



Recruitment patterns in four species of *Physaria* (Brassicaceae): implications for maintenance of population density over time in both native and cultivated stands

LUCIANA GONZÁLEZ-PALEO^{1,3,✉}; ALEJANDRO PASTOR-PASTOR²; MARLENE BÄRLAMAS^{3,4};
ALEJANDRA VILELA¹ & DAMIÁN RAVETTA^{1,3}

¹Museo Egidio Feruglio (CONICET). Trelew, Argentina. ²Museo Egidio Feruglio (FONCyT). Trelew, Argentina. ³Universidad Nacional de la Patagonia San Juan Bosco. Chubut, Argentina. ⁴Instituto Patagónico para el Estudio de Ecosistemas Continentales (CENPAT-CONICET). Puerto Madryn, Chubut, Argentina.

ABSTRACT. Seedling recruitment is a critical stage of a plant's cycle which determines population viability, the potential for invasiveness of a plant species and the success of establishment of a crop, among other processes. We evaluated the most relevant stages leading to recruitment (seed-rain, the time of seedling emergence, and seedling survival) in four species of *Physaria* (*P. gracilis*, *P. angustifolia*, *Physaria pinetorum* and *P. mendocina*) in a field experiment in Patagonia, Argentina, to assess the possibility of using spontaneous recruitment to understand population dynamics and to evaluate the potential of this process as a tool for crop reestablishment. We determined the effect of water availability and initial seedling density on final stand density. The total amount of dispersed seed was higher in *P. gracilis* and *P. pinetorum* than in the other two species. *Physaria pinetorum* germinated in late summer, while *P. angustifolia* and *P. gracilis* germinated in spring. No germination was registered for *P. mendocina*. In the three species whose seeds germinated, seedling survival was modulated by a density-dependent mechanism. For *P. pinetorum* seedling density was stable over time in low-density plots, while it decreased in high- and medium-density plots. Still, the highest final density was found in those plots with high initial density. Final density of *P. gracilis* also responded to irrigation treatment. The amount of dispersed seeds was adequate for the re-establishment of the crop in all four species, although the following stages were species-dependent. An appropriate control of seedling density at the initial stage of crop establishment may play a relevant role in the proper regeneration of the crop.

[Keywords: *Lesquerella*, arid environments, seed-rain, seedling survival, seedling density, water availability]

RESUMEN. Patrones de reclutamiento en cuatro especies de *Physaria* (Brassicaceae): implicancias para el mantenimiento de la densidad en poblaciones silvestres y en cultivo. En zonas áridas, el reclutamiento de nuevos individuos es un proceso crítico que determina la viabilidad poblacional, el potencial de invasión de plantas alóctonas y el éxito en el establecimiento de cultivos. Se evaluaron las principales etapas del reclutamiento (lluvia de semillas, fecha de emergencia y supervivencia de las plántulas) en cuatro especies de *Physaria* (*P. gracilis*, *P. angustifolia*, *P. pinetorum*, y *P. mendocina*) en un experimento a campo en la Patagonia argentina, con el objetivo evaluar el potencial de este proceso para entender la dinámica poblacional y su utilidad como una alternativa sustentable de restablecimiento del cultivo. Se estudió el efecto de la disponibilidad de agua y de la densidad inicial de plántulas sobre la densidad final del cultivo. La cantidad total de semillas dispersadas fue mayor en *P. gracilis* y *P. pinetorum* que en las otras especies. No hubo germinación en *P. mendocina*. Las semillas de *P. pinetorum* germinaron a fines del verano, mientras que el resto de las especies germinó en primavera. La supervivencia estuvo modulada por un mecanismo denso-dependiente. En *P. pinetorum*, la densidad de plántulas fue estable en el tiempo en las parcelas de baja densidad inicial, mientras que decreció en las parcelas de densidades media y alta. A pesar de esto, la densidad final fue mayor en las parcelas de alta densidad inicial. La densidad final de *P. gracilis* respondió a la frecuencia de riego. Concluimos que la cantidad de semillas es adecuada para el restablecimiento de la población en las cuatro especies, aunque los procesos que resultan en la densidad final fueron dependientes de la especie. El control apropiado de la densidad inicial de plántulas jugaría un rol relevante para que el restablecimiento se produzca a densidades apropiadas para el cultivo en *P. pinetorum*.

[Palabras clave: *Lesquerella*, zonas áridas, lluvia de semillas, supervivencia de las plántulas, densidad de plántulas, disponibilidad de agua]

INTRODUCTION

Arid environments have strong environmental limitations that constrain seedling establishment and plant growth. In agricultural settings, these constraints require innovative agronomic management to avoid negative environmental impacts (DePauw 2004). One alternative to reduce environmental impacts and to generate economic returns in these low resource environments has been the domestication of wild plant species and the development of new crops that possess conservative resource use strategies (Ravetta and Soriano 1998; González-Paleo and Ravetta 2015). These developments have to be accompanied by low cost production strategies to make these crops profitable (Tilman et al. 2002). Among other aspects of cropping systems in arid environments, the establishment of the crop has remained fairly unchanged and has been copied from more mesic cultivation settings.

The process by which new individuals create a new standing population or are added to an existing population (i.e., recruitment) is one of the most critical stages in the plant's life cycle (Kitajima and Fenner 2000). Seedling recruitment represents the interface between the seed and the reproductive plant and includes three basic processes: seed germination, seedling survivorship and seedling growth, which need to be sequentially successful, and are, thus, not always easy to be completed (Busso et al. 2012). A comprehensive, sequential assessment of this process may be the best approach for addressing regeneration constraints (Giménez-Benavides et al. 2008).

In an agricultural context, the knowledge of critical stages of seedling recruitment may determine the success of the establishment of a crop in marginal lands (Aiken et al. 2015). Spontaneous seedling recruitment could have the potential to restore plant density in perennial crops. Similarly, in annual crops, spontaneous recruitment could be a potential alternative to mechanical re-seeding in fragile cropping environments such as those in arid lands, in which traditional agronomic technology increases the cost of crop production and the risk of soil erosion (Pimentel et al. 1995; Pimentel et al. 2012; Carr et al. 2005; Kim et al. 2008). Recruitment studies are also useful in ecological studies to predict plant population viability (Weiher and Keddy 1999), species range (Giménez-Benavides et al. 2008) and the invasive potential of a given exotic species (Tilman 1993).

Recruitment can be considered a temporal and spatial sequence of stages modulated by biotic and abiotic factors (Nathan and Müller-Landau 2000; Sagnard et al. 2007; Aicher et al. 2011). Within this sequence, seed-rain (i.e., the total input of new seeds that provides an individual plant to the seed bank) (Álvarez-Buylla and Martínez-Ramos 1990) is the first critical step for the generation of a new cohort of plants. Spatial and temporal variability in seed-rain may provoke irregularities in the distribution and density of seedlings (Utsugi et al. 2006). The second critical stage is seedling emergence. The date and site of emergence regulate the duration of the growing season and modulate the intensity of processes such as freezing or pathogen's attacks on seedlings (De la Cruz et al. 2008; James et al. 2011), thus determining the success of recruitment (Escudero et al. 2005), total biomass and seed-production (Ortiz-Monasterio et al. 1994). After emergence, seedling mortality is the main restriction to reaching an adequate stand and to completing the plant's life-cycle (Wang and Smith 2002). Seedling mortality is mainly controlled by water availability in the top layer of the soil (Lauenroth et al. 1994; Bertiller et al. 1996; Defosse et al. 1997; Novoplansky and Goldberg 2001) and by intra-specific competition for soil resources, which is a function of seedling density (Firbank and Watkinson 1987; Lortie and Turkington 2002; Spiegel and Nathan 2012).

We evaluated the recruitment process of four *Physaria* species after a first cropping cycle, in order to assess their population viability in a resource limited environment and the potential for the spontaneous re-establishment of crop density in perennial and annual species. All four species: *P. gracilis* (Hook.) Watson, *P. angustifolia* Nutt. (annuals), *P. mendocina* (Phil) Kurtz and *P. pinetorum* Wootton and Standley (perennials), are under evaluation as new oil-seed crops for irrigated valleys in semi-arid Patagonia, Argentina (Ravetta and Soriano 1998; González-Paleo and Ravetta 2011). Perennial new crops for grain production could provide environmental benefits such as improvements of nutrient- and water-uptake efficiencies (Tilman and Wedin 1991) while storing organic carbon in the root zone (i.e., carbon sequestration) (Poepplau et al. 2011). Furthermore, the continuous soil cover ensured by perennials reduces soil erosion and water and nutrient losses, and improves nutrient availability (i.e., water and nutrient regulation) (Pimentel et al. 2012; Culman et al. 2013; Crews and Brookes 2014).

Our experiments could also contribute to the understanding of population maintenance of these little-known species native to South and North American deserts.

In previous field experiments we observed that *P. pinetorum* and *P. gracilis* had high fruit dehiscence; we also observed seed germination in the fields (González-Paleo, unpublished data), what lead us to the hypothesis that these two species had the potential to establishing a new, spontaneous stand, after the crop is harvested. On the other hand, *P. mendocina* and *P. angustifolia* seemed to have lower fruit dehiscence and lower and less stable rates of seed germination than *P. pinetorum* and *P. gracilis*, which should restrict the possibility of re-establishment.

Regardless of the potential agro-ecological advantage of using the seed that is lost from the plants to restore stand density in perennials, seed shattering is considered a disadvantage, because it implies a significant loss of yield (Zanetti et al. 2013), but also because the development of a seed bank might mean an increase in the risk of invasion when introducing a new crop (Chimura et al. 2010).

Having a mature crop as a starting point, we evaluated seed-rain, time of emergence, and survival of seedlings, and we assessed the effect of irrigation and initial seedling density as modulators of final density of the new stand. We used this experiment as an approach to improve our understanding of the recruitment patterns in forbs of low resources environment, and to generate criteria to evaluate benefits and drawbacks of spontaneous recruitment to restore the crop density in perennials or to re-establish the crop in annual cultivated *Physaria*.

MATERIALS AND METHODS

Study site and species description

A field experiment was performed in Gaiman, Chubut, Argentina (43°21'31" S - 65°38'39" W). This target area for increased cultivation is characterized by semi-desert Mediterranean climate, with cold, wet winters and dry summers. Irrigation is possible from spring (September) to early fall (April). In this area the mean annual precipitation is 179 mm, mean low temperature of the coldest month (June and July) is 1 °C and absolute minimum air temperature is -10.8 °C.

We evaluated four species of *Physaria* (Brassicaceae) native to arid lands of America: two annual species native to Oklahoma and Texas (*P. gracilis* [Hook.] Wats. and *P. angustifolia* [Nutt.]) and two perennial species (*P. pinetorum* Wootton and Standley, native to Arizona, and *P. mendocina* [Phil] Kurtz, native to Argentina [La Pampa]). The areas to where these species are native and from where seeds were collected have similar environments regarding water availability: low total annual precipitation (200-400 mm), winter-spring seasonality, and a clear summer water-deficit (González-Paleo 2010).

All four species have been proposed as potential new oil-seed crops because they contain high levels of hydroxy fatty acid in their seed-oils (Dierig et al. 1993). The target area for their cultivation is irrigated valleys in Patagonia, of the need of supplemental irrigation during the critical period for yield determination (Puppala et al. 2004), which is coincident with the dry season in this area. Periods of water shortage significantly reduce the reproductive success of these partly-domesticated accessions (González-Paleo 2010). Thus, we applied at least three supplemental irrigations (every 25-30 days) from later September to early January (González-Paleo and Ravetta 2011). These species can tolerate periodic water shortages, and this low irrigation should allow reducing the risk of soil salinization in this valley environment (Pérez-Álvarez 2015).

Physaria plants have an acaulescent rosette in the vegetative state, which develops elongate stems bearing leaves, flowers and capsules in the reproductive state. The four accessions evaluated have retained characteristics of their wild ancestors, such as high fruit dehiscence, because they are in an incipient stage of domestication. However, the amount of seed lost by fruit dehiscence has not been quantified. In previous experiments we found differences in potential seed-yield among domesticated accession of these species: *P. gracilis* and *P. mendocina* (have higher seed-yield than of *P. angustifolia* and *P. pinetorum* (González-Paleo and Ravetta 2012). The number of fruits per plant and the number of seed per fruit also differed between species (González-Paleo and Ravetta 2012).

Experimental design

The initial plant population used to evaluate seed-rain belonged to an experiment in which

Table 1: Initial stand density for three *Physaria* species (low, medium and high δ_i) in high and low irrigation treatments, according to the range established previously in Materials and methods. *See that both medium and high initial densities of *P. pinetorum* are higher than the range reported.

Tabla 1. Densidad inicial para tres especies de *Physaria* separadas en sub-parcelas de baja, intermedia y alta δ_i , en tratamientos de alta y baja irrigación, de acuerdo a los rangos establecidos previamente en Materiales y métodos.*La densidad inicial y media de *P. pinetorum* son más altas que el rango reportado.

	Initial seedlings density (δ_i)		
	High	Medium	Low
High irrigation-w1			
<i>P. angustifolia</i>	980 ± 188	440 ± 68	220 ± 37
<i>P. gracilis</i>	2780 ± 385	780 ± 139	350 ± 62
<i>P. pinetorum</i>	8280 ± 1170*	3820 ± 512*	1620 ± 381*
Low irrigation-w0			
<i>P. angustifolia</i>	940 ± 168	420 ± 146	220 ± 97
<i>P. gracilis</i>	980 ± 124	460 ± 116	260 ± 25
<i>P. pinetorum</i>	6880 ± 2695*	2900 ± 783*	800 ± 202

the effect of irrigation on seed production was tested on the four species of *Physaria* (syn *Lesquerella*). The experimental design was a two factor split-plot (Gómez and Gómez 1984). The first factor was irrigation treatment (main plot = 3x3.5 m) and the second factor was species (sub-plots = 1x0.8 m). Sub-plots corresponding to each species were set-up within each main plot (1 sub-plot per species per main plot, 4 sub-plots in total per main plot; 12 plants per sub-plot). Plant density was 10 plants/m².

The irrigation treatments had two levels consisting in differential frequency of irrigation: high irrigation plots (w1, 6 replicates), which were flood-irrigated weekly

to field capacity, and low irrigation plots (w0, 6 replicates), which had an intermittent irrigation frequency (Figure 1). For the low irrigation treatment (w0), flood-irrigation was applied when CO₂ assimilation rate decreased down to 50% (average for the four species), compared to that of control plants. The use of CO₂ assimilation rate as the response variable resulted in an irrigation frequency between 20-25 days (González-Paleo 2010; Vilela and González-Paleo 2015). The irrigation treatments were applied all along the experiment, except during the winter in which water for irrigation it is not available in the Valley of the Chubut River.

Seed-yield, fruit dehiscence and seed-rain

Seed traps were made with PVC tubes with a circular collecting surface of 0.038 m² and a height of 0.5 cm. The traps were planted in the ground under an individual plant per sub-plot (6 traps per species and irrigation treatment). We monitored seed-rain weekly, as the number and weight of the seed in each trap, during the summer 2007-2008, after the first fruits ripe (late December), through mid-January. In these plants we also measured potential seed yield (González-Paleo and Ravetta 2012) and the proportion of seed that was lost by dehiscence, as the difference between potential seed-production and measured seed-yield.

Seedling emergence and survival

The total number of seedlings was monitored in sub-sub-plots (0.1x0.1 m, 100 cm², 3 sub-sub-plot per sub-plot) placed randomly

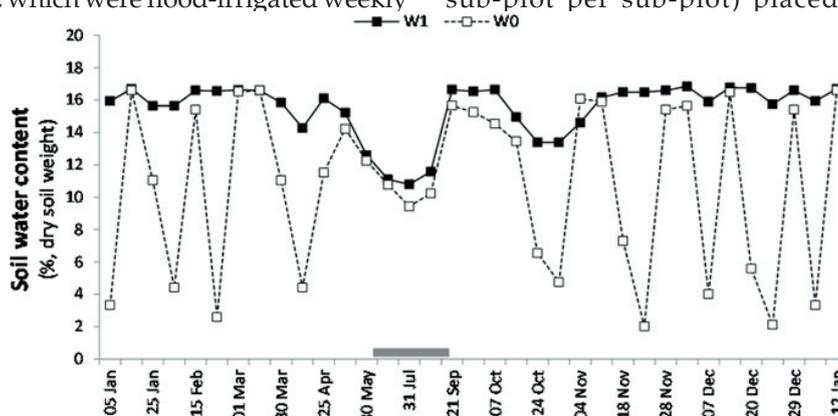


Figure 1. Soil water content (% dry soil weight) for the high (W1; black squares) and low (W0; white squares) irrigation treatments. Each point is the mean of 12 gypsum blocks (two per main plot, 6 main plots per irrigation treatment). Grey line on the X axis indicates the period in which water is not available for irrigation in the Valle Inferior del Río Chubut (from May to September 21).

Figura 1. Contenido hídrico del suelo (% peso seco) para los tratamientos de alta (W1, cuadrados negros) y baja (W0, cuadrados blancos) frecuencia de riego. Cada punto representa la media de 12 bloques de yeso (2 por parcela principal, 6 parcelas principales por tratamiento de riego). La línea gris sobre el eje X indica el período en el cual no hay agua disponible para riego en el Valle Inferior del Río Chubut (desde mayo hasta el 21 de septiembre).

within each species sub-plot. We chose three initial seedling density (δ_i) levels per sub-sub-plot: 1) low density (<400 seedling/m²), 2) medium density (400-700 seedling/m²), and 3) high density (>700 seedling/m²), because of previous observations that showed an aggregated seedling distribution. This aggregated pattern in seedling distribution was also observed in other species of *Physaria*, and it has been related to limited seed dispersion. When seeds are dispersed they remained close to the mother plant (<1 m); the density of seeds and seedlings decreases with distance from the mother plant (Cabin et al. 2000; Masnatta et al. 2012). The initial seedling density for the three species and both irrigation treatments is shown in Table 1. We established these sub-sub plots after 15 days of the germination pulse, because it has been shown that more than 60% of the seeds present in the seed-bank germinate in *P. fendleri* after germination starts (Windauer et al. 2007). The measurement of seedling density started 10 days after establishment of the sub-sub-plots, when seedlings had one pair of leaves. This happened on February for *P. pinetorum*, and October for *P. gracilis* and *P. angustifolia* (Time 1 in Figure 3). We monitored the number of seedlings per sub-sub-plot every ten days until plants reached anthesis. The two annual species were monitored from October to November. The perennial *P. pinetorum* was monitored from February to September. Survival was calculated as: final plant density / initial seedling density*100.

Statistical analysis

To evaluate differences in potential seed-yield, the proportion of seed lost by dehiscence, and seed-rain, among species and irrigation treatments, we carried out a split-plot, two-way factor ANOVA. The main plot was irrigation treatment and the sub-plot was species. To assess the effect of irrigation treatment and initial seedling density on seedling survival, we performed a three-way repeated measures general linear model (GLM; irrigation treatment, time and δ_i) for each species. In those cases in which the triple interaction was significant, we tested for each irrigation treatment, differences in seedling survival throughout time (double interaction, time x δ_i). In those cases in which interaction time x δ_i was significant, we test seedlings survival through time, for each initial density. We compared final stand density among δ_i levels and species. In all cases post-hoc mean comparison were done with Tukey's test. We carried out Levene's and Shapiro-Wilk's tests

in order to check homogeneity of variances and normality, respectively. To control Type I error rates, we adjusted our analyses using the Bonferroni correction by the Sidak method.

RESULTS

Seed-yield, fruit dehiscence and seed-rain

Potential seed-yield and proportion of seed lost by fruit dehiscence differed among species and irrigation treatments (significant interaction irrigation treatments and species; $F=18.78^{***}$ and $F=16.91^{***}$). Under high irrigation treatments, *P. mendocina* and *P. gracilis* had a higher seed-yield than the others (7.99 ± 1.85 versus 3.47 ± 1.21 g of seeds/plant). The amount of seed lost was higher in *P. pinetorum* and *P. gracilis* ($32\pm 12\%$ and $28\pm 13\%$ of the potential seed yield, respectively) than in *P. mendocina* and *P. angustifolia* ($15.5\pm 9\%$ and $19.5\pm 8\%$ of the potential seed yield, respectively). We did not find differences between species in the low irrigation treatments neither for seed-yield ($F=2.24^{ns}$; 2.80 ± 0.98 g of seeds/plant, on average) nor for percentage of seed lost ($F=1.29^{ns}$, $28\pm 9\%$ of potential seed-yield, on average, for the four species).

All four species of *Physaria* had similar timing of dehiscence, starting in late December, with a maximum on early January and ending near mid-January (Figure 2). The amount of irrigation supplied to the crop did not have an effect on seed-rain ($F=0.37^{ns}$). Accumulated seed-rain (number of seeds per unit area) was higher in *P. pinetorum* and *P. gracilis* than in *P. mendocina* and *P. angustifolia* ($F=12.23^{***}$; Figure 2).

Seedling emergence

Seeds of *P. angustifolia* and *P. gracilis* germinated in Spring, after 9 months on the soil. Seedlings completed their life-cycle in three months, from October to December (date of anthesis was 13 November). On the other hand, seeds of *P. pinetorum* germinated in late summer after only 30-45 days on the soil. Seedlings showed a longer growing season, from February to January of the following year (date of anthesis was September) (Figure 3). No germination was recorded for seeds of *P. mendocina*.

Survival

Seedling survival of *P. pinetorum* decreased over time in plots with high and medium initial density (significant interaction between

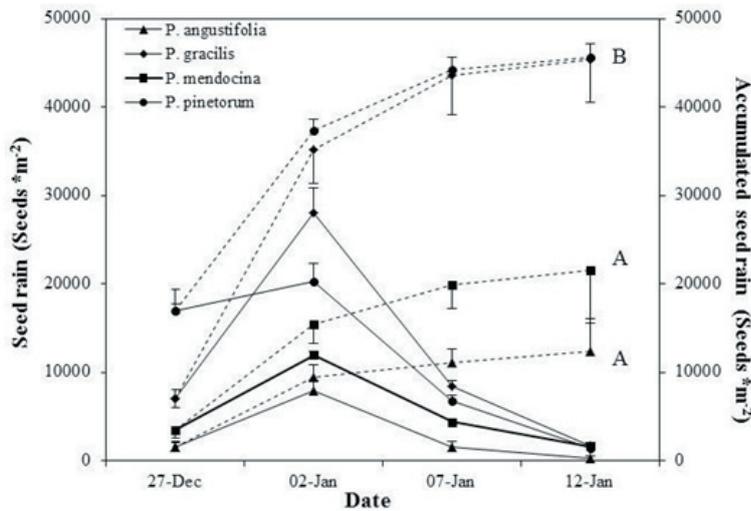


Figure 2. Seed-rain (seeds/m²) for four species of *Physaria*. Full lines represent the amount of seeds lost for each date. Dotted lines are the total accumulated seed-rain. Different letters indicate significant differences in the total amount of seeds that reached the ground. Each point represents mean value±S.E.

Figura 2. Lluvia de semillas (semillas/m²) en cuatro especies de *Physaria*. Las líneas continuas representan la cantidad de semillas caídas por fecha, mientras que las líneas punteadas muestran la lluvia de semillas total acumulada. Las letras indican diferencias entre especies en la cantidad total de semillas que alcanzaron el suelo.

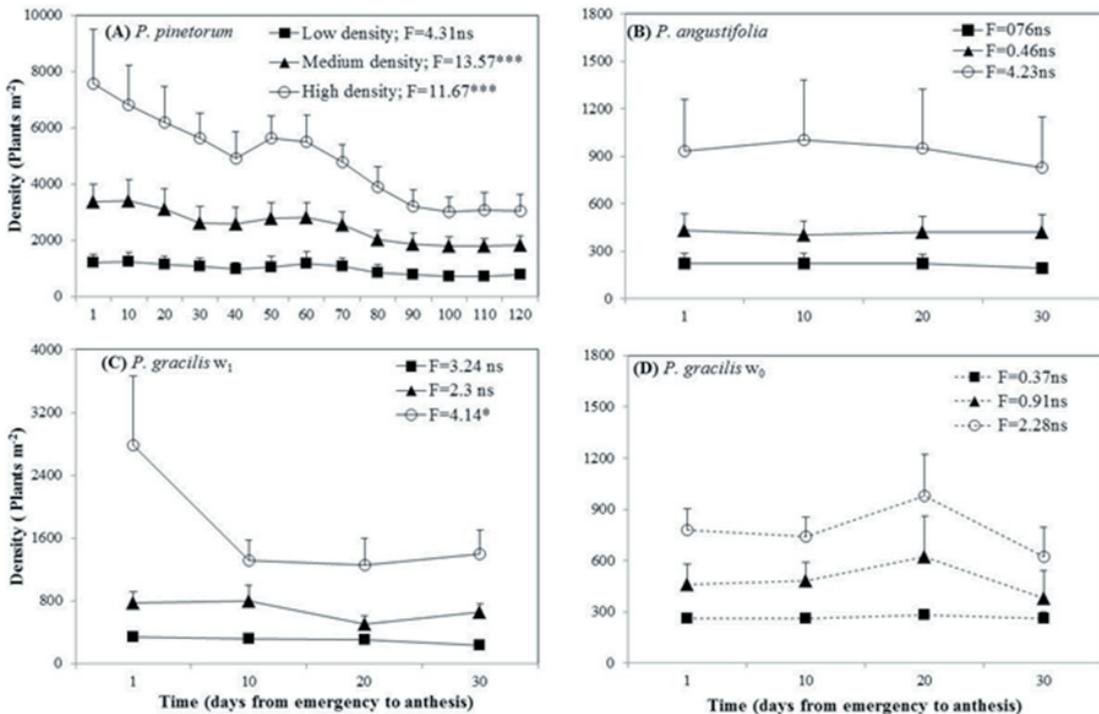


Figure 3. Seedlings survival (plants/m²) over time in patches of low-, medium-, and high- initial density (δ_i) for *Physaria pinetorum* (A), *P. angustifolia* (B) and *P. gracilis* (C and D). For *P. pinetorum* (A) and *P. angustifolia* (B), each point represents the mean value±S.E. of both water treatments (w1-high, and w0-low) since there were no significant interactions (Table 1). For *P. gracilis*, high (C) and low (D) water treatments were separated because of a significant triple interaction (Table 1). In (A), time 1 (emergence date) corresponds to February 19 and time 240 (anthesis date) to September 13, while in (B), (C) and (D), time 1 corresponds to October 13 and time 30 to November 13. Squares indicate low density treatment, triangles indicate medium density treatment and circles indicate high density treatment. For each density treatment, repeated measures GLM were applied for the effect of time. GLM statistics are *F*-values. *P*-values <0.05 remained significant after Bonferroni correction by the Sidak method. **P*<0.05; ****P*<0.001, ns=non-significant.

Figura 3. Supervivencia de las plántulas (plantas/m²) en el tiempo en parches de baja-, media- y alta- densidad inicial (δ_i) para *Physaria pinetorum* (A), *P. angustifolia* (B) and *P. gracilis* (C y D). Para *P. pinetorum* (A) y *P. angustifolia* (B), cada punto representa el valor promedio±E.E. para ambos tratamientos de riego en conjunto ya que la interacción fue no significativa (Tabla 1). Para *P. gracilis*, los tratamientos de alta (C) y baja (D) frecuencia de riego fueron analizados de forma separada debido a que la interacción triple fue significativa (Tabla 1). En (A), el tiempo 1 (fecha de emergencia de las plántulas) se corresponde con el 19 de febrero y el tiempo 240 (fecha de antesis) con el 13 de septiembre, mientras que en (B), (C) y (D), el tiempo 1 corresponde con el 13 de octubre y el tiempo 30 con el 13 de noviembre. El tratamiento de baja densidad inicial se indica por medio de cuadrados, los triángulos el tratamiento de densidad media, y los círculos el tratamiento de densidad alta. En cada tratamiento de densidad se aplicó un análisis de medidas repetidas para testear el efecto del tiempo.

Table 2. Results of the repeated measurements ANOVA on the effects of irrigation treatment, initial density (δ_i), time and their interactions in the seedling density dynamics of three species of *Physaria*. Degrees of freedom (df), mean squares (MS) and significance level (^{ns} $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$) are shown.

Tabla 2. Resultados del ANVA de medidas repetidas que evalúa el efecto del tratamiento de riego, la densidad inicial de plántulas (δ_i), el tiempo y sus interacciones sobre dinámica de la densidad de plántulas en tres especies de *Physaria*. Se muestran los grados de libertad, los cuadrados medios y el nivel de significancia (^{ns} $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$).

	<i>P. gracilis</i>		<i>P. angustifolia</i>		<i>P. pinetorum</i>	
	df	MS	df	MS	df	MS
Between subjects						
Water availability	1	437**	1	1.8 ^{ns}	1	10975 ^{ns}
Initial density (δ_i)	2	947***	2	542**	2	53370**
Water availability \times δ_i	2	216 ^{ns}	2	0.3 ^{ns}	2	2104 ^{ns}
Error	24	66	24	108	24	2548
Withinsubjects						
Time	3	55**	3	2.1 ^{ns}	13	1759***
Time \times Water availability	3	71***	3	0.8 ^{ns}	13	119 ^{ns}
Time \times δ_i	6	41**	6	1.7 ^{ns}	26	450***
Time \times Water availability \times δ_i	6	42***	6	0.7 ^{ns}	26	88 ^{ns}
Error	72	16	72	0.6	312	74.34

Table 3. *Physaria* species final stand density in low, medium and high δ_i . Comparisons were performed only in high water availability (w1) treatments. Low cases letters are used to compare the effect of initial seedlings density for each species (F_{δ_i}). Capital letters compare species for each δ_i (F_{species}). Values are means \pm SE (n=5). Significance levels: * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Tabla 3. Densidad final de las parcelas de tres especies de *Physaria* creciendo en condiciones iniciales de baja, media, y alta densidad inicial (δ_i). Las comparaciones fueron realizadas para el tratamiento de alta disponibilidad de agua (w1). Letras minúsculas comparan el efecto de δ_i para cada especie (F_{δ_i}). Letras mayúsculas comparan especies para cada δ_i (F_{species}). Los valores son promedios \pm SE (n=5). Niveles de significancia: * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Species	Initial seedlings density (δ_i)			F_{δ_i}
	High	Medium	Low	
<i>P. angustifolia</i>	830 \pm 316.8 bA	420 \pm 110.7 abA	190 \pm 34.5 aA	4.19*
<i>P. gracilis</i>	1400 \pm 298.3 bB	660 \pm 107.7 aA	240 \pm 67.8 aA	22.13***
<i>P. pinetorum</i>	3060 \pm 575.5 cC	1840 \pm 335.2 bB	880 \pm 213.8 aB	15.91***
F_{species}	17.41***	25.21***	12.14**	

δ_i and time) (Table 2), and remained stable in the low δ_i plots, independently of irrigation treatment (non-significant triple interaction) (Figure 3a; Table 2). Seedling survival was 55% in medium- and 40% in high- δ_i plots. There was no effect of irrigation treatment on the dynamics of seedling density (non-significant interaction between irrigation treatment and time or density) (Table 2). In *P. angustifolia* there was no effect of initial density on seedling survival (Figure 3b), initial seedling density was maintained in time.

Physaria gracilis seedling survival was affected over time both by irrigation treatment and δ_i (significant triple interaction time \times irrigation treatment \times δ_i) (Table 2). Hence, the effect of initial seedlings density on survival was tested for each irrigation treatment. Under high irrigation level seedling density decreased only in high-density plots (significant interaction $\delta_i \times$ time, $F=2.80^{**}$) (Figure 3c). Seedling mortality in these plots was as high as 50% (Figure 3c). In low irrigation treatment, the initial seedling

density did not affect survival (non-significant interaction $\delta_i \times$ time; $F=0.74^{ns}$) (Figure 3d).

Final stand density (δ_f) was determined for those individual plants that survived and reached the reproductive stage. All annual survivors bloomed, while 90% of the perennial plants flowered. Final stand density was different for the three species and it was dependent on initial density (Table 3). Although the highest mortality was found in the high δ_i , it was under this treatment where the highest final density was found for all three species (Table 3). Final stand density was higher in *P. pinetorum* in all three δ_i plots and there were no differences between *P. gracilis* and *P. angustifolia* (Table 3).

DISCUSSION

Arid lands have strong environmental limitations that constrain seedling establishment and survival, and require innovative agronomic management to avoid

negative environmental impacts of irrigation and fertilizers (De Pauw 2004) and to achieve an adequate plant stand. The domestication of perennial grain crops with conservative resource use strategies (Ravetta and Soriano 1998; González-Paleo and Ravetta 2015) added to the use of low-cost production technology based on perennity (Tilman et al. 2002), are proposed as an option to reduce soil degradation and sustain productivity (De Haan et al. 2014). Using four *Physaria* species as a case study, we tested the idea that seed dispersal due to fruit dehiscence could be an alternative to re-establish decaying perennial stands. A comprehensive, sequential assessment of the recruitment process of desert forbs may be the best approach for addressing crop establishment constraints. We evaluated three stages in the recruitment processes: seed-rain, seedling emergence and seedling survival.

Seed-yield, fruit dehiscence and seed-rain

The amount of seed dispersed by a crop is positively related to the crop's seed-yield and to the degree of fruit dehiscence (Sagnard et al. 2007). Although seed-yield is lower in wild plant species undergoing domestication than in crops, fruit dehiscence is higher in the former (Cox 2009). The consequence is usually high seed losses, which have a negative impact on harvestable yields and crop economics. Because of this, the reduction in fruit dehiscence usually takes high priority in breeding programs (Cox 2009), although the results of the selection in this area have been relatively limited (Child et al. 1998). Still, these unharvested seeds are incorporated into the soil and if predation is low. This seed-bank is readily available for new plant establishment, which could be used to create the next season's stand or to re-establish stand density in a perennial crop. An appropriate management of crop re-establishment by spontaneous recruitment might avoid negative impacts derived from tillage and mechanical re-seeding. In our experiment, seed-rain was detected in all four species of *Physaria*, although the amount of seed was dependent on the species.

Seed-rain was greater in *Physaria pinetorum* and *P. gracilis* than in the other two species in spite of differences in seed-yield (*P. gracilis* and *P. mendocina* had higher yields than *P. angustifolia* and *P. pinetorum*). This result seems to be more dependent on interspecific differences in fruit dehiscence than in seed

yield. For instance, *P. pinetorum* which had the lowest seed-yield, had the highest amount of seed-rain, due to its greater dehiscence (about of 32% of potential seed-yield). Moreover, water availability had no effect on seed rain although it did affect seed-yield; these contrasting effects of water availability might be caused by an increase in fruit shattering under low water availability that increased the proportion of seed-yield lost. In any case, dehiscence appears to provide more seeds than the adequate amount for the establishment of a new stand in all four species, since seed density was much higher than the crop density proposed for other similar crops, such as partly domesticated *P. fendleri* (Brahim et al. 1998).

Dehiscence and seed shattering are a major problem in many crops (Price et al. 1996), especially in those in an incipient degree of domestication. It has been shown that around 10-25% of the yield is lost by dehiscence in many crops (Sedbrook et al. 2014). Moreover, it seems that conventional breeding has so far been unable to produce new cultivars which are more resistant to opening (Child et al. 1998). Our results shown that for *Physaria* species, seed loss is not much higher than for domesticated crops, and reached between 17% and 32% of potential seed-yield.

Seedling emergence

Recruitment is determined by the effect of processes occurring during emergence. Those effects are modulated by environmental variables such as freezing temperature, development of physical soil crusts, drought, and pathogen attacks on germinated seeds (James et al. 2011). Plants have developed mechanisms to avoid these effects by controlling the timing of germination (Baskin and Baskin 2001). In *P. mendocina* the lack of germination may be due to seed dormancy, which is commonly found in non-domesticated species native to arid environments, as a mechanism to prevent germination, preceding unfavorable environmental conditions (Cardwell 1984; Baskin and Baskin 2004). This mechanism has been described for wild accessions of *P. fendleri* in central Arizona, in which seed germination is found during the fall or early winter (Dierig et al. 1993). Dormancy might be mediated by the presence of germination inhibitors in seed teguments. These inhibitors must be washed away prior to germination (Raven et al. 1986). Our observations on stands

of *P. mendocina* support this hypothesis since seed germination and spontaneous seedling establishment have been observed only after unusual heavy rains (unpublished data). On the other hand, *P. pinetorum* seeds had no dormancy and an early emergence, whereas the annuals took about four months in the ground to germinate the following spring. This pattern in annuals could be also related to seed dormancy, in this case broken by annual temperature cycles, as found by Marone et al. (2000) for some forbs in the arid Monte region or could be due to unfavorable germination conditions during the winter time.

Several studies have shown that early-emerged seedlings have higher chances for survival than late emerged seedlings (Cavieres and Peñaloza 2012). In our experiment the germination timing of *P. pinetorum* coincided with the sowing time proposed for this crop in Patagonia (Ploschuk et al. 2003). An early establishment in the fall results in greater biomass production and, thus, greater seed-yield, compared to crops sown in spring (Ploschuk et al. 2003). Also, an earlier germination should reduce seed exposure to predation, pathogens attacks, etc, avoiding, thus, the loss of seeds or reductions in viability. Also, in annual species late emergence should lead to lower yields, due to a shorter life-cycle and lesser biomass production. Dierig et al. (2012) showed that *P. fendleri* fall plantings produce higher yields than spring and winter plantings, due to a longer growth cycle.

Seedling survival

Soil-water availability has been pointed out as the most relevant factor determining seedling survival in arid environments (Soriano and Sala 1986; Cipriotti et al. 2008). Hence, we expected lower seedling survival in our low-irrigation treatment, rather than in the high-irrigation. However, we found no response of *P. pinetorum* and *P. angustifolia* to irrigation treatment, while seedling survival for *P. gracilis* was lower in the high-irrigation level and higher initial seedlings density. This higher seedling mortality under high-irrigation was a direct consequence of the higher rate of germination and concomitant increase of intra-specific competition observed under non-limiting water conditions. Thus, the negative effect of water availability was indirect and modulated by density-dependent mechanisms. In spite of this, high δ_i plots under high irrigation had the greatest final stand density.

In *P. pinetorum*, the main factor explaining changes in seedling survival was the initial density (δ_i). The importance of density-dependent processes in reducing seed-to-adult survival is widely recognized and reflects several non-exclusive mechanisms such as seed predation, herbivory, pathogens and seedling competition (Donohue 1997; Nathan and Müller-Landau 2000; Mari et al. 2008; Spiegel and Nathan 2012; Cavieres and Peñaloza 2012). Density-dependent processes during early stages affect seedling survival and thus may influence the structure of the population (Lambers and Clark 2003). In our experiment, the overall result of these processes was an irregular-aggregate distribution of seedling patches, with large bare-soil spaces between patches with aggregated seedlings. Within these patches we found that final stand density was directly correlated to initial density (δ_i) in *P. angustifolia* and *P. pinetorum*. These results indicate that density-dependent processes are relatively less important to determine final density than the number of seedlings initially recruited.

Implications towards the design of sustainable agricultural practices

The final aggregate distribution found in our plots must have relevant implications for the spontaneous reestablishment of the crop and its use in the agronomic context. On the one hand, the final distribution of the seedlings could represent an unsolvable problem in annuals, producing an undesired patchy distribution. On the other hand, in the perennial, density-dependent processes, such as intra-specific competition, would result in a more even distribution of plants compared to the uneven seed-rain found mostly close to the mother plants. In a perennial crop, the re-seeding is not needed to recover a new complete stand but to have enough plants to replace those plants that die as the stand gets older. Traditional sowing systems might be more efficient in achieving an optimal distribution. Nonetheless, it would mean inter-seeding or a complete replacement of the stand. In the case of the perennial *P. pinetorum*, this extra cost of re-establishment of a new stand should be added to the 32% of the potential seed-yield lost by fruit shattering. Since breeding for non-shattering pods has proved to be difficult (Chid et al. 1998), we proposed the use of the seed lost by shattering as a way to re-establish crop density in perennial herbs. In our experiment, the final

density was higher than that recommended for other similar crops (e.g., *P. fendleri*) (Brahim et al. 1998) and acquired an aggregate distribution. Hence, an appropriate control of density and distribution of seedlings at the initial stage is needed, for instance using a controlled removal of selected seedlings before the end of the vegetative stage.

CONCLUSIONS

The amount of seed dispersed for all four species of *Physaria* evaluated in this study was higher than the minimum crop density recommended for *P. fendleri*, and it seems adequate for the re-establishment of the new crop cycle. We conclude that crop re-establishment following seed-loss before harvest, has the potential for re-establishing the following crop-stand. However, the feasibility of using spontaneous recruitment for crop establishment depends on several processes that follow seed-rain. For example, in *P. mendocina*, seeds did not germinate, probably due to seed-dormancy. Therefore, spontaneous seedling recruitment is not an option under these conditions.

The time of germination (Spring in annuals vs. Fall in *P. pinetorum*) plays an important role determining crop productivity. Crop

establishment in spring has been shown to be inadequate for crop production because it produces a very short growth-cycle, rendering low final biomass and seed-yield (Ploschuk et al. 2003). Factors regulating the final stand density were different for each of the species we evaluated. For *P. gracilis* and *P. angustifolia*, the influence of initial seedlings density and irrigation treatment were relatively minor in reducing the final stand.

The best scenario for the use of recruitment for the re-establishment of the crop was that of *P. pinetorum*: 1) seed-rain was not limiting, 2) seedling emergence takes place in fall, and 3) seedling survival was modulated by a density-dependent mechanism, although this process did not compensate for unevenness in initial seedling density. The consequence would be a heterogeneous and somehow patchy final stand density. An appropriate control of density and distribution of seedlings at the initial stage is also a very relevant issue that should be further investigated.

ACKNOWLEDGMENTS. This work was funded by Agencia Nacional de Promoción Científica y Tecnológica (PID 363) and Ministerio de la Producción de la Provincia del Chubut, Argentina.

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