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PRIMARY DISPERSAL OF *Cytisus multiflorus* SEEDS[1]

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ABSTRACT. Current work relates to the primary dispersal of Cytisus multiflorus *seeds: seed production, dispersal mechanisms, distribution of seed after dissemination and dormancy were investigated. The distribution of seed was recorded before collection; seed viabilaty and dormancy were assessed. The results indicate that the dispersion is assisted by an explosive dehiscence of the seed pod in that only 35% of the seed drop directly beneath the plant, the remainder falling further away, some reaching distances greater than 3 m. Dormancy index was found to be 98.9%.*

RESUMEN.- En el presente trabajo se estudia la dispersión primaria de las semillas de Cytisus multiflorus: *cuantificación de la producción, mecanismos de dispersión, distribución de las semillas tras la diseminación, y su estado de latencia. Para ello se colocaron dispositivos de recogida de las semillas debajo y alrededor de las plantas, anotando la cantidad y distancia de la caída; posteriormente eran sembradas para comprobar la viabilidad y dormición de las semillas. Los resultados indican la existencia de una dispersión por dehiscencia explosiva; solamente el 35% de las semillas caen bajo la planta, haciéndolo el resto en sus alrededores; algunas alcanzaron distancias superiores a los 3 m. El índice de dormición es de 98.9%.*

RÉSUMÉ.- Dans le present travail on étudie la dispersion primaire des graines de Cytisus multiflorus: *quantification de la production, mécanismes de dispersion, distribution des graines après la dissémination et leur état de latence. Pour ce faire on a placé des dispositifs de récolte des graines au-dessous et autour des plantes, enregistrant la quantité et la distance de la chute; après elles etaient semées pour tester la viabilité et dormance des graines. Les résultats indiquent l'éxistence d'une dispersion par déhiscence explosive; seulement 35% des graines tombent au-dessous de la plante, et le reste dans les alentours; quelques-unes atteignent des distances supérieures à 3 m. L'index de dormition est de 98.9%.*

Key-words: *Dispersal, explosive dehiscence, seed density, dormancy, Cytisus multiflorus.*

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Recent interest in matorral formations is beginning to result in their serious consideration in any concrete proposals for land use or environment conservation. Hence the growing importance of studies into their natural dynamics.

Cytisus multiflorus is a woody leguminous species indegenous to the Central Western-North Western part of the Iberian peninsula. It is very abundant in this area where it constitutes vast monospecific formations. Its great abundance and expansion, especially be colonizing abandoned and/ or burned fields, makes the study of its reproduction very interesting. Numerous data have been recently furnished as regards its regeneration and demography (FERNÁNDEZ SANTOS, 1991). They show the relatively small significance of generative as opposed to vegetative reproduction following different types of human disturbances. However, there are certain conditions, such as topography, formation age, etc..., under which the importance of regeneration by seed may be greater or even predominant. Furthermore, seedlings emerge in the in-between disturbance periods pointing to this as a way of colonization. Seed dispersal is therefore one of the many important factors to be considered if we are to contribute to the knowledge of the reproductive strategies of species.

The study of seed dispersal is of interest in many aspects of ecology, among which the following are worth pointing out: colonization of new sites; predador-prey conflict; parent-offspring relationship; gene flow; population's genetic structure; etc... (GREEN, 1983). It includes the reproductive efforts made by a species to enlarge its occupied area as well as to survive in an already colonized site.

The study present here deals with the initial spatial seed dispersal —later on there may be further dispersal— in *Cytisus multiflorus* including the following specifics: seed production, dispersal mechanisms, distribution of dispersed seeds, seed viability and dormancy. At the same time soil seed bank (MORENO MARCOS, 1991) and vegetative reproduction as well as by seedlings (FERNÁNDEZ SANTOS, 1991) were also studied.

1. Material and methods

The study area is situated in the vincinity of Vitigudino, in the North Western part of the province of Salamanca. It is a region of old fields abandoned for up to 10-12 years. Soils are typically dystric cambisols with some lithosols and large massive rock-outcrops. The rocks are calc-alkaline granites such as leucogranites. The mean yearly precipitation and temperature are 650 mm and 11.5°C respectively; with the resulting climate being cool subhumid. Grasslands with young and vigorous matorral, of mainly *C. multiflorus*, and few trees, predominate here.

Eight adult plants, between 7-9 years of age, of medium size and with good flower and seed setting (avoiding extreme cases) were selected. Another important criterium of choice was that the plants be isolated. Therefore it was necessary to cut out some neighbouring plants.

Four furrows, 40 cm wide and 10 cm deep, were made around the plants. They were perpendicular to each other and oriented to the SW, SE, NE and NW. They measured 380 cm in length (60 cm towards the interior and 320 towards the exterior of the plant) starting from the plant's projection on the ground. An area, in the centre, of about 1.2 m^2 wasn't sampled. The furrows were covered with plastic sheets fastened to the ground and subdivided by marking 20 cm intervals.

Seeds were counted for each plant with orientation and distance. The count was carried out every 2-3 days from 9 July to 6 August 1989 covering the whole seed dispersal period.

Seed production per plant was estimated from the number of collected seeds by the following calculation:

$$\sum_{i=1}^{n} x_i A_i + Cx_1 \qquad \text{where:}$$

xi - mean seed sensity at the distance i, calculated for values obtained for the four orientations;

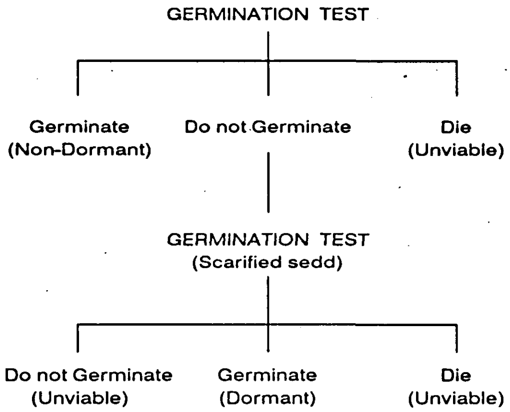
Ai - ring area, of 20 cm radius, around the plant, at the distance i from the central axis of the plant;

C - Central-zone area, i.e. the not studied area, variable with plant but about 1.2 m^2;

xi - seed density found in the first ring. It was assumed that seed density in this 1st section was similar to that of the central-zone (basing the assumption on the obtained results).

For the calculation we also assumed that the plants were hemispherical and of an almost circular projection. Since the selected plants grew in isolation it wasn't far from true. Seeds that fell at a longer distance than 3.2 m from the plants were not included. However, as can be seen in Fig. 2, they represent only an insignificant percentage.

A sample of 1500 seeds was taken for testing seed dormancy and viabilty Within this sample 30 replicas of 50 seeds were carried out. Seeds were washed in 3.5% sodium hypochrorite solution (bleech) and placed in Petri dishes following the method by PUENTES GRAÑA (1984). They were kept in a dark cool place (AÑORBE, 1988) and checked every two days for germinated and rotten seeds while removing both kinds. Seeds were considered germinated when the radicle extension was > 1 mm (VIGNA *et al.*, 1983). Those that had not germinated after one month were classified as dormant (AÑORBE, 1988 and HOLMES, 1989). Dormant seed were scarified mechanically by hand to promote imbibition and those germinating within a further one month were considered to be viable (see next diagram).



$$\text{VIABILITY INDEX} = \frac{\text{TOTALS - UNVIABLES}}{\text{TOTALS}}$$

$$\text{DORMANCY INDEX} = \frac{\text{DORMANTS}}{\text{VIABLES}}$$

2. Results

2.1. *Seed dispersal mechanism*

Initial seed dispersal in *C. multiflorus* is by explosive dehiscence of its legume and hurling of part of the contained seeds; i.e. it is the autochory type of seed dispersal. The explosive action is produced by an hygroscopic mechanism through desiccation. This desiccation becomes explosive due to the tension created on contracting, by drying out of dead cells, of different cell layers at different angles (STRASBURGER & col., 1988; FAHN, 1985). It is a purely physical mechanism not requiring any additional energy input from the plant. In our study the seed dispersal ocurred between the second week of July and the first week of August, when the fruit was mature; and between 14.00-20.00 hours with lower relative air humidity.

The way in which the pod opens varies. It may open completely or partially; start opening at the basal or apical end; get completely open with both halves of the pod apart or stay twisted with the pod halves close together. In some of the instances, only some seeds are hurled on explosion of the pod. The other seeds stay in the pod either because it doesn't open entirely or because it doesn't release them easily even after its full opening. Thus only a few seeds are cast each time, although the pod contains more of them inside, optimizing the launch of a few at the cost of the rest that are not cast outside of the plant. This hurl or launch of seeds, individually or in small batches, is characteristic of the explosive seed dispersal (STAMP & LUCAS, 1983). Owing to the marginal position of most of the pods and their direction towards the exterior of the plant their seeds fall in their majority outside the plant.

2.2. *Seed production*

The obtained number of seeds is shown in Fig. 1. It is worth pointing out that mature seed production is very high in these plants, especially if we consider that only 37.8% of the produced seeds reach maturity. The rest are aborted, eaten, or not fully developed (AÑORBE, 1988). GRIME (1981) reports that the majority of species growing in severely and repatedly disturbed environments have a high proportion of reproductory resources. What is also striking are the tremendous differences found between individual plants (maximum 89430 and minimum 3841 seeds per plant) in spite of their similar age, size, and site (all plants eight plants grew in the same plot). it might be a reflection of a great genetic variability; which in itself presents an advantage under such conditions of frequent disturbances and important fluctuations of environmental factors.

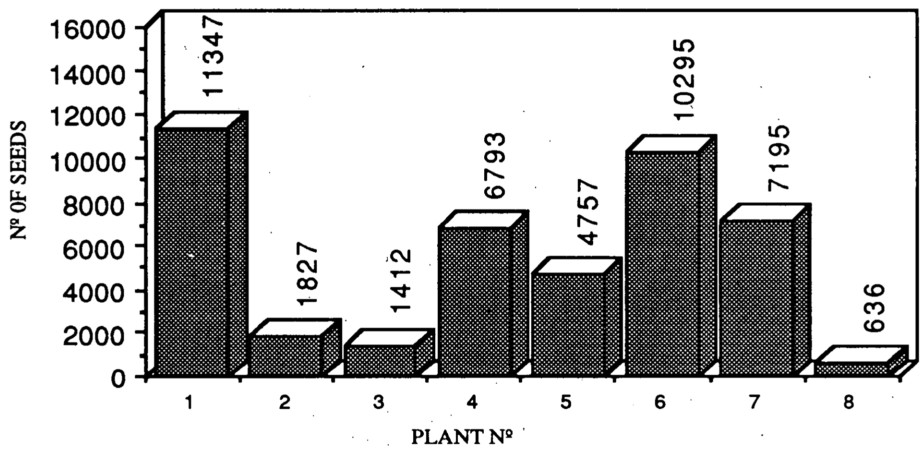


Fig. 1. The estimated number of seed produced per plant. *(Número estimado de semillas producidas por planta).*

2.3. *Seed density curve*

Table 1 and Figure 2 show the dispersed seeds density curves, expressing it in the percentage of seeds fallen at each of the distances. This type of curve is very interesting because neither the maximum distance nor the mean distance of seed dispersal give us enough information as to the result of seed dispersal (GREEN, 1983).

TABLE 1
Mean values and coefficients of variation of the percentage of seeds fallen at each of the distances (metres). Each distance indicates the middle of each 20 cm ring intervals; i.e. 0.9 represents the ring intervals from 0.8-1 m distance. The outer limit of the plant is at 0.6 m (see methods).

DIST	MEAN	CV	DIST	MEAN	CV	DIST	MEAN	CV
0.10	25.12	13.0	1.50	2.86	26.0	2.9	1.40	52.2
0.30	19.38	11.3	1.70	2.74	26.2	3.10	1.32	51.0
0.50	12.60	18.3	1.90	2.44	24.0	3.30	1.11	45.2
0.70	8.31	12.2	2.10	2.00	25.5	3.50	0.82	61.4
0.90	5.69	11.6	2.30	1.92	28.6	3.70	0.45	53.8
1.10	4.75	15.0	2.50	1.81	34.9			
1.30	3.65	18.3	2.70	1.54	44.9			

The carried out regression analysis gave the following result:
$y = -1.59 + 7.90\ (1/x) - 0.52\ (1/x^2)$ $R^2 = 96.7\ \%$ $p < 0.0001$
Significance: $(1/X) = P < 0.0001$ $(1/X^2) = P < 0.0001$
Confidence interval (95%): $(1/X) = 7.52, 8,28$ $(1/X^2) = -0.56, -0.49$
Were x = distance from the plant (in metres). y = % of seeds fallen at each of the distances.

This corresponds to a hyperbolic curve (a + b* 1/X) with a sigmoidal tendency near the origin ($-c^*\ 1/X^2$), which indicates that the slope decreases near the origin. It is even more evident in plants as plant n.º 4 (Fig. 2). Presumably seed density stabilizes towards the centre of the plants —the zone we have not studied—. Such type of curve in which the maximum density is found at a short distance from the centre of the plant and considerably decreasing with moving away from it, ocurrs quite often in nature (HARPER, 1977; HOWE & SMALLWOOD, 1982; GREEN, 1983; FENNER, 1985).

If we take the number of seeds fallen at each of the distances instead of their density (Fig. 3) the curve adopts a very different form, with the slope less pronounced. This is quite logical, since the area corresponding to each of the distances increases in arithmentic progression with distance from the plant. It is evident that the quantity of seeds cast outside of the plant constitutes a high proportion of the total seed production (65%); 28, 21 and 15% fell within the 1st, 2nd, and 3rd metres respectively. Although these percentages could represent a small number of all the collected seeds, the number that is found, for instance at 3.2 m from the plant is considerable; in some cases up to 125-185 seeds/m^2. That means that some seeds might possibly go well beyond 3 metres and even reach 4 m.

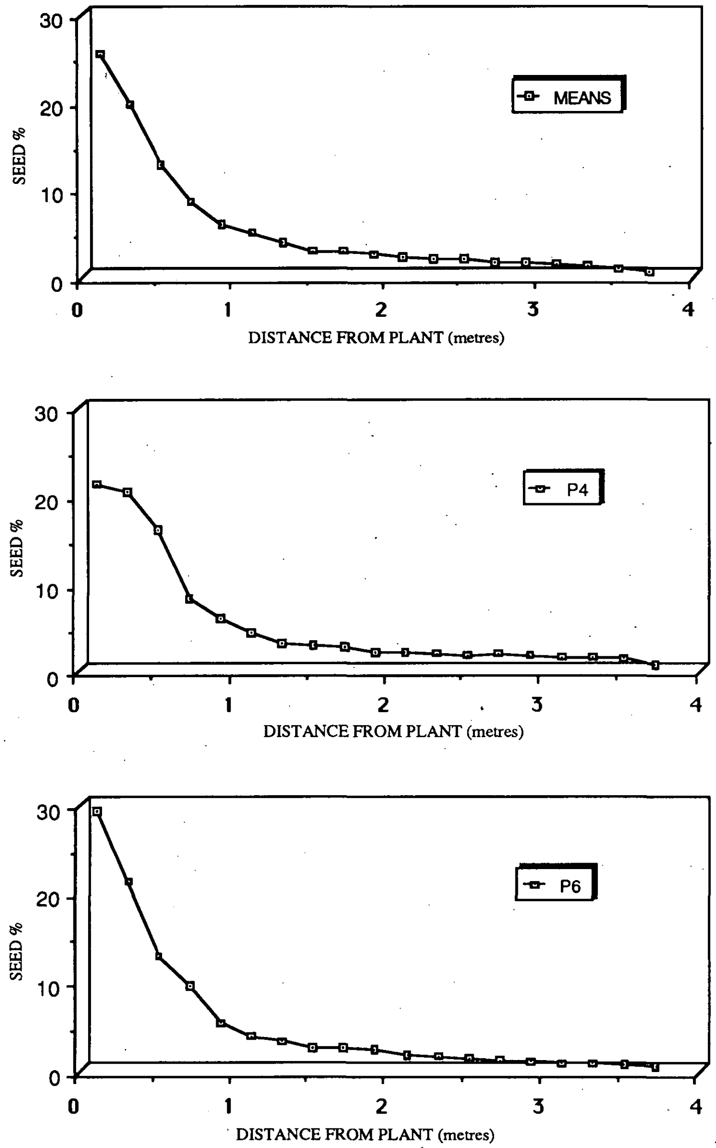
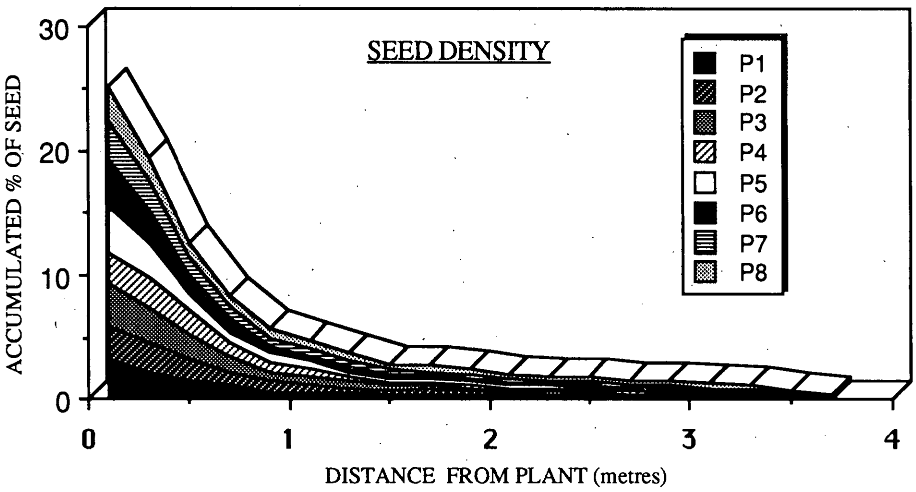


Fig. 2. Seed dispersal curves: mean values, plant n.º 4, and n.º 6 (the latter two represent extreme cases). Distance expressed in metres from the parent plant in 20 cm intervals. The three first intervals are right below the plant and the 4th interval is the first one outside of the boundary of the plant. *(Curvas de dispersión de semillas: valores medios, planta n.º 4 y n.º 6; las dos últimas representan los casos extremos. La distancia se expresa en metros desde la planta origen en intervalos de 20 cm. Los tres primeros intervalos están debajo de la planta y el cuarto intervalo es el primero que queda fuera de los límites de la planta).*



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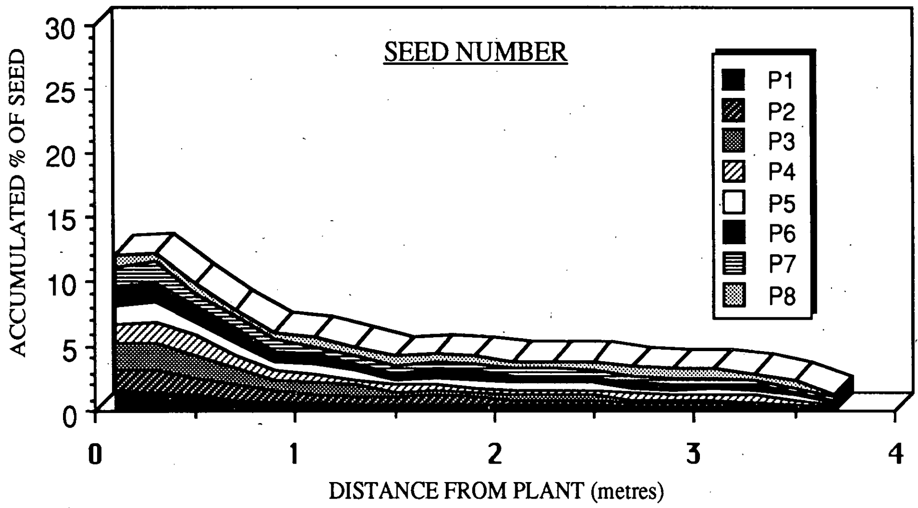

-B-

Fig. 3. Distribution of seed density (A) as compared to the distribution of the seed number fallen at each distance (B). It shows the accumulated percentages of the eight plants, using the same specific weight for all of them. *(Distribución de la densidad de semillas -A- comparada con la distribución del número de semillas caídas a cada distancia -B-. Muestra los porcentajes acumulados de las ocho plantas, utilizando el mismo peso específico para todas ellas).*

2.4. *Distribution of seeds according to orientation*

The results are shown in Table 2 and Figure 4.

TABLE 2
Mean values and coefficients of variation of the percentages of seeds fallen at each of the orientations. Also the results of the multiple comparison of means are shown (* = p < 0.01 and + = p > 0.1).

			COMPARISON OF MEANS			
	MEANS	CV	SW	SE	NE	NW
SW	36.5	30.6	—	*	*	*
SE	19.7	26.9		—	+	*
NE	18.4	28.6			—	*
NW	25.4	18.1				—

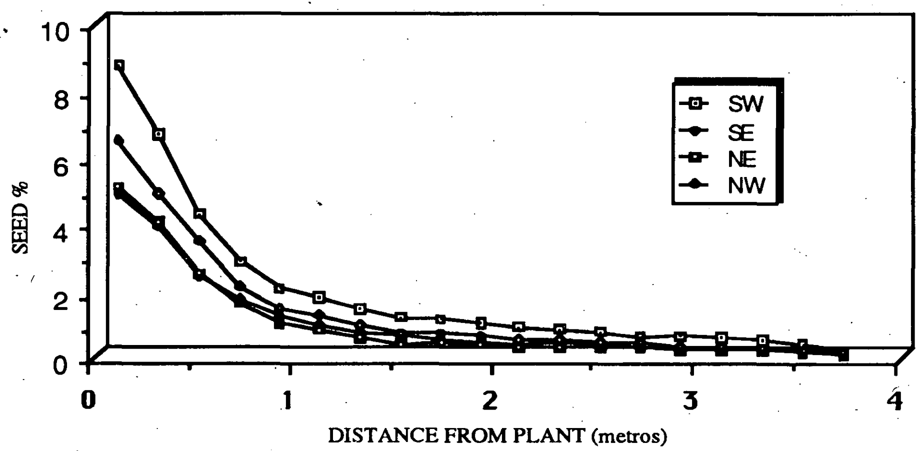

Fig. 4. Seed dispersal curves for the four orientations. It also ilustrates the relative amount of seeds fallen at each of orientations. *(Curvas de dispersión de semillas para las cuatro orientaciones. También ilustra la cantidad relativa de semillas caída en cada orientación).*

Two-way analysis of variance (orientation and distance) was carried out in order to prove the significance of the found differences. The difference in the number of seeds fallen at each orientation is highly significant:

Fexp = 94.79 g.l. = 3 p < 0.01

The posteriori test of this significance was carried out using the T-Tukey and Newman-Keuls' method. Table 2 shows the result of this test.

The highest seed production is found in the western orientation, especially in the SW.

This result agrees with those found for *Cytisus balansae* with bigger fruit setting in the West than in the East orientation (GONZÁLEZ BARTOLOMÉ, 1985). The prevailing humid West and South-West winds as well as the longer hours of sunshine and warmth of these orientations could be the determining factors of these differences.

Although the number of dispersed seeds differs with orientation their dispersal curves are very similar. No significant differences were found between them.

Fexp = 0.4103 g.l. = 54 p > 0.1

2.5. *Seed dormancy and viability test*

Of the total number of tested seeds 1.2% did not show germinating capacity (they were not viable); 2.13% germinated readily without any stimulation (they were non-dormant); and the rest germinated only after mechanical scarification (they were dormant) (see fig. 5).

This gives us a 98.8% viability index and 98.9% that of dormancy; thus placing *C. multiflorus* among those species with the highest dormancy index. These seeds form a soil seed bank which creates a dispersal mechanism in time (VENABLE & BROWN, 1988).

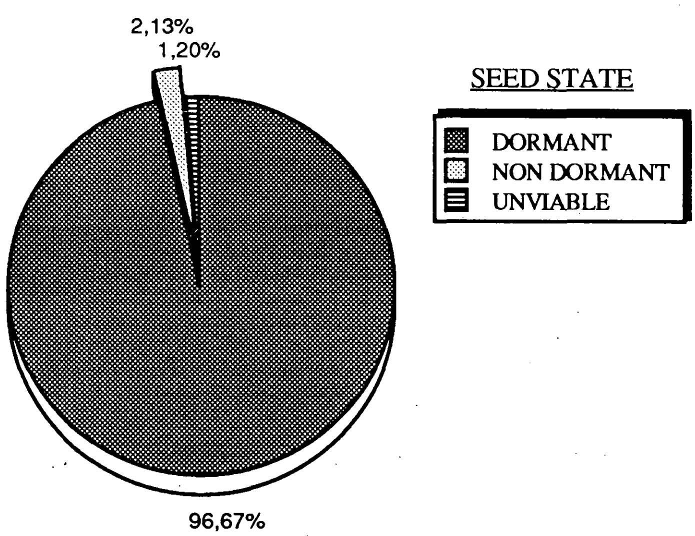

Fig. 5. The state of seeds at the time of their dispersal. *(Estado de las semillas en el momento de su dispersión).*

The percentage of viable non-dormant seeds, 2.13 %, is of great importance because they might never become dormant (AÑORBE, 1988). This implies an efficient source for seedling establishment without the need for stimulation by any environmental factor.

Seed production in the non-dormant state can be explained by the fact that impermeability is acquiered gradually by desiccation on maturing of the seed. This desiccation takes place through the *hilum* —abcision scar left when the seed detaches from the *funiculus*—, which works like a one-way-valve and is activated higroscopically. This valve lets humidity out through the hilar fissure which opens and closes in response to changes in the surrounding humidity. As the seed desiccates a contraction and sealing of Malpighi cells takes place so producing impermeability. Hence, the drier the environment the greater the impermeability effect (TRAN & CAVANHAGH, 1984).

In the present study we found that 2.13% of seeds were non-dormant. But this figure could very significantly depending on the surrounding conditions (drought/dryness) under which seed maturity was reached. AÑORBE (1988) reports 12.08%, although in his study seeds were collected directly from the plants, possibly not having fully matured yet.

Discussion and conclusions

Cytisus multiflorus reproduces mainly by vegetative means; nevertheless, seedling emergence is quite frequent following disturbances as well as during the in between periods (FERNÁNDEZ SANTOS, 1991). This is in perfect agreement with our results on the double type of seed dispersal mechanism, i.e. the spatial-temporal seed dispersal.

The initial seed dispersal by explosive dehiscence facilitates efficient seed dispersal by casting seeds in a wide area. This together with the small non-dormant proportion of seeds allows new seedlings to establish themselves, which is of great importance for colonization as well as rejuvenation of any population without waiting for drastic disturbances such as fire.

Furthermore this seed dispersal is important as an efficient response to spatial heterogeneity on a small scale. ANTONOVICS & col. (1987) demonstrated how plants react to spatial heterogeneity of few centimetres as well as some metres.

Nevertheless, it is a simple seed dispersal mechanism which doesn't facilitate the seeds reaching long distances —about 4 m is the maximum— and leaves a large number of seeds (35%) right below the plant. But with the great advantage that it does not require any additional effort from the plant for their dispersal. We have found that the explosive seed dispersal is quite common in other leguminous matorral species, such as the generas: *Cytisus, Adenocarpus, Ulex, Genista,...* Explosive seed dispersal in these generas has been reported by other authors (FONT QUER, 1979; GRIME & col., 1981; WILLIAMS, 1981; FAHN, 1985). DAVEY (1982; quoted by KEELEY, 1987) found that seed dispersal in different *Ceanothus* species (plants with explosive capsules) is limited and the majority of seeds fall within the first metres from the plant. These are examples similar to that of *Cytisus multiflorus*. Other ones, however, let all their seeds fall right below the plant; as does *Retama* sp. (personal observation). The same happens with *Cistus* sp. (TROUMBIS & TRABAUD, 1986) and *Erica* sp. (MALIK *et al.*, 1984).

HERRERA (1984) argues that due to the presence of gaps in the seral matorral they don't need a very specialized seed dispersal mechanism. Actually, passive seed dispersal or by not complicated mechanisms is common in matorrals such as the: chaparral (PARKER & KELLY, 1989), brezal (HOBBS *et al.*, 1986), and *Cistus* (TROUMBIS & TRABAUD, 1986).

The other, major, part of dispersed seeds is dormant, which permits the formation of a persistent soil seed bank (MORENO, 1992) creating in this way a seed dispersal mechanism in time (VENABLE & BROWN, 1988). These seeds will later, when stimulated, form part of the population. It will generally ocurr when there is drastic disturbance such as fire, soil turning over, etc.

There are species with seminal dimorphism that may be morphological or physiological (in this case it is not so evident and is difficult to recognize). Physiological dimorphism shows various types of dormancy, or the same type of dormancy, but with different requirements for seed germination (FENNER, 1985; UNGAR, 1987). STONE and JUHREN (1952; quoted by CHRISTENSEN, 1985) found that a proportion of annual seed production germinated readily the same year but the rest needed a high temperature treatment to germinate. WILLIAMS (1981) reported the same for *Cytisus scoparius*. And this is exactly what occurs in *Cytisus multiflorus*, i.e. that shows a physiological seed dimporphism —perhaps not genetically coded— which implies the creation of a seed pool to germinate during the year and other pool (more important quantitatively) to form a soil seed bank. One might speculate that the proportion of dormant seeds depends on the probability of their sucess in establishing seedlings; in as far as such probability decreases the proportion of dormant seeds increases (PARKER & col., 1989).

It is difficult to tell the relative importance of a seed dispersal mechanism in terms of demography. However, if we base our deliberation on the productive effort of the plant it becomes clear that *C. multiflorus* hazards and bids for seed dispersal in time.

Seeds of *C. multiflorus* are subject to enormous predatory pressures such as the one befores seed dispersal; between 8.4 and 25% of seeds are eaten (AÑORBE, 1988). But even after seed dispersal levels of predation are still high. Thus the number of seeds accumulated in the soil, proceeding from different years, is smaller than the one produced in one year (MORENO, 1992).

Seed dispersal on a short distance from the plant might mean a dramatic increase in the probability of seed survival (HOWE & SMALLWOOD, 1982). Some authors interpret this type of seed dispersal as an "escape" from predation. Explosive seed dispersal avoids the predispersal predation, since mature seeds do not stay on the plant for such an extended period of time could result in high predation indeces (HARPER, 1977). Besides, explosive seed dispersal makes all the seeds reach the ground in a relatively short time, thus favouring the saturation of seed predatos' food (HARPER, 1977; ANDERSEN, 1987). Other authors, however, argue that seed dispersal hinders the finding of seeds by their predators because it reduces seed density and increase the search area of foraging (JANZEN, 1970 and CONNEL, 1971; quoted by HOWE & SMALLWOOD, 1982).

Furthermore, *C. multiflorus* is characterized by a very high seed production and its high variability between plants; characteristics which have also been reported and interpreted as an "escape" from predation (JANZEN, 1970, 1974 quoted by HARPER, 1977).

Considering all the above we come to think that the high seed production and the explosive seed dispersal together with the consequent seed dispersal on a limited distance from the plant imply and escape mechanism from predation. Thus allowing the creation of a soil seed bank which becomes the principal way of seed dispersal in *Cytisus multiflorus.* Hence, it is a species better adapted to maintaining rather than to extending its occupied area. However, its spatial seed dispersal shouln't be minimized nor disregarded for 2.13% of seeds (non-dormant seeds) in absolute terms is a high number that facilitates the colonization of gaps in the slow advance of a formation.

Finally, we should point out that this discussion could have become even more complicated, since *C. multiflorus* seed, similarly to many other leguminous matorral species, has a kind of aril which could serve as a elaiosome. In some instances we have observed that seeds, once fallen to the ground, were transported by ants and that some ant-nests contain thousands of *C. multiflorus* seeds. Does this create a secondary seed dispersal mechanism —myrmechory—? Is it a simple predation? Or both?

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