to seed size and shape (dimensional variance) according to their location in the soil seed bank along a vertical gradient (see text for details).

If these assumptions are true, then seeds should be distributed along a vertical gradient, in such a way that seed-dimensional variance decreases and their size increases with depth. The expected seed distribution with the soil seed bank, as predicted by our model, is illustrated in Fig. 1. Each of the quadrants should include seeds of the two characteristics defining each quadrant.

Additionally, agricultural practices can be expected to alter the soil seed-bank profile (Levassor *et al.* 1991; Milberg 1995; Bakker at al. 1996; Kalamees & Zobel 1998). If the soil from which seeds originate has not been altered, we could assume that vertical seed distribution is solely as a consequence of natural factors. These factors would be the size and shape of seeds, the texture and structure of the soil, or the activity of seed predators, worms, etc. (Sheldon, 1974; Rees, 1995). However, tilling and grazing would give rise to a spatial distribution of seeds, which is different from the "natural" one, since disturbing or distorting factors are introduced into the environment (Janzen 1981; Bekker at al. 1998; Meissner and Facelli 1999).

For this study, we have used data obtained on seeds from a soil seed bank of *C. multiflorus* which were located at different depths and which also display different germinative capacities. We applied a modification of Thompson's method (Thompson *et*

Table 1. Morphological seed characteristics to predict their vertical distribution in the soil

Depth (cm)	Size	Variance	Morphology
D1 (0-2.5)	Small	High	Low weight. Flat and/or elongated
D2 (2.5-5)	Medium	High	Greater weight than those at D1. Flat and elongated
D3 (5-10)	Small	Medium	Similar weight to those in D1. Round
D4 (10-15)	High	Low	Greater weight that those at D3. Round

al. 1993) to determine whether there is a relationship between the depth at which seeds of this species are buried in the soil and their size (i.e. weight) and shape. The working hypothesis presented above was tested on a plot that had never been cultivated as well as on one that had been.

Material and Methods

Seed material and description of the sampling areas

The seeds studied were collected on the 26th of March 1999, approximately eight months following their dispersal from the parent plants. Seeds were taken from 12 soil samples divided into four layers from the selected depths: up to 2.5 (D1); 5.0 (D2); 10.0 (D3); and 15.0 cm (D4), which came to a total of 48 samples. Each of the samples consisted of the amount of soil in a quadrant of 20 x 20 cm^2. The sampling sites were at Sanchón de la Rivera and at Sardón de los Frailes, both in Salamanca province (Spain) (29TQF172522 U.T.M. and 29TQF281651 U.T.M. coordinates respectively). Both sites are situated in a semiarid region with a strongly seasonal climate, i.e. very cold humid winters and hot dry summers. The soils are cambisol (distric and humic), very sandy, acid, oligotrophic, and on granite bedrock (FAO 1966). These soils are poorly-structured and contain colloidal clay, therefore prone to becoming swampy because of their low permeability. The plot at Sanchón de la Rivera has never been cultivated and is used as pastureland for cattle. The plot at Sardón de los Frailes was cultivated until 1968 and then abandoned; this land has not been subject to grazing animals and terriculous insects were not evident in 1999.

Seeds were extracted from the soil seed bank by flotation with carbon tetrachloride (William 1981). Weight (mg) and three dimensions of every individual seed were determined. The measured dimensions were length, width and depth. A precision GMBH (Gottingen, Germany) balance and a digital caliper (Lyman, China) were used for all measurements. All measurements were performed by the same operator. The individual variance value of the three dimensions was estimated prior to data standardisation by accepting the largest of the dimensions, i.e. seed length, as unity (Thompson, *et al.* 1993).

Results

Uncultivated land used for grazing (pastureland)

The distribution of seed in the soil samples taken in Sanchón de la Rivera are presented in Fig. 2.

Almost all seeds at D1 are of low weight and flat and/or elongated as indicated by their high variance values. Thus, they are mainly restricted to quadrant I (Fig. 2a). The only exceptions were three seeds taken from this depth that are plotted in quadrants III and IV.

The variance values for seeds extracted from D2 (2.5 - 5 cm) are in quadrants II and IV (Fig. 2b). Very irregularly shaped (high variance), heavy seeds were found at this depth, but there were also seeds of low variance and high weight and only one seed of high variance and low weight.

At D3, seeds were found of all shapes and sizes except of high variance and high weight (Fig. 2c) representing I, III and IV type seeds. At D4 (Fig. 2d) we found seeds of the shape and weight corresponding to quadrant IV. Only one of the seeds showed D1 characteristics, but it was very close to D4.

Cultivated and abandoned land

The distribution of seeds in the soil samples from Sardón de los Frailes are presented in Fig. 3. Seeds at D1 (Fig. 3a) are predominantly of quadrant I type, showing low weight and high variance. A small proportion of them were of the shape and weight of quadrants II and III type seeds.

Seeds from D2 (2.5 - 5.0 cm) and D3 (5.0 – 10.0 cm) included all shapes and sizes, and correspond to quadrant I to IV type seeds (Fig. 3b). Therefore, when land has been cultivated, seeds of any type can be found at these depths. In D3 (5 - 10 cm), the number of seeds was lower than in D3. Interestingly, quadrant III type seeds (the seed type predicted for this depth) were not the most abundant at this depth (Fig. 3c). Finally, in D4 all seeds but one are quadrant IV type seeds (Fig. 3d).

Discussion

A remarkable regularity was observed in the morphology of seeds at D1 (0.0 - 2.5 cm) and D4 (10.0 - 15.0 cm) irrespective of the cultivation status of the plots. In both cases the predictions of the starting hypothesis were fulfilled. At D1 (0.0 - 2.5 cm) there are seeds of high variance and low size (quadrant I type) whereas at D4 (10.0 - 15.0 cm) there is a predominance of seeds of low variance and high size (quadrant IV type).

The absence of quadrant II, III and IV type seeds at D1 may be because those seeds:

a) germinate, and the seedlings as well as the seed themselves are eaten by herbivores (Harper 1977; Schupp 1988; Bertiller and Defossé 1990; Milberg 1995),

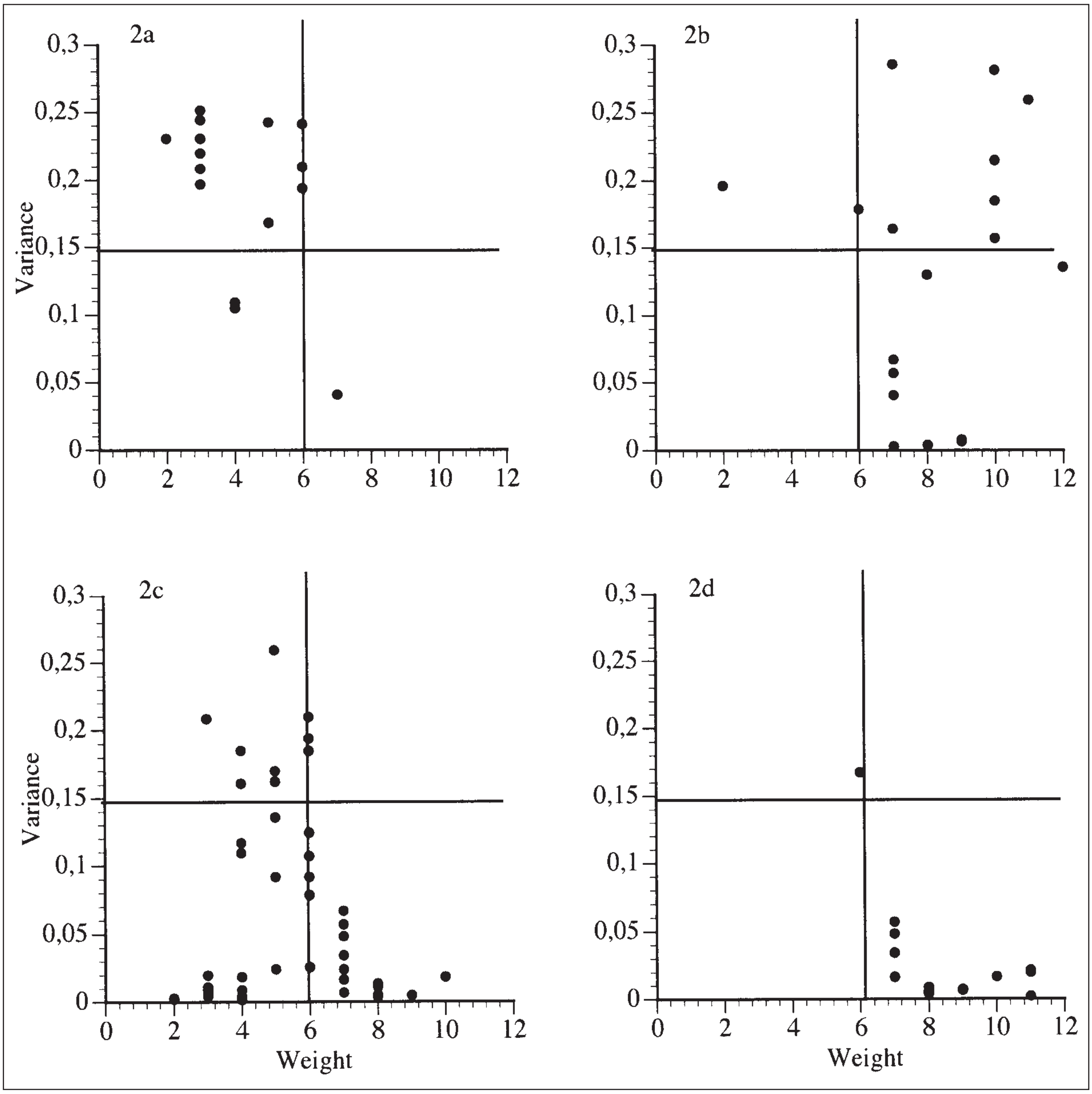

Fig. 2: Seed distribution in relation to seed size and shape according to their location in the soil seed bank at four depths a) 0-2.5 cm; b) 2.5-5.0 cm; c) 5.0 – 10.0 cm; d) 10.0- 15 cm, in uncultivated land (Sanchón de la Rivera, Salamanca, Spain).

b) they penetrate the soil because they are more spherical (Thompson 1987; Grime 1989; Thompson *et al.* 1993),
c) they are transported to lower layers by insects or earthworms (McRill and Sagar 1973; Grant 1983; Andersen 1987, 1988; Escala and Xena de Enrech 1991; Setterfield 1997), and/or
d) they are eaten by rodents, which are very active in these habitats (Malo *et al.* 1995; Madsen and Shine 1996; Wurm 2000).

The results confirm the working hypothesis that seeds at D4 should be the most suitable for penetrating the soil and remaining viable because of their size and spherical shape, thus conforming to quadrant IV of our predictive model. With only two exceptions, all seeds at D4, in either cultivate or uncultivate plots, conformed to quadrant IV.

Seeds with quadrant IV characteristics were also found at other depths (Fig. 2b, c, Fig. 3b, c) in both cultivated and uncultivated land, but it is quite logical to assume that with time they would descend to

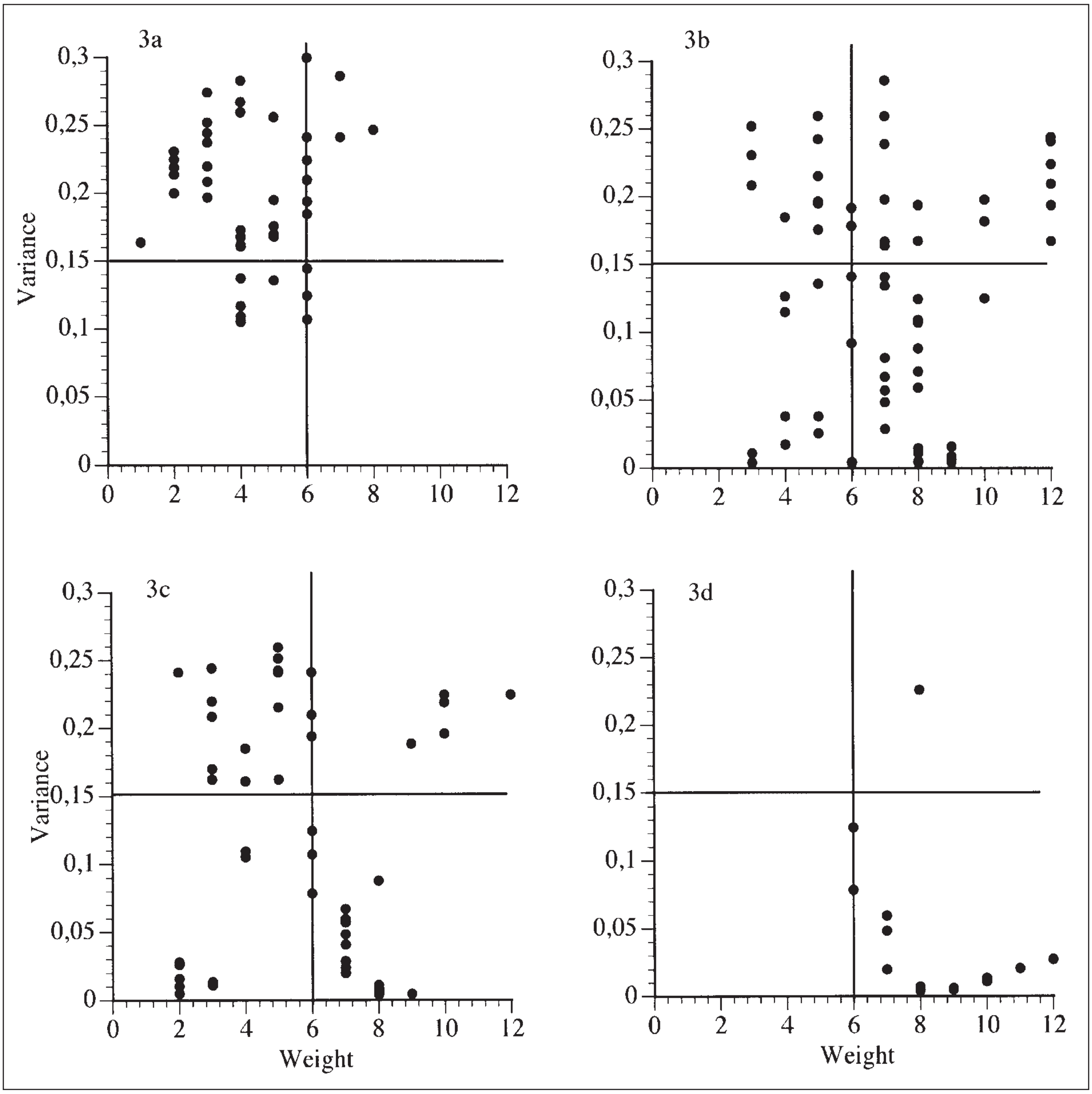

Fig. 3: Seed distribution in relation to seed size and shape according to their location in the soil seed bank at four depths a) 0-2.5 cm; b) 2.5-5.0 cm; c) 5.0 – 10.0 cm; d) 10.0- 15 cm, in uncultivated land (Sardón de los Frailes, Salamanca, Spain).

D4. This observation is consistent with the pattern followed by seeds of annual and woody species from a seed bank in Sweden, where seeds from colonising species were found below a depth of four cm; and shows that seeds deep in the soil are likely to be very old (Milberg 1995). Eight months, the time elapsed between shedding and sampling, is therefore not enough for seeds to complete their distribution across the soil profile, according to their size and shape.

At D2 (2.5 - 5 cm) and D3 (5.0 - 10.0 cm), seeds of all types were collected, except those corresponding to quadrant I for D2 of non-cultivated land. The presence of quadrant IV type seeds are likely once again to represent seeds still moving to greater depth. An explanation for the presence of quadrant I and II type seeds at depths greater than predicted requires the consideration of the soil characteristics as well as the presence of hooved animals (Julita 1998). Cambisol soils are poorly-structured and show very low permeability (FAO 1966). Consequently, with the autumn rains the soil becomes soft and gives way under the weight of domestic hooved animals, whose hooves sink to depths of 10 cm or even deeper. Similarly, ants and in particular, various worms, transport seeds to depths of up to 10-15 cm (Andersen 1987; Thompson *et al.* 1994).

The effects of land use are also pronounced. The sampling plot at Sardón was under cultivation with cereals during the years following the Spanish Civil War (1939-1968) and has been abandoned since 1968 (direct information from the landowner). Comparing the results from these sites (Fig. 2) with those from uncultivated land (Fig. 3), two distinct differences in seed distribution are conspicuous. Firstly, the presence, in previously cultivated plots, of quadrant II type seeds in the D1 profile (Fig. 3a), which were absent in the D1 profile of non-cultivated plots (Fig. 2a). Second, in the D2 profile of previously cultivated land (Fig. 3b) there were seeds of all the sizes and shapes, whereas seeds in the D2 profile of uncultivated land essentially followed the predictive model, i.e. they were quadrant II type (Fig. 2b). In this profile there was also a high representation of quadrant IV type seeds, that we assume are seed descending to D4. Quadrant IV type seeds present in the D3 layer, are also likely to represent seeds descending to D4 and it would not be surprising to find quadrant III and IV type transient seeds in the uncultivated D2 profile.

Obviously, point distribution in groups is not strictly defined, and in all the quadrants there are points corresponding to seeds extracted from other depths different to those expected. Nevertheless, distributions according to size and shape variance values, is shown here to be a valid method for determining seed distribution in the soil seed bank.

Cytisus multiflorus displays several characteristics of a ‘pioneer’ species. They produce seeds destined to germinate and establish themselves almost immediately, thus ensuring a rapid establishment of new individuals and seeds that will remain dormant within the soil over time. By producing both types of seeds this species is capable of occupying/colonising a high number of niches -horizontally, vertically and temporarily.

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