

Sex-related spatial patterns of *Poa ligularis* in relation to shrub patch occurrence in northern Patagonia

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Abstract. *Poa ligularis* is a dioecious species and a valuable forage plant which is widespread in the arid steppe of northern Patagonia (Argentina). The vegetation in these areas consists of a system of perennial plant patches alternating with bare soil areas defining contrasting micro-environments. We hypothesized that (1) male and female individuals of *P. ligularis* are spatially segregated in different micro-environments, (2) the intensity of spatial segregation of sexes depends on plant structure and (3) spatial segregation of sexes is enhanced by competitive interactions between the sexes within the vegetation patches. We analysed the spatial distribution of female and male individuals in relation to the spatial pattern of vegetation in two areas differing in their vegetation structure. The location of *P. ligularis* within patches where either male, female or both sexes occurred was also analysed. The results indicate that different patterns of spatial distribution of sexes of *P. ligularis* may be found at the community level depending on the dominant life forms and geometric structure of plant patches. Where patches are of a lower height, with a high internal patch cover, individuals of both sexes are concentrated within patch canopies. In sites characterized by large, tall patches and less internal patch cover suitable microsites for female and male *P. ligularis* occur both within and outside the patch with males located at further distances from the patch edge. Where the patch is large and tall enough to allow the establishment of males and females at relatively high numbers, males occupy the patch periphery or even colonize the inter-patch bare soil. These spatial patterns are consistent with selective traits in which females better tolerate intraspecific competition than males, while males tolerate wider fluctuations in the physical environment (soil moisture, nitrogen availability, wind intensity, etc.).

Keywords: Dioecy; Patchy environment; Reproductive system; Sexual specialization.

Nomenclature: Correa (1969-1988).

Introduction

It has been hypothesized that the division of sexual labour would increase the reproductive efficiency of dioecious plants in comparison with similar monoecious species (Lloyd 1982; Lovett Doust & Lovett Doust 1988). Dioecy is present in only 5% of angiosperms (Charnov 1984), but many plant communities have dioecious species as stable components (West 1983; Beeskov et al. 1987). Many authors have identified morphological and functional differences between genders of dioecious plants that may eventually result in habitat segregation between them. The higher reproductive costs of females compared with males (Harper 1977; Lloyd & Webb 1977; Lovett Doust et al. 1987; Lloyd & Bawa 1984; Gehring & Linhart 1993) and the aerodynamic requirements for pollen dispersal and reception in anemophilous species (Cox 1981) have been suggested as important factors that might have driven natural selection in the direction of sexual specialization (Freeman et al. 1997). In many dioecious species, females are frequently found in nutrient-rich microsites while males growth is frequently associated with open microsites of lower quality in terms of environmental extremes and resource availability (Freeman et al. 1976; Lovett Doust et al. 1987; Lyons et al. 1994; Havens et al. 1995; Soldaat et al. 1997). Faliński (1998) reported increased dieback of female trees of *Salix caprea* in relation to herbivore pressure.

Plant patchiness creates a gradient of microsite qualities from just below the patch crown to the more open intra-patch areas and may be considered as the main source of spatial environmental heterogeneity in desert and semidesert ecosystems (Klemmedson & Barth 1975; Garner & Steinberg 1989; Soriano et al. 1994; Bisigato & Bertiller 1997; Mazzarino et al. 1996). Vinton & Burke (1995) stressed the importance of local plant effects on soil in arid and semi-arid ecosystems. Their results indicated that plant cover patterns were more important for soil processes than the particular plant

canopy composition. Tall and large vegetation patches may also have a positive shelter effect extending beyond their crowns which may facilitate the establishment of vegetation around them (e.g. Callaway 1995; Callaway & Davis 1998). On the other hand, below-ground competition, particularly among species of the same functional group, may occur in the neighbourhood of established vegetation (Casper & Jackson 1997). Thus, biophysical and chemical conditions may change dramatically from the patches of bare soil towards the center of vegetation patches. This environmental variability may provide suitable scenarios for spatial segregation of sexes of dioecious species which may be stronger in ecosystems with marked vegetation patchiness rather than in those with small and diffuse vegetation plant patches. Additionally, many studies have reported biased sex ratios in different environments or microsites as a response to competition between sexes (Freeman et al. 1976; Cox 1981; Weiner 1989; Houssard et al. 1994). Lovett Doust et al. (1987) reported that in some dioecious species female biased ratios found at high plant densities are consistent with a higher tolerance to intraspecific competition compared to males.

The vegetation in Patagonia, as in many other arid ecosystems, is distributed in a spatial pattern constituted by well-defined vegetation patches alternating with areas of bare soil. Patches offer a relatively more predictable environment than bare soil in terms of soil moisture, nutrient and seed supply and shelter from winds (Rostagno & del Valle 1988; Rostagno et al. 1991; Mazzarino et al. 1996, 1998; Bertiller 1998). Mazzarino et al. (1998) found that the presence of large and dense plant patches (irrespective of their botanical composition) significantly increased the labile-N pool in the underlying soil.

The dioecious *Poa ligularis* is widespread in Patagonia (Argentina) and is one of the most preferred species for herbivores (Soriano 1956a; Boelcke 1957; Soriano 1959; Correa 1978; Ares et al. 1990; Soriano et al. 1995). We hypothesized that (1) male and female individuals of *P. ligularis* are spatially segregated in different microsites defined by the distribution of bare soil and vegetation. Specifically, we suggest that females would be more frequent than males in more protected and nutrient-rich micro-environments associated with plant patches, while males would occur in open micro-environments; (2) spatial segregation is stronger at sites with large and tall patches; (3) spatial segregation of sexes is enhanced by competitive interactions between the sexes within the patches. We predict that in the absence of plants of the other sex, both males and females would be accommodated inside the patches while in bisexual patches, males would occur near the edges or towards the exterior of the patches.

Material and Methods

Study area

Two sites in northeastern Patagonia were selected: Laguna Blanca (42° 48' S, 65° 08' W; elevation: 120 m a.s.l.) and Bahía Cracker (42° 59' S, 64° 34' W; 90 m a.s.l.) near Puerto Madryn, Chubut province. The climate of the area is arid, and the two sites differ in some microclimatic conditions and in the spatial pattern of their vegetation. In Laguna Blanca (LB), mean annual precipitation is 188 mm with a high mean interannual variation ($\gamma=6$, Barros & Rivero 1982) The mean annual temperature is 13.7 °C. Soils are a complex of typical palaeorthid-typic calciorthid (soil taxonomy follows Anon. 1992). In the upper soil, the clay content ranges from 4-6% beneath vegetation patches to 7-8% in the bare soil. The vegetation is characteristic of the southern portion of the Monte Phytogeographic Province (Soriano 1950) and covers less than 40-60% of the soil. The plant canopy is dominated by:

Tall shrubs:	<i>Larrea divaricata</i>	<i>Chuquiraga hystrix</i>
	<i>Lycium chilense</i>	<i>Schinus johnstonii</i>
Intermediate shrubs:	<i>Atriplex lampa</i>	
Small shrubs:	<i>Nassauvia fuegiana</i>	<i>Acantholippia seriphioides</i>
	<i>Junellia seriphioides</i>	

Shrubs cover ca. 35-40% of the soil in a patchy pattern (Bertiller et al. 1991; Mazzarino et al. 1996; Bisigato & Bertiller 1997). The grass layer, which covers ca. 5-15% of the surface, is dominated by *Stipa tenuis*, *Poa ligularis* and *Stipa speciosa*. In Bahía Cracker (BC), the mean annual precipitation is 254 mm, with high mean interannual variation ($\gamma=8$; Barros & Rivero 1982) and the mean annual temperature is 12.5 °C. Soils are xerollic haplargids with some xerollic calciorthids and typic torriorthents. The vegetation is characteristic of the Patagonia phytogeographic Province with some components of the Monte phytogeographic Province (Soriano 1950; Soriano 1956b) and covers less than 40-50% of the soil. The dominant species are intermediate (*Chuquiraga avellanadae*) and small shrubs (*Nassauvia fuegiana*), which cover ca. 30-40% of the soil and are organized in a patchy pattern. The grass layer is dominated by *Stipa tenuis*, *Poa ligularis*, *Piptochaetium napostaense* and *Stipa speciosa* (Beeskow et al. 1995).

Sampling

The characteristics of the vegetation and the spatial distribution of *P. ligularis* with respect to perennial vegetation patches were evaluated along four 40 m and six 50 m linear transects in LB and BC, respectively. Half the transects at each site were oriented in the W-E direction (direction of the dominant winds) and the

other half in the S-N direction. For the purpose of this study, a patch was defined as a group of perennial plants including at least one shrub individual, where the projection of the patch canopy over the soil is separated from neighbouring patches by at least 15 cm of bare ground. The number of patches and the length intercepted by each patch, as well as the sex and the distance of each individual of *P. ligularis* intercepted along the transect to the center and edge of the closest intercepted patch were measured. Distances to the closest patch defined in this way can correspond to plants inside or outside the border of patches, depending on their radius. The relative frequency of males and females, with respect to occurrence inside or outside vegetation patches, was used to test hypothesis 1. Also, the height, internal cover (total and by functional group: shrubs or grasses) at each intercepted patch and the cover of grass in the spaces between intercepted patches were visually estimated. These data, along with the relative frequency of males and females inside or outside of vegetation patches, were utilized to test hypothesis 2. Hypothesis 3, was tested by analysing the mean distances to the closest patch edge of plants of *P. ligularis* in relation to the mean radius of the closest patches in cases where plants of only one sex occurred, and also in patches where both sexes were present. These were called unisexual and bisexual patches, respectively.

The distributions of relative frequencies of occurrence at varying distances from vegetation patch edges of *P. ligularis* males and females were compared with a χ^2 -test. The significance of different means of the non-normally distributed distances to patch edges was analysed by the Mann-Whitney test (Norusis 1993).

Results

As predicted by hypothesis 1, males in LB were more frequent than females outside patches or were found at relatively larger distances (up to 4 m) from the edge of the closest patch (Fig. 1).

In BC however, both sexes of *P. ligularis* were located inside the crown of the patches (Fig. 1). As predicted by hypothesis 2, these differences in the intensity of spatial segregation between sites were related to characteristics of the vegetation structure. In LB, the plant cover consisted of larger patches per unit area compared to BC (Table 1). Vegetation patches also differed in their internal characteristics. Patches in LB were taller and with lower total internal cover than those in BC. Shrub cover was higher in patches at LB than at BC. At both sites, interspaces between shrub patches were partially colonized by different perennial grass species.

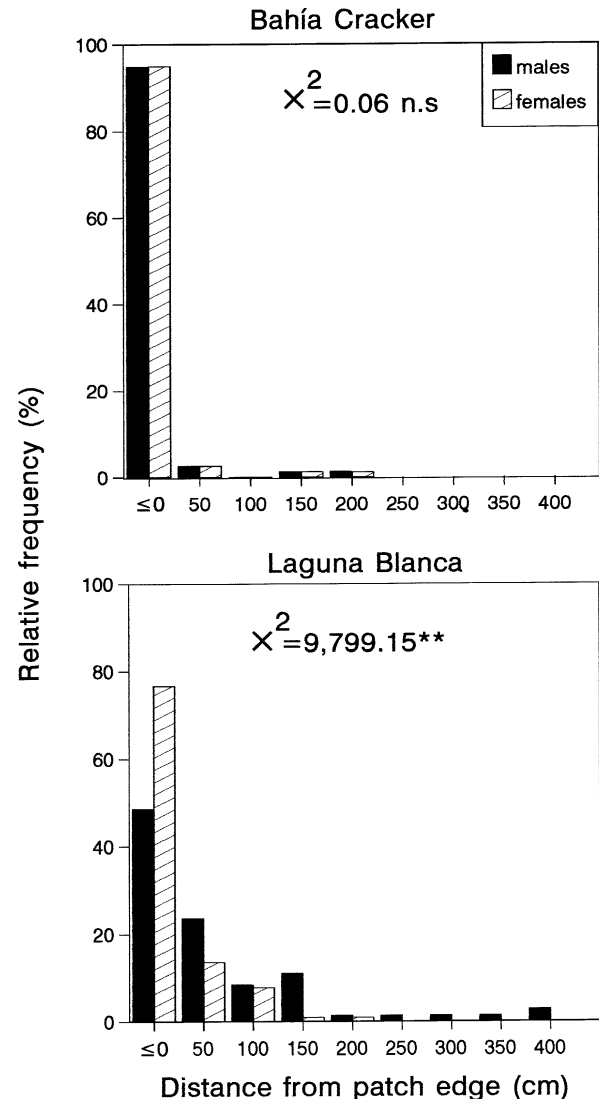


Fig. 1. Distributions of relative frequencies of male and female *P. ligularis* at different distances from patch edge (inside: distance ≤ 0 ; outside: distance > 0).

Table 1. Characterization of the vegetation structure at Bahía Cracker and Laguna Blanca sampling sites. Different lower case letters indicate significant ($p \leq 0.05$) differences between sites based on ANOVA-test. Sample sizes in parentheses.

	Bahía Cracker	Laguna Blanca
Mean patch radius (cm)	34.2a (171)	49.9b (54)
Mean radius of patches with <i>P. ligularis</i>	40.0a (94)	50.0b (53)
Mean height of patches (cm)	49.8a (171)	120.6b (54)
Mean internal patch cover (%)	75.2a (171)	66.1b (54)
Mean shrub cover of patches (%)	39.3a (171)	58.1b (54)
Mean grass cover between patches (%)	14.8a (6)	9.7a (4)

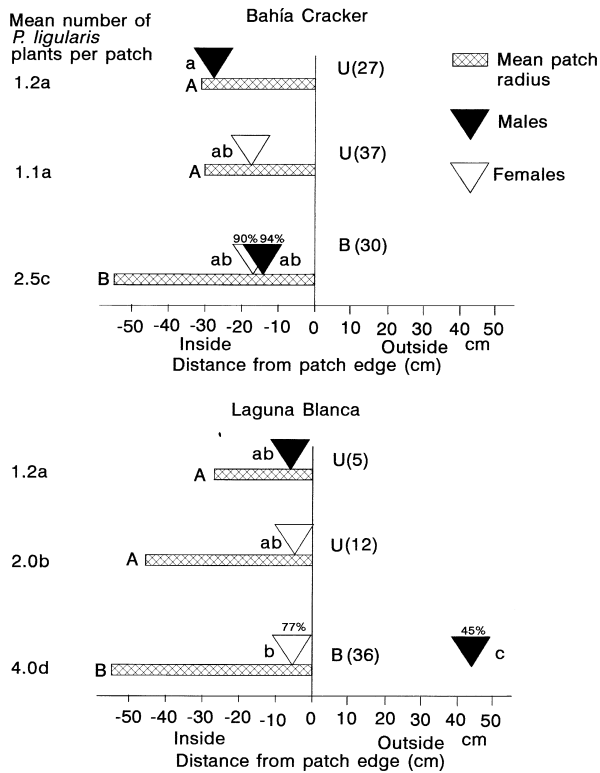


Fig. 2. Mean number of *P. ligularis* plants per patch. Plant symbols are located at mean distances from unisexual (U) or bisexual (B) patch edges. Different upper case letters indicate significant differences in patch mean radii (all possible comparisons, ANOVA-test). Different lower case letters indicate significant differences in distances of *P. ligularis* from the patch edge or in numbers of plants per patch (all possible comparisons, Mann-Whitney-test). Sample sizes in parentheses. Numbers above male and females symbols in bisexual patches indicate the percentage of individuals inside patch crowns.

In relation to hypothesis 3, it should be noted that only large patches (mean radius > 50 cm) accommodated bisexual groups of *P. ligularis* while small patches contained only either female or male individuals. The density of plants of *P. ligularis* in the bisexual patches was twice as high in LB than in BC. In the case of LB, 55% and 45% of the males were found outside/inside the patches, respectively, while females dominated inside patches. Conversely, in the bisexual patches of BC, most males and females were found inside patch crowns (94% and 90%, respectively, Fig. 2).

Discussion

Our results indicate that spatial segregation of sexes of *P. ligularis* occurs in arid environments of northern Patagonia depending on the structure of plant patches. In BC, where patches are shorter with a high internal cover, a sharp contrast exists between the sheltered intra-patch environment and the external soil. Individuals of both sexes of the species are found almost entirely within the patch canopies. In contrast to this, patches in LB have less internal cover and are taller, thus creating a whole gradient of microsite qualities from inside the patch crown to the more open intra-patch areas. As a result, suitable microsities for both female and male *P. ligularis* occur within and outside the patch crowns, with males located further from their closest patch (Fig. 1). These results are consistent with our first and second hypotheses.

However, males occupy external microsities only in the case of LB-bisexual patches (Fig. 2). The number of individuals that can accommodate each bisexual patch also varies in relation to the variations in the dominant life forms and geometric structure of patches. At a similar patch size, LB-bisexual patches accommodate significant higher numbers of individuals of *Poa ligularis* than BC-bisexual patches. Within patches, the density of *P. ligularis* is probably limited by the availability of suitable microsities, consisting of small open areas among shrub branches or crowns or stems of perennial grasses and herbs rather than by seed availability (Bertiller 1998). Female and/or male *P. ligularis* would compete for these microsities, as is the case in other dioecious species (Cox 1981). In the areas of bare soil between patches, microsite quality and seed number may limit *P. ligularis* establishment (Aguilar 1994; Soriano et al. 1994; Bertiller 1998). Greater chances exist for taller LB-patches to shelter a large number of individuals than the shorter BC-patches, resulting in higher numbers of individuals associated with them. Under these conditions the outcome of competitive exclusion and/or successful establishment may be more marked in LB-bisexual patches. This will result in concentration of females inside patches and exclusion of males to the edges of or outside patches. This is consistent with our third hypothesis and with a higher tolerance of females to intraspecific competition compared to males, as reported in other dioecious species (Lovett Doust et al. 1987). Conversely, males better tolerate microsities of lower quality in terms of environmental extremes and resource availability. These mechanisms also allow the maintenance of an adequate distance from females that minimizes intersexual competition while allowing successful fertilization (Freeman et al. 1976).

These results prompt the formulation of further hypotheses in relation to the competitive exclusion and the adaptive value of spatial segregation between the *P. ligularis* sexes. In tall patches of LB, which provide a full range of microsite quality, spatial segregation would minimize intraspecific competition while maximizing reproductive success. Males, which are more precocious than females during the flowering season, stop vegetative and reproductive growth when pollen is dispersed, this is when females are expected to have high resource requirements. Accordingly, males are less limited than females in their cycle because pollen dispersal occurs in spring, when soil water has been recharged after the relatively humid winter season in northern Patagonia. Thus, the reproductive effort of males can be maintained even at relatively more exposed sites i.e. distant from a patch. Females require a constant water supply during the growing season, which can only be found in the shelter of vegetation patches, during the drier spring and beginning of summer, long after pollen production has ceased (Bertiller et al. 1991; Coronato & Bertiller 1997; Bertiller unpubl.).

The occurrence of spatial segregation of sexes in the largest patches of LB is consistent with other observations of dioecious plants where males were found to be less sensitive to water stress and nutrient availability than females (Freeman et al. 1976; Lovett Doust et al. 1987; Lyons et al. 1994; Havens et al. 1995). In this scenario, a differentiation in space and time of sexual labour is expected to increase reproductive efficiency, giving an advantage to dioecy over monoecy as reported by Lloyd (1982).

The tendency for the sexes of dioecious species to be spatially separated can result from differential survival induced by natural selection acting upon functional differences, or from the plasticity of sex expression under varying environmental conditions (Freeman et al. 1976; Lloyd & Bawa 1984; Freeman et al. 1993). We have observed marked plants of *P. ligularis* growing in a wide range of conditions in both the field and greenhouse for over 5 years and have not yet observed sex-lability in this species. In microsites where there is no seed limitation for the establishment of this species, we interpret the pattern of sexual segregation as having resulted from the selective survival of individuals of *P. ligularis* in microsites within patches and in the inter-patches of bare soil.

Acknowledgements. We thank Dr. D. Goldberg and two anonymous reviewers for their comments on an earlier version of this paper. This research was funded by PIP-CONICET 4270/97.

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Received 18 May 1998;

Revision received 6 November 1998;

Accepted 29 March 1999.

Coordinating Editor: D.E. Goldberg.