Reproductive traits in four spontaneous *Pappophorum vaginatum* populations in arid Argentina

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A B S T R A C T

Arid zones, where native rangelands are common, are essentials for millions of people livelihood. These areas support 50% of the world's livestock and are where 44% of the world's food is grown. In rangelands of Central Argentina, *Pappophorum vaginatum* is basically the unique, warm-season perennial grass species palatable to grazing livestock. Our major objective was to determine variability in reproductive characteristics among four spontaneous, overgrazed populations (i.e., P1, P2, P3, P4) of that species to identify promissory materials for domestication. Studies were conducted during three consecutive growing seasons within the southwestern part of the Phytogeographical Province of the Monte, in southwestern Buenos Aires, Argentina. Measured reproductive characteristics were related to flowering initiation, seed production and natural reseeding potential. Significant differences were found for flowering initiation and natural reseeding potential, but not for viable anthecia per plant among the four populations of *P. vaginatum*. This species fructified from the beginning to the end of the studied growing seasons with a great anthecia production per plant. The light weight of these anthecia and their awns would favor a great wind dispersal and most likely the establishment of new seedlings of *P. vaginatum*. This suggests that sexual reproduction might have a relatively greater importance than asexual reproduction (i.e., tillering) in the persistence of the overgrazed *P. vaginatum* in the plant communities of the studied region. Selection of plant materials with a late flowering initiation will allow to extend the forage production of a better quality. The variability among and within populations found on this study support the idea that would be promissory to start selection programs to obtain improved germplasm to reincorporate to grasslands of the south of the Phytogeographical Region of the Monte (Argentina) not only to increase livestock production but to recover and maintain biodiversity.

1. Introduction

Grassland cover 40.5% of the total land surface of the world (White et al., 2000) and has been lived in and use by people throughout human history (Gibson, 2009). In arid zones, where native rangelands are common, live approximately 2.5 billion people who depend on this ecosystem services for their livelihoods (UN EMG, 2010). According to Gaur and Squires (2018) these arid zones support 50% of the world's livestock where 44% of the world's food is grown. The three greatest threat to native grassland are agriculture, fragmentation and invasion of non-native species (Gibson, 2009). Thus, it is crucial to optimize the use of resources and knowledges, like those informed by Kassahun et al.

(2008), Smith et al. (2010a), Tälle et al. (2016), Dubeux Jr. et al. (2017), Al- bukhari et al. (2018), Muir et al. (2018), Koncz et al. (2020), and Belesky et al. (2020) in order to harmonize rangeland utilization and biodiversity conservation.

Production of meat by livestock in 75% of continental Argentina, characterized by arid and semi-arid zones, is based on grazing of native vegetation (Busso et al., 2018). Thus, rangelands are important as a production factor (because they are the main food source for animals) and a biodiversity reservoir since they provide an ecological or environmental service with the subsequent social-economical impact (Mujica, 2010a, b).

Pappophorum Schreb is a grass genus native to the American

continent with 10 species, 7 of which live in arid and semiarid zones of Argentina and boundary regions (Pensiero, 1986). It is considered mainly autogamous because of the presence of cleistogamy (Campbell et al., 1983; Pensiero, 1986). Rangelands of central Argentina are characterized by the scarcity of warm-season, native perennial grasses, palatable to livestock grazing (Busso et al., 2004). Within this region, at the South of the Phytogeographical Province of the Monte, one important species is *Pappophorum vaginatum* Buckley (Poaceae). This is basically the unique palatable perennial grass species during the warm-season for grazing livestock (Giorgetti et al., 1997). This situation exposes *P. vaginatum* to overgrazing and is currently considered as a decreasing species (Torres et al., 2013a). Within Argentina *P. vaginatum* can be found not only in the Phytogeographical Region of the Monte but also in those of the Pampas, Espinal and southeast of Chaco (Pensiero, 1986).

A valuable contribution for the recovery, maintenance and increase of biodiversity is the domestication of native and naturalized species with forage value, and the successful introductions (Mujica, 2010a, b). In addition, establishment of improved forages, among other technologies, can substantially increase the stocking rate of semiarid areas in Argentina (Garbulsky and Deregibus, 2004). Thus, much research has focused on the study of introduced species adapted to semiarid conditions since several decades (Ferri, 2014). However, the native germplasm of the semiarid region of Argentina is of a special interest and value in terms of genetic improvement. This is due to its evolutionary history and adaptation to the climatic and edaphic constraints of such region (Martin, 2005). Besides, several studies to a global scale have reported that the native species are the most adequate for ecosystem restoration in arid and semiarid regions (Waters and Shaw, 2003). Nevertheless, such species must go through successive steps of evaluation previous to their utilization (Tyler et al., 1987). This includes studies from their characterization and initial evaluation either at the greenhouse or at the field as isolated plants to comparative yield and grazing studies.

Studies of variability in characteristics of agronomic interest and elucidation of the strategies of adaptation to biotic and abiotic disturbances on the native or naturalized species is of critical importance. Genetic improvement should focus in combining the effects of natural selection to the local environment with those coming from artificial selection on agronomic characteristics, specially those linked to the control of transplanting and the production of forage and seeds (Mujica, 2010a, b). In this sense, various studies were made on native, perennial, warm-season forage grasses. For example, some of these studies were related to (1) elucidate strategies of competitive ability on *P. vaginatum* (Torres et al., 2013a, b) and *Trichloris crinita* (Lag.) Parodi (Greco and Cavagnaro, 2005); (2) study the phenotipic variation for various characteristics of agronomic interest in populations of *T. crinita* (Kloster et al., 2016), *Setaria lachnea* (Pensiero et al., 2011) and *P. vaginatum* (Entio et al., 2014b, c), and (3) evaluate the genetic variability on *T. crinita* (Cavagnaro et al., 2006). The strategic incorporation of forage, native species was also studied to recuperate degraded areas (Quiroga et al., 2009) and increase animal stocking rate (Passera et al., 1992).

More specifically, the variability in seed germination and on characteristics related to the initial seedling growth were studied in populations of *P. vaginatum* (Entio et al., 2014b; Entio et al., 2014c). Additional studies were made on reproductive characteristics on populations of *Setaria lachnea* such as the variability in (1) germination, seed weight and production, and cleistogamy (Pensiero et al.,1995), and panicle emergence and fecundity (Pensiero et al., 2011); and (2) flower phenology, number of panicles and percentage fructification (Exner et al.,2010).

One important mechanism which contributes to plant species persistence on rangelands is natural reseeding which depends on viable seed contribution into the soil seed bank. This was proved at the field under grazing conditions; for example, with the variety Aguapé of *Lotus tenuis* (Entio and Mujica, 2011). The soil seed bank can work as such as

long as the disseminules preserve their viability (Baker, 1989). In addition, persistance of the soil seed bank is critical because it is a reserve of accumulated genetic adaptability for the population over which can act natural selection (Simpson et al., 1989). Perennial grasses at the Monte form transient soil seed banks; however, such transience appears to be little associated with losses due to germination (Marone et al., 2003). The main factor of seed losses can be attributed to predation by granivores (Marone et al., 2000). Anyhow, Entio et al. (2014a) suggested a positive effect of ants in the establishment of new seedlings of *P. vaginatum* from seeds obtained from plants at the stage of seed dispersal.

The hypothesis of this study is that there is variability in reproductive characteristics important for domestication (i.e. flowering initiation, viable seed production, and potential of natural reseeding) among spontaneous populations of *P. vaginatum* in the semiarid region of the Province of Buenos Aires. This will allow to identify promissory materials with later flowering initiation and greater viable seed production and potential of natural reseeding to select in programs of genetic improvement to use in grasslands restoration. In this way, an increase in the abundance of *P. vaginatum* either by artificial sowing, natural reseeding or both, will be important not only to increase forage availability for livestock grazing but for the recovery and maintenance of biodiversity. The objective of this study was to analize the variability of various reproductive characteristics on four spontaneous native populations of *P. vaginatum* within the semiarid region of the Buenos Aires Province to identify promissory materials for domestication.

2. Materials and methods

2.1. Study site and sites of seed sampling

This study was conducted during the growing seasons (spring-summer-fall) of 2013/2014; 2014/2015 and 2015/2016 at the Chacra Experimental Patagones, Ministry of Agrarian Affairs-Buenos Aires (40° 39′ S; 62° 54′ W). A meteorological station located 5 m from the experimental plots provided climate information during the duration of the study (2013–2016) (Table 1).

A voucher/specimen was collected by Nicora, E.G. under the collection number 6712 on December 29, 1959 in Caseros, Partido de Daireaux, Buenos Aires, Argentina. It was deposited in the herbarium of La Plata, Buenos Aires (Fernando O. Zuloaga, personal communication, Instituto de Botánica Darwinion, Pcia. Buenos Aires). This information is crutial to ensure the species identification throughout time and the testimony material of the experiment. Seeds of *P. vaginatum* were sampled from four spontaneous populations (P1, P2, P3, P4) in December 2012 covering the north (P1, P2), center (P3) and south (P4) of the semiarid region of the Province of Buenos Aires (Fig. 1). Details of the sampling sites are shown in Table 1.

2.2. Field study

On October 25, 2013, on the first 2013/2014 growing season, 6 plants of each of 9 genotypes per population (i.e., 9 different plants/population; pure lines; n = 9) were transplanted to field plots. There were 0.5 m among each of 9 lines (i.e., 1 line/genotype) x 0.25 m among each of 6 plants/genotype within each line. A completely randomized block design using 2 blocks (within which there were 2 replicate plots/population) was utilized. There was a total of 432 plants for all populations [6 plants/genotype x 9 genotypes/population x 4 populations x 2 replicate plots/population]. Each replicate plot/population had 54 plants (i.e., 6 plants/genotype x 9 genotypes/population) (Fig. 2). Irrigation was initially applied until flooding each furrow at the beginning of each month (December, January, February) during the first summer to secure plant survival.

Table 1
Details of seed collecting sites of the studied spontaneous populations of P. vaginatum and climatic details at the experimental site (Patagones) during the study period.

Details	Populations			
	P1	P2	P3	P4
Municipality	Saavedra	Adolfo Alsina	Villarino	Patagones
Coordinates	37°26′51.2″S 62°28′1.2″W	37°21′37.6″S 62°27′52.1″W	38°49′32.4″S 62°43′13.2″W	40°40′25.86″S 62°54′3.06″W
Precipitations (mm):	665.1	665.1	648.5	434.2
- Long-term mean annual				
- mean annual during the study				527
Temperatures (Max/Min) (°C):	14.9 (21.3/8)	14.9 (21.3/8)	15.4 (22.8/9)	14.1 (20.9/7.4)
- Long-term mean annual				
- mean annual during the study				14.3 (21.1/7.4)
Long-term Max/Min absolute temperature (°C)	42.5/−12	42.5/−12	43.8/−11.8	42.1/−8.6
Relative humidity (%):	66.25	66.25	63.7	65.5
- Long-term mean annual				
- mean annual during the study				68.3
Typical relief	steppe with an herbaceous stratum cover	steppe with an herbaceous stratum cover	undulated steppe with sandy hills, herbaceous stratum cover and secondary shrub communities	steppe with an open shrub stratum and a herbaceous stratum

Long-term data: INTA Informa, 2013; Servicio Meteorológico Nacional (SMN), and Ministerio de Agroindustrias (provincia de Buenos Aires) (MA-BA), 2016.
Data at the experimental site: Ministerio de Agroindustrias (provincia de Buenos Aires) (MA-BA), 2016.
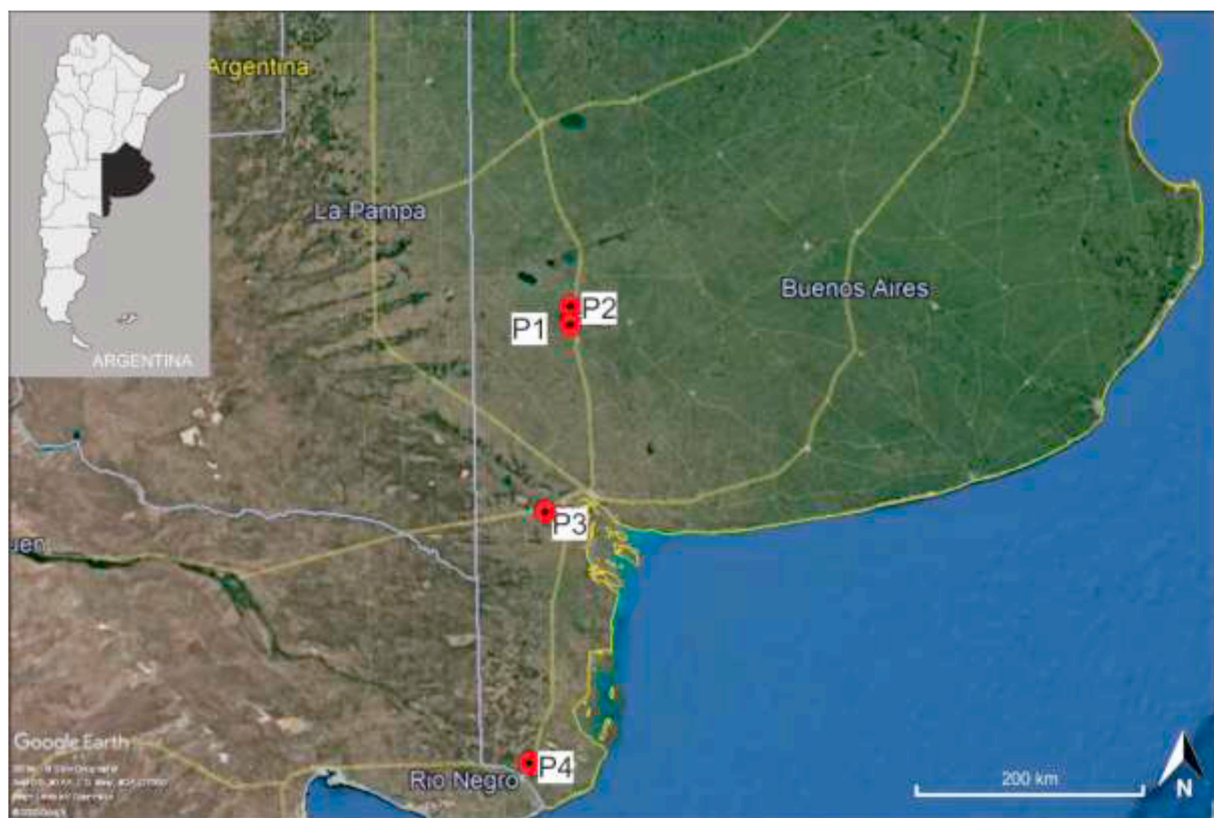

Fig. 1. Geographic location of the seed collecting sites of the studied spontaneous populations of *P. vaginatum* (June 2020, Google Earth Pro, 7.January 3, 4507).

2.2.1. Reproductive characteristics

During the studied period, several variables related to reproductive characteristics were determined. They included determinations of the (1) total number of reproductive tillers, (2) number of reproductive tillers at different stages of developmental morphology (Fig. 3), (3) number of anthecia/panicle/plant, (4) number of anthecia/plant, and (5) panicle length. Potential reseeding was calculated as described in Table 2. The number of viable anthecia was determined as a measure of seed production and quality on all populations. This value was obtained adjusting the number of anthecia per plant by the percentage of cumulative germination (see Table 2). This latest value was obtained in a germination study made in the laboratory as described below.
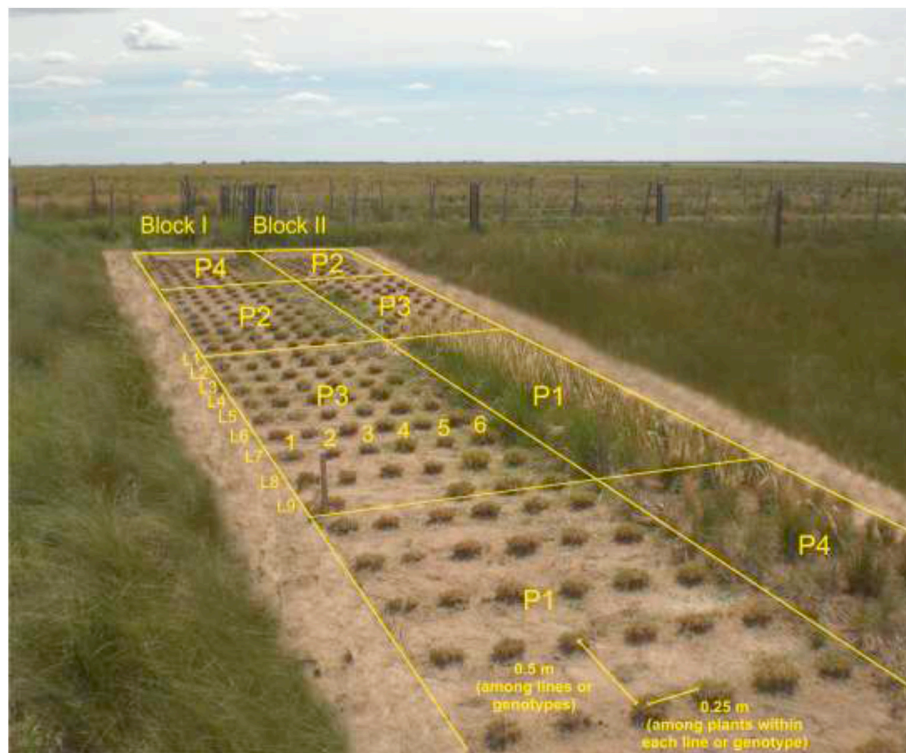
Fig. 2. Details of the experimental design of the field essay carried out at the Chacra Experimental Patagones. The distribution of plants within each of the four randomized plots (P1 to P4) per block is shown. Within each plot there were 9 lines or genotypes and 6 plants per line or genotype (54 plants per plot). A zone of 1 m around de plots were periodically weeded to avoid radical competence from other plants.

2.2.2. *Plant morphology and survival characteristics*

2.2.2.1. Basal area. Plant total crown diameter was measured at a plant scale to determine total plant basal area. These measurements were conducted at the sampling dates as detailed in Table 2.

2.2.2.2. Plant survival. The success of transplanting was determined as the mean percentage of alive plants per plot at the end of the study (i.e., in 2016) with respect to the initial number of plants per plot (i.e., in 2013).

2.3. *Laboratory study*

This experiment was conducted in September 2016 with the seeds harvested on January 5, 2016 from the cultivated plants. It had a completely randomized experimental design (n = 6) and the experimental unit was a Petri dish (9 cm diameter) with 50 anthecia. Such anthecia were placed with their covers (lemma and palea) on wet filter paper to obtain their germination. The filter paper was maintained wet during the whole study. After 24 h of imbibition, the number of germinated anthecia (radicle $\geq$ 3 mm) was determined every 24 h during the study duration. The study finished after four consecutive days without germination (from day 18–22 from imbibition). We determined the percentage of cumulative germination. Temperature was determined with a digital thermometer (ThermoMeter TA318). The mean maximum and minimum temperatures ± 1 standard error during the study in the laboratory were from 22.9 °C $\pm$ 0.44–20.1 °C $\pm$ 0.44, respectively. Such temperatures were within the range of mean monthly air temperatures measured close to the field plots during the reproductive stage of *P. vaginatum* (data not shown). In addition, a potential reseeding value was calculated. This value was obtained after adjusting the number of viable anthecia per plant by the percentage of cumulative seedling emergence (this latest value was taken from a previous study under controlled conditions: means = P1: 38%; P2: 52%; P3: 65.5%; P4:

48%; Entio, 2019).

Sampling dates and timing during each growing season, the predominant developmental morphology stage at each sampling date, and all reproductive, morphological and plant survival characteristics determined at each date of sampling are described in Table 2.

2.4. *Statistical analyses*

The experimental design of the field studies allowed application of nested ANOVA (genotypes nested in populations) in a split-plot design (being the populations the large plot, and the genotypes the subplot) which allowed to compare most of the variables among populations. One-way ANOVAs were also used to compare the variables among populations in the studies under controlled conditions.

When F tests were significant, mean comparisons were made using the Tukey test with a significance level of 0.05. Several variables were transformed on the field studies (see details in Table 1) to comply with the assumptions of normality and homocedasticity of variance (Sokal and Rohlf, 1984). Non-transformed values are presented in Tables.

All statistical analyses were made using the program Statistica 7.1 (StatSoft, Inc, 2005).

3. Results

3.1. *Field study*

3.1.1. *Reproductive characteristics*

On December 10, 2013, late spring of the first 2013/2014 growing season, there were significant differences (p<0.001; P1>P3>P2>P4; Table 3) among the populations in the total number of reproductive tillers per plant. There were also significant differences (p < 0.001) among populations in the number of reproductive tillers per plant (1) Stage 1 (boot stage; P1>P3>P2>P4; Table 3); (2) Stage 2 (<of 50% of exposed panicles), values on P1 were greater (p $\leq$ 0.05) than those in the

Fig. 3. Details of reproductive tillers at different stages of developmental morphology in an individual of *P. vaginatum*.

remaining populations, which did not differ (p > 0.05) among them (Table 3); (3) Stage 3 (>of 50% of exposed panicles; p = 0,005; Table 3). Population 1 was significantly different (p ≤ 0,05) to P4. In addition, P2 and P3 did not have significant differences (p > 0.05) to P4 (Table 3). However, there were no significant differences (p = 0.5) among populations in the number of reproductive tillers at Stage 4 (100% of exposed, immature panicle) (Table 3). Finally, there were significant differences (p = 0.007) among populations in the number of reproductive tillers Stage 5 (100% of exposed, mature panicles) per plant. Population 1 was at least 30.4% greater (p ≤ 0,05) than the other populations, which did not differ significantly (p > 0.05) among them (Table 3). Significant intrapopulation differences (p ≤ 0.05) were detected for the total number of reproductive tillers per plant (P2) and for the number of reproductive tillers at Stage 1 (P1) and 3 (P2), and at Stage 4 (P1, P2).

On February 11, 2014, mid-summer of the 2013/2014 growing season, there were significant differences (p = 0,002) among the populations in the total number of reproductive tillers per plant. P1 were greater (p ≤ 0.05) than those in the remaining populations, which did not differ (p > 0.05) among them (Table 3). For this variable, significant intrapopulations differences (p ≤ 0,05) were detected in P2.

On November 5, 2014, mid-spring of the second 2014/2015 growing season, there were not significant differences (p = 0,063) among populations in the number of reproductive tillers Stage 1 (boot stage) per plant (Table 3). There were significant differences (p < 0.001) among populations for the set of reproductive tillers per plant of Stages from 2 to 5 (Table 3). Thus, P1 was greater than (p ≤ 0.05) the remaining populations. Population 4 was greater than (p ≤ 0.05) P2 and P3 (Table 3). In addition, P2 and P3 were not significantly different (p > 0.05, Table 3). Finally, there were not significant differences (p = 0.186)

among populations in the total number of reproductive tillers per plant (Table 3). Significant intrapopulation differences (p ≤ 0.05) were detected for the total number of reproductive tillers per plant (P2) and for the number of reproductive tillers at Stage 1 (P2, P4).

At the initiation of fructification (December 16, 2014: beginning of fructification during the second 2014/2015 growing season): (1) There were not significant differences (p = 0.287) among populations in the total number of reproductive tillers per plant (Table 3). (2) Populations differ significantly (p < 0,001) in the length of mature panicle per plant (Table 3). Thus, P1 was shorter (p ≤ 0.05) than the remaining populations which were similar (p > 0.05) among them (Table 3). (3) Populations showed significant differences (p < 0.001) in the number of anthecia per panicle on a plant basis (Table 3). This was because of P3 and P4 were similar (p > 0.05) between them, but greater than (p ≤ 0.05) P1 and P2; at the same time, P2 was greater (p ≤ 0.05) than P1 (Table 3). (4) Finally, populations did not differ (p = 0.295) in the number of anthecia per plant (Table 3). Significant intrapopulation differences (p ≤ 0.05) were detected for the total number of reproductive tiller per plant (P2, P3, P4), anthecia per panicle on a plant basis (P1, P2, P3, P4), and for the number of anthecia per plant (P2).

On January 05, 2016, early summer of the third 2015/2016 growing season, there were significant differences (p ≤ 0.05) among populations (1) on the total number of reproductive tillers per plant (Table 3). Thus, P4 was lower (p ≤ 0.05) than the remaining populations which were similar (p > 0.05) among them (Table 3); (2) in the number of reproductive tillers Stage 5 per plant (Table 3). As a result, P1 and P2 were similar (p > 0.05) between them, but greater (p ≤ 0.05) than P3 and P4 (Table 3). In addition, P3 and P4 were similar (p > 0.05) between them (Table 3); (3) in the number of reproductive tillers Stage 4 per plant (Table 3). Thus, P3 was greater (p ≤ 0.05) than the remaining populations; P1 showed intermediate values, and P2 and P4 were lower (p ≤ 0.05) than the remaining populations, and similar (p > 0.05) between them (Table 3). Significant intrapopulation differences (p ≤ 0.05) were detected for the total number of reproductive tiller per plant (P2), and number of reproductive tiller at Stage 4 and 5 (P1, P2, P3, P4 and P3, P4, respectively).

Also, in the first week of January 2016, there were significant differences (p < 0.001) among populations in the panicle length per plant (Table 3). Thus, while P3 and P1 showed the greatest (p ≤ 0.05) and lowest (p ≤ 0.05) values, respectively, P2 and P4 were similar (p > 0.05) between them (Table 3). At this time, populations also differed (p < 0.001) in the number of anthecia per panicle per plant (Table 3). While P2 and P4 were similar (p > 0.05) between them, P3 and P1 showed the greatest (p ≤ 0.05) and lowest (p ≤ 0.05) values, respectively (Table 3). At the same time, there were not significant differences among populations neither in the number of anthecia per plant (p = 0.075: Table 3) nor in the number of viable anthecia per plant (p = 0.56; Table 3). Significant intrapopulation differences (p ≤ 0.05) were detected for the panicle length (P1, P4), anthecia per panicle on a plant basis (P2, P3, P4), number of anthecia per plant, and number of viable anthecia per plant (P2, P4).

Regarding to the number of potential seedlings for natural reseeding per m², there were significant differences (p = 0.005) among populations (Table 3). Population 3 showed the greatest (p ≤ 0.05) value, P2 was greater (p ≤ 0.05) than P1 and P4 which resulted similar (p > 0,05) between them.

3.1.2. Plant morphology and survival characteristics

3.1.2.1. Basal area. Measurements on the third (September 17, 2014) and fourth (November 05, 2014) sampling dates, on the second 2014/2015 growing season, did not indicate significant differences (p > 0.05) in basal area (mean ± 1 E.E.: September 17, 2014 = 11.5 ± 0.7 cm²; November 05, 2014 = 18.4 ± 1.1 cm²) among populations (Table 3).

Table 2
Details of the sampling dates and study variables.

Sampling date (Number)	Predominant developmental morphology	Abbreviation	Study variable [transformation for statistical analysis]
Timing of each study growing season	stage		
December 10, 2013 (1)	Boot stage	**RTS1**	number of **R**eproductive **T**illers **S**tage **1** per plant (boot stage) number of **R**eproductive **T**illers **S**tage **2** per plant (<50% of emerged panicle) [ln (x+0.5)]
		RTS2	number of **R**eproductive **T**illers **S**tage **3** per plant (>50% of emerged panicle) [ln (x+0.5)]
		RTS3	number of **R**eproductive **T**illers **S**tage **4** per plant (immature emerged panicle) [ln (x+0.5)] number of **R**eproductive **T**illers **S**tage **5** per plant (mature emerged panicle) [ln (x+0.5)] the number of **T**otal **R**eproductive **T**illers was calculated per plant (S1+S2+S3+S4+S5) [$\sqrt{x}$]
		RTS4	
		RTS5	
Late spring of the first growing season (2013/2014)		**TRT**	
February 11, 2014 (2) Mid-summer of the 2013/2014 growing season	Seed dispersal mature grain	**RTS5**	see previous description
17 Sept 2014 (3) Early spring of the 2014/2015 growing season	Vegetative growth initiation (end of winter dormancy)	**Bd**	the **B**asal **d**iameter was measured per plant (cm)
Nov 5, 2014 (4) Mid-spring of the 2014/2015 growing season	Boot Stage	**Bd**	see previous description.
		RTS1	see previous description
		RTS2-5	the number of **R**eproductive **T**illers S2 to S5 was counted per plant
		TRT	the **T**otal number of **R**eproductive **T**illers was counted per plant (RTS1+RTS2 to 5)
December 16, 2014 (5) Late spring of the 2014/2015 growing season	boot stage; immature grain; mature grain	**TRT AP**	see previous description [$\sqrt{x}$]
		PL	the number of **A**nthecia per **P**anicle per plant (average
		APl	of 2 panicles per plant) [ln (x+0.5)] the **P**anicle **L**ength (cm) was determined per plant (average of 5 panicles per plant) the number of **A**nthecia per **Pl**ant was calculated (TRT x AP)
Jan 5, 2016 (6) Early summer of the 2015/2016 growing season	Immature grain; mature grain; seed dispersal	**RTS4**	see previous description [$\sqrt{(x+0.5)}$]
		RTS5	see previous description [$\sqrt{x}$]
		TRT	the **T**otal number of **R**eproductive **T**illers per plant was
		AP	calculated (S1+S2+S3+S4+S5) [$\sqrt{x}$]
		PL APl VAPl	see previous description [$\sqrt{(x+0.5)}$]
		PR	see previous description [$\sqrt{x}$]
		CG	see previous description [$\sqrt{x}$] the number of **V**iable **A**nthecia per **Pl**ant was calculated: APl adjusted by the cumulative germination percentage obtained from a laboratory study conducted after plant harvesting [$\sqrt{x}$] (Entio, 2019) **P**otential **R**eseeding per m^2 was calculated: value **VAPl** Adjusted by the percentage of cumulative emergence obtained from a previous study under controlled conditions [$\sqrt{x}$] (Entio, 2019) the percentage of **C**umulative **G**ermination was determined
June 6, 2016 (7) Late fall of the 2015/2016 growing season		Survival	the percentage of alive plants was calculated at the end of the study period

3.1.2.2. Plant survival. Survival values were high and similar (>95%; p > 0.05; data not shown) among populations on 17 September and 05 November of 2014, on the second 2014/2015 growing season. At the end of the study in 2016, on the third 2015/2016 growing season, once again there were no significant differences (p > 0.05) among populations in the number of established individuals (Table 3).

3.2. Laboratory study

Results of the germination study made with the seeds harvested on Jan 5, 2016 showed significant differences (p ≤ 0.05) among populations in the percentage of cumulative germination. Population 1 showed a higher (p ≤ 0,05) cumulative germination percentage than P2, P2 was similar (p > 0.05) to P3 and P4 (Table 3).

4. Discussion

4.1. Field study

A few weeks before a year from transplanting (i.e., on September 17, 2014: time of the 2014/2015 growing season initiation), all populations showed high (>95%) and similar (p > 0.05) survival values. This would indicate that the four studied populations would have a similar, high plant establishment potential under field conditions. However, we need to point out that irrigation was applied up to flooding each groove at the beginning of each month (December 2013, January and February 2014: late spring and early summer, respectively, of the 2013/2014 growing season) during the first summer after transplanting to secure its success. On Nov 05, 2014, mid-spring of the 2014/2015 growing season, plant survival was also >95% which confirmed the high and uniform plant establishment of the studied native species. Torres et al. (2013b) also determined survival values of 94% (May 2007) and 92.5% (May 2008)

Table 3
Characteristics evaluated (mean ± SE) during the three-year study on four spontaneous population of *P. vaginatum*. Different small cap letter within each characteristic indicate significant differences (p ≤ 0.05) among populations. The test of Tukey was used for mean comparisons.

Character (sampling n°)	Populations			
	P1	P2	P3	P4
TRT (1)	15.78 ± 0.98 a	10.58 ± 0.78 c	13.03 ± 0.88 b	8.44 ± 0.7 d
RTS1 (1)	13.68 ± 0.82 a	9.51 ± 0.74 c	12 ± 0.78 b	7.5 ± 0.68 d
RTS2 (1)	1.06 ± 0.2 a	0.49 ± 0.14 b	0.44 ± 0.14 b	0.54 ± 0.28 b
RTS3 (1)	0.64 ± 0.2 a	0.38 ± 0.14 ab	0.34 ± 0.12 ab	0.18 ± 0.08 b
RTS4 (1)	0.24 ± 0.09 a	0.19 ± 0.08 a	0.21 ± 0.08 a	0.15 ± 0.07 a
RTS5 (1)	0.15 ± 0.06 a	0 b	0.03 ± 0.02 b	0.05 ± 0.04 b
RTS5 (2)	4.63 ± 0.64 a	3.4 ± 0.6 b	3.34 ± 0.5 b	2.8 ± 0.48 b
Bd (3)	3.71 ± 0.2 a	3.68 ± 0.22 a	3.91 ± 0.24 a	3.98 ± 0.22 a
Bd (4)	5.07 ± 0.26 a	4.66 ± 0.28 a	4.93 ± 0.24 a	4.78 ± 0.28 a
TRT (4)	8.75 ± 0.7 a	7.24 ± 0.62 a	8.17 ± 0.64 a	8.08 ± 0.64 a
RTS1 (4)	4.66 ± 0.46 a	5.26 ± 0.56 a	5.89 ± 0.54 a	4.96 ± 0.52 a
RTS2-5 (4)	4.08 ± 0.46 a	1.98 ± 0.34 c	2.28 ± 0.36 c	3.12 ± 0.46 b
TRT (5)	16.83 ± 1.5 a	16.72 ± 1.63 a	14.42 ± 1.4 a	14.45 ± 1.5 a
PL (5)	8.86 ± 0.22 b	10 ± 0.74 a	10.61 ± 0.32 a	10.8 ± 0.38 a
AP (5)	44.59 ± 2.6 c	57.07 ± 3.2 b	71.37 ± 4.44 a	64.76 ± 4.18 a
APl (5)	789.98 ± 94.32 a	997 ± 126.2 a	1087.9 ± 145.4 a	967.85 ± 124.6 a
TRT (6)	32.03 ± 1.56 a	30.76 ± 1.42 a	29.87 ± 1.32 a	22.15 ± 1.56 b
RTS4 (6)	10.45 ± 1.56 b	7.37 ± 1.48 c	13.43 ± 1.62 a	6.34 ± 1.06 c
RTS5 (6)	21.58 ± 1.66 a	23.61 ± 1.88 a	16.8 ± 1.64 b	16.11 ± 1.36 b
PL (6)	9.95 ± 0.3 c	10.85 ± 0.28 b	11.84 ± 0.36 a	10.98 ± 0.3 b
AP (6)	55.94 ± 3.28 c	69.04 ± 3.82 b	85.43 ± 5.3 a	74.91 ± 4.8 b
APl (6)	1890.76 ± 214.28 a	2248.42 ± 259 a	2672.3 ± 184.68 a	1726.9 ± 177.22 a
CG (6)	68.33 ± 8.14 a	57.33 ± 6.58 b	54 ± 5.46 ab	64.66 ± 5.98 ab
VAPl (6)	1291.95 ± 146.42 a	1289 ± 148.48 a	1443.04 ± 153.7 a	1116.61 ± 114.6 a
PR (6)	3954 ± 448.16 c	5486 ± 631.94 b	7647 ± 822.76 a	4311 ± 444.72 c
Survival (7)	96.29 ± 5.74 a	95.37 ± 5.9 a	96.29 ± 4.3 a	96.29 ± 3.36 a

RTS1: number of **R**eproductive **T**illers **S**tage **1** per plant (boot stage); **RTS2:** number of **R**eproductive **T**illers **S**tage **2** per plant (<50% of emerged panicle); **RTS3:** number of **R**eproductive **T**illers **S**tage **3** per plant (>50% of emerged panicle); **RTS4:** number of **R**eproductive **T**illers **S**tage **4** per plant (inmature emerged panicle); **RTS5:** number of **R**eproductive **T**illers **S**tage **5** per plant (mature emerged panicle); **TRT:** number of **T**otal **R**eproductive **T**illers was calculated per plant (S1+S2+S3+S4+S5); **Bd:** the **B**asal **d**iameter was measured per plant (cm); **RTS2-5:** the number of **R**eproductive **T**illers **S**2 to **S**5 was counted per plant; **TRT: T**otal number of **R**eproductive **T**illers was counted per plant (RTS1+RTS2 to 5); **AP:** number of **A**ntheica per **P**anicle per plant; **PL: P**anicle **L**ength (cm) was determined per plant; **APl:** number of **A**ntheica per **Pl**ant was calculated (**TRT x AP**); **VAPl:** number of **V**iable **A**ntheica per **Pl**ant; **PR: P**otential **R**eseeding per m^2; **Survival:** the percentage of alive plants at the end of the study period.
(1): Late spring of the 2013/2014 growing season; **(2)**: Mid-summer of the 2013/2014 growing season; **(3)**: Early spring of the 2014/2015 growing season; **(4)**: Mid-spring of the 2014/2015 growing season; **(5)**: Late spring of the 2014/2015 growing season; **(6)**: Early summer of the 2015/2016 growing season; **(7)**: Late fall of the 2015/2016 growing season.

after $1^{1/2}$ and $2^{1/2}$ years from transplanting on *P. vaginatum* within an exclosure.

By mid September 2014, at the initiation of the 2014/2015 growing season, plant basal diameter (range = 3.71–3.98 cm), and thus basal area (range = 10.81–12.44 cm^2), were also similar (p > 0.05) among populations. Torres et al. (2013b) reported greater values of basal area [from 27 (May 2006) to 42 cm^2 (May 2007)] on undefoliated plants of *P. vaginatum* growing within an exclosure to domestic herbivory at the end of their studied growing seasons.

Taking into account the production of total reproductive tillers as an indicator of initial growth after transplanting [sampling dates (1) December 10, 2013, and (2) February 11, 2014: late spring and mid-summer, respectively, of the 2013/2014 growing season], P1 was superior (p ≤ 0.05) to the remaining populations (Table 3). In addition, observing the results obtained on December 10, 2013 it might be that P1 would initiate flowering earlier than P2, P3 and P4 because it presented 47.7% more total reproductive tillers early in the reproductive cycle than the average of the other populations (Tabe 3). Even more, it presented at least three times more reproductive tillers of Stage 5 (100% of mature emerged panicle) than the other populations (Table 3).

On December 10, 2013 (late spring of the 2013/2014 growing season), reproductive tillers of Stage 1 (boot stage) were dominant in all populations (86.7%, 88.9%, 89.9% and 92.1% from the total reproductive tillers per plant on P1, P2, P3 and P4, respectively). On February 11, 2014 (mid-summer of the 2013/2014 growing season), only reproductive tillers of Stage 5 (100% mature emerged panicle) were observed. Gil Báez et al. (2015) also found significant differences among

populations of *Trichloris crinita* in the Monte region taking into account the number of reproductive tillers per plant (100% mature emerged panicle) as an indicator of initial growth during the first reproductive cycle after the transplanting.

At the beginning of November 2014 (mid-spring of the 2014/2015 growing season), populations did not show differences (p > 0,05) in the number of total reproductive tillers (Table 3). Also, P1 was on average 70% greater (p ≤ 0.05) than the other populations in the number of reproductive tillers S2–S5 (Table 2). This result, similarly to that obtained on December 10, 2013, highlighted that P1 was the earliest population in initiating flowering. This was because of P1 had a greater number of mature reproductive tillers per plant than the other populations at the initiation of the reproductive cycle. Exner et al. (2010) also reported differences in flowering initiation among different populations of *Setaria lachnea*. Initiation of the reproductive cycle is an important variable to take into account in selection programs on forage species (Allard, 1999). Selection of plant materials with a late flowering period would allow to extend the forage production of a better quality, because the initiation of flowering is associated with a reduction of forage quality (Pontes et al., 2007). We emphasize that high values of heredability, and thus a great response to selection, are expected for this developmental morphology stage (i.e., initiation of flowering) in grasses and other, various families (Weis and Kossler, 2004).

It is critical to take into account seed production on forage species not only for selected-germplasm seed multiplication but for its subsequent natural dispersion. At the same time, seed production of any given species can also be very important for the persistance of that species via

natural reseeding in environments exposed to various product production (e.g., meat, milk, wool, etc.) (Entio and Mujica, 2011). Most of the measured variables on December 16, 2014 and January 05, 2016 (late spring and early summer of the 2014/2015 and 2015/2016 growing seasons, respectively) showed the existence of inter and intra population variability. The sampling on December 16, 2014 was made during the first third of the fructification developmental morphology stage of development in the 2014/2015 growing season. Although the number of total reproductive tillers (range: 14.4–16.8) did not show significant differences (p > 0.05) among populations (Table 3), P1 showed a higher value than the remaining populations. This shows once again the tendency of P1 to a greater precocity for initiating the reproductive cycle, with possible implications with regard to forage quality as it was previously discussed (Pontes et al., 2007). Torres et al. (2013a) reported a maximum average value of 18 reproductive tillers per plant by mid December 2006 on undefoliated genotypes of *P. vaginatum* at the same study site than ours. Precipitation during their warm-season growing cycle 2006/2007 (i.e., from October 2006 to May 2007) was 276.4 mm. On the other hand, despite P1 had a lower (p ≤ 0.05) panicle length and number of anthecia per panicle than the other populations (Table 3), its production of anthecia per plant was similar (p > 0.05) to that on the remaining populations. This was because P1 showed the greatest number of reproductive tillers among all four populations (e.g., Table 3).

Measurements on Jan 05, 2016 (early summer of the 2015/2016 growing season) were conducted in the third reproductive cycle from plant establishment, and at this time plants were in the fructification stage of developmental morphology. The number of total reproductive tillers per plant varied between 22 and 32 depending on the population, and its average was about 80% greater than the average on December 16, 2014 (late spring of the 2014/2015 growing season). Populations 1 and 2 were among the populations with a greater number of total reproductive tillers per plant; in addition, they were the two populations with the greatest (p ≤ 0.05) number of reproductive tillers Stage 5 per plant (Table 3). This suggested an earliest initiation of the reproductive cycle on P1 and P2 than on P3 and P4. Cavagnaro et al. (2006) and Gil Báez et al. (2015) also reported variability on the number of reproductive tillers per plant between populations of *Trichloris crinita*. Exner et al. (2010) also showed variability in such parameter between populations of *Setaria lachnea*. On the other hand, P1 was smaller (p ≤ 0.05) than the other populations for panicle length and number of anthecia per panicle per plant (Table 3). Despite this, its per plant anthecia production was similar (p > 0.05) to that on the other populations (Table 3) because of its hight reproductive tiller production (Table 3). In this study, mean panicle length was 10 and 10.9 cm on December 16, 2014 (late spring of the 2014/2015 growing season) and January 05, 2016 (early summer of the 2015/2016 growing season), respectively. However, Smith (2010) and Smith et al. (2010b) reported mean values around 18.5–20 cm for a selected material of *P. vaginatum*. Other studies also reported variability among populations for various reproductive variables on warm-season perennial grasses: for (A) flowering initiation (Exner et al., 2010); extension of the period of panicle emergence (Exner et al., 2010; Pensiero et al., 2011); percentage of fructification (Exner et al., 2010; Pensiero et al., 2011); degree of cleistogamy (Pensiero et al., 2011), and germination responses (Pensiero et al., 2011; 2011) on *Setaria lachnea*; and (B) panicle length on *Panicum virgatum* (Price and Casler, 2014).

With the anthecia harvested on Jan 05, 2016 (early summer of the 2015/2016 growing season), a germination study was conducted. In this study, cumulative germination varied between 54 and 67% among populations. Thereafter, there was not variability (p > 0.05) among populations for the number of viable anthecia per plant (range: 1116–1443), although P3 showed higher values. The mean precipitation of the study years was 39% greater than the long-term mean annual precipitation (1981–2016: 434.2 mm). In addition, it did occur within a period of humid years (2010–2016) for the region which mean annual precipitation (522.6 mm) was greater than 20% of the long-term mean annual precipitation. *Pappophorum* spp. Produces twice as much seeds in

humid than in dry years (Pol et al., 2010). However, Pol et al. (2010) also reported that among seven warm-season perennial grass species, *Trichloris crinita* was the only one that significantly produced more seed in a dry than in a humid year in the region of the Central Monte in Argentina.

The number of established individuals per unit surface area was of 8 plants/m^2, and it did not vary significantly for any of the populations until the end of the studied period. Population 3 showed the greatest (p ≤ 0.05) potential of natural reseeding with at least 28.3% more seedlings in the next generation than the other three populations (Table 3). This greater potential of natural reseeding on P3, could be associated to its high values of viable anthecia production per plant (Table 3) and cumulative emergence (Entio, 2019). Anyhow, all studied populations of *P. vaginatum* might achieve a high potential of natural reseeding considering that the number of potentials seedlings in the next generation per m^2 was at least almost 500 times greater than the individuals implanted at the beginign of the study per m^2 (Table 3). Yang et al. (1988) indicated that the establishment efficiencies as a result of natural reseeding of *Dactylis glomerata* varied between 0.96 and 5.32% under different grazing systems. Assuming for *P. vaginatum* an intermediate efficiency of 3.14%, according our study it might be expected a minimum of 325, 324, 359, and 280 established potential seedlings per m^2 for P1, P2, P3, and P4, respectively.

The results obtained in this study, even taken into account that are potential values of reseeding, would allow to suppose that sexual reproduction is critical to explain such a long-term persistance of *P. vaginatum* in the rangelands of central Argentina. Asexual reproduction (tiller production from axillary buds) is the main way of reproduction in the rangeland perennial grasses according to Briske and Richards (1995). However, and in agreement with the results of this study, Torres et al. (2013a) demonstrated that plants of *P. vaginatum* produce abundant anthecia during its growing cycle. These anthecia plus their awns can have a very good wind dispersal because of their small size (anthecium = 1.5–3.5 mm + awns: 6–9 mm: Rúgolo de Agrasar et al., 2005; Entio, 2019). As a result, Torres et al. (2013a) proposed that the most relevant form of reproduction (either sexual or asexual) should be explored in *P. vaginatum* to explain its wide distribution and persistence to long-term disturbances (i.e., mostly herbivory) in arid and semiarid zones of central Argentina. An early and high seed production in *P. vaginatum* populations would imply a great seed dispersal that could germinate and establish in appropriate microsites. Since the studied populations can produce up to around 1400 viable anthecia per plant (Table 3), it is likely that sexual reproduction has a relatively greater role than that asexual (i.e., daughter tiller production per plant) in determining the persistence of *P. vaginatum* in a region where grazing, drought and wildfires are frequent disturbances (Peláez et al., 2001; Flemmer et al., 2003). Our results in *P. vaginatum* thus differ from the report of Briske and Richards (1995), and they could be specially true where wild fires kill a greater proportion of undesirable than desirable grasses (Boo et al., 1996), thus leaving potential microsites for the establishment of new plants of *P. vaginatum*.

Research results showed interpopulation variability for several of the reproductive characteristics during the years of study, although some of them also showed intrapopulation variability. This is expected in autogamous species (Jain, 1976; Loveless and Hamrick, 1984; Ramakrishnan et al., 2004) such in *Pappophorum* spp. because of the presence of cleistogamy (Campbell et al., 1983; Pensiero, 1986). Further research will determine if the variation among populations is higher than expected by drift alone or by distance following a test proposed by Ovaskainen et al. (2016).

Finally, this warm-season specie, with high palatability, considered as "decreasing" due to overgrazing and adapted to local environmental conditions, not only presents a high production of viable anthecia and natural reseeding potential but presents differences in flowering initiation. Selection of plant materials with a late flowering initiation will allow to extend the forage production of a better quality. The variability

among and within populations found on this study support the idea that would be promissory to start selection programs in order to obtain improved germplasm suitable to increase livestock production and to recover and maintain biodiversity in grasslands of the south of the Phytogeographical Region of the Monte (Argentina).

Author contributions

Author contributions LE and MM conceived and designed the study. LE and MM performed the study. LE analyzed the data. LE wrote the manuscript in Spanish and CAB wrote it in English. LE was in charge of all paper revisions. CAB made all editorial work from the time the manuscript was submitted to *Acta Oecologica* until it was finally published. All authors approved the final version. YAT contributed to make the statistical analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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