Research article

Abiotic factors affect the recruitment and biomass of perennial grass and evergreen shrub seedlings in denuded areas of Patagonian Monte rangelands

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ABSTRACT

Assessing the ability of key species to cope with environmental stresses in disturbed areas is an important issue for recovery of degraded arid ecosystem. Our objective was to evaluate the effect of soil moisture, exposure to UV radiation, and presence/absence of litter with different chemistry on soil N, recruitment and biomass of seedlings of perennial grass (*Poa ligularis* and *Nassella tenuis*) and evergreen shrub species (*Atriplex lampa* and *Larrea divaricata*) in denuded areas. We carried out a microcosm experiment with soil blocks (28 cm depth) sowed with seeds of the target species, subjected to different levels of litter type (perennial grass-evergreen shrub mixture, evergreen shrub mixture, and no litter), UV radiation (near ambient and reduced UV), and soil water (high: 15–25% and low 5–15%). Periodically, during 6 months, we assessed soil-N (total and inorganic) at two depths and species seedling recruitment at microcosms. Additionally, emerged seedlings of each species were transplanted to individual pots containing soil and subjected to the same previous factors during 12 months. Then, all plants were harvested and biomass assessed. Only inorganic soil-N at the upper soil varied among treatments increasing with the presence of evergreen shrub litter, exposure to ambient UV, and high soil water. Inorganic soil-N, promoted by near ambient UV and high soil water, had a positive effect on recruitment of perennial grasses and *A. lampa*. Both litter types promoted the recruitment of perennial grasses. Evergreen shrub litter and high soil water promoted the recruitment of *L. divaricata*. Seedling biomass of perennial grasses increased with high soil water and reduced UV. Ambient UV had positive or null effects on biomass of evergreen shrub seedlings. High soil water increased biomass of *L. divaricata* seedlings. We concluded that soil water appeared as the most limiting factor for seedling recruitment of all species whereas inorganic soil N limited the recruitment of the small-seeded perennial grasses and *A. lampa*. Ambient UV had negative effects on seedling biomass of perennial grasses. These complex relationships among abiotic factors and seed and plant traits should be taken into account when planning management actions after disturbances.

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1. Introduction

Livestock grazing affects the structure and functioning of plant communities in arid and semiarid rangelands, shifting vegetation from stable states with high cover of perennial grasses to alternative stable states dominated by shrubs or annual species with a significant increase in the size of denuded areas (Ares et al., 1990; Bestelmeyer et al., 2015; Fick et al., 2016; Milchunas and Lauenroth, 1993; Okin et al., 2009). In this context abiotic drivers are relevant and ecosystem changes may be difficult or impossible to reverse towards desirable states without an active human intervention (Fick et al., 2016; James et al., 2012, 2013).

Plant regeneration by seeds is an essential process to restore plant species diversity, and community structure and dynamics in disturbed arid ecosystems of the world where the majority of plant species reproduce by seeds (Bertiller and Carrera, 2015; Grime and Hillier, 2000; Larson et al., 2015). Accordingly, seed availability across space and time is the first step for plant cover recovery in these environments (De Falco et al., 2009; Fick et al., 2016). A

second step is that seeds reach safe microsites for germination and plant establishment (Bertiller and Carrera, 2015; Fick et al., 2016; Larson et al., 2015). The early stages in plant development are expected to be more sensitive to environmental variability than adult stages, and consequently represent a major constraint for plant regeneration processes (Walk et al., 2011; Wellstein, 2012). Early processes such as seedling emergence may have different abiotic drivers that those leading to the later seedling survival and biomass accumulation (Fay and Schultz, 2009; Lloret et al., 2004).

The increase in the size of denuded areas due to disturbance is associated with a major incidence of abiotic factors over biotic factors related to the established vegetation such as the facilitation/competition balance (Fick et al., 2016; Mollard et al., 2014; Schlesinger et al., 1990). Negative interactions with established plants may constitute a main biotic control for plant reestablishment processes in small soil gaps or vegetated areas (Funk et al., 2008; Hulvey and Aigner, 2014; Luzuriaga et al., 2012) where microclimatic conditions, soil resources (water, nutrients), and protection from herbivores are more favorable than in denuded areas for seedling emergence and survival, and biomass accumulation (Barberá et al., 2006; Bertiller et al., 2002; Mollard et al., 2014; Smit et al., 2006).

Litter accumulation on the soil surface could improve the microenvironmental conditions in denuded areas since this layer may reduce soil temperature fluctuation, and increase soil water conservation, microbial activity and nutrient levels thus promoting plant regeneration processes (Loydi et al., 2013; Xiong and Nilsson, 1999). However, the presence of litter could have facilitative to inhibitory effects on seedlings depending on either the amount (physical effect) or the chemical properties (Hovstad and Ohlson, 2008; Rotundo and Aguiar, 2005). Additionally, C/N ratios or the presence of secondary compounds in litter could influence microbial litter decomposition thus favoring either microbial N release or N immobilization processes (Arriaga and Maya, 2007; Bosco et al., 2016; Gartner and Cardon, 2004). However, litter N dynamics in arid ecosystems may be decoupled from microbial processes due to abiotic processes such as photo-degradation (Brandt et al., 2010; Parton et al., 2007). Decomposition and N release processes in litter layers, depending on their chemistry, may be differentially affected by abiotic factors such as soil water content and exposition to UV radiation (Bosco et al., 2016) with different effects on seedling establishment.

The success of plant survival in contrasting soil microsites may differ among different plant species depending on their functional traits (Gilardelli et al., 2015; Navas et al., 2010). Perennial grasses and shrubs are the dominant plant life forms in arid ecosystems (Bär Lamas et al., 2016; Navas et al., 2010). In general, perennial grasses are opportunistic species with shallow rooting depth and active growth usually coupled with water inputs in the upper soil whereas shrubs with deep or dimorphic root systems and high diversity of structural and chemical defenses against water shortage, UV radiation exposure and herbivory develop vegetative growth decoupled from water inputs (Bertiller et al., 1991; Carrera et al., 2003; Navas et al., 2010). Therefore, shrub species may be better able to colonize large denuded areas with low fertility and harsh microclimatic conditions than perennial grass species (Bertiller and Bisigato, 1998). However, species of the same life form in arid environments may have differences in functional traits among them (Bär Lamas et al., 2016). Moreover, some studies found adaptive or plastic differences in functional traits within the same perennial grass species in arid environments (Moreno and Bertiller, 2015; Valladares et al., 2007).

Knowledge about the capabilities of different key species to cope with environmental filters imposed by land degradation after disturbance is an important issue in relation to the recovery of degraded areas in arid ecosystems (James et al., 2011; Madsen et al., 2016) but this topic still remains as one main issue of research in restoration ecology (Gilardelli et al., 2015; Hulvey and Aigner, 2014; Larson et al., 2015). The aim of this study was to evaluate the capability of seedlings of dominant species of the main plant life forms in arid ecosystems (perennial grasses and evergreen shrubs) to cope with different abiotic environments (conditioned by soil moisture, exposure to UV radiation, and presence/absence of litter mixtures with different chemistry) in areas denuded by disturbances. We hypothesized that differences in seedling recruitment and biomass accumulation induced by different abiotic scenarios in the regeneration microsites will be less between species of the same life form than between life forms (Fig. 1). We predicted that soil water content has a direct effect on plants promoting recruitment and growth of perennial grass species while evergreen shrub species are less dependent of this factor. Soil water content exert an indirect effect on recruitment and growth throughout litter decomposition mediated by microbial activity with higher soil water content promoting soil microbial activity. The incidence of UV radiation impacts directly on seedling recruitment and growth with negative effects on perennial grass species (low concentration of protective compounds) but with negligible effects on evergreen shrub species (high concentration of protective compounds), while impacts indirectly on both life forms throughout litter photo-degradation. Litter presence has a direct positive effect on seedling recruitment of perennial grass species by improving seedbed microclimate conditions while bare soil impacts negatively on this life form. The presence or absence of litter has lower impact on evergreen shrub than on perennial grass species. Litter chemistry modulates soil N availability, being recruitment and growth of perennial grass species higher dependent on soil N availability than evergreen shrub species. Litter with low C/N ratio and high concentration of secondary compounds (- C/N; + secondary compounds) releases inorganic N to soil throughout microbial activity while litter with high C/N ratio and low concentration of secondary compounds (+C/N, - secondary compounds) immobilizes N in microbial biomass.

2. Materials and methods

2.1. Study area and species

The study area is located in the southern portion of the Monte Phytogeographical Province (Patagonian Monte), Argentina. Mean annual temperature is 13.4 °C, mean annual precipitation is 235.9 mm and mean annual speed of wind (prevailing from west-southwest) is 4.6 m s^{-1} (22-year average, Centro Nacional Patagónico, 2009). Soils are a complex of Typic Haplocalcids and Typic Petrocalcids (del Valle, 1998; Soil Survey Staff, 1998). Vegetation corresponds to the shrubland of *Larrea divaricata* Cav. and *Stipa* spp. (León et al., 1998). Perennial grasses and shrubs are the main plant life forms and are arranged in a patchy structure (dominated by shrubs) covering less than 40% of the soil alternating with denuded areas (Bertiller and Ares, 2011). Within this area, we selected six representative study sites of at least 3 ha each (minimal area *sensu* Mueller-Dombois and Ellenberg, 1974) with large denuded areas (>2 m in diameter without vegetation cover) induced by sheep grazing (43° 06′ 13.4S; 65° 43′51.3W; 150 m a.s.l.; 43° 08′ 52.0S, 65° 42′49.6W; 151 m a.s.l., 42° 11′ 38.7S, 64° 59′ 37.3W; 75 m a.s.l.; 42° 12′ 27.8S, 64° 59′ 34.5W; 94 m a.s.l. and 42° 12′ 13.7S, 64° 58′ 55.6W; 92 m a.s.l.) or fire disturbances (42° 49′ 15.6S, 65° 00′ 24.5W; 63 m a.s.l.). Additionally, we selected a further study site characteristic of the Patagonian Monte located at 42° 47′ 10.4S, 65° 00′28.2W; 5 m a.s.l. to perform the manipulative experiments. This site was characterized by large denuded areas
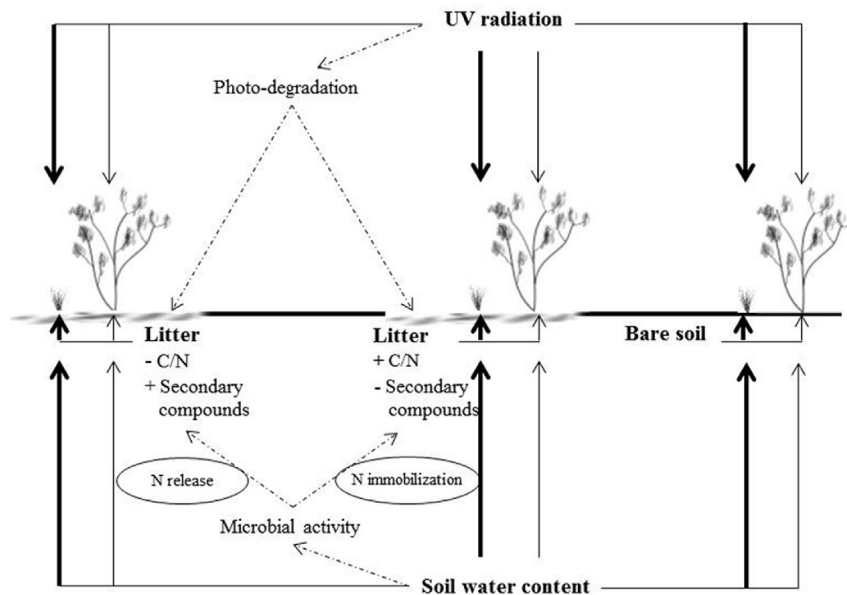
Fig. 1. Conceptual model for direct (solid lines) and indirect (dotted lines) effects of abiotic factors on seedling recruitment and growth of perennial grass and evergreen shrub species. The thickness of the arrows indicates the size of the effect.

generated by anthropic disturbance through the patchy removal of vegetation. In this experimental site, we selected six large (>5 m in diameter) bare soil areas.

For this study, we selected four dominant plant species which are abundant in the conserved areas of the Patagonian Monte, three species highly preferred by grazers: two species of perennial grasses (*Poa ligularis* Nees ex Steud and *Nassella tenuis* (Phil.) Barkworth) and the evergreen shrub *Atriplex lampa* Gill. ex Moq and one non preferred species (*Larrea divaricata*) (Bertiller et al., 1991). The selected perennial grasses are fast growing species that produce short lifespan tissues with low concentration of secondary compounds and usually prosper in microsites with high soil resources availability (Campanella and Bertiller, 2008; Carrera et al., 2005). The selected evergreen shrubs are slow growing species with high concentration of chemical defenses against herbivory and water shortage (Bertiller et al., 2006; Moreno et al., 2010).

2.2. Sampling

Within the study area, we collected seeds of the four dominant species (*P. ligularis, N. tenuis, A. lampa* and *L. divaricata*) during the seed dispersal period (spring/summer 2011/2012) at different sites and pooled them by species. Additionally, we randomly selected 12 plant patches dominated by evergreen shrubs and 12 plant patches dominated by both perennial grasses and evergreen shrubs at each study site and collected the litter accumulated on the soil surface up to 2 cm underneath each patch canopy within a plot (30 × 40 cm). The litter collected was cleaned of attached soil particles with a brush, pooled into one sample per patch type, homogenized by mixing, and dried at 45 °C for 48 h. Litter from evergreen shrub dominated patches (ESL) mostly consisted in a mixture of leaves and fine woody stems of evergreen shrub species, predominantly *L. divaricata*. Litter from perennial grass and evergreen shrub dominated patches (PGL) consisted in a mixture dominated by leaves of perennial grasses (*N. tenuis*) accompanied by leaves of different species of evergreen shrubs. Litter chemistry of each litter mixture was assessed using the protocols followed by Bertiller et al.

(2006). The litter mixture from ESL had higher concentrations of N, soluble phenols and lignin and lower C/N ratio (24.5 ± 0.6 mg g^{-1}, 11.8 ± 0.8 mg g^{-1}, 198.8 ± 11.4 mg g^{-1} and 15.5 ± 0.4, respectively) than litter mixtures from PGL (9.1 ± 0.2 mg g^{-1}, 5.1 ± 0.4 mg g^{-1}, 113.3 ± 14.4 mg g^{-1} and 48.9 ± 1.6, respectively). Finally, we selected 12 denuded areas (>2 m in diameter) at each study site and extracted one block of the upper soil (30 cm × 40 cm × 14 cm deep) without altering its structure burying a sharp metal frame and the sub-superficial soil (30 cm × 40 cm × 14−28 cm deep) corresponding to each block with a shovel. Blocks of the surface soil and the collected sub-superficial soil from each denuded area were placed in individual waterproof wooden boxes (30 cm × 40 cm × 28 cm deep) reconstructing the soil stratigraphy (microcosm) resulting in 12 microcosms per study site.

2.3. Seedling recruitment and soil N microcosms experiment

We performed a factorial microcosm experiment to evaluate the simultaneous effect of litter type (three levels), UV radiation (two levels) and soil water (two levels) on total and inorganic ($NH_4^+ + NO_3^-$), soil nitrogen (N) concentration and on plant recruitment of the selected species (Fig. 2a). Accordingly, one set of microcosms (6 microcosms) from each study site was submitted to a reduced UV radiation treatment by covering them with a Mylar-D polyester filter (Dupont) blocking 55% of incident UV-A, 85% of incident UV-B (280−400 nm) and 15% of PAR (Re-UV). The other set (6 microcosms) was submitted to near ambient UV radiation treatment by covering them with an Aclar fluorocarbon plastic filter (Allied chemical) which transmitted approximately 85% of the incident UV-A, UV-B and PAR (Am-UV). Filters were supported by a PVC structure placed 40−45 cm above the soil surface of the microcosms (Mylar and Aclar, respectively) and both excluded natural precipitation. Spectral properties of both filters were monitored twice a month in cloudless days at the same hour (13:30 h) with a radiometer SKYE SpectroSense 2 and periodically cleaned or replaced to avoid changes in their spectral properties. During the experiment, values of UV-A and UV-B radiation under Re-UV treatment were lower ($p \leq 0.05$) than under Am-UV while there
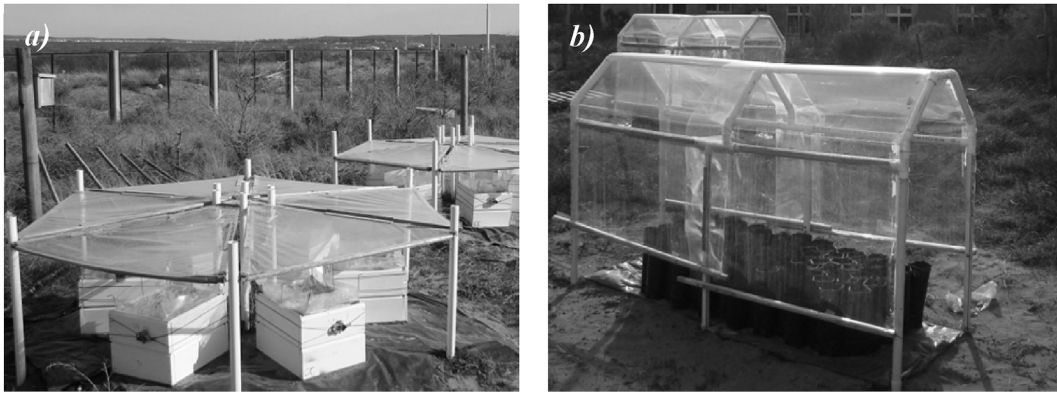
Fig. 2. View of *a)* seedling recruitment and soil N, and *b)* seedling growth experiments.

were no differences in PAR transmittance among filters ($p > 0.05$). Temperature under both filters was hourly monitored with iButton Thermochron sensors model 1921G (Maxim Integrated Products Incorporated, Sunnyvale, CA, U.S.A.). We did not find significant differences in mean soil temperatures between filters across the study period ($p > 0.05$). At each set (6 microcosms), two microcosms were submitted to the effect of litter cover of evergreen shrub dominated patches (ESL), other two to the effect of litter cover of perennial grass and evergreen shrub dominated patches (PGL) and the last two microcosms remained as controls without litter (no litter cover: NL). Previous to litter addition, the surface of all microcosms was cleaned from superficial litter. After that, the surface of each microcosm was divided into 48 cells of 5 cm × 5 cm each. About 1 g of litter per cell, either ESL or PGL litter was added to the respective litter treatment. This litter amount is equivalent to the litter mass on the soil surface reported in the study area ($350-400$ g m^{-2}) (Carrera and Bertiller, 2010) and in other arid and semiarid ecosystems (Eckstein and Donath, 2005). One of the microcosms of each litter treatment was submitted to high soil volumetric water content (range $15-25\%$; HSW) and the other microcosm was subjected to low soil volumetric water content (range $5-15\%$, LSW). These levels of volumetric soil water content corresponded to the mean values of soil moisture assessed in the study area in fall-winter (wet season) and spring-summer (dry season), respectively (Coronato and Bertiller, 1997). The soil water level at each microcosm was controlled every two or four days depending on the season with an IMKO TDR probe. The microcosm surface was homogeneously watered with tap water when needed (i.e. when soil volumetric water content reach the lowest value of the respective treatment) using a manual sprinkler.

Finally, at each microcosm, we randomly assigned 4 cells per species (16 cells per microcosm) and sowed between 4 and 6 seeds per cell and species (*P. ligularis, N. tenuis, A. lampa* and *L. divaricata*) below the litter cover. In cells of the NL treatment, seeds were slightly buried to avoid removal by wind. Seeds were sown in January 2013 and in August 2013 seedlings with the first true leaf fully expanded, considered as established seedling (Fenner and Thompson, 2005), were recorded. Recruitment was calculated as the percentage of seedlings established relative to the seeds sown. The remaining 32 cells per microcosm (without seeds) were used to evaluate total and inorganic soil N ($NH_4^+ + NO_3^-$) concentration. We randomly selected a cell and extracted a soil sample from 0 to 5 and from 5 to 28 cm depth at each microcosm at 2, 4 and 7 months from the beginning of the experiment (1, 2 and 3 sampling dates respectively). The last soil extraction date was 20 days after seedling harvest. Samples were taken with a 2 cm diameter soil core tool. After extraction, soil samples were placed into a plastic bag, transported to the laboratory and fresh soil samples sieved to pass a

2 mm mesh. We extracted a subsample of 5 g in 25 ml of KCl 1M (1:5 soil:solution ratio) and assessed N–NH_4^+ by the indophenol-blue method and N–NO_3^- by the copperised Cd reduction method (Keeney and Nelson, 1982) with an SkalarSan auto-analyzer. Soil inorganic N concentration was expressed on the basis of oven-dried soil (105 °C for 48 h). Total soil-N concentration was determined via combustion on a LECO-CN628 analyzer.

2.4. Seedling growth experiment

We performed a factorial experiment in pots to evaluate the simultaneous effect of litter type (three levels), UV radiation (two levels) and soil water (two levels) on the biomass of the established plants of the four selected species. For this purpose, sixty emerged seedlings per species (1 seedling per pot) were transplanted to black polyethylene pots (40 cm height and 12 cm of diameter) filled with 4.5 kg of a mix of superficial soil ($0-15$ cm) from the study sites. Pots were maintained at field capacity in a greenhouse until the seedlings reached two true fully expanded leaves (established seedlings). From this moment, pots were subjected to the same conditions as in the recruitment experiment (three levels of litter type, two levels of UV radiation, and two levels of soil water content). For doing this, we constructed two pairs of PVC structures of 130 cm height and 80 cm width. One pair of the structures was covered with Mylar-D polyester filters (Dupont) (Re-UV) and the other pair of structures was covered with Aclar fluorocarbon plastic filters (Allied chemical) (Am-UV). These structures excluded natural precipitation. Fifteen pots per species were placed under each structure and five of them were randomly assigned to a different litter level (litter dominated by evergreen shrubs (ESL), litter dominated by perennial grasses and evergreen shrubs (PGL) and no litter addition (NL)). Litter was added in the same proportion than in recruitment experiment ($350-400$ g m^{-2}). Finally, one structure of each UV radiation level was submitted to high soil volumetric water content (range $15-25\%$, HSW) and the other was submitted to low soil volumetric water content (range $5-15\%$, LSW). The experiment lasted one year (from May 2014 to May 2015) (Fig. 2b). During the experiment, volumetric soil water content, UV radiation filter spectral properties and superficial soil temperature of pots were controlled with the same instruments and methodology used in the species recruitment experiment. At the end of the experiment, total biomass (above + belowground biomass) of each juvenile plant was harvested, briefly cleaned with tap water, dried at 45 °C for 48 h and weighted.

2.5. Data analysis

We used a paired *t*-test to compare initial chemistry (N, C/N,

soluble phenolics and lignin) between litter types. The significance of the differences in total and inorganic soil N concentration at each extraction date among treatments was assessed by three-way ANOVA, including litter, UV radiation, soil water content as fixed factors and their interactions. Tukey's test was used for multiple comparisons between treatments. ANOVA assumptions were tested before analyses and soil inorganic N was logarithmically transformed to meet ANOVA assumptions at date 2 and 3. The significance of the differences in the proportion of seedlings recruitment of perennial grass and evergreen shrub species among single and combined factor levels was analyzed by a Generalized Linear Model (GLM) with binomial distribution and logit link function (McCullagh and Nelder, 1989). In this model, seedling recruitment was the dependent variable, species (nested within plant life form), litter, soil water content and UV radiation were included as factors and soil inorganic N concentration was included as a continuous covariate. Akaike's information criterion (AIC) was used to compare models, and the model with the minimum AIC was selected as the best fit estimator. LSD test was used for multiple comparisons between treatments. Relationships between soil inorganic N concentration and seedling recruitment by species were tested by linear regression models.

The significance of differences in total plant biomass among single and combined factor levels was analyzed by GLM with normal distribution and identity link function. Robust indicator for the covariance matrix was used as there was not homogeneity of variances. In these models, total biomass was the dependent variable while species (nested within plant life form), litter, soil water content and UV radiation were included as factors. AIC was used to compare models, and the model with the minimum AIC was selected as the best fit estimator. LSD test was used for multiple comparisons between treatments.

3. Results

3.1. Total and inorganic soil N concentration

Total soil N concentration (soil-N_t) did not vary among treatments at any depth (0–5 and 5–28 cm) and sampling date ($p > 0.05$; data not shown). We found significant ($p \leq 0.05$) effects of single factors on soil inorganic N concentration (soil-N_i: $NO_3^- + NH_4^+$) but we did not find significant effects of combined factors on this variable at any soil depth and sampling date ($p > 0.05$). Soil-N_i at 0–5 cm depth varied significantly ($p \leq 0.05$) with the effect of single factors at the second and third date while values at 5–28 cm depth did not vary at any date ($p > 0.05$; Table S1). Litter type significantly ($p \leq 0.05$) affected soil-N_i at 0–5 cm depth at sampling dates 2 and 3, with the highest values at the soil underneath litter dominated by evergreen shrubs (ESL) (Fig. 3a). Soil-N_i varied significantly ($p \leq 0.05$) with soil water content only at sampling date 2, being ca. 100% higher at high (HSW) than at low (LSW) soil water content (Fig. 3b). The exposure to near ambient UV radiation (Am-UV) significantly ($p \leq 0.05$) enhanced soil-N_i concentration at sampling date 2 and 3 (Fig. 3c).

3.2. Seedling recruitment

Seedling recruitment ranged between 0 and 33% depending on species and treatments (*P. ligularis*: 0–28%, *N. tenuis*: 3–33%, *A. lampa*: 1–14% and *L. divaricata*: 0–5%; Table S2a). Among factors, soil inorganic N (soil-N_i: $NO_3^- + NH_4^+$) had a significant ($p \leq 0.05$) and positive effect on seedling recruitment (Table 1a) being this effect highly significant ($p \leq 0.05$) on seedling recruitment of both perennial grass species (*P. ligularis* and *N.* tenuis) and the evergreen shrub *A. lampa* (Fig. 4a, b, and c, respectively) and marginal
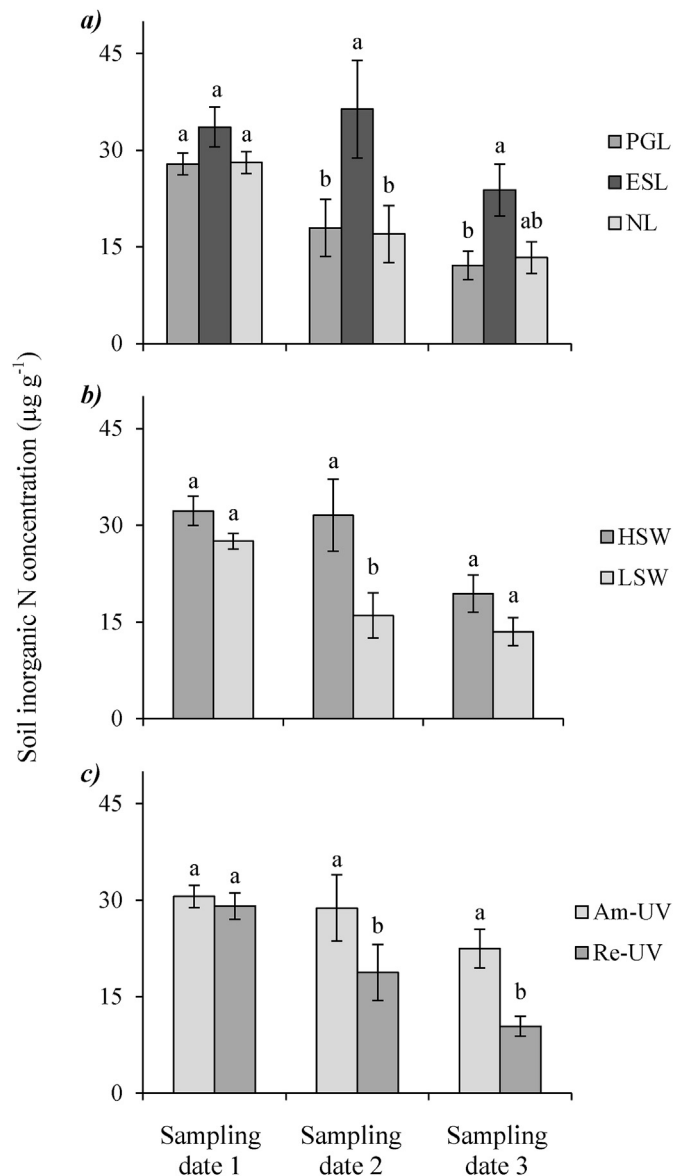
Fig. 3. Mean values ± 1 SE of soil inorganic N ($NO_3^- + NH_4^+$) concentration (μg g^{-1}) by sampling dates at microcosms with *a)*, perennial grass and evergreen shrub litter (PGL), litter dominated by evergreen shrubs (ESL) and no litter cover (NL); *b)* high and low soil water content (15–25%: HSW and 5–15%: LSW, respectively), and *c)* exposure to near ambient UV radiation (Am-UV) and reduced UV radiation (Re-UV). Different letters indicate significant differences (Tukey's test; $p \leq 0.05$) in soil inorganic N concentration between levels of each factor.

($p > 0.05$) on seedling recruitment of *L. divaricata* (Fig. 4d). Among species, *P. ligularis* was the most responsive to soil-N_i levels ($p \leq 0.01$). Seedling recruitment was also affected by the combined effects of species (nested within life forms), soil water, litter type, and UV radiation ($p \leq 0.05$) (Table 1a). Seedling recruitment of *P. ligularis* was mostly affected by litter type showing the lowest recruitment in the treatment without litter addition (NL) irrespectively of the soil water levels (Fig. 5a). Seedling recruitment of *N. tenuis* was enhanced by the combination of PGL and HSW (Fig. 5b). Seedling recruitment of the evergreen shrub *A. lampa* was not affected by the combined effect of litter and soil water content (Fig. 5c) while that of *L. divaricata* was enhanced by the combination of ESL and HSW (Fig. 5d). The recruitment of both perennial grass species (*P. ligularis* and *N. tenuis*) and the evergreen shrub *A. lampa* was also promoted by the exposure to near ambient UV

Table 1
Results of the generalized linear model (GLM) for effects of soil inorganic N, litter, soil water, UV radiation and species (nested within plant life form) on **a)** seedling recruitment and on **b)** total plant biomass of perennial grass and evergreen shrub species.

	a) Seedling recruitment			b) Total plant biomass		
	χ^2	d.f.	p-value	χ^2	d.f.	p-value
Soil-N_i (NO_3^- + NH_4^+)	5.22	1	**0.02**	–	–	–
Litter	6.52	2	**0.04**	27.36	2	**0.00**
Soil water	0.00	1	1.00	207.00	1	**0.00**
UV radiation	0.00	1	1.00	5.57	1	**0.02**
Species (life form)	35.19	3	**0.00**	508.78	3	**0.00**
Species (life form) × litter	7.32	6	0.29	27.36	2	**0.00**
Species (life form) × soil water	13.38	3	**0.00**	39.87	3	**0.00**
Species (life form) × UV radiation	5.87	3	0.12	15.88	3	**0.00**
Species (life form) × soil water × litter	18.24	8	**0.02**	14.86	8	0.06
Species (life form) × UV radiation × litter	4.15	8	0.84	18.67	8	**0.02**
Species (life form) × UV radiation × soil water	15.19	4	**0.00**	20.00	4	**0.00**

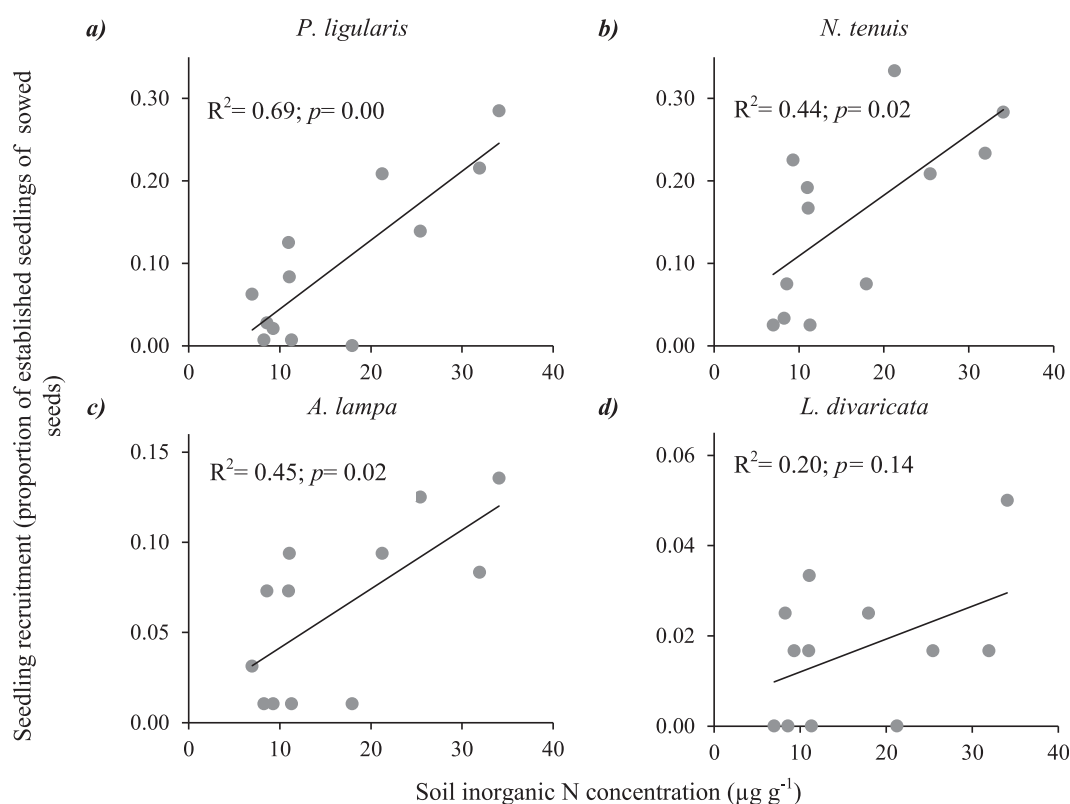Bold values indicate significant effects ($p \leq 0.05$).

Fig. 4. Linear regression between soil inorganic N (NO_3^- + NH_4^+) concentration (µg g^{-1}) and seedling recruitment (proportion of established seedlings of sowed seeds) of perennial grass species: **a)** P. ligularis and **b)** N. tenuis; and evergreen shrub species: **c)** A. lampa and **d)** L. divaricata.

radiation (Am-UV) irrespective of the soil water level (Fig. 5e, f, and g). The recruitment of *L. divaricata* was not significantly affected by the combined effect of soil water content and UV radiation levels although it was null under LSW and Re-UV (Fig. 5h).

3.3. Plant biomass

Plant biomass ranged between 4.3 and 38.4 g depending on species and treatments (*P. ligularis*: 14.9–38.4 g, *N. tenuis*: 9.8–19.2 g, *A. lampa*: 6.3–20.6 g and *L. divaricata*: 4.3–11.3 g; Table S2b). Plant biomass was affected by the interaction among single factors (species, litter, exposure to UV radiation, soil water content) ($p \leq 0.05$) (Table 1b). The plant biomass of *P. ligularis* was significantly reduced by Am-UV only in presence of ESL although this trend was observed in the other litter levels (PGL and NL)

(Fig. 6a). The plant biomass of *N. tenuis* was significantly reduced by Am-UV in presence of PGL and NL without effect of UV levels under ESL (Fig. 6b). Total biomass of *A. lampa* was enhanced by the combined effect of Am-UV and PGL with the same trend (marginal) with Am-UV and ESL (Fig. 6c). The combined effect of litter and UV radiation did not affect the plant biomass of *L. divaricata* (Fig. 6d). Plant biomass of both perennial grass species was enhanced by HSW and Re-UV radiation exposure (Fig. 6e and f) while that of *A. lampa* was only negatively affected by Re-UV radiation under LSW (Fig. 6g). Plant biomass of *L. divaricata* was only affected by soil water content at both levels of exposure to UV radiation (Fig. 6h).

4. Discussion

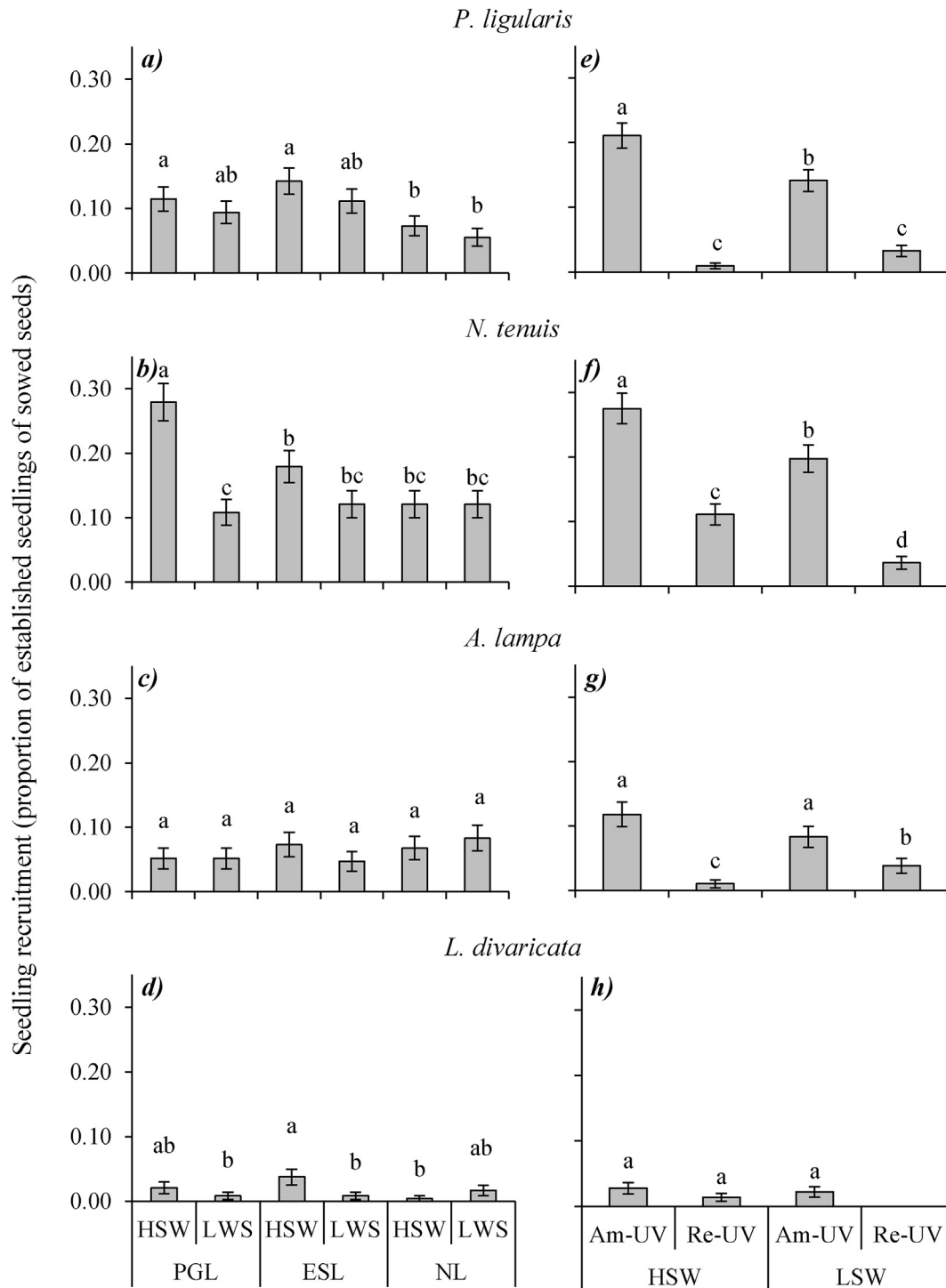The development of a practical guidance for plant and

Fig. 5. Mean values ± 1 SE of seedling recruitment (proportion of established seedlings of sowed seeds) of perennial grass (*P. ligularis* and *N. tenuis*) and evergreen shrub (*A. lampa* and *L. divaricata*) species under the combined effects of litter type (perennial grass and evergreen shrub litter: PGL; litter dominated by evergreen shrubs: ESL and no litter: NL) and high and low soil water content (15–25%: HSW and 5–15%: LSW) factors (*a*) to *d*)) and under the combined effects of high and low soil water content and exposure to UV radiation (near ambient UV radiation: Am-UV and reduced UV radiation: Re-UV) factors (*e*) to *h*)). Different letters indicate significant differences (LSD test; $p \leq 0.05$) on seedling recruitment among combined treatments.

ecosystem function restoration requires of knowledge about the ecology of key species and their performance in disturbed environments (James et al., 2011; Larson et al., 2015; Svejcar et al., 2014). The life form approach has been extensively used to describe plant responses to disturbances in arid ecosystems (Bernhardt-Römermann et al., 2011; Díaz et al., 2007; Gilardelli

et al., 2015; Grime, 1977). However, contrary to our expectations, our results showed that responses in plant recruitment and biomass accumulation of seedlings in disturbed bare soil patches conditioned by different levels of soil water, UV radiation, and litter varied among species irrespective of the life form. Inorganic soil N independently of the other abiotic factors enhanced the seedling
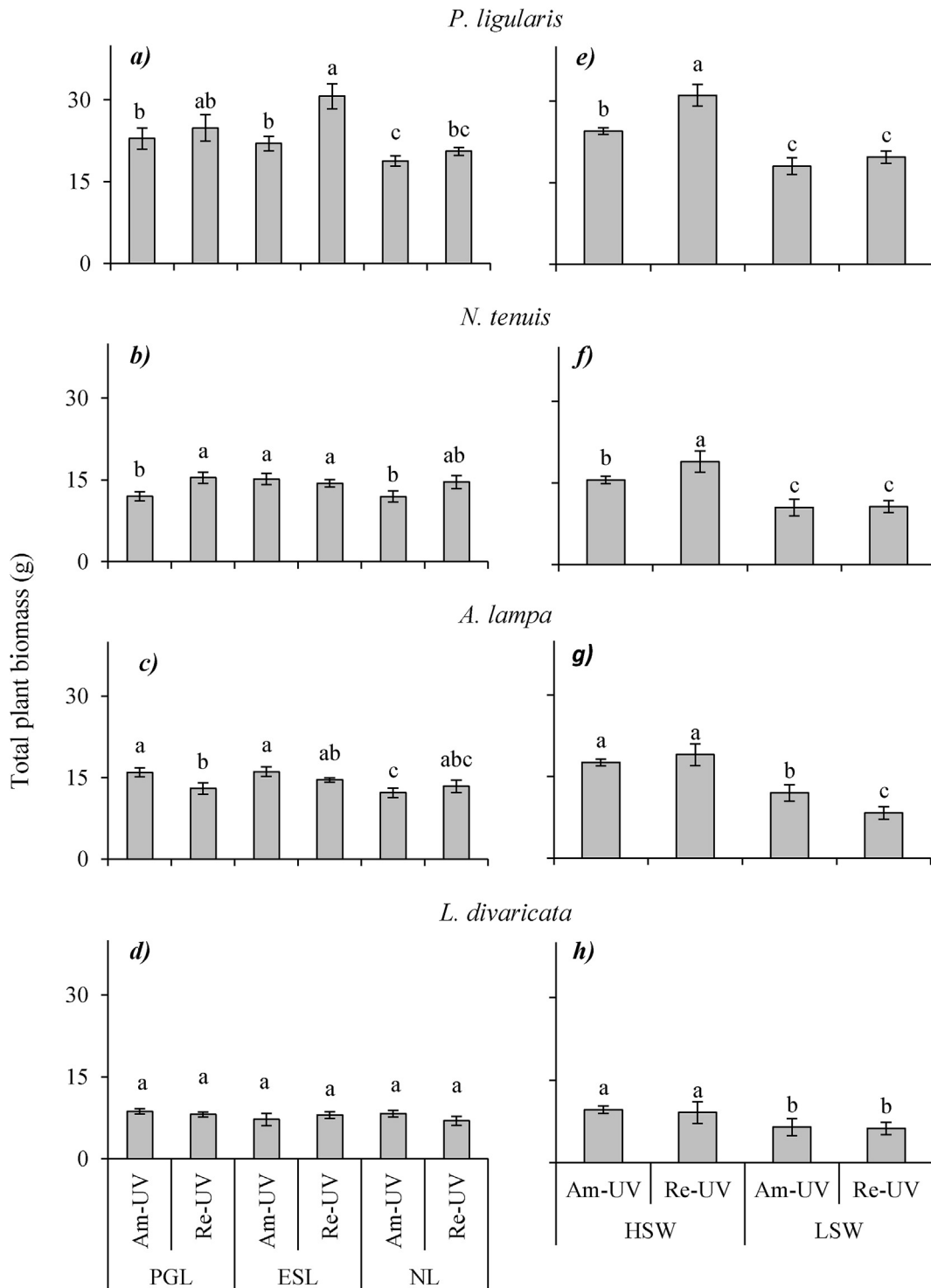
Fig. 6. Mean values ± 1 SE of total plant biomass (g) of perennial grass (*P. ligularis* and *N. tenuis*) and evergreen shrub (*A. lampa* and *L. divaricata*) species under the combined effects of litter type (perennial grass and evergreen shrub litter: PGL; litter dominated by evergreen shrubs: ESL and no litter: NL) and UV radiation (near ambient UV radiation: Am-UV and reduced UV radiation: Re-UV) factors (*a)* to *d)*) and under the combined effects of high and low soil water content (15–25%: HSW and 5–15%: LSW) and UV radiation factors (*e)* to *h)*). Different letters indicate significant differences (LSD test; $p \leq 0.05$) on total plant biomass among combined treatments.

recruitment of both perennial grass species (*P. ligularis* and *N. tenuis*) and the evergreen shrub *A. lampa*, while its effect was less evident in the case of *L. divaricata*. As we expected, soil inorganic N was influenced by the three abiotic factors considered in our study (presence/absence of litter mixtures with different chemistry, soil water content, and UV radiation exposure). Nitrogen dynamics in

arid and semi-arid ecosystems is primarily regulated by microbial activity, which is strongly dependent on microbial stoichiometry, and by high levels of UV radiation enhancing photodegradation processes (Manzoni et al., 2010; Parton et al., 2007). In our study, litter mixtures dominated by evergreen shrubs (ESL), with the lowest C/N ratio, released the greatest amount of inorganic N to the

soil during the decomposition process. In contrast, litter dominated by a mixture of perennial grass and evergreen shrub species (PGL), with the highest C/N ratio released the lowest amount of inorganic N to the soil with values comparable to those levels found in the soil without litter. This could be attributed to high N retention in microbial biomass during decomposition due to high C/N ratio in this litter (Bosco et al., 2016; Parton et al., 2007; Wardle, 2002). Additionally, exposure to UV radiation through photodegradation processes and soil water positively affected inorganic N release in both litter types as observed in other arid ecosystems (Austin et al., 2004; Parton et al., 2007). Moreover, the lack of differences in soil inorganic N concentration between high and low soil water levels at the end of the experiment may be the result of the accumulation of dead microbial biomass during the dry periods and the subsequent high inorganic N release from decaying microbial biomass with readily mineralizable N, due to low C/N ratio, during wet periods (Austin et al., 2004; Cui and Caldwell, 1997).

Our results contrast to other studies showing differential responses in the early establishment of species with different ecological strategies in relation to increasing inorganic N in soil (Kitajima and Fenner, 2000; Salonen and Setälä, 1992). We suggest that the similar recruitment responses between perennial grass species and the evergreen shrub *A. lampa* may be related to the similar size of their seeds contrasting to recruitment response to soil inorganic N in the large-seeded *L. divaricata* (Correa, 1978). In this sense, the early establishment of small-seeded species may be highly dependent on external N sources immediately after emergence (Kitajima and Fenner, 2000; Moles and Westoby, 2004) while the decelerated response of *L. divaricata* recruitment to soil inorganic N could be associated with larger nutrient reserves in seeds than the former (Fenner and Thompson, 2005; Moles and Westoby, 2004). Similarly to soil N, UV exposure had a positive effect on seedling recruitment of perennial grass species and *A. lampa* and no effects on recruitment of *L. divaricata*. This response might be associated with an indirect positive effect of exposure to UV radiation through litter photodegradation promoting N release (Parton et al., 2007) rather than to a direct effect on seedling recruitment.

In contrast to soil inorganic N and exposure to UV radiation, we found marked species specific responses to the combined effect of litter traits and soil water. Litter presence promoted the recruitment of *P. ligularis* while *N. tenuis* and *L. divaricata* recruitment was promoted by high soil water and the presence of litter with contrasting chemistry (litter mixtures of both life forms and evergreen shrub litter, respectively). The positive response of *P. ligularis* recruitment to the presence of both types of litter could be attributed to the improvement of regeneration microsites against seed desiccation (Boeken and Orenstein, 2001; Loydi et al., 2013; Xiong and Nilsson, 1999). This is consistent with field observations showing that *P. ligularis* recruitment occurs in protected microsites (Bertiller et al., 2002). Differences in seedling recruitment between perennial grass species could be related to the thicker seed coat in *N. tenuis* than in *P. ligularis* (Correa, 1978) indicating that the former requires higher levels of soil water to reach an adequate seed humectation to promote seed germination and the subsequent seedling emergence and recruitment than the latter one (Bosco et al., 2015; Gutterman, 1993). Furthermore, *N. tenuis* recruitment was enhanced in microsites with litter mixtures of perennial grasses and evergreen shrubs having low concentration of soluble phenolics (Bosco et al., 2015, 2016). Secondary compounds such as soluble phenolics could have negative effects on early processes of plant regeneration (germination, emergence and establishment) thus regulating seedling recruitment (Castells et al., 2005; Inderjit et al., 2011; Knipe and Herbel, 1966).

Biomass responses to the abiotic factors also varied among species irrespective of the life form. Reduced UV radiation had a positive effect on biomass of both perennial grass species depending on the litter type (litter dominated by evergreen shrubs in *P. ligularis* and litter dominated by a mixture of both life forms in *N. tenuis*). In contrast, the reverse response was found in the biomass of *A. lampa* in litter dominated by a mixture of both life forms and no response in biomass of *L. divaricata*. UV radiation effects on species biomass might be related to the protective mechanical or physiological barriers in plants (Bernal et al., 2013, 2015; Tosserams et al., 2001). In our study, the positive effects of the reduction of exposure to UV radiation on perennial grass biomass could be related to low concentrations of secondary compounds in their photosynthetic active tissues (Campanella and Bertiller, 2008; Carrera et al., 2009). In contrast, evergreen shrub species (*L. divaricata* and *A. lampa*), with high concentration of phenols and lignin, respectively in their photosynthetic active tissues (Campanella and Bertiller, 2008; Moreno et al., 2010), are more protected from the incidence of ambient UV radiation. The promoting effect of reduced UV radiation on biomass of perennial grass species occurred with high soil water content while the promoting effect on biomass of exposure to UV radiation in *A. lampa* occurred with low soil water content. In this sense, previous studies suggested that plants could get benefits from the cross-tolerance of drought and UV radiation acting together (Bernal et al., 2013; Caldwell et al., 2007; Paoletti, 2005). Since UV radiation induces xeromorphic characteristics, negative effects of low soil water content on total plant biomass of perennial grasses under the combined effect of exposure to UV radiation and low soil water could be compensated (Bernal et al., 2013, 2015; Caldwell et al., 2007). Moreover, the effects of exposure to UV radiation on *A. lampa* seemed to enhance drought resistance when growing in microsites with low soil water content. Furthermore, biomass in the immature seedling stage of all species responded to increasing soil water, contrasting with plant responses in mature stages. Mature plants of perennial grasses are often fast growing species with acquisitive traits (*sensu* Díaz et al., 2004) that generally demand high amount of soil resources and water (Aerts and Chapin, 2000; Campanella and Bertiller, 2008; Navas et al., 2010) while mature plants of evergreen shrubs are often slow growing species with conservative traits (*sensu* Díaz et al., 2004) and generally deep rooting depth mostly independent of superficial water inputs (Aerts and Chapin, 2000; Bertiller et al., 2006; Navas et al., 2010). However, previous studies indicated that some evergreen shrubs have active and opportunistic root systems that could develop fine roots as a response to upper soil water availability with an improvement of plant growth performance (Reynolds et al., 2004; Rodríguez et al., 2007; Schwinning et al., 2002).

In conclusion, abiotic factors in disturbed bare soil patches such as soil water availability, the presence or absence and chemical quality of litter, the exposure to UV radiation and soil inorganic N levels differentially modulated seedling recruitment and biomass of species independently of life form. Among these factors soil water appeared as a limiting factor for seedling recruitment of all species and soil inorganic N as a limiting factor particularly in small-seeded species. The presence of different litter types was also relevant for seedling recruitment of perennial grass species probably in relation to the maintenance of soil water and inorganic N availability. In contrast, UV radiation in combination to soil water was the main factor affecting seedling biomass. The differential effect of UV radiation on seedling biomass could be associated with the concentration of secondary compounds in aboveground tissues. Accordingly, these complex relationships between abiotic factors at a microsite scale along with seed and plant traits should be important for planning management actions for vegetation recovery after disturbance.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jenvman.2018.04.020.

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