EFFECT OF FINE-SCALE SPATIAL VARIATION OF SOIL NITROGEN ON THE PERFORMANCE OF THE SEXES OF *POA LIGULARIS* IN PATCHY ECOSYSTEMS OF NORTHERN PATAGONIA

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In patchy environments of arid Patagonia, males of the dioecious grass *Poa ligularis* dominate in N-poor microsites, while females are more common in N-rich microsites. In order to explore functional differences related to spatial segregation of the sexes, we analyzed biomass allocation and tissue N concentration in males and females of *P. ligularis* growing in a range of soil N concentrations (sN). Based on the general patterns of responses described for plants from N-rich and N-poor habitats, we hypothesized that (1) females, which dominate in N-rich microsites, would increase biomass allocation with increasing sN, while males, frequent in N-poor microsites, would show a limited response and (2) tissue N concentration would display a wider variation in males than females in response to changes in sN. At three sites in northern Patagonia, we randomly selected 15 plants of each sex of *P. ligularis* growing inside shrub patches and 15 in the interpatch areas and evaluated the biomass and N concentration of aboveground (vegetative and reproductive) and belowground structures. Biomass allocation to belowground structures and N concentration in roots increased with increasing sN for both males and females. Aboveground biomass increased with increasing sN only in females. In the N-poorest sites, we found higher N allocation to tiller crowns with increasing sN in males relative to females. In both sexes, biomass allocation to sexual reproductive structures (panicles) did not change significantly with variations in sN. These results provide partial evidence on morphological and functional dimorphism in a dioecious species with spatial segregation of the sexes.

Keywords: biomass allocation, dioecy, nitrogen concentration in plant tissues, nitrogen concentration in roots, nitrogen gradients in soil, spatial segregation of the sexes.

Introduction

Spatial segregation of the sexes in dioecious species could reflect differential mortality of males and females in different microsites and/or physiological specialization of the sexes on sites of different resource quality. The latter is an important adaptive plant trait, allowing each sex to tap resources required for successful growth and reproduction, thus enhancing reproductive efficiency and plant fitness (Freeman et al. 1976, 1997; Cox 1981; Lloyd 1982; Dawson and Ehleringer 1993; Gehring and Linhart 1993). A pattern of female-biased sex ratios in favorable habitats and male-biased ratios in stressful habitats is commonly observed in dioecious species with spatial segregation of the sexes, and it has often been related to higher reproductive costs in females than males (Freeman et al. 1976; Cox 1981; Gehring and Linhart 1993; Ågren et al. 1999; Dawson and Geber 1999).

Plants from nutrient-poor habitats tend to reduce the rate of nutrient cycling, and, often, their growth rate is less affected by variations in the external nutrient supply than that of plants from nutrient-rich habitats (Berendse and Elberse 1990; Chapin et al. 1990; Chapin 1991*a*, 1991*b*; Lambers and

Poorter 1992; Aerts and van der Peijl 1993). Furthermore, tissue N concentration usually exhibits more variability in relation to an external nutrient supply in plants from nutrient-poor rather than nutrient-rich habitats (Garnier 1998). In agreement with these general patterns, higher responses in growth to increasing resource supplies have been reported in females than in males of dioecious species with spatially segregated sexes and a prevalence of females in nutrient-rich habitats (Bierzchudek and Eckhart 1988; Geber 1999).

Canopy composition, diversity, and spatial structure may have strong effects on nutrient pools, cycling, and supply (van Breemen 1995; Vinton and Burke 1995; Scott and Binkley 1997; Epstein et al. 1998; Hooper and Vitousek 1998), creating spatial heterogeneity in soil resources that may favor the spatial segregation of the sexes with different physiological requirements in dioecious species. In patchy arid ecosystems, the soil beneath plant canopies concentrates greater amounts of microbial biomass, organic detrital matter, and nutrients, particularly nitrogen, than the interpatch soil, creating fertility islands (Charley and West 1977; Skujins 1981; Moorhead et al. 1986; Garner and Steinberger 1989; Horn and Redente 1998). Shrub-induced patchiness in N-fertility and sheltering is common in arid ecosystems of northern Patagonia (Mazzarino et al. 1996, 1998) and results in a wide range of microsites that are differentially colonized by the sexes of the dioecious grass *Poa ligularis* (Bertiller et al. 2000, 2001).

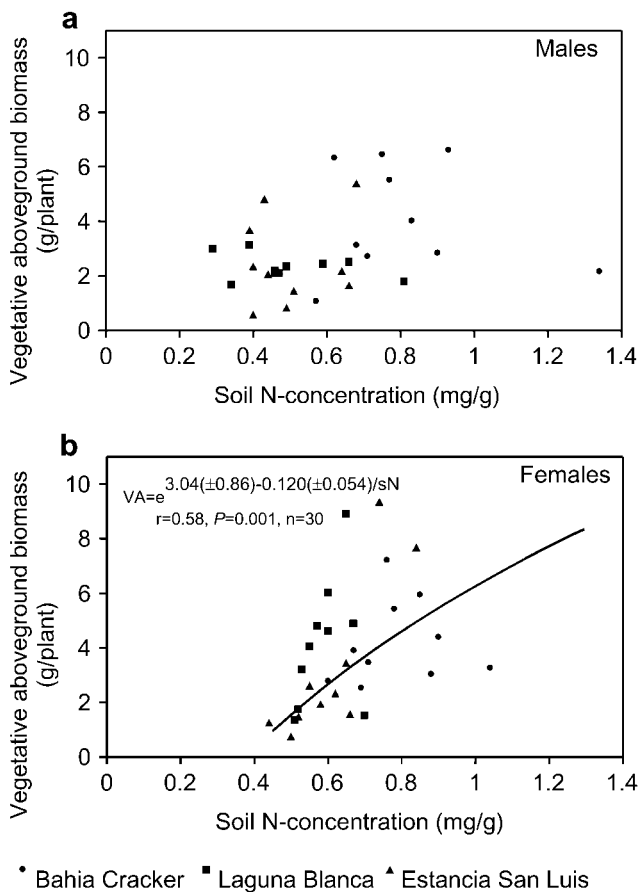[1] Author for correspondence; e-mail bertil@cenpat.edu.ar.

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Fig. 1 Vegetative aboveground biomass (*VA*) in males (*a*) and females (*b*) as a function of the N concentration in the soil. Confidence intervals (*P* = 0.05) shown in parentheses after equation parameters.

Poa ligularis Nees. ap. Steudel is a widespread wind-pollinated dioecious bunchgrass in arid ecosystems of Patagonia (Correa 1978; Ares et al. 1990; Bisigato and Bertiller 1997; León et al. 1998). Previous investigations indicated that sex expression in *P. ligularis* is constant and females dominate in sheltered (low air evaporative demand) and N-rich microsites beneath shrub canopies, while males are frequent at N-poor interpatch areas or at patch borders (Bertiller et al. 2000, 2001). This indicates that spatial segregation of the sexes in *P. ligularis* could be the result of sexual specialization for some aspects of the habitat. We hypothesized that (1) females, dominant in N-rich microsites, would increase biomass allocation with increasing soil N (sN), while this trait would show a limited response in males frequent in N-poor microsites and (2) N concentration in tissues would display a wider variation in response to changes in sN in males than in females.

Material and Methods

Study Area

This study was carried out in northern Patagonia in sites along a 60-km W-E transect, where mean annual precipitation

Table 1

Maximum and Minimum N Concentration in Soil (mg/g) beneath *Poa ligularis* Plants at the Different Microsites and Sites

	Microsite	
Site	Inside shrub patch	Outside shrub patch
Estancia San Luis (ESL)	0.39–0.84	0.40–0.62
Laguna Blanca (LB)	0.39–0.81	0.29–0.57
Bahía Cracker (BC)	0.69–1.34	0.57–0.90

ranges from 160 mm in the west to 200 mm in the east (Barros and Rivero 1982). We selected three study sites of ca. 2 ha each, where grazing by large herbivores had been excluded for at least the last 5 yr (Estancia San Luis [ESL]: 42°39′S, 65°23′W, 115 m a.s.l.; Laguna Blanca [LB]: 42°48′S, 65°08′W, 120 m a.s.l.; and Bahía Cracker [BC]: 42°59′S, 64°34′W, 90 m a.s.l.). At all sites, the vegetation is dominated by shrubs and grasses arranged in a patchy pattern. The morphological aspects of plant patches at these sites have been described elsewhere (Bertiller et al. 2001). The diameter and height of the patches do not differ significantly between ESL (44 cm diameter, 112 cm height) and LB (50 cm diameter, 121 cm height), whereas patches in BC are smaller (32 cm diameter, 50 cm height) than in the other two sites. The mean cover of individual patches is significantly higher in LB (66%) and BC (75%) than in ESL (54%). The density of *Poa ligularis* is higher in LB than in ESL and BC (11 vs. four and five plants per 10-m transect, respectively). The modal diameter of the mature plants at the three sites is 10 cm. The mean N concentration in the soil differs significantly among sites as follows: ESL < LB < BC. The spatial N variability in soil also differs among sites. Soil N decreases suddenly in LB and ESL and gradually in BC from the center to the interpatch area.

Evaluation by Sex of Performance in Relation to Soil N

During the flowering period (October 1998), 15 mature non-senescent plants of each sex of *P. ligularis* growing inside shrub patches and 15 at the interpatch areas were randomly selected at BC, LB, and ESL (five plants per combination of sex, mi-

Table 2

Multivariate ANCOVA of All Plant Traits by Sex, Microsite, Site, and Soil N (sN) Concentration as Covariate

Effect	F	P
Intercept	31.1	<0.001
Sex	3.4	0.004
Microsite	2.2	0.042
Site	6.2	<0.001
sN	3.2	0.006
Sex × sN	2.4	0.031
Sex × site	3.3	<0.001

Note. Plant traits include vegetative aboveground biomass; square-root-transformed panicle biomass and belowground biomass; N concentration in green leaves, dry leaves, culms, and flowers; and square-root-transformed N concentration in roots. Nonsignificant results on two-, three-, and four-way interactions are not shown. *P* ≤ 0.05 shown in bold.

Table 3

**Significance (*P*) of the ANCOVA of Biomass and N Concentration by Fixed Factors (Sex and Microsite),
Random Factor (Site), and Soil N Concentration as Covariate**

Source	df	Vegetative aboveground biomass (a)	Panicle biomass (b)	Belowground biomass (c)	N in green leaves (d)	N in dry leaves (e)	N in culms (f)	N in flowers (g)	N in tiller crowns (h)	N in roots (i)
Intercept	1	0.715	0.107	0.099	0.000	0.046	0.002	0.022	0.032	0.003
Main effects:										
Sex	1	0.089	0.904	0.277	0.798	0.611	0.479	0.641	0.442	0.191
Microsite	1	0.693	0.873	0.390	0.147	0.299	0.252	0.387	0.611	0.667
Site	2	0.181	0.064	0.148	0.823	0.191	0.538	0.296	0.555	0.664
sN	1	0.157	0.661	**0.050**	0.597	0.905	0.788	0.725	0.284	**0.013**
Interactions:										
Sex × sN	1	**0.050**							**0.039**	
Sex × site	2	**0.037**	**0.017**					**0.001**	**0.001**	
Sex × site × sN	2								**0.001**	

Note.   Nonsignificant results on two-, three-, and four-way interactions are not shown. $P \leq 0.05$ shown in bold.

crosite, and site). Senescent plants in this species have dead tillers at the center of the bunch and can be easily sorted. For the purpose of this study, we define a "patch" as a group of perennial plant species including at least one shrub life form, such that the projection of its canopy over the soil was separated from neighbor patches by at least 15 cm of bare ground. The total aboveground biomass of each selected *P. ligularis* plant was harvested, and a cylindrical soil core (10 cm depth, 10 cm diameter) centered in the basal area of the harvested plant was also extracted. The aboveground biomass was sorted into categories as follows: green leaves (G), dry leaves (completely dry, yellow, without signs of deterioration) (D), culms (C), and flowers (F). Tiller crowns (T) and roots (R) were separated from each soil core and washed. We estimated that the root biomass removed in this procedure was more than 80% of the total root biomass of each plant (Soriano et al. 1987).The sorted categories of above- and belowground biomass were dried at 45°C for 48 h and weighed (Carrera et al. 2000). The soil from the cores was air-dried and sieved (0.5-mm mesh). Nitrogen concentration of each biomass category (G, D, C, F, T, and R) was determined by the Kjeldahl acid-digestion method (Coombs et al. 1985), and total N concentration in the soil of each core was determined by the Kjeldahl technique (Bremner and Mulvaney 1982). In addition, the following biomass variables were computed: vegetative aboveground biomass (VA; VA = G + D), panicles (P; P = C + F), and belowground biomass (B; B = T + R).

Before statistical analyses, homogeneity of variance and normal distribution were tested for each variable. In case variables did not meet these requirements, they were square root transformed (Sokal and Rohlf 1981). A multivariate ANCOVA of all traits (biomass or tissue N concentration) considered simultaneously was used to explore the significance of the effect of sex, microsite, site, sN, and two-way interactions between them. Subsequently, we used ANCOVA to test for differences in individual plant traits (biomass or tissue N concentration) between sexes (two levels, fixed factor: male or female), microsites (two levels, fixed factor: inside or outside shrub patches), and site (three levels, random factor: BC, LB, or ESL) with N concentration in soil as covariate. For each fixed factor, the mean squares used to test the significance of the factor were a linear combination of the mean squares of interaction fixed factor × random factor and the mean square of the error based on the Type III sum of squares (Norusis 1997). The relationship between plant traits (biomass or tissue N concentration) and sN was described by regression analysis. We selected the best least squares fit between a linear and a nonlinear

Table 4

**Mean Values of Vegetative Aboveground Biomass (g/plant)
by Sex and Site**

Site	Males	Females
ESL	2.49[a]	3.23[b]
LB	2.33[a]	4.11[b]
BC	4.09[b]	4.19[b]

Note.   Different lowercase letters indicate significant differences between means.
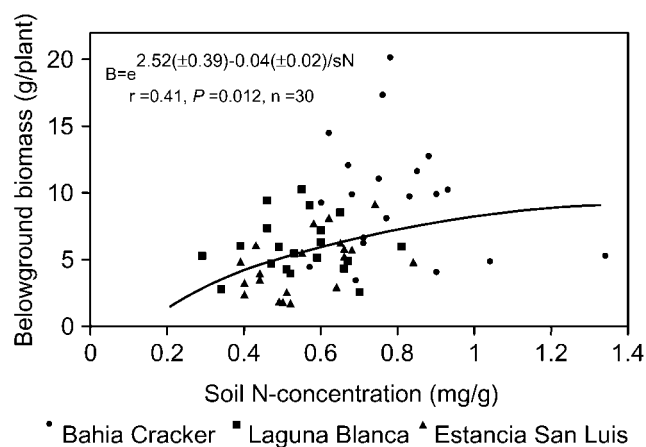

Fig. 2   Belowground biomass of both sexes as a function of the N concentration in the soil. Confidence intervals ($P = 0.05$) shown in parentheses after equation parameters.
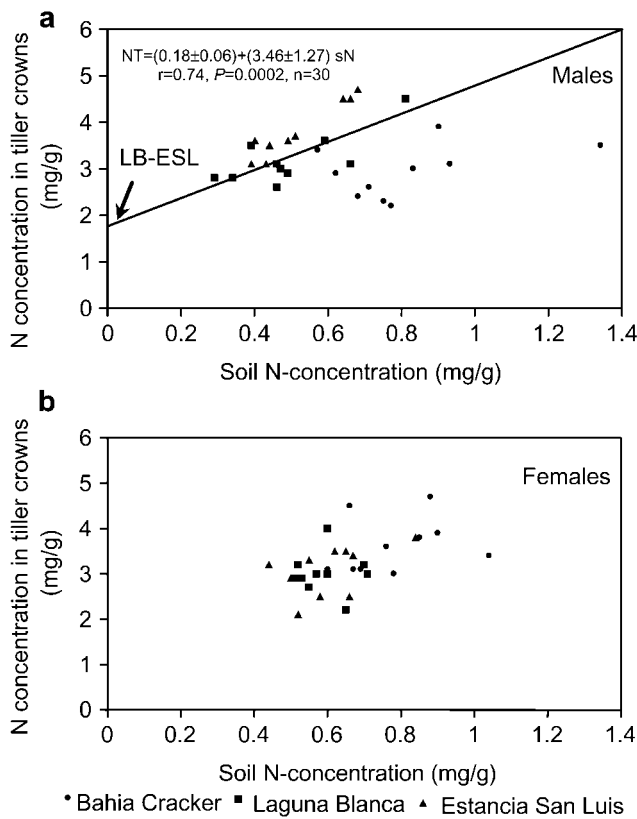
Fig. 3 N concentration in tiller crowns in males (*a*) and females (*b*) as a function of the N concentration in the soil. Confidence intervals ($P = 0.05$) shown in parentheses after equation parameters.

saturation function depending on the shape of the variable response to N soil concentration (Norusis 1997).

Results

Poa ligularis plants were found in soil N concentrations that ranged from 0.29 to 1.34 mg/g (table 1). The highest sN, both inside and outside shrub patches, was found in BC. Soil N values found under *P. ligularis* plants were similar at LB and ESL. All the analyzed factors (sex, microsite, site), the co-variable (sN), and the two-way interactions (sex × sN and sex × site) had significant effects on all plant traits considered simultaneously (table 2). The VA varied between sexes in re-

lation to site and sN (table 3, col. a, significant sex × site and sex × sN interactions). The VA did not differ significantly between sexes in BC. In ESL and LB, however, the VA was significantly lower in males than in females (table 4). The VA changed differently in both sexes in relation to sN. In males, the VA did not vary significantly with changes in sN (fig. 1*a*), whereas in females, it increased significantly with increasing sN (fig. 1*b*). Panicle biomass (P) did not vary significantly among sites in males. In females, P was higher in LB than in ESL and BC (table 3, col. b, significant sex × site interaction; table 5). The belowground biomass (B) changed only in relation to sN (table 3, col. c, significant sex × sN interaction). We did not find effects of microsite, site, sex, or interactions among factors on B. In both sexes, B increased significantly with increasing sN (fig. 2).

The N concentration in the VA (green and dry leaves) and in the culms did not change significantly with sex, microsite, site, sN, or interactions among them (table 3, cols. d, e, and f, respectively). The N concentration in flowers, however, varied between sexes in relation to site (table 3, col. g, significant sex × site interaction). It was significantly higher in males than in females in ESL and BC (table 6). The N concentration in tiller crowns varied between sexes in accordance with site and sN (table 3, col. h, significant sex × site × sN interaction). In males, the N concentration in tiller crowns increased significantly with increasing sN in LB and ESL (the N-poorest sites; fig. 3*a*) while in females, the N concentration in tiller crowns did not change with increasing sN (fig. 3*b*). The N concentration in roots did not vary with site, microsite, sex, or interactions between them (table 3, col. i). In both sexes, the N concentration in roots increased significantly with increasing sN (fig. 4).

Discussion

In female *Poa ligularis*, frequent in N-rich microsites of shrub steppes at northern Patagonia, biomass allocation to vegetative (above- and belowground) structures and N concentration in roots were positively correlated with increases in sN. In males, which are dominant in N-poor microsites, biomass and N concentration responses to increasing sN were restricted to belowground structures, a common trait in plants from nutrient-poor soils (van der Maarel and Titlyanova 1989; Eissenstat 1992; van Breemen 1995; Garnier 1998; Lambers et al. 1998). Increased N concentration in roots with increasing sN may be related to an increase in fine roots (Atkinson 1985; Jackson and Caldwell 1989; Bilgrough and Caldwell 1995; Gordon and Jackson 2000) and, consequently, to an improved capacity to acquire nutrients and water (Fitter 1985, 1998;

Table 5

Mean Values of Biomass (g/plant) by Sex and Site: Culm, Flower, and Panicle (Flower + Culm)

Site	Culm biomass		Flower biomass		Panicle biomass	
	Males	Females	Males	Females	Males	Females
ESL	0.49	0.95	0.65	1.35	1.14[a]	2.30[a]
LB	0.87	1.89	1.12	3.12	1.99[a]	5.01[b]
BC	0.89	0.74	0.80	0.99	1.69[a]	1.73[a]

Note. Different lowercase letters indicate significant differences between means.

Table 6

Mean Values of N Concentration in Flowers (mg/g) by Sex and Site

Site	Males	Females
ESL	18.42[A]	11.86[B]
LB	10.35[B]	11.89[B]
BC	18.61[A]	12.26[B]

Note. Different superscript letters indicate significant differences between means.

Plot equation shown on figure:
$$NR = (0.41 \pm 0.08) + (2.41 \pm 1.21)sN$$
$$r = 0.40, \ P = 0.01, \ n = 30$$

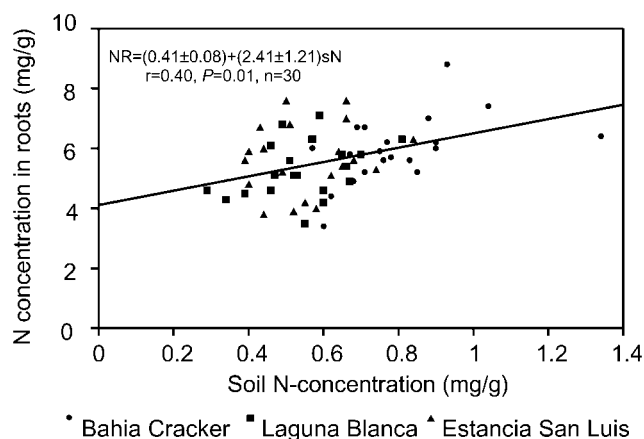Legend: • Bahia Cracker ■ Laguna Blanca ▲ Estancia San Luis

Fig. 4 N concentration in roots of both sexes as a function of the N concentration in the soil. Confidence intervals ($P = 0.05$) shown in parentheses after equation parameters.

dispersal such as those in ESL and LB. These results indicate that microenvironmental variables associated with plant patches, other than sN, also can account for reproductive differential physiological responses of the sexes in *P. ligularis*.

Neither the evidence for physiological adaptation of the sexes in dioecious species with spatial segregation nor the evolutionary origins of sexual dimorphism in flowering plants are well documented (Dawson and Geber 1999). Our results partially support our hypotheses (greater biomass and lower N tissue concentration responses to sN in females than in males) and are in accordance with some trends reported for dioecious species with physiological specialization and spatial segregation of the sexes (Freeman et al. 1976; Bierzchudek and Eckhart 1988; Dawson and Bliss 1989; Dawson and Ehleringer 1993; Dawson and Geber 1999; Geber 1999). The existence of intersexual differences in biomass allocation to aboveground structures and in N allocation to tiller crowns with increasing sN could be the result of different selection processes upon the sexes related to their individual fitness. A consistent female bias in favorable microhabitats and male bias in stressful microhabitats may reflect physiological specialization of the sexes on sites of different resource quality. In this scenario, selection would be expressed on traits related to reproductive costs in females and improved pollen dispersal in males. Selection may favor higher rates of dry matter production and increased offspring vigor in females. In males, selection may be on characters relevant to improve the acquisition of resources in stressful habitats and to gain reproductive advantage in windy interpatch areas by enhanced pollen dispersal (Freeman et al. 1976, 1997; Dawson and Bliss 1989; Geber 1999). Since females show a higher competitive ability over males (Bertiller et al. 2001), our results suggest that functional dimorphism itself contributes to the maintenance of habitat segregation. These alternatives are being explored further in new experiments that take into consideration larger timescales (including several growing seasons) and in manipulative experiments at our sites and/or in greenhouses with controlled climatic conditions and different N levels.

Eissenstat 1992; Lambers et al. 1998). In the N-poorest sites (ESL and LB), males showed higher N allocation to tiller crowns with increasing sN than females, in accordance with general responses observed in plants from stressful habitats (Garnier 1998).

In both sexes, biomass and N allocation to panicles did not change with increasing sN. This contrasts with reported cases in which higher biomass allocation to reproductive structures with increasing nutrient supply in females relative to males were described (Dawson and Geber 1999). Some intersexual differences in biomass and N allocation to reproductive parts found in this study were related to site features other than sN. Sites in this study differ significantly in patch height/radius (LB = ESL > BC), cover (LB = BC > ESL), and in the size of the sheltered areas that they induce (LB > ESL > BC) (Bertiller et al. 2001). At LB, where a markedly spatial segregation of the sexes occurs (Bertiller et al. 2000, 2001), we found higher biomass allocation to panicles in females than in males, probably related to larger patch sheltering effects. We speculate that this could be a consequence of physiological adaptation leading to higher carbon uptake in females compared with males at favorable habitats, as observed in other dioecious species (Dawson and Geber 1999). At ESL and LB where patches are large, we found higher N allocation to flowers in males than in females or in males growing at BC. The dispersal of N-rich pollen with eventual higher performance (Bertin 1988) could represent an important adaptive trait for improving male performance in habitats with restricted pollen

Acknowledgments

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