

Seed rain in and between vegetation patches in arid Patagonia, Argentina (With 1 Table & 4 Figures)

LLuvia de semillas dentro y entre parches de vegetación en Patagonia árida, Argentina

(Con 1Tabla y 4 Figuras)

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Abstract. Seed rain has ecological consequences on plant community structure. This study was conducted in the Monte Austral Neuquino nearby the town of Picún Leufú, Province of Neuquén, Argentina, within an area of 15 km x 15 km (39° 20' 32" S; 69°19' 30" W). Studies were conducted at two sites, distant 1.5 km from one another. Vegetation is distributed on the soil surface as vegetation patches. Four superficial locations may be found in the soil of these patches: location 1, small dune accumulated under the lee; location 2, found at the edge of the small dune, and below the major grass canopies and tallest shrubs; location 3, located at the edge of the vegetation patch, and location 4 which includes the uncovered corridors among vegetation patches. Seed rain was measured by collecting seeds from traps located in the four study locations. Our working hypotheses were that (1) seeds of the study species arrive to all locations of the vegetation patches and the nude corridors among patches, and (2) the magnitude of the seed rain depends on time of the year. *Larrea divaricata* showed the greatest values in the corridors among vegetation patches and in the periphery of such patches. A similar pattern was found for *S. neaei* although this species dispersed seeds further from the mother plant. *Atriplex lampa* distributed seeds homogeneously in all four locations. *Elymus erianthus* only contributed 1 seed to the seed rain. *Larrea divaricata* showed a greater proportion of its total seed rain between December

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and March in all locations. Seed rain in *A. lampa* was almost permanent throughout the year while in *S. neaei* was concentrated in December and January, although it showed some seed rain until April.

Key words: Seed rain, shrub and grass species, vegetation patches, arid Argentina.

Resumen. La lluvia de semillas tiene consecuencias ecológicas en la estructura de las comunidades vegetales. Este estudio se llevó a cabo en el Monte Austral Neuquino cerca del pueblo de Picún Leufú, Provincia de Neuquén, Argentina, en un área de 15 km x 15 km (39° 20' 32"S; 69°19' 30'O). Los estudios se condujeron en dos sitios distantes 1,5 km. La vegetación está distribuída sobre la superficie del suelo como parches de vegetación. En el suelo de estos parches se pueden observar cuatro lugares superficiales: ubicación 1, duna pequeña ubicada a sotavento; ubicación 2, en los bordes de la pequeña duna, y debajo del follaje de las principales gramíneas perennes y arbustos más altos; ubicación 3, en los bordes de los parches de vegetación, y ubicación 4 que incluye los corredores descubiertos de vegetación entre los parches vegetados. La lluvia de semillas se midió recolectando semillas de las trampas ubicadas en los cuatro lugares estudiados en cada parche de vegetación. Nuestras hipótesis de trabajo fueron que (1) las semillas de las cuatro especies estudiadas llegan a todos los lugares de los parches de vegetación, y (2) la magnitud de la lluvia de semillas varía con la época del año. *Larrea divaricata* mostró los mayores valores en los corredores entre los parches de vegetación y en la periferia de dichos parches. Un modelo similar se observó para *S. neaei* aunque esta especie dispersó semillas más lejos desde la planta madre. *Atriplex lampa* distribuyó semillas homogéneamente en los cuatro lugares. *Elymus erianthus* solo contribuyó una semilla a la lluvia de semillas. *Larrea divaricata* mostró una mayor proporción de su lluvia total de semillas entre Diciembre y Marzo en todos los lugares. Mientras que la lluvia de semillas fue casi permanente durante el año en *A. lampa*, en *S. neaei* se concentró en Diciembre y Enero, aunque ésta mostró lluvia de semillas hasta Abril.

Palabras clave: Lluvia de semillas, especies de gramíneas y arbustos, isletas de vegetación, Argentina árida.

INTRODUCTION

Seed rain has ecological consequences on plant community structure (Willson & Traveset, 2000). The dynamics of a plant population in environments with vegetation patches depends not only on its survival on a specific phenological stage and growth in different patches, but also of

the degree of the vegetation patch suitability through those stages. The degree of vegetation patch suitability can have an important impact on the quantity and the spatial pattern of recruitments. In addition, site suitability can not be independent of seed arrival because of density-dependent mortality factors. Regarding colonization and community structure, early colonizers can inhibit later colonizations if the first establish so densely that constraint plant growth among them. Thus some aspects of the spatial pattern of plant succession can be related with dispersion. In U.S.A. desertic areas, what appears to be limiting the initiation of primary succession is not seed dispersal but the low permanency of seeds in these habitats (Kollmann & Pirl, 1995; Schupp, 1995; Schupp & Fuentes, 1995; Kollman & Schill, 1996; Aguiar & Sala, 1997; Russell & Schupp, 1998).

Aguiar & Sala (1997) emphasize that new plant recruitment depends not only on seedling establishment but also on seed availability which in turn depends on seed production and dispersal. Seed dispersal has two different phases (1) seed movement from the plant to the soil surface, and (2) the subsequent movement of these seeds on that surface. The relationships between wind speed and direction, height of the seed source and seed characteristics determine the position of landing of seeds which are dispersed by wind. The lateral seed movement is mainly controlled by soil roughness and the seed size and shape. It has been recognized as a very significant part of seed dispersal in environments with sparse vegetation. Seeds are captured by uncovered soil only if they are smaller than the size of soil particles or if they possess a morphology and/or appendages which can allow them to anchor in crevices or soil irregularities.

Seeds and seedlings of most populations often interact with individuals of other species. Thus studies at a scale of communities are necessary to evaluate the importance of seed rain in population dynamics and interactions among populations. Peart (1989) emphasized the lack of studies which relate seed rain density to species abundance in the plant community.

The seed flow either into or out of a habitat unit determines the population of that habitat. Seeds which fall on a piece of land can be a function of several variables: (1) the height and origin of the seed source, (2) the seed source concentration, (3) the seed dispersal capacity (i.e., its weight, presence of appendages, etc) and (4) the activity of distribution agents (i.e., wind speed and velocity, herbivory and granivory animals, etc.) (Harper, 1977).

Our working hypothesis was that the seeds of the study species arrive to all microenvironments of the vegetation patches and the nude corridors among patches. The magnitude of the seed rain depends on the time of the year.

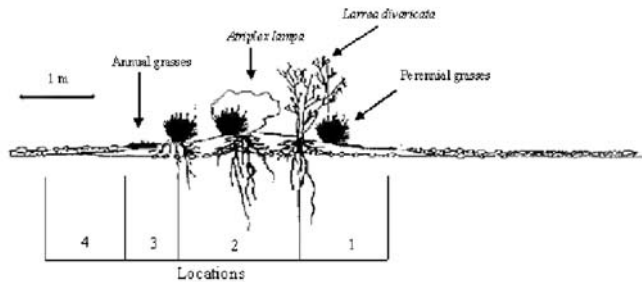
Objectives included to (1) determine the magnitude of the seed rain of *Larrea divaricata*, *Atriplex lampa*, *Stipa neaei* and *Elymus erianthus* in the different locations of the vegetation patches (spatial variability), and (2) characterize its seasonal dynamics (temporal variability).

MATERIALS AND METHODS

Study site. This research was conducted in the shrubby steppe of *L. divaricata* and *A. lampa*, nearby the town of Picún Leufú, Province of Neuquén, within the Monte Austral Neuquino (MAN). As in other arid and semiarid environments of the world, vegetation at this study site had a scattered distribution and a patchy structure (Aguiar et al., 1992; Aguilar & Sala, 1999). Studies were effected within an area of 15 x 15 km (39° 20-32' S; 69° 19-30' W) and conducted at two sites, distant 1.5 km from one another. Four superficial locations may be found in the soil of these vegetation patches: location 1, small dune accumulated windward which generally presents a litter cover; location 2, it is found at the edge of the small dune, and below the major grass canopy and tallest shrubs; location 3, under the lee and located at the edge of the vegetation patch, and location 4 which are the uncovered corridors among vegetation patches (Fig. 1). In each of the two study sites, four vegetation patches were selected and four locations investigated within each patch: (1) windward,

Fig. 1. Vegetation patch description. The location of annual and perennial grasses, *Larrea divaricata* and *Atriplex lampa* is indicated in the patch.

Fig. 1. Descripción de un parche de vegetación. En el parche se indican la ubicación de las gramíneas anuales y perennes, *Larrea divaricata* y *Atriplex lampa*.



(2) below *L. divaricata*, (3) under the lee, and (4) in the bare corridors among vegetation patches (Fig. 1).

Climate. In Picún Leufú, average long-term (1928-1950) annual precipitation is 137.2 mm, and average annual precipitation during 1999-2005 was 200 mm. Extreme values of precipitation during 1928-1950 have been 62.7 and 245.3 mm (Morello, 1958). Maximum and minimum precipitations occur during winter and spring, and summer, respectively. Monthly average values for diurnal and nocturnal temperatures are 28 and 15 °C in January, respectively, and 7 and 2 °C in July, respectively. Mean annual wind speed is 13 km/h (Servicio Meteorológico Nacional, 1958). Summer is the windy season. November, December and January have the greatest wind speed, with a mean of 17 km/h at 2 m from the soil level.

Vegetation. The shrubby steppe of the dominant *L. divaricata* and the co-dominant *A. lampa* occupies approximately 1,080,000 hectares in the MAN. The average height of this steppe is 1.20 m. It is usually present either in plain areas or in those with very little slope (< 5%) (Movia et al., 1982). Three strata can be found within each of the vegetation

patches in this steppe (Movia et al., 1982): (1) *L. divaricata*, *Bougainvillea spinosa* (Cav.) Heimerl, *Monttea aphylla* (Miers) Bentham et Hooker and *L. cuneifolia* Cav. are present with a mean height of 1.50 m, but which can be reduced to 0.80 m on stony or fine-textured soils, (2) the second stratum varies between 0.70-1.00 m and is characterized by the presence of *A. lampa* (0.5-0.8 m height). This species is present either on sandy mounds together with *Prosopis alpataco* Philippi, *Schinus polygamus* (Cav.) Cabr., *Lycium chilense* Miers (ex Bertero), *Chuquiraga erinacea* D. Don and *Fabiana peckii* Niederlein or alone in the interspaces, (3) small shrubs (*Acantholippia seriphioides* (A. Gray) Moldenke, *Gutierrezia solbrigii* Cabr., *Verbena seriphioides* Gilles & Hook, *Senecio aff. filaginoides* DC., *Cassia aphylla* Cav. and *Grindelia chiloensis* (Corn.) Cabr.) and perennial grasses (*Stipa neaei* (Nees ex Steudel), *Poa lanuginosa* (Poir et ap. Lamarck), *Poa ligularis* (Nees ap. Steudel), *Stipa speciosa* (Trinius et Ruprecht), and *Elymus erianthus* Philippi) form the third stratum, which is 0.05-0.60 m height. There are ephemeral species (*Schismus barbatus* Thellung and *Plantago patagonica* Jacquin) 0.05 m height which do not have a plant cover greater than 15%.

Soils. Aridisols dominate the area. There are mostly old structural plains. Landscape is controlled for the horizontal disposition of the sub-jacent mantle. It includes Typic Paleortids, Petrocalcic Calciortids, Petrocalcic Paleargids and Typic Torriorthents, with shallow and saline phases (Ferrer & Irisarri, 1989). According to the soil classification (Soil Survey Staff, 1975) no water is available during long periods. The annual average precipitation is approximately 140 mm and it does not have a clear seasonal distribution (Italconsult Argentina, 1966). However, a light tendency to the Mediterranean type could be observed, with greater humidity during the winter (Morello, 1958). When temperature is sufficient for plant growth, soil water potentials are ≤ 1.5 MPa most of the time. During the warm season, a continuous period of three or more months with available moisture does not exist (Soil Survey Staff, 1975). In addition, the scarce rain has a low infiltration, especially in the corridors between vegetation patches, and most of it is lost by runoff (Bonvissuto, personal observation, EEA INTA Bariloche, Argentina).

Sampling methods. Wind speed behind the shrub protection in the patch, in the patch interspaces at the soil surface level and at 1.5 m height from the soil surface was measured using a portable anemometer.

The magnitude in which seeds arrive to the four microenvironments (within and between vegetation patches, Fig. 1) was studied, which is a measure of its lateral movement. Seed traps were installed in each of the four locations in undisturbed vegetation patches under field conditions. Traps were constructed using plastic from soft drinks of 10 cm diameter. The upper part of each was inverted and utilized as a funnel. This rested on the rest of the plastic container. Traps were 16.5 cm deep and were buried so that the upper part was at the soil surface level. These traps had small holes at the other extreme which allowed for water drainage.

The total of traps was 1 trap/location x 4 locations/vegetation patch x 4 vegetation patches/site x 2 sites = 32 traps. Traps were installed in 1999 and the number of seeds of each species trapped on them was counted every 15 days during more than a year. The diverse seed or fruit structure and sizes of the study species, which would eventually influence its distribution in space, were described by Correa (1978, 1984, 1988) and can be seen in Fig. 2.

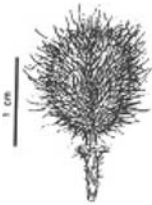
RESULTS

There was times when wind speed was greater than 30 km/h at 1.5 m height from the soil surface, and it reached values close to 25 km/h at the soil surface in the interspaces between vegetation patches (Fig. 3). Under the shrubs, values were from 0 to 5 km/h throughout the year.

The total amount of seeds trapped in all sectors of the vegetation patches varied with the study species (Table 1). *Larrea divaricata* showed the greatest values in the corridors among vegetation patches (location 4) and in the periphery of such patches (location 3). A similar pattern was found for *S. neaei* although this species dispersed seeds further from the mother plant. *Atriplex lampa* distributed seeds homogeneously in all 4 locations. *Elymus erianthus* only contributed 1 seed to the seed rain.

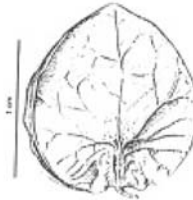
Fig. 2. Characteristics of the seeds and/or fruits of the study species (Correa, 1978, 1984 and 1988).

Fig. 2. Características de las semillas y/o frutos de las especies en estudio (Correa, 1978, 1984 y 1988).



Larrea divaricata

Orange-red fruit with white pubescence. Easily detachable in five mericarpos, with one seed each. Smooth seeds of + 4 mm.



Atriplex lampa

Fruits with bracts of 6-12 × 5-12 mm, membranaceous, free up to the base, oval-rhomboid or subcordadas, obtuses, entire or dentiforms, finely reticulated dorsum at maturity, briefly pediceladas. With one seed each.



Stipa neaei

Fusiform, lineal anthercium; thinned in its upper third, of 9-14 mm, hairy up to either its middle or upper portion with short hairs. Beardless awn of 20-40 mm, bowed subula of 65-110 mm with hairs of up to 4 mm. Lined, fusiform caryopsis of 7-8 mm



Elymus erianthus *

Lanceolated lemma with beardless dorsum, slightly rough in the upper part and densely hairy at its margins. White, silky hairs up to 5 mm. Bidentate apex with 2 sharp teeth. Between these teeth, an awn which can be 1 to 10 mm length is born. Bicarinate palea, either equal or shorter than its lemma. Hairy carinate with the dorsum shortly hairy and a thin, hairy apex. Caryopsis of 5-6 mm.

* Note: To date is *Leymus erianthus* (Dubcovsky et al. 1997)

Fig. 3. Wind speed (km/h) at the soil surface and at 1.50 m height from it in the corridors (location 4) and below the vegetation patches (location 2). Dates: (1) 5 Aug. 1999, (2) 29 Sept., (3) 15 Oct., (4) 27 Oct., (5) 12 Nov., (6) 23 Nov., (7) 13 Dec., (8) 23 Dec., (9) 7 Jan. 2000, (10) 20 Jan., (11) 21 Jan., (12) 3 Feb., (13) 4 Feb., (14) 3 Mar., (15) 24 Mar., (16) 7 Apr., (17) 5 May, (18) 2 Jun., (19) 7 Nov. Each histogram is the mean of 100 measurements which were effected with a hand anemometer. Vertical bars represent 1 s.e. of the mean. Where there is no histograms, wind speed was 0 km/h.

Fig. 3. Velocidad del viento (km/h) en la superficie del suelo y a 1,50 m de altura de ésta en los corredores (sector 4) y debajo de los parches de vegetación (sector 2). Fechas: (1) 5 Ago. 1999, (2) 29 Sept., (3) 15 Oct., (4) 27 Oct., (5) 12 Nov., (6) 23 Nov., (7) 13 Dic., (8) 23 Dic., (9) 7 Ene. 2000, (10) 20 Ene., (11) 21 Ene., (12) 3 Feb., (13) 4 Feb., (14) 3 Mar., (15) 24 Mar., (16) 7 Abr., (17) 5 Mayo, (18) 2 Jun., (19) 7 Nov. Cada histograma es el promedio de 100 mediciones que fueron efectuadas con un anemómetro de mano. Las barras verticales representan un error estándar de la media. Donde no hay histogramas, la velocidad del viento fue 0 km/h.

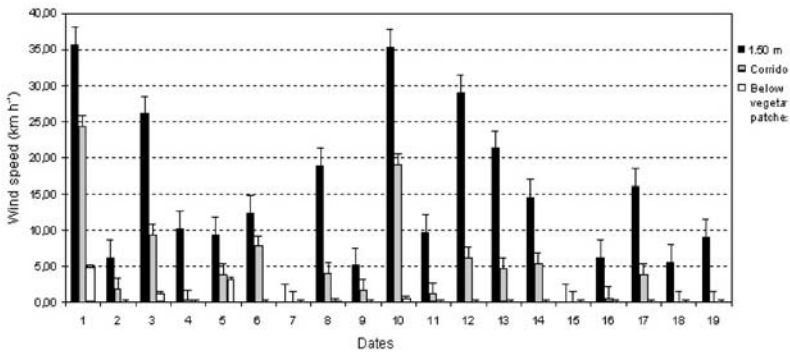


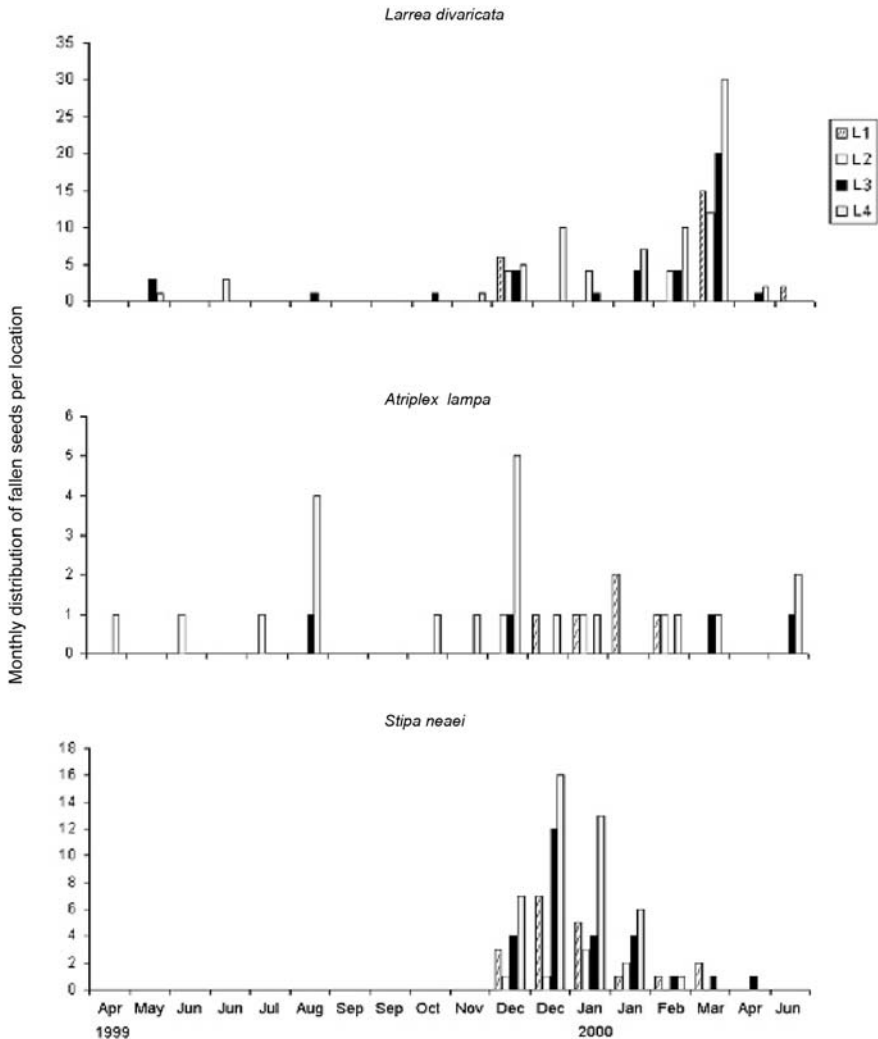
Table 1. Total of seeds fallen per location at the field in 8 vegetation patches from March 1999 to June 2000 in the study species

Tabla 1. Número total de semillas caídas en cada sector en el campo en 8 parches de vegetación desde Marzo 1999 hasta Junio 2000 en las especies en estudio.

Location	<i>Larrea divaricata</i>	<i>Atriplex lampa</i>	<i>Stipa neaei</i>	<i>Elymus erianthus</i>
1	23 (14.65%)	7 (17.50%)	20 (20.83%)	0
2	27 (17.20%)	5 (12.50%)	7 (7.29%)	0
3	35 (22.29%)	6 (15.00%)	26 (27.08%)	0
4	72 (45.86%)	22 (55.00%)	43 (44.79%)	1 (100%)
Total	157	40	96	1

Fig. 4. Monthly distribution of seed rain per location in 8 vegetation patches from March 1999 to June 2000 in the study species. L1: location 1, L2: location 2, L3: location 3, L4: location 4. Notice the change of scale between species.

Fig. 4. Distribución mensual de la lluvia de semillas por sector en 8 parches de vegetación desde Marzo 1999 hasta Junio 2000 en las especies estudiadas. L1: sector 1, L2: sector 2; L3: sector 3; L4: sector 4. Note el cambio de escala entre especies.



Larrea divaricata showed a greater proportion of its total seed rain between December and March in all locations (Fig. 4). Seed rain in *A. lampa* was almost permanent throughout the year; the greatest seed quantities were found in sector 4 (4 in August and 5 in December). Seed rain in *S. neaei* was concentrated in December and January, although there was some seed rain until April (Fig. 4).

DISCUSSION

There was an important seed rain to location 4: 46% of *L. divaricata* seeds, 55% of the seeds of *A. lampa*, 45% of the seeds of *S. neaei* and only one seed of *E. erianthus*. However, seeded seeds in that location produced numerous seedlings, but none of them survived until the time of harvesting which was conducted after the summer drought (Bonvissuto, 2005). Many seeds of all 4 species arrived to location 4 (Table 1), but there were relatively few in the soil seed bank (Bonvissuto, 2005).

Seeds do not necessarily stay in the places they fall while seed rain is occurring. Lateral movement has been recognized as a significant part of secondary seed dispersal in environments with scarce vegetation (Reichman, 1984). Wind speed and direction are important in secondary seed dispersal. Wind can reach 25 km/h in some cases in the corridors among vegetation patches (Fig. 3). Looking at this figure, we can realize that in the corridors will very likely be more lateral seed movement than in the microenvironments located behind the vegetation patches as a result of wind intensity differences among locations. Wind speed and direction combined with height of the seed source and seed characteristics (i.e., biomass, morphology) to determine the position of seed landing of seeds dispersed by wind (Green, 1983). When precipitation is intense it can also contribute to secondary seed dispersal through runoff (Bonvissuto, personal observation, E.E.A. INTA Bariloche, Río Negro, Argentina).

The total seed rain contributed from all 4 species (*L. divaricata*, *A. lampa*, *S. neaei* and *E. erianthus*) increased at increasing distance from below the shrub canopies (location 2) (Table 1). The study species demons-

trated its dispersion capacity. This is because it was abundant the amount of their seeds which arrived to the most distant locations (corridors among vegetation patches), very likely as a result of the appendages in their fruits. *L. divaricata* has strong and firm radial trichomes in all seed directions (Fig. 2); this implies that little wind is necessary for making seeds to roll (www.fs.fed.us/database/feis/plants...nical_and_ecological_characteristics.html, 2000). *Atriplex lampa* presents light bractlets with paper consistency (Fig. 2) which can collaborate in wind dispersal (Osmond et al., 1980). *Stipa neaei* has a large, beardless awn and very likely is dispersed by wind (www.botany.utoronto.ca/courses/BOT307/307prairie3.html, 2005).

Time from seed maturity is an important component which influences seed rain. This is because there are seeds which are released as soon as they mature while others need a post-maturation time in the plant before seed dispersal will occur. Seeds of *S. neaei*, for example, are released from the plant as soon as they mature. Maximum seed rain in this species was during December and January. It is also the case of *L. divaricata*, which maximum seed dispersal occurred between December and March. On the other hand, *A. lampa* showed an homogeneous seed rain during the whole year. In this case, seeds were kept in the plant and then released either at once or slowly throughout a prolonged period.

Numerous ecological factors can contribute to seed dispersal (Willson & Traveset, 2000). Ideally, seed maturation should adjust to dispersal agent availability and germination conditions. Limitations to this ideal can derive from natural selection which contributes to avoid (1) seed predators, (2) changes in flowering time and (3) changes in the amount of time required for fruit maturation. In addition, there is environmental variation regarding the timing of (1) maturation and (2) activity of the dispersal agents in any given area. This ultimately will affect rates and quality of seed dispersal.

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