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**Title:** Arid community responses to nitrogen and carbon addition depend on dominant species traits and are decoupled between above- and belowground biomass

**Running title:** Above- and belowground plant responses

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## **Abstract**

Questions: Arid communities are strongly limited by soil resources including water and nitrogen (N). Plants compete for N with other plants and microorganisms, which are also limited by carbon (C). We propose that above- and belowground plant responses to soil resources are modulated by community structure (species relative abundances, ‘mass ratio hypothesis’) and species traits (relative growth rates ‘RGRs’). We evaluated the single and combined effects of soil N and C addition on the above- and belowground biomass accumulation of perennial grass patches in an arid community, and the mechanisms involved in their responses.

Location: Patagonian steppe, Argentina.

Methods: We added N ( $2\text{gN}\cdot\text{m}^{-2}$ ;  $\text{NH}_4\text{NO}_3$ ) and C ( $330\text{gC}\cdot\text{m}^{-2}$ ; sucrose) to  $1\text{m}^2$  field plots in a factorial design. After two years, we harvested aboveground ( $n=5$  plots) and belowground biomass ( $n=10$  soil cores) and sorted it by species. We measured potential soil respiration as a proxy of microbial activity.

Results: Total aboveground biomass increased 55% by N and decreased 45% by C addition, in relation to controls. C addition reduced total belowground biomass by 42%. The aboveground differences were associated with changes in the biomass of dominant species according to their RGRs. *Poa ligularis* (dominant, high RGR) increased 92% by N addition while *Pappostipa speciosa* (dominant, low RGR) decreased 55% by C addition. Intermediate and subordinate grasses

did not modify their biomass, independently of their RGR. Potential soil respiration was three times higher in C addition than in control plots.

**Conclusions:** Community biomass was explained by a combination of mass ratio hypothesis and specific RGR, as dominant grass controlled aboveground community responses to N (high RGR species) and C addition (low RGR species). Our findings highlight the independence between the above- and belowground processes and the importance of considering community equitability and species characteristics to predict plant community responses to changes in soil resources.

**Key words:** Mass ratio hypothesis, dominant species, subordinate species, Relative Growth Rates (RGR), potential soil respiration, biomass accumulation, perennial grasses, Patagonian Steppe.

## Introduction

The ecological processes in arid communities are not only strongly limited by water availability (Noy-Meir 1973), but also by other soil resources (Austin 2011). The above- and belowground plant responses to soil resources' availability could be modulated by differences in the abundance ('mass ratio hypothesis'; Grime 1998) and relative growth rates ('RGRs', the increase in dry mass per unit of plant mass in a given time interval; Grime & Hunt 1975) of the individual plant species present in the community. The mass ratio hypothesis states that the most abundant species (i.e., dominants) determine the biomass accumulation of their community, while the subordinate species have a minor role in this function (Grime 1998; Finegan et al. 2015; Prado-Junior et al. 2016; Sonkoly et al. 2019). Additionally, specific RGR determines how that species will respond to changes in resource availability (Chapin 1980; Chapin et al. 1987; Zhang et al. 2020). In response to soil nutrient pulses, the biomass of high RGR species (competitive species

*sensu* Grime 1977) increases more than the biomass of lower RGR species (stress tolerant species *sensu* Grime 1977; Chapin 1980; De Kroon & Mommer 2006). But stress tolerant species maintain their growth due to their low nutrient requirements in comparison with higher RGRs species (Chapin 1980; De Kroon & Mommer 2006). Therefore, community response to nutrients could be explained by a combination of these two mechanisms (Vile et al. 2006). In this way, RGRs of dominant species may control the plant community biomass in response to changes in soil resources. But it remains to be tested if the above- and belowground portions of arid plant communities respond similarly.

The response of plant above- and belowground biomass to labile soil nitrogen (N) and carbon (C) remains an open question in plant communities of arid ecosystems. In arid ecosystems the microbial community is extremely limited by soil C (Gonzalez-Polo & Austin 2009; Soong et al. 2020), due to the patchy distribution of vegetation and the photodegradation of aboveground plant litter (Austin & Vivanco 2006). Dead roots and rhizodeposition are the main inputs of organic C to soils (Villarino et al. 2021) and explain much of the variation in soil organic N contents (Carrera & Bertiller 2010). In conditions of high availability of readily assimilable C, microorganisms increase their biomass (Austin & Vivanco 2006) while releasing carbon dioxide (CO<sub>2</sub>; Ekblad & Nordgren 2002; Schimel & Weintraub 2003). This shifts microbial growth limitation from C to N (Ekblad & Nordgren 2002) and promotes microbial N uptake, thus increasing N immobilization (Schaeffer et al. 2003; Bleier & Jackson 2007; Perry et al. 2010; Wild et al. 2017) and reducing N available to plant consumption (Eschen et al. 2007). As a result of this microorganism – plant competition for soil N (Kaye & Hart 1997; Schimel & Bennett 2004; Kuzyakov & Xu 2013), plants could reduce their growth (Schmidt et al. 1997b; Bleier & Jackson 2007; Eschen et al. 2007). By contrast, available N inhibits microbial respiration and biomass (Liu

& Greaver 2010) while promoting plant growth (Hooper & Johnson 1999; Yahdjian et al. 2011). The balance between labile C and N availability regulates the outcome of the competition between soil microorganisms and plants (Hodge et al. 2000b). In addition, microorganisms are better competitors in the short-term, but plants are better in the long-term because of their longer lifespan (Hodge et al. 2000a; Bleier & Jackson 2007; Kuzyakov & Xu 2013).

We evaluated the combined effect of soil N and C addition on the above- and belowground biomass accumulation of grass dominated patches in an arid community and inferred possible mechanisms involved in its response. First, we hypothesized that the biomass of grasses, both above- and belowground, increases with soil N addition. By contrast, it decreases with C addition to soil due to competition for soil resources with microbial decomposers. Our second hypothesis is that the response of the entire plant community will be determined by changes in the biomass of the dominant grasses (mass ratio hypothesis) and by the responsiveness of the high RGRs grass species to N and C additions. Finally, we hypothesized that the activity of soil microorganisms, estimated by potential soil respiration, increases by C addition and is even higher with C and N addition due to the elimination of their limiting resources. To test these hypotheses, we conducted a field experiment with factorial addition of N and C. Plots were in the grass dominated patches of the Patagonian steppe inside a domestic grazing enclosure to warrant the presence of plant species that are preferred by sheep. Fences allow the free movement of wild herbivores.

## **Methods**

### Study system and species description

We conducted a field experiment in an arid steppe of the Patagonian Region (Occidental District of Patagonia in the Southwest of Chubut province, Argentina). The site, strongly limited

by soil resources, has been used as a model system to study the plant ecology of arid communities for several decades (> 50 years now). The average annual precipitation is  $131 \pm 8$  mm (1982-2011; average  $\pm$  SE), most of which occurs during winter and early spring months (INTA 2022). The soil texture is sandy with stones and gravel, which facilitates working with grass roots. The site is characterized by a two-phase mosaic community: a matrix with sparse tussock grasses (75 % of the community) and high cover patches composed by shrubs and grasses that cover the remaining 25% (Aguiar & Sala 1994; Soriano et al. 1994; Cipriotti & Aguiar 2005). We focused on the grass dominated matrix composed of few plant species that present contrasting abundances and RGRs (Leva et al. 2009; Oñatibia 2013; Oñatibia et al. 2017). This offers a unique opportunity to test the importance of the mechanisms that control above- and belowground plant biomass responses to N and C additions in natural conditions.

In the Patagonian Steppe, the grass community has low richness and equitability (Soriano 1956; Oñatibia et al. 2017) and includes eight perennial graminoid species. We worked with the four most abundant and frequent species, all Poaceae, in a 30-year sheep grazing enclosure. These four grass species constitute a perennial grass guild that included (from the highest to the lowest belowground RGRs under optimal condition in glasshouse): *Bromus pictus* Hook.f. ( $2.67 \pm 0.22$  % $\cdot$ day $^{-1}$ ); *Poa ligularis* Nees ex Steud. ( $1.58 \pm 0.35$  % $\cdot$ day $^{-1}$ ); *Pappostipa speciosa* (Trin. & Rupr.) Romasch. ( $0.57 \pm 0.05$  % $\cdot$ day $^{-1}$ ) and *Pappostipa humilis* (Cav.) Romasch. ( $0.50 \pm 0.34$  % $\cdot$ day $^{-1}$ ; Leva et al. 2009). The same pattern of RGR is observed when considering total above- and belowground biomass of each species (Couso 2011). The first two species are commonly in low density or locally extinct in commercial paddocks because of high grazing intensity (Oñatibia & Aguiar 2016). Therefore, in the enclosure we defined *P. ligularis* ( $7.2 \pm 0.3$  ind. $\cdot$ m $^{-2}$ ) and *P. speciosa* ( $4.3 \pm 0.1$  ind. $\cdot$ m $^{-2}$ ) as dominant species, *P. humilis* ( $2.8 \pm 0.3$  ind. $\cdot$ m $^{-2}$ ) as intermediate,

and *B. pictus* ( $1.5 \pm 0.2$  ind.m<sup>-2</sup>) as a subordinate species, according to their abundances (Oñatibia & Aguiar 2016). These four species represent 93% and 82% of the total above- and belowground biomass of the grass dominated patches, respectively. The grasses have 54% of their roots growing in the first 10 cm of the soil, distributed horizontally (Soriano et al. 1987). Our study focused on this soil layer as it is the one directly affected by treatments and in which the soil biological activity concentrates (Austin & Vivanco 2006).

### Experimental design and data collection

We conducted a factorial experiment of C and N addition in a randomized complete block design, to separate the variability of the microenvironmental conditions from the net effects of the addition treatments on the studied variables (n = 10 blocks; Appendix S1: Experimental design). The blocks, floristically homogeneous, were distributed in an area of 8 ha excluded from sheep grazing. Each block consisted of an area of 10 m x 10 m, with a minimum distance of 2 m among plots. We added 330 g.m<sup>-2</sup> of C as sucrose and 2 g.m<sup>-2</sup> of N as granulated ammonium nitrate (NH<sub>4</sub>NO<sub>3</sub>) in 1 m<sup>2</sup> plots during two consecutive years (2010 and 2011). Sucrose and ammonium nitrate were incorporated in the corresponding plots raking the first cm of soil in July (beginning of winter in the South Hemisphere), to secure changes in nutrient availability before the beginning of the growing season (Soriano et al. 1976). Therefore, the treatments were: control (without additions), N, C, and NC. It has been tested that the addition of C in the form of sucrose is an efficient management method to reduce N availability for plants (Eschen et al. 2007). The amount of C and N were determined according to a previous experiment performed in the same site (Austin & Vivanco 2006). The addition of N and C increased soil N and microbial biomass, respectively, eliminating their limitation for plants and microorganisms (Austin & Vivanco 2006).

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To measure total and specific grass responses to N and C additions (first and second hypothesis), we sampled above- and belowground biomass of the grass dominated patches ( $\text{g}\cdot\text{m}^{-2}$ ) at growing season peak during the second year of fertilization (December 2011). The biomass value is a good estimator of plant productivity (Sala & Austin 2000). We sampled aboveground biomass in five blocks. We clipped all standing plant material inside each plot and sorted biomass by species. We sampled soil cores in 10 blocks to measure belowground plant biomass. We extracted the first 10 cm of soil with a 5 cm diameter drill from bare ground surrounded by at least three of the four grass species, close to the center of every plot. In doing so our intention was to avoid favoring the belowground biomass of the dominant tussock species in the sampling. As the spatial resolution of the area sampled for the belowground plant biomass is lower than the aboveground' one, we decided to increase the number of soil samples to better represent the spatial scale of the plant community processes, which differ between these two portions of vegetation (Van Der Putten et al. 2009). In the laboratory, we separated grass roots by species based on their morphological characteristics using a validated identification protocol (Leva et al. 2009; Reyes & Aguiar 2017a). We dried all the samples at  $62^{\circ}\text{C}$  for 72 hours and weighed them (0.001 g and 0.0001 g resolution for above- and belowground biomass, respectively).

We measured potential soil respiration to characterize soil microbial activity (third hypothesis). During the second growing season we extracted 200 g of the first 10 cm soil depth in each plot ( $n = 10$ ) and we incubated it for several days in greenhouse conditions, without lid to avoid inhibitory effects due to  $\text{CO}_2$  accumulation. Temperature was semi-controlled at  $\sim 25^{\circ}\text{C}$  and soil gravimetric water content was maintained at field capacity by adding distilled water by daily evaluation. This allowed us to separate  $\text{CO}_2$  emissions due to root activity, present in the field, from emission due to microorganism activity (Le Dantec et al. 1999; D'Acunto et al. 2018).



Potential soil respiration was measured with a portable respirator, a closed dynamic chamber that quantifies their variation in CO<sub>2</sub> concentration during a limited time lapse (PP Systems SRC-1, Soil CO<sub>2</sub> Flux System, UK, 2003).

Finally, during the second growing season, we extracted soil samples from five blocks (five samples per treatment) to measure total soil N by Kjeldahl method and total soil organic C concentration by Walkley & Black method (INGEIS – UBA/CONICET, Buenos Aires, Argentina). With these data we also estimated total soil C:N ratio per plot.

### Statistical analyses

We performed statistical analyses with R (R version 3.6.2, R Core Team 2018) using mixed-effects models (*lme* function in ‘nlme’ package, Pinheiro et al. 2017). We modelled total and specific above- and belowground biomass of grasses, potential soil respiration, and total soil C, N and C:N as a factorial design of N and C addition (fixed factors). Random structures included blocks (n = 10 for belowground biomass and potential soil respiration, and n = 5 for aboveground biomass and total soil C, N and C:N). *P. humilis* aboveground biomass, potential soil respiration, total soil N and C:N were log(1+X) transformed, while *P. speciosa*, *P. humilis*, *P. ligularis* and total belowground biomass, and *B. pictus* aboveground biomass were  $\sqrt{(x)}$  transformed to ensure that residuals were normally distributed (Shapiro–Wilk test). We modeled variance heterogeneity of *P. speciosa* and *P. humilis* aboveground biomass, *B. pictus* belowground biomass, potential soil respiration, and total soil organic C (*varIdent*; Pinheiro et al. 2017). When interactions were significant ( $P < 0.05$ ), we performed post hoc comparisons through Tukey tests.

## **Results**

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There were differences in response to the two-year N and C addition between the total above- and belowground biomass of the grass dominated patches at the end of the experiment (Fig. 1; Appendix S2: Results from mixed-effect models). Total aboveground biomass increased 55% in N fertilized plots and decreased 45% in the C addition plots compared to control plots. Combined N and C addition had no effect (Fig. 1, top panel). Total belowground biomass was not affected by N addition (single or with C) but decreased 42% in C addition plots (Fig. 1, bottom panel).

Individual grass species responses to N and C addition varied according to their RGRs and their relative abundance (Fig. 2; Appendix S2: Results from mixed-effect models). Aboveground biomass of the dominant species *P. speciosa* decreased 55% after C addition (Fig. 2.a) while *P. ligularis* increased 92% after N fertilization (Fig. 2.b). There were no significant effects of N or C additions on the aboveground biomass of *P. humilis* (intermediate species) and *B. pictus* (subordinate species; Fig. 2.c-d). Surprisingly, the belowground biomass of the four species considered did not change in response to treatments (Fig. 2). The belowground biomass of *P. humilis* decreased in response to N addition, but this effect was only marginally significant ( $F_{1,27} = 3.56, P = 0.07$ ).

Potential soil respiration (CO<sub>2</sub> liberation) changed in response to C addition. After two years, potential soil respiration increased three times in the C addition plots, being an order of magnitude higher than at the beginning of the experiment (Fig. 3; Appendix S2: Results from mixed-effect models). The level of total soil C and N at the time of biomass harvest was  $0.551 \pm 0.032\%$  and  $0.045 \pm 0.003\%$ , respectively. There were no differences in response to treatments on total soil C and N, but the addition of N reduced total soil C:N ratio by 12% in relation to control plots (from 11.53 to 10.16;  $F_{1,12} = 4.47, P = 0.06$ ).

## Discussion

According to our hypotheses, we found different responses to soil N and labile C addition on the grass-dominated patches of the arid community. Both the above- and the belowground portions of the grass patches reduced their biomass accumulation in response to labile C addition (first hypothesis; Fig. 1), while aboveground biomass increased with N addition (Fig. 1). These changes in the perennial grass community resulted from complex species responses. Only dominant plant species responded to fertilization with N and C, as suggested by the mass ratio hypothesis. Intermediate and subordinate grasses did not modify their biomass, independently if they have low or high RGR. The amount of above- and belowground biomass that the two dominant species produced depended on their specific RGRs (second hypothesis; Fig. 2). Aboveground biomass of *P. speciosa* (low RGR) decreased with C addition, while that of *P. ligularis* (high RGR) increased when N was added (Fig. 2). Finally, potential soil respiration was higher under C addition (third hypothesis; Fig. 3), which agree with the idea that soil microbial activity is controlled by the availability of soil C (Austin & Vivanco 2006). We evaluated the net response of the perennial grass community to soil N and C enrichment. The plants of these grass-dominated patches of the Patagonian steppe are surrounded by bare soil and the plant cover is low (Soriano et al. 1994). Therefore, aboveground competition for light is not as intense as belowground competition for soil resources, particularly between low- and high-RGR grass species in the absence of sheep grazing (Graff et al. 2007).

The identity and characteristics of the plant species explained the net responses of the perennial grass patches of this arid community to changes in soil resources. We found that only aboveground biomass accumulation increased in response to N availability (Fig 1). Our results

suggest that in this Patagonian steppe belowground plant accumulation might be decoupled from the availability and uptake of soil resources (Kulmatiski et al. 2017; Dybzinski et al. 2019). This is supported by a previous study, with the same four species at the same site, where it was observed that the  $^{15}\text{N}$  absorbed by roots was rapidly allocated to the aboveground biomass (Reyes & Aguiar 2021). Also the four species included in our plots do not differ in resource acquisition rates (Reyes & Aguiar 2021). However, high and low RGR species have clear ecological trade-offs between allocating resources to aboveground leaf biomass or reproductive tillers. In addition, high RGR species showed rapid growth when soil in their zone of influence was fertilized with N (Reyes & Aguiar 2019). Coincidentally, in our plots N fertilization only promoted the accumulation of aboveground biomass of *P. ligularis*, the dominant high RGR species (Fig. 2b).

We propose that the measured decoupling between above- and belowground biomass responses was related to the differences on the decomposition rates of these two portions of vegetation. Photodegradation is important in arid communities, increasing decomposition of aboveground biomass and the loss of C fixed directly to the atmosphere (Austin & Vivanco 2006). Furthermore, roots, particularly of the low RGR species (Semmartin et al. 2004), have lower decomposition rates than the aboveground biomass (Austin et al. 2009; Freschet et al. 2013; Berenstecher et al. 2021). C addition inhibited root decomposition in this steppe (Berenstecher et al. 2021), which suggests that the decrease in total belowground biomass observed by C addition was due to a reduction in root productivity and not due to an increase in decomposition rate. We were able to identify plant species by the morphology of their roots, although we could not determine if their roots were alive or dead. As a result, we have a good comparison of treatment relative effect on total and specific belowground biomass but a poor estimation of absolute values of alive roots at the end of the experiment.

Soil respiration indicates that carbon addition increases the biomass of soil microorganisms, which probably immobilize N that are no longer available for grasses (Schaeffer et al. 2003; Austin & Vivanco 2006; Bleier & Jackson 2007; Wild et al. 2017). Our study indicates that the microbial community response showed a three-fold increase in potential soil respiration when labile C was added to soil, in relation to control or N addition conditions (Fig. 3). Microbial immobilization could explain the reduction in total above- and belowground biomass of the perennial grass community in response to C addition (Fig. 1; Schmidt et al. 1997b; Bleier & Jackson 2007; Eschen et al. 2007). But interestingly this response was mainly explained by the aboveground biomass response of *P. speciosa*. This dominant species with low RGR (stress tolerant *sensu* Grime 1977) was susceptible to microbial use of N, indicating the high intensity of microbial-plant competition (Fig. 2a). The long-lasting effect of C addition on this dominant grass with low RGR suggest an important reduction of their growth (Schmidt et al. 1997b; Bleier & Jackson 2007; Eschen et al. 2007) and a slow recovery of their biomass after N immobilization by microorganisms (Reyes & Aguiar 2019). We added C to soil in labile form (sucrose), and despite this, we observed changes in the grass patches several months after its addition. Instead, *P. ligularis*, dominant species with high RGR (competitive *sensu* Grime 1977), *P. humilis*, and *B. pictus*, intermediate and subordinate species, respectively, did not respond to the increase of microbial activity and successfully cancelled microbial competition. These plants did not reduce their biomass, or recovered it quickly, after N immobilization by soil microorganisms, thus not showing a long lasting effect of microbial competition for N (Hodge et al. 2000a; Bleier & Jackson 2007; Kuzyakov & Xu 2013). It is necessary to study the effect of less labile C forms (e.g., manipulating the quantity of leaf and root litter) to understand long lasting effects of changes in litter production in this arid communities.

Our study evaluated not only the total and specific aboveground responses of a perennial grass dominated patches in an arid community but also its total and specific belowground biomass, an aspect that has been relegated because of the methodological difficulties involved (Lauenroth 2000; Wilson 2014; Reyes & Aguiar 2017a; López-Mársico et al. 2020; Reyes & Aguiar 2021). The overrepresentation of pot experiments (Schmidt et al. 1997a; Schmidt et al. 1997b; Bleier & Jackson 2007) compared to field experiments remarks the importance and strength of our plot experiment, performed in the field without manipulating the species present (including wild animals but excluding domestic sheep). Also, this study complements previous experiments where microsite N and C addition tracked changes in perennial grass community composition at an individual plant scale (Reyes & Aguiar 2017a; Reyes & Aguiar 2017b). Experiments at plot scale in natural conditions are essential to predict possible vegetation outcomes of changes in the nutrient cycles in existing communities (Bardgett et al. 2005; Van Der Putten et al. 2009). Particularly, the increase with N addition of the aboveground biomass of *P. ligularis* (the dominant and high RGR's species, Fig. 2b) have direct management implications, as this species is highly preferred by large herbivores and constitutes one of the main forage resources for domestic grazing common in these arid rangelands (Golluscio et al. 2015; Oñatibia & Aguiar 2016). Grazing decreases *P. ligularis* abundance, which could potentially reduce the grass community response to N fertilization.

Water availability is the main constraint for arid communities. The plant species present in these communities show different strategies and traits to cope with this stress. However, other factors than water may also constrain arid plant communities (Hooper & Johnson 1999; Austin 2011; Yahdjian et al. 2011). Here we aimed at increasing our understanding the relationship between community and individual species responses to soil N and C availability. Specifically, we focused on above- and belowground biomass accumulation responses. Interestingly, we found that

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these responses depend on a community level attribute (dominance) and on an individual species trait (RGR). This finding supports our hypotheses derived from two general ecological principles: the mass ratio hypothesis and the central role of RGRs as the main determinant of plant responses to dramatic differences in resource availability (Chapin et al. 1987; Grime 1998). In conclusion, our findings highlight the importance of considering not only plant traits but also community attributes to predict plant community dynamics to the ongoing global changes in soil resource availability.

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**Author contributions:** Original idea and experimental design by M.R.A. M.F.R. refined experimental design and conducted the experiment; S.C. analyzed the data and led the writing of the manuscript. All authors contributed to successive drafts and gave final approval for publication.

### **Data availability**

All data generated during this study are available in the Supporting Information: Appendix S3.

### **Supporting information**

Appendix S1: Experimental design

Appendix S2: Results from mixed-effect models

Appendix S3: Data generated during the study

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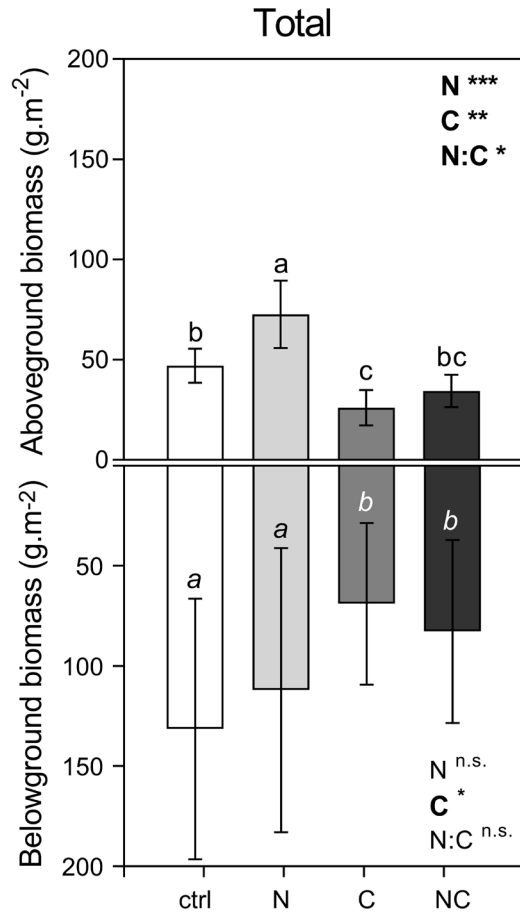
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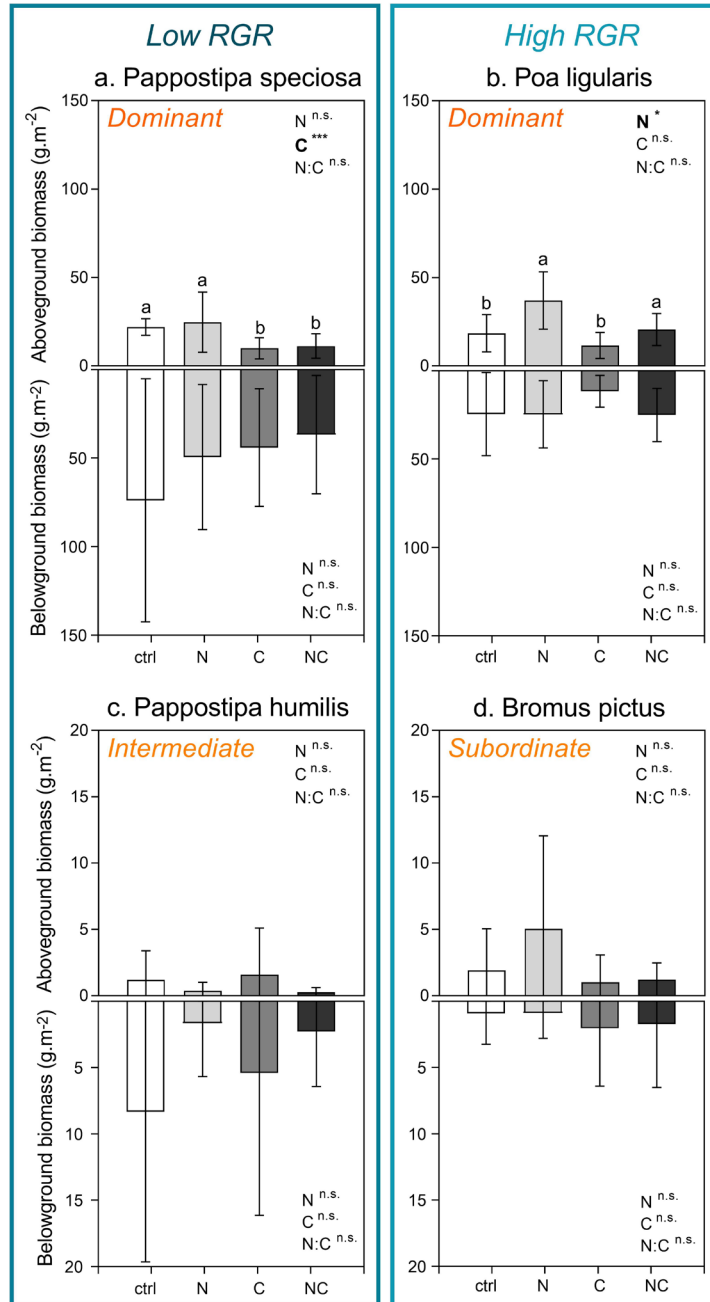
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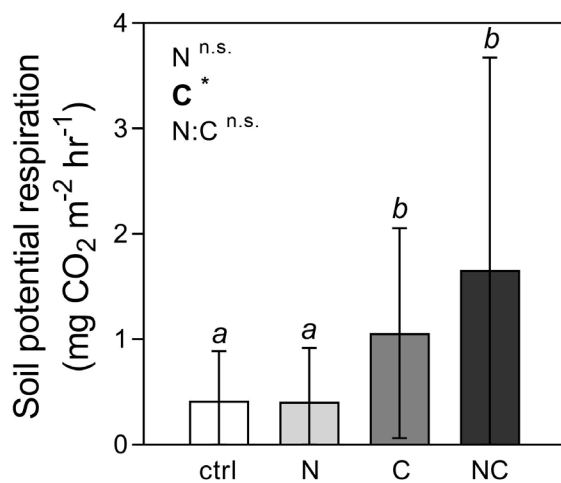


**Figure 1** Total above- and belowground biomass accumulation ( $\text{g}\cdot\text{m}^{-2}$ ) of grass dominated patches in response to N addition, C addition, and their interaction during growing season of the second experimental year. Treatments are: ctrl (control, no addition), N ( $2 \text{ gN m}^{-2}$ ), C ( $330 \text{ gC m}^{-2}$ ), NC ( $2 \text{ gN m}^{-2} + 330 \text{ gC m}^{-2}$ ). Bars indicate mean  $\pm$  SD (aboveground biomass:  $n = 5$ ; belowground biomass:  $n = 10$ ). Different lower-case letters indicate significant differences among treatments (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ )





**Figure 2** Above- and belowground biomass accumulation (g.m<sup>-2</sup>) of (a) *Pappostipa speciosa*, (b) *Poa ligularis*, (c) *Pappostipa humilis*, and (d) *Bromus pictus* in response to N addition, C addition, and their interaction during growing season of the second experimental year. Treatments are: ctrl (control, no addition), N (2 gN m<sup>-2</sup>), C (330 gC m<sup>-2</sup>), NC (2 gN m<sup>-2</sup> + 330 gC m<sup>-2</sup>). Bars indicate mean ± SD (aboveground biomass: n = 5; belowground biomass: n = 10). Different lower-case letters indicate significant differences among treatments (\* P < 0.05; \*\* P < 0.01; \*\*\* P < 0.001). Y-axis scale differs between dominant and intermediate/subordinate species



**Figure 3** Potential soil respiration (mg CO<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup>) in response to N addition, C addition, and their interaction. Soil samples were extracted during growing season of the second experimental year. Treatments are: ctrl (control, no addition), N (2 gN m<sup>-2</sup>), C (330 gC m<sup>-2</sup>), NC (2 gN m<sup>-2</sup> + 330 gC m<sup>-2</sup>). Bars indicate mean ± SD (n=10). Different lower-case letters indicate significant differences among treatments (\* P < 0.05)