LIGHT EFFECTS ON SEED GERMINATION OF TWO SPONTANEOUS POPULATIONS OF *Pappophorum vaginatum*

EFECTOS DE LA LUZ EN LA GERMINACIÓN DE SEMILLAS DE DOS POBLACIONES ESPONTÁNEAS DE *Pappophorum vaginatum*

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ABSTRACT

Our objectives were to (1) determine the effects of light on seed germination of 2 populations (P1, P2) of *Pappophorum vaginatum*, and (2) compare the germination responses between these populations. Because of this, two studies were conducted. The first study evaluated the effects of 2 light conditions (L0=darkness, and L1=14 h light) on the cumulative germination (%) after 4, 8, 15 and 19 days from imbibion. The second study was conducted only under L1 conditions, and it evaluated the (a) cumulative germination, (b) germination speed index, (c) time to 50% of cumulative germination (T50), (d) percentage of empty spikelets (i.e., without cariopsis), and percentage spikelets with imbibed, but not germinated cariopsis after 19 days from imbibion of seeds. *Pappophorum vaginatum* was the dominant species in both study communities, but total, live plant cover was 37.5% in community 1, and 62.5% in community 2. Both populations were sensitive to light. After 19 days from imbibion there was a significant, positive effect of light on cumulative germination. In the second study, cumulative germination and germination speed index were greater (p≤0.01) in P1 than in P2. At the same time, T50 and the percentage of spikelets with imbibed, but not germinated cariopsis, were greater (p≤0.01) in P2 than in P1; no differences were found in the percentage of empty spikelets. Our results demonstrated that light was important for seed germination in *P. vaginatum*, and that the timing for initiating germination as a response to light differed between the two study *P. vaginatum* populations.

KEY WORDS: germination, *Pappophorum vaginatum*, populations, light effects, natural reseeding, establishment, perennial grasses

RESUMEN

Nuestros objetivos fueron (1) determinar el efecto de la luz en la germinación de dos poblaciones (P1, P2) de *Pappophorum vaginatum*, y (2) comparar las respuestas de la germinación entre estas poblaciones. Se condujeron dos estudios. El primer estudio evaluó los efectos de dos condiciones de luz (L0=oscuridad, y L1=14 h de luz) en la germinación acumulada (%) después de 4, 8, 15 y 19 días desde la imbibición. El segundo estudio solo se condujo bajo las condiciones L1, y se evaluaron (a) la germinación acumulada, (b) el índice de velocidad de germinación, (c) el tiempo al 50% de germinación acumulada (T50), (d) el porcentaje de espiguillas vacías (sin cariopse), y el porcentaje de espiguillas con cariopses embebidos, pero no germinados. *Pappophorum vaginatum* fue la especie dominante en ambas comunidades estudiadas, pero la cobertura vegetal viva, total, fue 37.5% en la comunidad 1 y 62.5% en la

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comunidad 2. Ambas poblaciones fueron sensibles a la luz. Después de 19 días desde la imbibición, hubo un efecto positivo, significativo de la luz sobre la germinación acumulada. En el segundo estudio, realizado solo bajo las condiciones de luz indicadas para el primer estudio, la germinación acumulada y el índice de la velocidad de germinación fueron mayores (p≤0.01) en P1 que en P2. Al mismo tiempo, T50 y el porcentaje de espiguillas con cariopses embebidos, pero no germinados, fueron mayores (p≤0.01) en P2 que en P1; no se hallaron diferencias en el porcentaje de espiguillas vacías. Nuestros resultados demostraron que la luz fue importante para la germinación de las semillas en *P. vaginatum*, y que el momento de la iniciación de la germinación en respuesta a la luz difirió entre las poblaciones de *P. vaginatum* estudiadas.

PALABRAS CLAVE: germinación, *Pappophorum vaginatum*, poblaciones, luz, resiembra natural, establecimiento, gramíneas perennes

INTRODUCTION

Warm-season, perennial grasses palatable to domestic livestock are scarce in rangelands of central Argentina (Busso *et al*., 2004). The unique abundant, C4, palatable forage species in this region, and more specifically, at the South of the Phytogeographical Province of the Monte, is *Pappophorum vaginatum* Buckley (Giorgetti *et al*., 1997). This is currently a decreasing species because of it has been exposed to overgrazing during decades (Torres *et al*., 2013a). This native species can also be found in other Phytogeographical Provinces of Argentina like the Pampeana, of the Espinal and SE of the Chaqueña (Pensiero, 1986).

Re-establishment of *P. vaginatum* in rangelands of central Argentina would not only be important to increase forage availability to grazing livestock but also to recuperate and maintain plant biodiversity. Studies of traits related to the control of and environmental factors that affect plant establishment such as those which determine germination, and factors that affect this process (e.g., light) are critical. Germination is the first step of a series of events that will produce a new individual (Soriano, 1960). Some studies have reported differences in germination responses or vigor between populations of *P. vaginatum* when they were exposed to both fluctuating light conditions in the laboratory and permanent darkness (Casalla *et al*., 2010; Entío *et al*., 2011). Seed germination of *P. vaginatum* was positively influenced by light (Martinez *et al*., 1992). However, the variability in the germination response to light is not known among different spontaneous, native populations of this species.

Various plant species need light to germinate, and the effect of the either presence or absence of light varies among species (Medina, 1977). Germination responses to light are common in small-seed species, which are able to show seedling emergence after disturbances (Pons, 2000). Because of this, seed responses to light might be considered an indication that light exerts some kind of control on seed dormancy (Bewley & Black, 1994). However, Martinez *et al.* (1992) and Chilo *et al*. (2013) determined absence of seed dormancy in *P. vaginatum*, a small-seed producing species (Rúgolo de Agrasar *et al*., 2005). Alonso & Peretti (1995) found that the better and fastest germination in *Brisa subaristata*, a native species of Argentinian rangelands, occurred at 20°C under light conditions. Light also promoted germination in *P. vaginatum* (Martinez *et al*., 1992).

Another factor which influences germination success is soil N (Pons, 1989; Mandak and Pysek, 2001; Plassmann *et al*., 2008; Bird, 2013). It appears that N availability serves as a gap detection mechanism in nitrogen-limited systems, such as those in the arid and semiarid rangelands of Argentina, signaling seed germination when the availability of N increases (Pons, 1989).

The hypothesis of this work is that there are differences in the seed germination response to light between the two study native *P. vaginatum* populations. Our objectives were to evaluate the

effects of various light conditions on the seed germination of two spontaneous *P. vaginatum* populations, and compare the germination responses between them.

MATERIALS AND METHODS

Site of seed collection

Seeds of *Pappophorum vaginatum* were collected from two spontaneous populations at the West of the Province of Buenos Aires, Argentina, in December 2010. Collections sites were 37° 26′ 51.2′′ S; 62° 28′ 1.2′′ W for population 1 (P1), and 37° 21′ 37.6′′ S; 62° 27′ 52.1′′W for population 2 (P2). Distance between collection sites was 10 km. Long-term (1911 to 2011) mean annual precipitation in this region is 665.1mm. Mean annual temperature is 14.9°C; mean maximum and minimum values are 21.3°C (January) and 8°C (July) respectively. Absolute maximum and minimum temperatures are 42.5°C (January) and -12°C (July), respectively. Long-term (1962-2011) mean relative humidity is 66.25%. Relief is a typical steppe with a herbaceous stratum cover.

Selection of the study sites was made on the basis of their different plant cover of the soil surface area, and on the fact that they had different physico-chemical properties. Total alive plant and nude soil covers were 37.5% and 62.5%, respectively, at the site of P1. Plant cover was determined following (Daubenmire, 1959). Companion species in decreasing order were *Stipa papposa*, *Bouteloua spp.*, *Centaurea spp.*, *Nassella neesiana* and *Adesmia bicolor* at the site of P1. Soil was silty. Total alive plant and nude soil covers were 62.5% and 37.5%, respectively, at the site of P2. At this population, companion species in decreasing order were *Nassella clarazii*, *Bouteloua spp.* and *Medicago lupulina*. Soil was sand-silty. Differences in physico-chemical properties between both sites are indicated in Table 1 [EC, C, OM, TN, P, Ca+Mg, Na and absorption sodium relationship (ASR)].

Laboratory studies

Two germination studies were conducted with each of two spontaneous, native populations of *Pappophorum vaginatum*. A completely rando-

Table 1. Mean values (n=5) of soil characteristics at the collections sites of two populations (P1, P2) of *P. vaginatum*. Significant differences between populations for any given soil parameter are indicated after the Student *t* test

Tabla 1. Valores promedio (n=5) de características del suelo en los sitios de muestreo de las dos poblaciones (P1, P2) de *P. vaginatum*. Diferencias significativas entre poblaciones para cualquier parámetro de suelo se indican después de efectuar el test *t* de Student

Parameters	P1	P2
EC (ppm)	0.49 ns	0.51 ns
C (%)	2.29 **	1.53 **
OM (%)	3.96 **	2.63 **
TN (%)	0.22 *	0.16 *
P (ppm)	3.75	ND
Ca + Mg (meq/l)	4.90 ns	5.33 ns
Na (meq/l)	0.53 ns	0.55 ns
ASR	0.33 ns	0.35 ns

ns: not significant; *: $p \leq 0.05$; **: $p \leq 0.01$; ND: not detectable (concentration of analite was below detection limits)

mized experimental design was utilized. The experimental unit was each Petri dish containing 50 seeds. Seeds were placed on moistened filter paper for germination.

In the first study, the effects of two light conditions (L0 and L1) were determined on seed germination of each of P1 and P2. One light condition consisted of total darkness (i.e., L0). The other light condition (i.e., L1, 14 h light/10 h darkness under natural laboratory conditions) had a mean light intensity of 13.4 ± 1.08 μmol m^{-2}.sec^{-1} (mean ± 1 SE).

Under the L0 light condition, Petri dishes were placed within a black, plastic container. After each of 4, 8, 15 and 19 days from imbibtion, four Petri dishes (i.e., replicates) were taken out from the container for each of P1 and P2 exposed to L0 and L1 each (i.e., 4 dates from imbibition x 2 populations/date x 2 light conditions/population/date x 4 replicates/light condition/population/date= 64 Petri dishes). Germinated seeds (radicle≥ 3 mm) were counted after each day from imbibition. During extraction of Petri dishes from the container, it remained under darkness. This allowed that those Petri

dishes that were taken out from such container after the subsequent 8, 15 and 19 days from imbibition remained under continuous darkness. Measurements of L1 were determined with a solar radiation sensor: PAR CAVADEVICES. Similarly, after 4 days from imbibition, seeds germinated under L1 conditions were evaluated using the same procedure than that for seeds exposed to darkness. Counting of germinated seeds was repeated after 8, 15 and 19 days from imbibition. The study ended-up after 4 consecutive days with no germination (i.e., from day 15 to day 19 after imbibition). The percentage of cumulative germination was determined under both light conditions.

In the second study, seed germination of the P1 and P2 populations of *P. vaginatum* was evaluated only under L1 conditions in the laboratory, after determining that light increased germination of both populations in the first study. Eight replicates were used for each population (i.e., n=8). Germinated seeds (radicle ≥ 3 mm) were counted once a day during 19 consecutive days on the same Petri dishes (2 populations x 8 replicates / population= 16 Petri dishes); after counting, germinated seeds were taken out of the Petri dishes. The study ended-up when seeds did not germinate during 4 consecutive days (i.e., from day 15 to day 19 after imbibition). Thereafter, the (1) percentage cumulative germination; (2) germination speed index, (3) time to 50% of percentage cumulative germination (T50), (d) percentage of empty spikelets (i.e., without cariopsis), and percentage spikelets with imbibed, but not germinated cariopsis were determined. Identification of spikelets without cariopsis, and of those which had imbibed, but not germinated cariopsis was conducted using a stereo-oscopic microscope. Histological instrumentation was used to dissect the seed cover on those seeds which remained ungerminated. The germination speed index (GSI) was calculated as $GSI = G1/T1 + G2/T2 + \ldots + Gn/Tn$, where G=number of germinated seeds; T= day of germination; n= day of the last control of germination (Maguire, 1962). The range of temperatures in the laboratory, where both studies were conducted, was between 27.8°C and 21.0°C; mean maximum and minimum temperatures were 25.7°C ± 0.41 and 23.2°C ± 0.44, respectively. The range of temperatures within the black, plastic container was between 27°C and 20.8°C; mean maximum and minimum temperatures were 26.6°C ±1.02 and 21.2°C ±0.21, respectively.

Statistical analysis

A three-way ANOVA (Table 2; 2 populations x 2 light conditions x 4 sampling dates after imbibition of seeds) was conducted in the first study. The 3-way interaction was not significant

Table 2. Results of the three-way analysis of variance examining the effects of days from imbibition of seeds, population, and light on the cumulative germination percentage of *P. vaginatum* in a semiarid area near Patagones, Provincia de Buenos Aires, Argentina

Tabla 2. Resultados del análisis de varianza de 3 vías examinando los efectos de días después de la imbibición de las semillas, población y luz sobre el porcentaje de germinación acumulado de *P. vaginatum* en un área semiárida cerca de Patagones, Provincia de Buenos Aires, Argentina

Source	df	Mean sums of squares and significance level
		Cumulative germination (%)
Days from imbibition	3	3010.5 ***
Population	1	4317.5 ***
Light	1	4442.2 ***
Days from imbibition x Population	3	435.8 ***
Days from imbibition x Light	3	121.6 *
Population x Light	1	914.8 ****
Days from imbibition x Population x Light	3	42.7 ns
Error	48	30.9
Total	63	

* p<0.05, **** p<0.001, ns= not significant

(Table 2), but all two-way interactions were significant at p < 0.05 (Table 2). One-way ANOVA was used in the second study for comparing several variables in P1 versus P2 exposed to L1 conditions. In all cases, mean comparisons were made using the Fisher LSD test at a significance level of 0.05. All statistical analyses were conducted using Infostat version 2012 (Di Rienzo *et al*., 2012).

RESULTS

First study

Despite the three-way interaction was not significant (p>0.05), there were three two-way, significant (p<0.05) interactions: (1) Population x Light condition; (2) Date from imbibition x Light condition, and (3) Date from imbibition x Population (Table 2). Each of these interactions was studied (Figs. 1 to 3). Light increased (p<0.05) cumulative germination in both populations (Fig. 1), and at all four study dates from imbibition (Fig. 2) in comparison to continuous darkness. Also, cumulative germination was greater (p<0.05) in P1 than in P2 under both light conditions (Fig. 1), and after 4 and 8 days from imbibition (Fig. 3). However, P1 and P2 showed a similar (p>0.05) cumulative germination at 15 and 19 days from imbibition (Fig. 3). Finally, cumulative germination increased (p<0.05) from 4 to 8 days after imbibition, and remained similar (p>0.05) among 8 to 19 days from imbibition, under both light conditions (Fig. 2) and populations (Fig. 3).

Second study

Results of the second study showed differences in the germination response between the two study populations. One of the populations (i.e., P1) showed a greater (p≤0.01) cumulative germination and germination speed index, and a lower (p≤0.01) T50 than the other population (i.e., P2) (Table 3). At the same time, the percen-
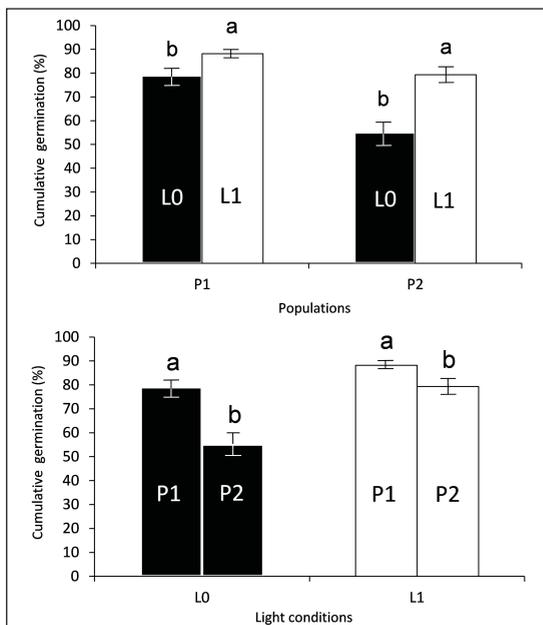

Figure 1. Cumulative germination (%) after seed imbibition of two *P. vaginatum* populations (P1, P2) exposed to two light conditions (L0=continuous darkness; L1=14 h light/10 h dark). Different letters indicate significant differences between light treatments within each population (uppermost panel) or between populations within each light condition (lowermost panel) after the Fisher´s LSD test (*= p≤0.05; **= p≤0.01)

Figura 1. Germinación acumulada (%) después de la imbibición de las semillas de dos poblaciones de *P. vaginatum* (P1, P2) expuestas a dos condiciones de luz (L0=oscuridad continua; L1=14 h luz/10 h oscuridad). Letras diferentes indican diferencias significativas entre condiciones de luz dentro de cada población (panel superior), o entre poblaciones dentro de cada condición de luz (panel inferior) después de la prueba de Diferencia Mínima Significativa de Fisher (*= p≤0.05; **= p≤0.01)

tage of imbibed, but not germinated cariopses was greater in P2 than in P1. The percentage of empty spikelets was similar among populations (Table 3).

DISCUSSION

Germination and dormancy mechanisms have a great adaptive importance because they contribute to assure that seedling emergence will occur at the most advantageous place and time

(Bewley & Black, 1994). In general, the response of germination to light is common in small-seeded species, like *P. vaginatum* (Rúgolo de Agrasar, 2005), which are able to emerge from the soil after any type of disturbance is produced (Pons, 2000). Because of this, responses of seeds to light are considered a sign that light has some kind of control on seed dormancy (Bewley & Black, 1994).

Our results showed a positive effect of light on seed germination of both populations of *P. vaginatum* (Fig. 1). This is in agreement with the results of Martínez *et al.* (1992) on this species.

Many species need light to germinate, although the effect of either the presence or absence of light varies with the species (Medina, 1977). In rangeland species of Argentina, various responses were obtained after the exposure of their seeds to light quantity and quality. The best and fastest germination was produced under light conditions at 20°C in *Brisa subaristata* (Alonso & Peretti, 1995).

Populations of *P. vaginatum* exposed to the natural light/dark fluctuation in the laboratory in our second study, showed greater cumulative germination percentage values (80.5 to 91.3%) than those in a previous study where 11 populations of *P. vaginatum* were compared under darkness conditions (30.5 to 73.5%), and the proportion of empty spikelets was greater (Entio *et al.*, 2011). Seeds of *Pappophorum*
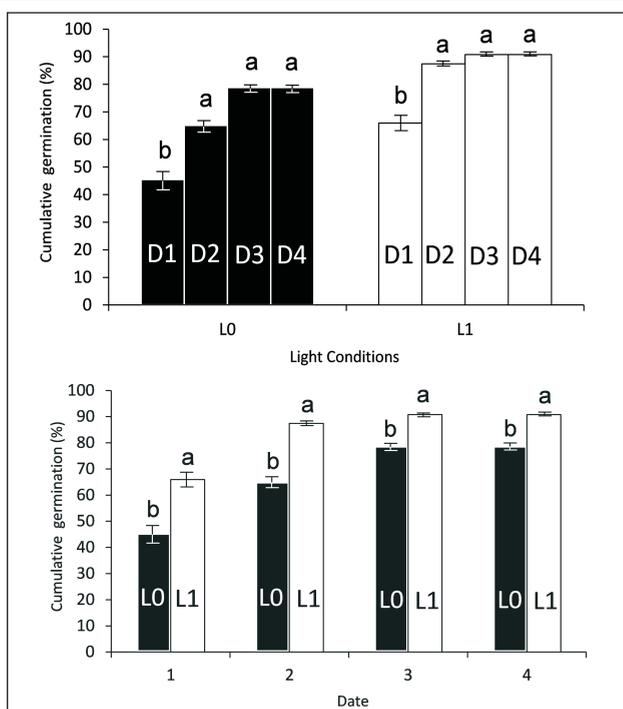

Figure 2. Cumulative germination (%) after seed imbibition of two *P. vaginatum* populations (P1, P2) exposed to two light conditions (L0=continuous darkness; L1= 14 h light/10 h dark). Different letters indicate significant differences among sampling dates within each light treatment (uppermost panel) or between light treatments within each sampling date (lowermost panel) after the Fisher´s LSD test (*= p≤0.05; **= p≤0.01)

Figura 2. Germinación acumulada (%) después de la imbibición de las semillas de dos poblaciones de *P. vaginatum* (P1, P2) expuestas a dos condiciones de luz (L0=oscuridad continua; L1= 14 h luz/10 h oscuridad). Letras diferentes indican diferencias significativas entre fechas de muestreo dentro de cada tratamiento de luz (panel superior) o entre tratamientos de luz dentro de cada fecha de muestreo (panel inferior) después de la prueba de LSD de Fisher (*= p≤0,05; **= p≤0,01)

caespitosum and *P. philippianum* collected in the Arid Chaco, Argentina, (aprox. 300 mm mean annual precipitation) showed germination percentages of 50 and 51%, respectively, in a germination study where seeds were kept moistened at 25-30 C (Quiroga *et al*., 2009).

The fact that cumulative germination was greater in P1 than in P2 (Fig. 1, Table 3) might par-

Table 3. Mean values of various germination parameters in two populations (P1, P2) of *P. vaginatum*. Different letters in the same row indicate significant differences (p ≤ 0.01) between populations after the Fisher's test LSD

Tabla 3. Valores promedio de varios parámetros de germinación en dos poblaciones (P1, P2) de *P. vaginatum*. Letras diferentes en la misma fila indican diferencias significativas (p ≤ 0.01) entre poblaciones después del test LSD de Fisher

Parameter	Population			
	P1		P2	
Cumulative germination (%)	91.31	a	80.50	b
Germination speed index	11.49	a	7.58	b
T_{50} (d)	4.10	b	6.00	a
Empty spikelets (%)	3.80	a	7.00	a
Spikelets with imbibed, but not germinated, cariopsis (%)	8.60	b	19.50	a

tially be attributed to its lower proportion of spikelets with imbibed, but not germinated cariopsis (Table 2). The greater proportion of imbibed, but not germinated cariopsis in P2 might be attributed to the presence of either dormancy mechanisms or loss of viability. Nevertheless, both *Pappophorum* populations reached a similar germination percentage after 15 and 19 days from imbibition in the first study (Fig. 3), when the number of replicates (n=4) was less than twice that in the second study (n=10). The percentage of empty spikelets was similar in both populations (Table 2). This might be attributed to similar environmental conditions during seed formation, since seed sampling in both populations was conducted in relatively nearby sites at a similar time.

In addition, P1 grew in a soil with a greater carbon, organic matter and total nitrogen contents than those found in P2 (Table 3). The ability of soil N to increase germination success is well documented (Pons, 1989; Mandak & Pysek, 2001; Plassmann *et al*., 2008). Bird (2013) reported that addition of ammonium nitrate to the soil increased percentage of germi-

nation in the grasses *Elymus canadensis*, *Panicum virgatum*, *Schizachyrium scoparium* and *Sorghastrum nutans*. The availability of N is thought to serve as a gap detection mechanism for plants within nitrogen-limited systems, signaling germination of seeds when such opportunities arise (Pons, 1989).

Casalla *et al*. (2010) determined that the germination response was variable among *P. vaginatum* populations when they were exposed to natural light/dark conditions in the laboratory. Similar results were obtained by Entío *et al*. (2011) under continuous darkness conditions. Even though differences were found in the germination responses between the two study *P. vaginatum* populations, we recognize that little can be said on the amplitude of that response because it is limited by the number of the study populations. Anyhow, the fact that germination showed a positive response to light in both study populations is important. This, combined with a greater germination speed in P1 than in P2, would be beneficial to rapidly take advantage of small precipitation events (≤ 5mm) which are common at the study site (Páez *et al*., 2005).

Disturbances like grazing livestock (e.g., via tissue removal, trampling) produce plant cover changes which open new spaces, and subsequent colonization opportunities, because seeds are exposed to variations in light quantity and quality (Fenner & Thompson, 2005). A mechanism of response to high irradiance might also exist, which inhibits germination in several plant species (Pons, 2000). This mechanism is relevant in arid ecosystems. This is because it constraints seed germination during the summer drought on those seeds which lie on the soil surface (Fenner & Thompson, 2005). Seed germination of several semiarid rangeland species, for example, was inhibited at high light intensities in the Mediterranean (Dobarro *et al.*, 2010). Investigation on
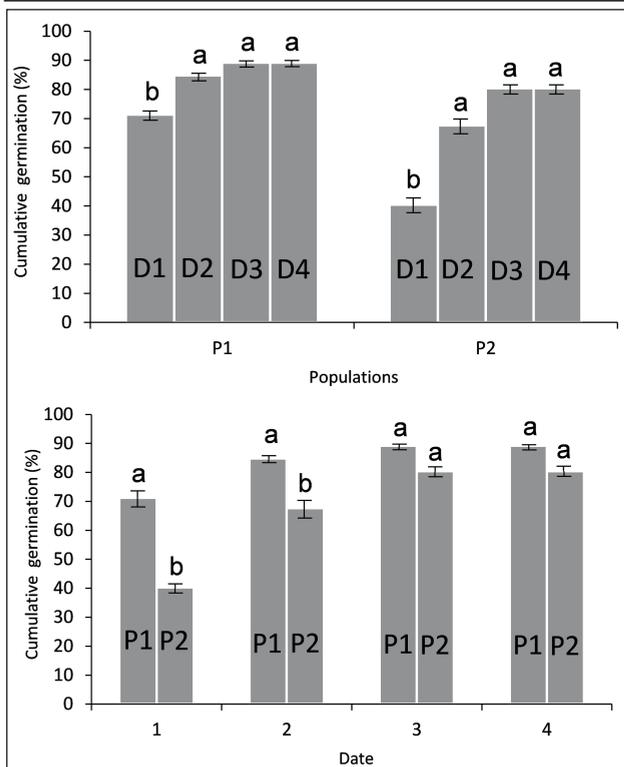
Figure 3. Cumulative germination (%) after seed imbibition of two *P. vaginatum* populations (P1, P2) exposed to two light conditions (L0= continuous darkness; L1= 14 h light/10 h dark). Different letters indicate significant differences among sampling dates within each population (uppermost panel) or between populations within each sampling date (lowermost panel) after the Fisher´s LSD test (*= p≤0.05; **= p≤0.01)

Figura 3. Germinación acumulada (%) después de la imbibición de las semillas de dos poblaciones de *P. vaginatum* (P1, P2) expuestas a dos condiciones de luz (L0= oscuridad continua; L1= 14 h luz/10 h oscuridad). Letras diferentes indican diferencias significativas entre fechas de muestreo dentro de cada población (panel superior) o entre poblaciones dentro de cada fecha de muestreo (panel inferior) después de la prueba LSD de Fisher (*=p ≤0.05; **= p≤0.01)

The anthecium and awns of *P. vaginatum* are very small (Rúgolo de Agrasar *et al*., 2005). Dispersion of seeds because of the wind is larger from the mother plant for light than heavy seeds (Chambers & MacMahon, 1994). Also, Mayor *et al*. (2003) reported that *P. vaginatum* was present in the soil seed bank at depths no greater than 4 cm from the soil surface in the Phytogeographical Province of the Espinal, a relatively close area to our study site. Sunlight scarcely penetrates the soil surface (Caldwell *et al*., 2007), and anthecia of *P. vaginatum* does not penetrate deep into the soil (Mayor *et al*., 2003). Because of this, that sunlight might be enough to stimulate (1) seed germination of *P. vaginatum* given appropriate conditions for the germination of this species (e.g., adequate soil both moisture and nutrient contents), and (2) the germination responses of *P. vaginatum* to light (i.e., Table 3).

Inter-population differences in the response of seed germination to light in the study *P. vaginatum* populations (Table 3) indicate that light should be considered on seed germination of *Pappophorum vaginatum* at the time of managing its implantation. Plants of *P. vaginatum* start producing abundant anthecia from the beginning to the end of the whole growing season (Torres *et al*., 2008). These anthecia may have a very good dispersal by wind because of its small size (anthecia= 1.5 to 3.5 mm + awns: 6-9 mm: Rúgolo

the existence of this mechanism in *P. vaginatum* is highly desirable. Response of seed germination to light is important because it will contribute to determine the timing of germination under field conditions. In turn, this is critical for the survival, and subsequent development, of the resulting seedlings (Pons, 2000).

de Agrasar *et al*., 2005). Briske and Richads (1995) reported that asexual reproduction (e.g., tiller production from axillary buds) is the major form of reproduction in rangeland perennial grasses. Thereafter, future studies should evaluate the importance of sexual versus asexual (i.e., tiller production) reproduction in plants of *P. vaginatum* given its early and abundant production of anthecia during most of the growing season. We hyphotesize that the persistence of the palatable *P. vaginatum* on long-term severely overgrazed rangelands in arid and semiarid Argentina is partially the result of its abundant natural, sexual reseeding (e.g., see Torres *et al*., 2013b), which may show a high germination percentage given appropriate conditions (e.g., Table 3, P1).

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