Seed production of common teasel (*Dipsacus fullonum*) and response to intraspecific competition in Buenos Aires province, Argentina

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ABSTRACT

Dipsacus fullonum L. (common teasel) is a short-lived perennial plant that has become an invasive weed in Argentina and many other countries. It reduces native species diversity and forage production in natural protected areas and grasslands. Reproduction is only through seeds. Field surveys were carried out to determine reproductive potential under natural populations growing in four different locations of Buenos Aires province, Argentina (Bahía Blanca, Saldungaray, Necochea and Energía). At the onset of flowering, 30 plants were randomly tagged at each location. Selected plants included those considered growing in a group and those growing alone (when no other plant was adjacent for at least 60 cm). Once plant senescence was identified, all heads were counted and harvested individually. A linear regression model that described the relationship between the weight of seeds from a single head and the number of seeds was used to estimate the total seed production of each plant. The number of heads per plant varied from 3 (Energía) to 62 (Bahía Blanca). No differences were detected in the number of seeds in the principal head at the different growth situations. Across growth situations, principal heads from plants growing in Bahía Blanca showed 16%, 12%, and 22% more seeds than Energía, Necochea and Saldungaray, respectively. Total seed production per plant ranged from 1,485 (Energía) to 15,551 (Bahía Blanca). Plants growing in Bahía Blanca produced a number of heads and seeds higher than the other evaluated locations. Plants growing alone showed 46% and 48% greater head production and seed production across locations than plants in groups, respectively. This high production potential of common teasel plants growing alone would encourage the invasion of new areas, when compared with plants growing in dense patches.

Keywords: invasive plant, weed, bioecology.

RESUMEN

Dipsacus fullonum L. (carda silvestre) es una especie perenne de vida corta considerada una maleza invasora en Argentina y en varios otros países. La carda silvestre compite con especies nativas en los sitios que invade reduciendo la diversidad florística en áreas protegidas y la disponibilidad de forraje en pastizales naturales. Su modo de reproducción es únicamente a través de semillas. El objetivo de este trabajo fue determinar el potencial reproductivo y el efecto de la competencia intraespecífica sobre este mismo parámetro, en poblaciones naturales de carda creciendo en cuatro localidades diferentes de la provincia de Buenos Aires, Argentina (Bahía Blanca, Saldungaray, Necochea y Energía). Al inicio de la floración, se marcaron 30 plantas al azar en cada población. Las plantas se seleccionaron incluyendo aquellas creciendo en grupos y creciendo aisladas (cuando ninguna otra planta de carda se encontraba creciendo dentro de un radio de al menos 60 cm). Una vez identificada la senescencia de la planta, todas las inflorescencias (capítulos) fueron cosechadas individualmente. Se utilizó un modelo de regresión lineal para describir la relación entre el peso de semillas de un solo capítulo y el número de semillas, con el objetivo de estimar la producción total de semillas de cada planta. El número de capítulos por planta varió entre 3 (Energía) y 62 (Bahía

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Blanca). No se detectaron diferencias en el número de semillas del capítulo principal en las diferentes condiciones de crecimiento. El capítulo principal de las plantas que se encontraban creciendo en Bahía Blanca mostró un número de semillas 16%, 12% y 22% más alto que Energía, Necochea y Saldungaray, respectivamente. La producción total de semillas registrada por planta osciló entre 1.485 (Energía) y 15.551 (Bahía Blanca). Las plantas que se encontraban creciendo en Bahía Blanca produjeron un mayor número de capítulos y semillas que el resto de las localidades. Las plantas que crecieron aisladas mostraron un 46% y un 48% más de producción de capítulos y semillas en todas las localidades censadas que las plantas en grupos, respectivamente. Este alto potencial de producción de semillas, en plantas de carda silvestre creciendo aisladas, fomentaría la invasión de nuevas áreas, en comparación con plantas que se encuentran creciendo en parches densos.

Palabras clave: *planta invasora, maleza, bioecología.*

INTRODUCTION

Common teasel (*Dipsacus fullonum* L.) is a native European short-lived perennial plant, which can be found invading a variety of places in several countries, including Argentina (Busso *et al.*, 2013; CABI, 2022). It generally grows in protected areas, pasturelands, roadsides, and railways (Werner, 1975b). Common teasel can be especially prolific in mesic environments, where a moderate level of humidity is maintained throughout the growth cycle. However, occasionally, it can be observed invading dry soils (Werner, 1975b; Solecki, 1993). Common teasel was apparently intentionally introduced to Argentina for cultivation purposes, as an ornamental plant, or it may have arrived as seed contamination (Novara, 2007). It has been observed in several provinces within Argentina, for instance Córdoba, Entre Ríos, Río Negro, Salta, and Santa Fe (Zuloaga and Morrone, 1999), but apparently the highest abundance of populations, and in continuous expansion, have been observed especially in Buenos Aires province. Common teasel outcompetes native species in protected areas (Werner, 1977; Solecki, 1993; Huenneke and Thomson, 1995). Moreover, due to the presence of rigid spines or prickles on the leaves and stem surface, it may reduce available forage for livestock in grasslands (Solecki, 1993; Werner 1975b). In addition, teasels usually invade roadsides or railways, and tall stems (about 2.5 m) negatively affect vehicle visibility (Bentivegna and Smeda, 2011a).

Common teasel grows as a rosette in the first year of growth and typically bolts in the second or subsequent years. It produces a flowering stalk with several branches (Werner, 1975b). At the end of each branch, the plant holds an inflorescence (capitulum) usually denominated 'head'. In Argentina, flowering has been observed in early summer when the flowers appear inside the heads, showing a reduced calyx, a lilac or dark pink corolla of four fused petals, four stamens, and an ovary with a single ovule. The flowers are protandrous (*i.e.,* the stamens mature earlier than the pistil), which promotes cross-pollination by insects, but an estimated 4% of self-fertilization is also reported (Werner, 1975b). After fertilization, grayish brown fruits called achenes develop (hereafter seeds) (Jurica, 1921). Seed dispersal by wind or animals is not possible due to the lack of morphological adaptations, such as pappus or spines (Werner, 1975b). Thus, more than 99% of seeds fall within 1.5 m from the parent plant, producing dense populations (Werner, 1975a). High seed germination rates (> 90%) following maturity have been found in local populations (Daddario *et al.*, 2017). Long-distance seed dispersal is encouraged by the ability of seeds to float on water courses (Werner, 1975b).

Since teasel seed dispersal is limited and no vegetative reproduction has been observed, common teasel invasiveness may be promoted by the production of an elevated number of seeds (Caswell and Werner, 1978). Knowledge of common teasel seed production can provide information about the potential for forming soil seed banks and its invasion risk to new areas. Furthermore, management of common teasel may be best achieved by preventing or substantially limiting the reproductive stage. Failure to prevent the production of seed results in increasing numbers of propagules in the soil bank. The quantification of common teasel seed production is also especially useful to test the effectiveness of a management strategy and for restoration programs of invaded areas (Zimdahl, 2007). There are no quantitative estimates of common teasel seed production in Argentina, and despite the existence of some previous reports in other countries (Werner, 1975b), these have not focused on the extent of the actual seed production for individual plants or demonstrations of the impact of intraspecific competition on seed production.

Due to the significance of common teasel as an invasive weed and the lack of detailed information regarding these aspects, we hypothesized that the success of this species is explained in part by a high reproductive potential, which is, at the same time, higher in the absence of intraspecific competition than competing with other teasel plants. The specific objectives of this study were to quantify the numbers of heads, total seeds per primary head, and total seed production for common teasel plants growing with and without intraspecific competition from different populations growing in the south of Buenos Aires province, Argentina.

MATERIALS AND METHODS

Study sites

Common teasel head and seed production was studied in four populations located in the south of Buenos Aires province, Argentina (fig. 1). Naturally occurring populations of the weed were searched during field trips and selected for the research. The first one was situated by the margin of a water course in Bahía Blanca city (38°42'1.05"S; 62°19'49.84"W). The second and third were growing along a railway near Saldungaray city (38°21'41.08"S; 61°48'16.84"W) and Necochea city (38°31'12.1"S; 58°41'39.9"W). The last one was growing on a roadside close to Energía town (38°32'35.5"S; 59°29'7.1"W).

All populations were located at about 30-185 m above sea-level. The mean daily temperatures for winter and summer seasons ranged from 6 to 30°C for Bahía Blanca and Saldungaray (Paoloni, 2010), and 10 to 21°C for Necochea and Energía (Merlotto and Piccolo, 2009). Average annual rainfall is about 650-850 mm for Bahía Blanca and Saldungaray, and 913 mm for Necochea and Energía. Soil characteristics of the sites, size of the populations, and accompanying vegetation are detailed in table 1.

Figure 1. Location of all sites visited at which common teasel reproductive potential was evaluated in the south of Buenos Aires province, Argentina.

Description of the experiment

At each location, a number of 15 plants growing in intraspecific competition (hereafter "in groups") were randomly selected and tagged. Plants were considered in groups when at least two other plants of teasel were growing within a radius of 60 cm, following the methodology described by Bentivegna and Smeda (2011b). Another set of 15 plants were also selected and tagged in the absence of intraspecific competition (hereafter "alone"), when no other teasel plant was growing within that same radius. Once the heads had matured and before natural seed release, heads were harvested for each plant and then placed individually inside a bag. Harvest dates were 27/02/2013, 28/02/2013, 14/02/2014, and 15/02/2014 for Bahía Blanca, Saldungaray, Necochea, and Energía, respectively. All bags containing heads were taken to the laboratory. Since the principal head, positioned in the center of the plant, is the first one to mature and may escape to control measures (*e.g.*, mowing) (Bentivegna and Smeda, 2011a), it was identified and separately analyzed. Firstly, all heads were counted for each plant. Then, ten heads were randomly selected for each location and growth situation, for which the length of each head was measured. Later, seeds from each selected head were carefully extracted and cleaned using a 0.1 cm mesh sieve and counted. Finally, total seed weight per head was registered at room temperature (20 ± 2°C) and 50% relative humidity using a precision scale.

Statistical analysis

The experiment was conducted as a completely randomized design. Data were subjected to two-way Analysis of Variance (ANOVA), considering location (Bahía Blanca, Saldungaray, Necochea, and Energía) and growth situation (alone or in groups) as fixed factors. Means were separated using Fisher's Protected Least Significant Difference test at $p<0.05$. Previously, normality and variance homogeneity were evaluated through analysis of residuals. When it was necessary, data were transformed using Ln(x) transformation to achieve ANOVA assumptions (Snedecor and Cochran, 1956). Data were pooled over locations or the growth situation when no location by growth situation interaction was detected ($p>0.05$). Linear regression models were adjusted between head length and seed number, and also between seed weight and seed number, to estimate the total seed production per plant. Since seed weight showed a higher goodness-of-fit measure, it was used as an estimator of the total seed production. Analyses were performed using the statistical software INFOSTAT (Di Rienzo *et al*., 2015).

RESULTS

Number of heads per plant, seeds per principal head, and total seed production per plant results are shown in table 2. No interaction between locations and growth situation for the number of heads was observed ($F=1.43$; $p=0.24$). However, significant differences were detected between locations ($F=25.78$; $p<0.01$) and between growth situations ($F=63.92$; $p<0.01$) for the number of heads. Across growth situations, the lowest number of heads per plant was three, detected in Energía, and the highest was 62 in Bahía Blanca. Across locations, head production of plants growing alone was 46% higher than plants growing in groups (fig. 2).

According to the adjusted regression, seed weight and number of seeds per head fitted the data with $R^2=0.84$ (fig. 3a), and head length and number of seeds data fitted regression with $R^2=0.64$ (fig. 3b). No interaction between locations and growing conditions for the number of seeds of the principal head of common teasel ($F=1.03$; $p=0.38$). While no significant differences between plants growing alone and in groups were detected for the principal head ($F=0.12$; $p=0.72$), differences between locations were observed ($F=4.23$; $p<0.01$). Across growth situations, principal heads from plants growing in Bahía Blanca showed 16%, 12%, and 22% more seeds than Energía, Necochea, and Saldungaray, respectively (fig. 4).

Regarding the total seed production, there was no interaction between locations and growing conditions in the populations evaluated in our study ($F=1.64$; $p=0.18$). Nevertheless, there were significant differences between locations ($F=9.22$; $p<0.01$) and between growing conditions ($F=68.28$; $p<0.01$) for the total number of seeds. Seed production per plant was 5,692 seeds on average, ranging from 1,485 (Energía, plants in a group) to 15,551 (Bahía Blanca, for plants alone). Seed production of plants growing alone was 48% higher than plants growing in groups (fig. 5).

	Bahía Blanca	Energía	Necochea	Saldungaray
pH	8.3	8.2	7.6	8.3
Organic matter (%)	3.58	4.23	7.89	4.77
Total nitrogen (%)	0.189	0.21	0.374	0.221
Extractable phosphorous (ppm)	26.8	22.2	81.8	12.6
Potassium (ppm)	778	597	661	486
Calcium (ppm)	3,469	4,170	3,863	4,666
Magnesium (ppm)	369	403	395	221
Sand (%)	55.6	52.3	51.7	39.5
Loam (%)	27.8	28.7	31.8	42.2
Silk (%)	16.6	19	16.5	18.3
Effective soil depth (cm)	*ca.* 65	*ca.* 85	*ca.* 80	*ca.* 70
Population size (m^2)	350	150	2500	350
Accompanying vegetation	*Conium maculatum*-like, *Sonchus oleraceous*, *Diplotaxis tenuifolia*, Grasses (*Bromus* sp., *Lolium* sp.), *Cyperus*-like, and undetermined aquatic species.	Mostly grasses (*Thinopyrum ponticum*, *Festuca arundinacea*, *Dactylis glomerata*, *Cortaderia selloana*). Broadleaved species (*Cynara cardunculus*, and *Rapistrum rugosum*)	Mostly *Conium maculatum*-like, also *Carduus* sp., and *Eryngium* sp.	Mostly broadleaved species (*Cynara cardunculus*, *Cirsium vulgare*, *Diplotaxis tenuifolia*, and *Medicago* sp.) and grasses.

Table 1. Chemical and physical soil properties, population size, and accompanying vegetation of common teasel at Bahía Blanca, Necochea, Energía, and Saldungaray locations in Buenos Aires province during seed production study.

	Bahía Blanca		Energía		Necochea		Saldungaray	
	Group	Alone	Group	Alone	Group	Alone	Group	Alone
				Head production				
Mean	16	33	7	13	8	15	10	13
Standard deviation	8.98	13.52	2.03	4.62	3.09	5.17	4.24	7.42
Minimum	6	11	3	6	5	8	4	6
Maximum	43	62	10	23	16	27	20	36
				Seed production of principal head				
Mean	1,139	1,095	922	952	898	1,056	905	833
Standard deviation	180	316	262	143	192	482	238	267
Minimum	849	425	476	714	642	550	550	475
Maximum	1,516	1,787	1,546	1,202	1,224	2,176	1,321	1,336
				Seed production per plant				
Mean	4,918	11,390	3,100	5,781	3,527	7,151	3,890	5,773
Standard deviation	2,585	3,570	979	2,144	2,017	3,008	1,937	2,788
Minimum	2,087	3,560	1,668	2,922	1,485	2,089	1,530	2,893
Maximum	11,547	15,551	4,637	10,991	9,223	12,577	7,863	11,548

Table 2. Mean, standard deviation, minimum and maximum head production, seed production per principal head and total seed production in Bahía Blanca, Necochea, Energía, and Saldungaray locations for common teasel plants growing alone (plant without another teasel plant closer than 60 cm) or in a group (plant with at least two teasel plants growing within 60 cm radius).

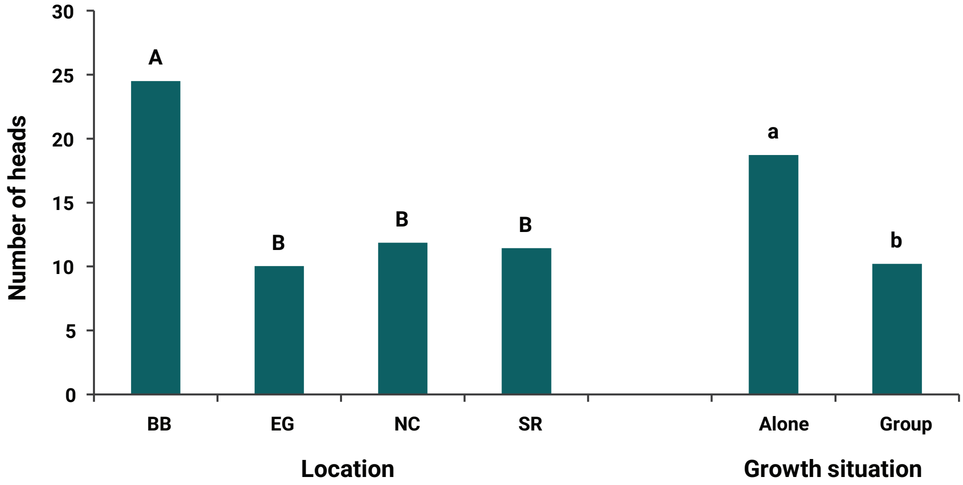

Figure 2. Number of heads of *Dipsacus fullonum* plants for four different locations in south Buenos Aires province and two growth situations ('Alone', when no other teasel plant was growing closer than 60 cm, and in 'Group', when there were as at least two plants growing within 60 cm radius). Abbreviations: BB = Bahía Blanca, EG = Energía, NC = Necochea, and SR = Saldungaray. Bars with the same letters do not differ statistically according to Fisher's protected test ($p<0.05$).

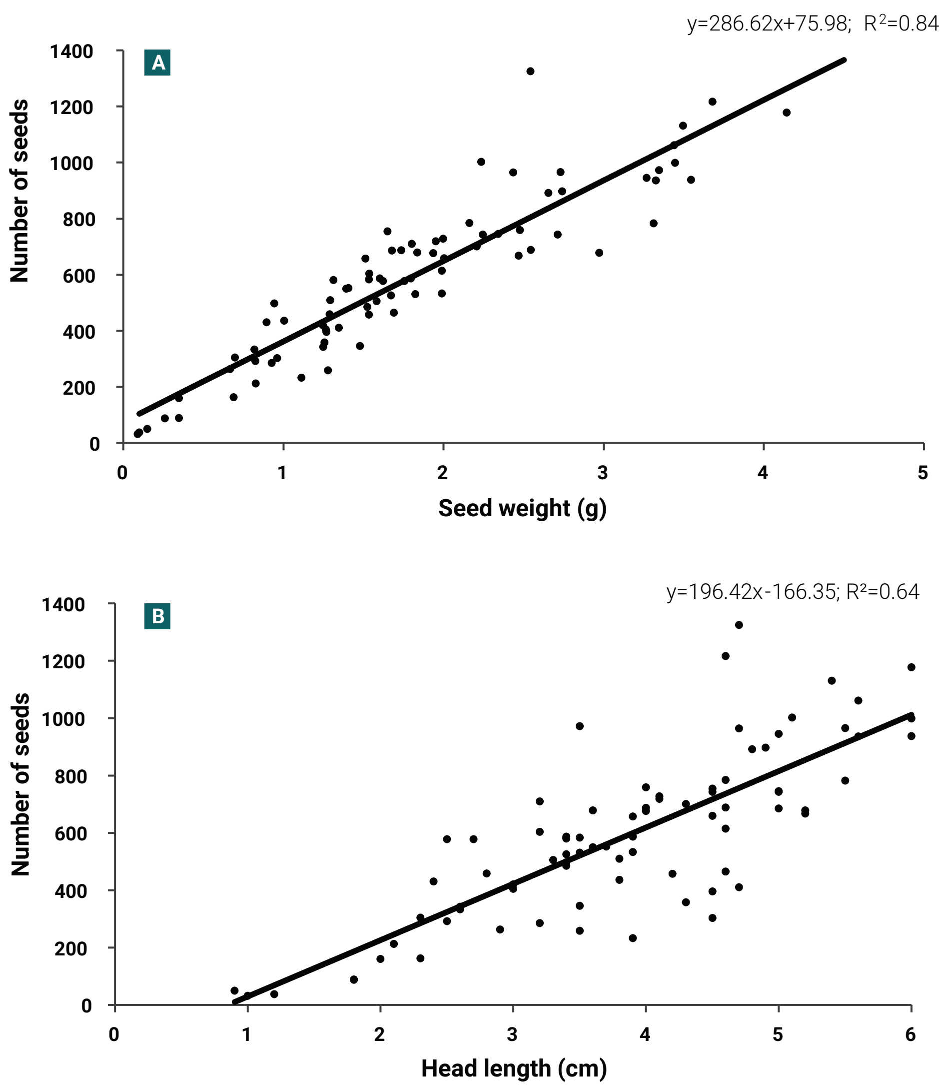

Figure 3. Number of seeds produced per individual head regressed against seed weight (**a**) and against head length (**b**) of *Dipsacus fullonum* from different locations in the south Buenos Aires province (Bahía Blanca, Saldungaray, Necochea, and Energía).

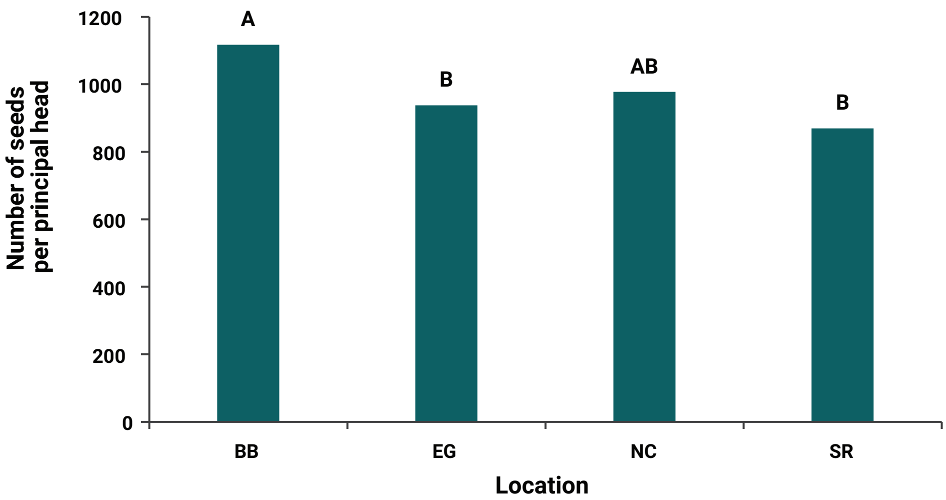

Figure 4. Number of seeds per principal head of *Dipsacus fullonum* plants for four different locations in south Buenos Aires province and two growth situations. Abbreviations: BB = Bahía Blanca, EG = Energía, NC = Necochea, and SR = Saldungaray. Data were pooled over the growth situation ('Alone', when no other teasel plant was growing closer than 60 cm, and in 'Group', when there were at least two plants growing within 60 cm radius). Bars with the same letters do not differ statistically according to Fisher's protected test (p<0.05).

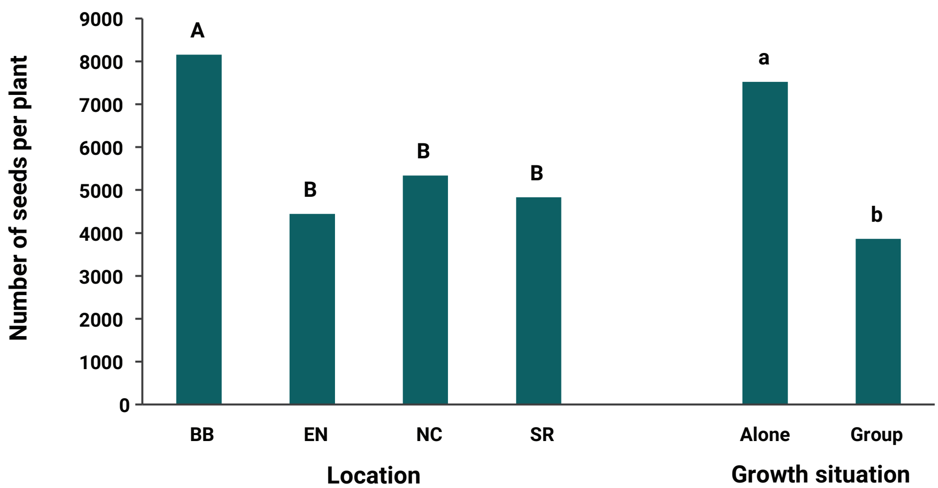

Figure 5. Total number of seeds of *Dipsacus fullonum* plants for four different locations in south Buenos Aires province and two growth situations ('Alone', when no other teasel plant was growing closer than 60 cm, and in 'Group', when there were as at least two plants growing within 60 cm radius). Abbreviations: BB = Bahía Blanca, EG = Energía, NC = Necochea, and SR = Saldungaray. Bars with the same letters do not differ statistically according to Fisher's protected test (p<0.05).

DISCUSSION

This work is the first report of the reproductive potential of common teasel populations growing in Argentina. The number of heads per plant, of seed per principal head, and total seed production was similar in most of the populations studied, with the exception of the one at Bahía Blanca for which it was greater, on average, as compared with those at other locations. Reproductive potential on teasel species may be determined by several factors, such as soil fertility (Jurica, 1921; Chuko and Hanyu, 1990), depth to rock, and climatic conditions (Bentivegna and Smeda, 2011b). In our study, some of the parameters of soil fertility (%MO, total N, Ca, and Mg), and effective depth, were lower in Bahía Blanca than in the other locations, especially compared with the Necochea site (table 1). Consequently, these factors would not explain the differences observed. Lower seed production can also be attributed, at least in part, to drier environmental conditions (Travlos, 2013). Our results suggest that although all the visited common teasel populations in southern Buenos Aires province received sufficient rainwater to produce seeds, the one at Bahía Blanca additionally had access to a continuous and abundant water supply because of its proximity to a water channel. This could explain the production of higher numbers of seeds which in turn would imply a higher invasive potential of this population.

Common teasel plants growing close to other species produced more heads and seeds than plants growing under intraspecific competition, for all the populations evaluated. This is consistent with reports provided by Bentivegna and Smeda (2011b) in *Dipsacus laciniatus,* another invasive species, in Missouri, USA. The density of reproductive individuals of teasels seems to be a strong source of variation in the number of seeds. Plants that invade a new site, represented by plants growing alone, would have a greater seed production capacity compared to plants in dense monospecific stands, likely to result in greater numbers of successful establishment events, thus a potentially faster rate of spread.

Populations of the province of Buenos Aires registered a maximum head production of 62 heads, which was higher than certain previous reports. Werner (1975b) indicated that it was common to find as many as 35 heads in common teasel in Canada, and Chessman (1998) reported from 1 to 40 in their native range (UK). Similar to our results, Chuko and Hanyu (1990) reported values from 60 to 100 heads in experiments performed in Japan. Bentivegna and Smeda (2011b) found a maximum of 56 heads in *Dipsacus laciniatus*. The maximum head production reported for teasel species in the literature was indicated by Mullins (1951), who stated a production potential of 100 in *D. sativus* (Indian teasel). Common teasel heads showed a broad range of sizes within a plant; consequently, a different seed production related to its length. This is consistent with Werner (1975b), who also found that the number of seeds per head was directly related with the size of the capitulum.

The principal head of teasel produces the greatest amount of the seeds and is the first one to mature, escaping to control measures, such as mowing (Bentivegna and Smeda 2011b). In the present study, maximum production in a single principal head was over 2,000 seeds. Bentivegna and Smeda (2011b) reported 1,487 seeds produced in the principal head of *Dipsacus laciniatus*. According to our results, the principal head was not affected by the type of competition. On the contrary, *D. laciniatus* plants produced more seeds in plants growing separated from plants of the same species, apparently taking advantage of available resources, and increasing seed production in each primary head (Bentivegna and Smeda, 2011b). In our case, one possible reason could be that plants growing in groups likely redirected resources to the principal heads achieving a seed number similar to plants growing in absence of intraspecific competition. Despite this fact, total seed production in plants in a group was observed to be low in correspondence to the lower number of heads produced.

In our study, it was observed that common teasel heads grew at different times, starting from late spring (December), and matured gradually until late summer (February). Apparently, the later the formation of a head, the smaller its size, and the last heads to form usually do not produce viable seeds (Chuko and Hanyu, 1990; Bentivegna and Smeda, 2011a). In Michigan (USA), Werner (1975b) suggested that 2,500 was the most typical number of seeds produced by a common teasel plant. Our results indicate a higher production than this previous report, which suggests a high invasion potential. In addition, Glass (1991) indicated that seed production could be over 3,000 seeds in *D. laciniatus* in Illinois (USA). However, Bentivegna and Smeda (2011b) reported in *D. laciniatus* a greater seed production of about 8,000 on average, with a maximum of 33,527 seeds.

CONCLUSIONS

Common teasel showed a high seed production in the environmental conditions of the province of Buenos Aires, which may explain in part its great expansion. The number of heads and seeds was higher when plants were growing alone compared with plants in dense patches. Consequently, plants invading a new site will produce a higher quantity of seeds that may encourage colonization. Since high seed germination rates following maturity have been found and seedling emergence has been observed to occur shortly after seed dispersal in Buenos Aires province, a great number of seedlings is expected from each plant (Daddario *et al*., 2017). This will quickly contribute to the formation of teasel dense patches and populations will increase rapidly in the areas of Argentina. As an interpretation of our study, invasive evaluation protocols should rate this species with a high score. Land-managers must avoid common teasel seed production in order to reduce extensive patches. The information presented in this study will be useful to assess techniques for controlling common teasel populations.

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DISCLOSURE STATEMENT

The authors declare no conflicts of interest.

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