IJANR
International Journal of Agriculture and Natural Resources

Int. J. Agric. Nat. Resour. 51(1):57-67. 2024
www.ijanr.cl

ANIMAL NUTRITION

DOI 10.7764/ijanr.51i1.2473

RESEARCH NOTES

How does the neighborhood of annual or perennial species affect the first one hundred days of the establishment of grasses?

Agustina Lavarello Herbin[1], María Laura Amalia Gatti[2], and Rodolfo Ángel Golluscio[2,3]

[1]Instituto Nacional de Tecnología Agropecuaria (INTA). Pergamino Experimental Agricultural Station. Pergamino, Buenos Aires, Argentina.

[2]Universidad de Buenos Aires. Facultad de Agronomía. Cátedra de Forrajicultura. Buenos Aires, Argentina.

[3]Universidad de Buenos Aires. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura (IFEVA), Facultad de Agronomía. Buenos Aires, Argentina.

Abstract

A. Lavarello Herbin, M.L.A. Gatti, and R.A. Golluscio. 2024. How does the neighborhood of annual or perennial species affect the first one hundred days of the establishment of grasses? Int. J. Agric. Nat. Resour. 57-67. Pastures that include annual and perennial grasses can play a strategic role in increasing the sustainability of temperate livestock systems. However, the impacts of the competition between annual and perennial genetically improved forage species on pastures has scarcely been studied. We evaluated the early dynamics of tillering, carbon partitioning and both intra- and interspecific competition in – or between – an annual (*Bromus willdenowii*; prairie grass; Bw) and a perennial (*Dactylis glomerata*; orchard grass; Dg) C_3 grass species. We sowed 24 0.18 m^2 microplots in May 2008. Each microplot constituted an experimental unit and contained five sowing lines spaced 0.175 m apart. On three of the lines, we sowed different combinations of the mentioned grasses, while on the two lines between them, we sowed red clover (*Trifolium pratense*). We randomly applied a factorial array of eight treatments—2 species (Dg vs. Bw) × 2 types of competition (intra vs. interspecific) × 2 levels of winter nitrogen fertilization (0 vs. 170 kg of N ha^{-1})—designed in three complete random blocks. Fertilization did not have any significant effect on any species. The evaluation period lasted 109 days after sowing (das), separated into three phases (0-53 das, 59-90 das and 90-109 das). The variables recorded were aerial biomass (leaves, sheets and senescent material), root biomass and tiller density per species. As expected, annual Bw inhibited the growth of perennial Dg at the latest stage of establishment but surprisingly promoted it at the earliest stage. This work suggested that a low initial density of an annual species should optimize the initial facilitating effect of the annual species on the perennial species with its subsequent inhibitory effect.

Keywords: *Bromus willdenowii*, competition, *Dactylis glomerata*, facilitation, orchard grass, prairie grass.

Received Oct 28, 2022. Accepted Mar 25, 2024
Corresponding author: lavarelloherbin.a@inta.gob.ar

Abbreviations

Bromus willdenowii Kunth (Bw); *Dactylis glomerata* (Dg); Relative interaction intensity index (RII).

Introduction

The expansion of agriculture has generated a series of changes in livestock husbandry practices throughout South America. Its main consequences have been the reduction in the area devoted to livestock and the territorial reorganization of this activity, which has been more concentrated in humid pampas in the past (Capdevielle, 2020). This process has promoted, on the one hand, a greater intensification of livestock and, on the other hand, an increase in stock densities in areas not suitable for agriculture (Paruelo et al., 2005).

Perennial pastures can play a strategic role in the context of livestock intensification because they are much more environmentally sustainable than other productive alternatives, as they reduce annual disturbances, which affects many biogeochemical cycles that are key to providing resilience and stability to agroecosystems (Islam et al., 2018). In particular, more diverse pastures have been shown to be more productive and more resistant to weed invasion. However, their management needs new strategies to obtain dense canopies in the field, according to site conditions and the objectives of each producer (Sanderson et al., 2013).

In temperate pastures, plants grow as members of a community in which intra- and interspecific competition generally affect growth (Gatti et al., 2015). Competition is defined as the interaction between individuals coming from the shared use of a resource that is in limited supply, resulting in a decrease in the survival, growth and/or reproduction of at least one of the individuals involved (Begon, 1996). In fact, the ability of a species to persist and prosper in a community is generally determined by its competitive interactions with other species (Connell, 1983).

Seedling establishment is a critical phase in pasture production because it determines the space that each species will later occupy in the canopy, subsequently affecting the future composition of pastures (Skinner, 2005). The rapid development of a critical root biomass, together with the development of aerial biomass and foliar area, are necessary factors to ensure the survival of seedlings (Sanderson et al., 2002). In fact, perennial species are considered to be established when their seedlings have developed between 4-6 leaves and at least two adventitious roots (Ries & Svejcar, 1991). At the community level, successful pasture establishment is defined as the survival of plants of a given species for at least one year after sowing, which includes the first summer, when environmental stress levels are usually the highest (Thom et al., 2011).

The sowing of *Bromus willdenowii* Kunth (prairie grass; Bw) and *Dactylis glomerata* (orchard grass; Dg) in alternate lines with erect legumes, such as alfalfa or red clover, is common in temperate–humid environments in Argentina (Scheneiter et al., 2008; Gatti et al., 2013). Bw, an annual or biannual grass (Scheneiter & Rimieri, 2001), can establish rapidly and can competitively exclude other species with a lower speed of establishment (Sanderson et al., 2002). Its great competitive ability results from its high growth rate and tiller weight, two properties that give it a great ability to compete for light (Sugiyama, 1999). In contrast, Dg, a perennial species, has low competitive ability due to its slow initial root growth, which is related to low nitrogen capture, both of which are characteristics that contribute to the lower competitiveness of this species relative to other species (Nurjaya & Tow, 2001). As shown in Hume (1991), Bw had greater leaf appearance rates (leaves per tiller per day) and lower site filling (tillers per tiller per leaf appearance interval) than did ryegrass species. The tillering rates (tillers per tiller per day) were also lower, except under vegetative conditions at 4 °C. The low tiller number in Bw was not due to a lack of tiller sites but rather to poor filling of these sites. Lower site filling occurred because of increased delays in the appearance of the youngest axillary tiller and a lack of axillary tillers emerging from basal tiller buds. In Bw, no tillers originated from coleoptile buds, while prophyll buds developed tillers only occasionally. A low tiller number in Bw was compensated for by greater tiller weight. Bw had more live leaves per tiller, a greater area per leaf and a greater leaf area per plant.

The application of small doses of nitrogen at the time of implantation and toward the end of winter is usually recommended (Berardo, 1996). The winter application of nitrates can mitigate the deficit in the winter supply of forage, anticipate spring regrowth and significantly increase annual forage production. The response doses in these systems usually range between 75-150 kgN ha^{-1} (Guaita et al., 1999; Berardo, 1996), although winter applications of up to 170 kg of nitrogen per hectare produce a linear increase in growth (Fernández Greco et al., 1995).

The results of competition between wild annual and/or perennial species, both in poor environments and/or in those improved by the addition of nutrients, have been extensively studied in the literature (e.g., Wilson & Tilman, 1993). In contrast, competition between genetically improved annual and perennial forage species has scarcely been studied. Some of the few related studies were the experiments of Gatti et al. (2013, 2015). They found (a) that the annual *Bromus willdenowii* reached greater aerial and belowground biomass than did the perennial *Dactylis glomerata* at 109 days after sowing and (b) that plants of both species reached greater biomass—both above- and belowground—and tiller density when surrounded by plants of the perennial species than when surrounded by plants of the annual species. However, there is no information on interactions between annual and perennial forage species during the very early phase of pasture establishment (<3 months).

This work analyzed the early (i.e., during the first 3.5 months after sowing) competition relationships in the sowing line between the annual grass *Bromus willdenowii* and the perennial grass *Dactylis glomerata*. Our objectives were as follows:

1) Evaluate the early dynamics of tillering and carbon partitioning between aboveground and belowground biomass in plants of both species when they were surrounded by individuals of the same species (intraspecific competition) or of the other species (interspecific competition) and evaluate the influence of nitrogen application on those dynamics.

2) Evaluate the early dynamics of the intensity of competition between the two species and analyze whether this intensity of competition is modified by nitrogen application.

Materials and Methods

We worked on an experimental layout similar to that of Gatti et al. (2013, 2015). In the experimental field of Facultad de Agronomía, Universidad de Buenos Aires (34° 35’ 29” S, 58° 29’ 0” W), we sowed 24 microplots of ~0.18 m^2 on May 27th, 2008 (1.056 m × 0.17 m). Each microplot constituted an experimental unit and contained five 0.17 m long sowing lines (lines 1 to 5) spaced 0.176 m apart. On lines 1, 3 and 5, we sowed an annual (*Bromus willdenowii*; prairie grass; Bw) and a perennial grass (*Dactylis glomerata*; orchard grass; Dg) 1.5 cm from each other, while on lines 2 and 4, we sowed legumes (*Trifolium pratense* L.; red clover) at the same distance between seeds (Figure 1). Legume seeds inoculated with specific *Rhizobium* strains were sowed with the sole purpose of simulating a common sward under our climatic conditions. Therefore, we did not consider *T. pratense* for any analysis.

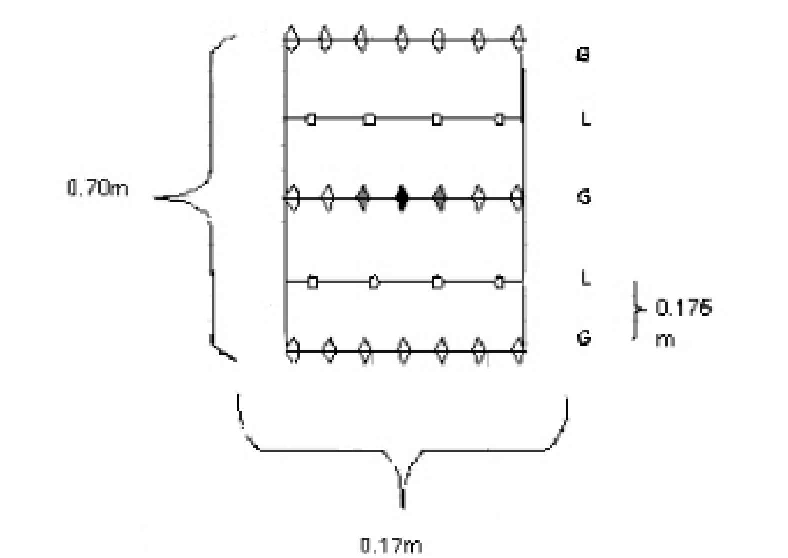

Figure 1. Schematic representation of each experimental unit. RhombI represents grasses, and squares represent legumes. Colored rhombi represent a sampling triplet composed of a central target plant (in black) flanked by two neighbor plants (in gray). G = grass line and L = red clover line.

The microplots differed in the composition of the lines of grasses according to four different situations of intra- and interspecific competition (each species surrounded by plants of the same or the other species). As a result, Bw target plants could be surrounded by Bw or Dg neighbors and Dg target plants could be surrounded by Bw or Dg neighbors. There were six microplots for each combination of species: Three were fertilized, and the other three were not (see details in Gatti et al., 2013, 2015). Over this experimental layout, we randomly applied a factorial array of eight treatments: 2 species (Dg vs. Bw) × 2 types of competition (intra vs. interspecific) × 2 levels of winter nitrogen fertilization (0 vs. 170 kgN ha^{-1}), designed in three complete random blocks. In all the experimental units, we carried out phosphorous fertilization (50 kg P ha^{-1}) and supplementary irrigation to avoid both P and water deficits. The nitrate soil level recorded before fertilization was 1.86 ppm ± 0.53. Nitrogen fertilization at 170 kg N ha^{-1} was carried out on July 19, which coincided with the first harvest date. The average temperature during the experimental period was 11.77 ± 2.78 °C, with minimum and maximum daily averages of 6.4 and 18.9 °C, respectively.

The experimental period covered both the early establishment stage and the late establishment stage of the pasture, the latter coinciding with the active vegetative growth of the species. The effects of competition for resources, directly related to the vegetative development of plants, are expected to be especially evident in the second stage (Lemaire & Millard, 1998). To observe tillering dynamics, biomass partitioning and competition intensity, we performed harvests on different dates: July 19th (53 days after sowing [das] and immediately before nitrogen fertilization), August 25th (90 das and 37 days after fertilization [daf]) and September 13th (109 das and 56 daf). This first harvest corresponds to fertilizer application at a rate of 170 kg N ha^{-1}, an application rate that usually allows a linear response in most C_3 grass species of the Humid Pampa (Fernández Greco et al., 1995). At 53 das, plants had one to three tillers per plant and five to six leaves on the main stem, a size corresponding to the beginning of the plant establishment phase (Ries & Svejcar, 1991; Sanderson et al., 2002). The number and length of expanded and growing or expanding leaves were monitored weekly on three tiller age cohorts: The main tiller and the largest ones that appeared 20 and 30 days after fertilization (20-daf and 30-daf tillers, respectively), i.e., 50 and 60 days after emergence (50-dae and 60-dae tillers, respectively) (Gatti et al., 2013). The data were recorded at the beginning of the reproductive period of Bw (13 September; 85 d after emergence and 56 daf) because competition for resources is considered to be directly linked to the vegetative development of plants (Lemaire & Millard, 1999). After fertilization on the central grass row of the mini-sward, data were collected to avoid border effects from external grass rows in a sequence of three central individual plants. The target plant on which the measurements were taken was the one marked and flanked by two grass neighbors. We did not expect a border effect of the rows with legumes owing to their very low initial growth and plant biomass in the experimental period with a low mean daily temperature (see Figure 1; see details in Gatti et al., 2013, 2015). On each day, we measured the tiller density, aerial biomass and root biomass (after washing the roots very carefully to remove the excess soil) of the target plants. The root system of the plants was manually excavated to > 20 cm depth; the surrounding soil was carefully removed, and then the roots were rinsed with water (Fang et al., 2012). We performed all biomass measurements after drying the different fractions (aboveground organs and roots) in an oven at 65 °C for 48 hours (more details are provided in Gatti et al., 2013, 2015).

To quantify the intensity of competition, we used the relative interaction intensity index (RII; Armas, 2004). This index is calculated as the difference between the biomass of a given species A when it grows accompanied by another species B (AB) and the biomass obtained when A grows accompanied by plants of its own species (AA), divided by the sum of both values (RII= (AB-AA)/(AB+AA)). Therefore, when A reaches an RII greater than zero, then B has a facilitating effect on A, while when A has a negative RII, B has a competitive effect on A. Among the several indices developed to quantify the magnitude of competition, the RII has been documented as the most suitable index for the analysis of plant interactions. It ranges between +1 and -1, it is symmetrical around zero with identical absolute values for competition and facilitation, its sampling properties are known and accurate, and it is safe to use in statistical and mathematical operations because it is linear and does not have discontinuities within its range (Armas et al., 2004).

We analyzed biomass and tiller density data with a two grass target species × two grass neighbor species × two fertilization levels factorial ANOVA and RII data with a two species × two fertilization levels factorial ANOVA, both with a repeated measures array, to analyze the differences among dates and a significance level of 5%. When we detected significant interaction effects, we used Tukey's test to make post hoc comparisons among means. We assessed all traits for normality using the Shapiro–Wilk test. We used the statistical package Infostat (Di Rienzo et al., 2008).

Results

Tillering and biomass partitioning

For all the measured variables, we found a significant interaction between date and neighbor. The other interactions (date × neighbor, date × species) were not significant for this variable. Independent of the identity of the target plant, tiller density and both above- and belowground biomass increased during the experimental period. However, all variables reached higher values with an annual neighbor than with a perennial neighbor at 90 days after sowing but with a perennial neighbor than with an annual neighbor at the final harvest—109 days after sowing. We did not detect any effect of fertilization, and in the case of aerial biomass, we detected a significant species × date interaction. Although the aerial biomass was similar between species at the beginning of the assay, Bw tended to produce more aerial biomass in the middle of the period evaluated and produced more aerial biomass at the end of the assay (Figure 2).

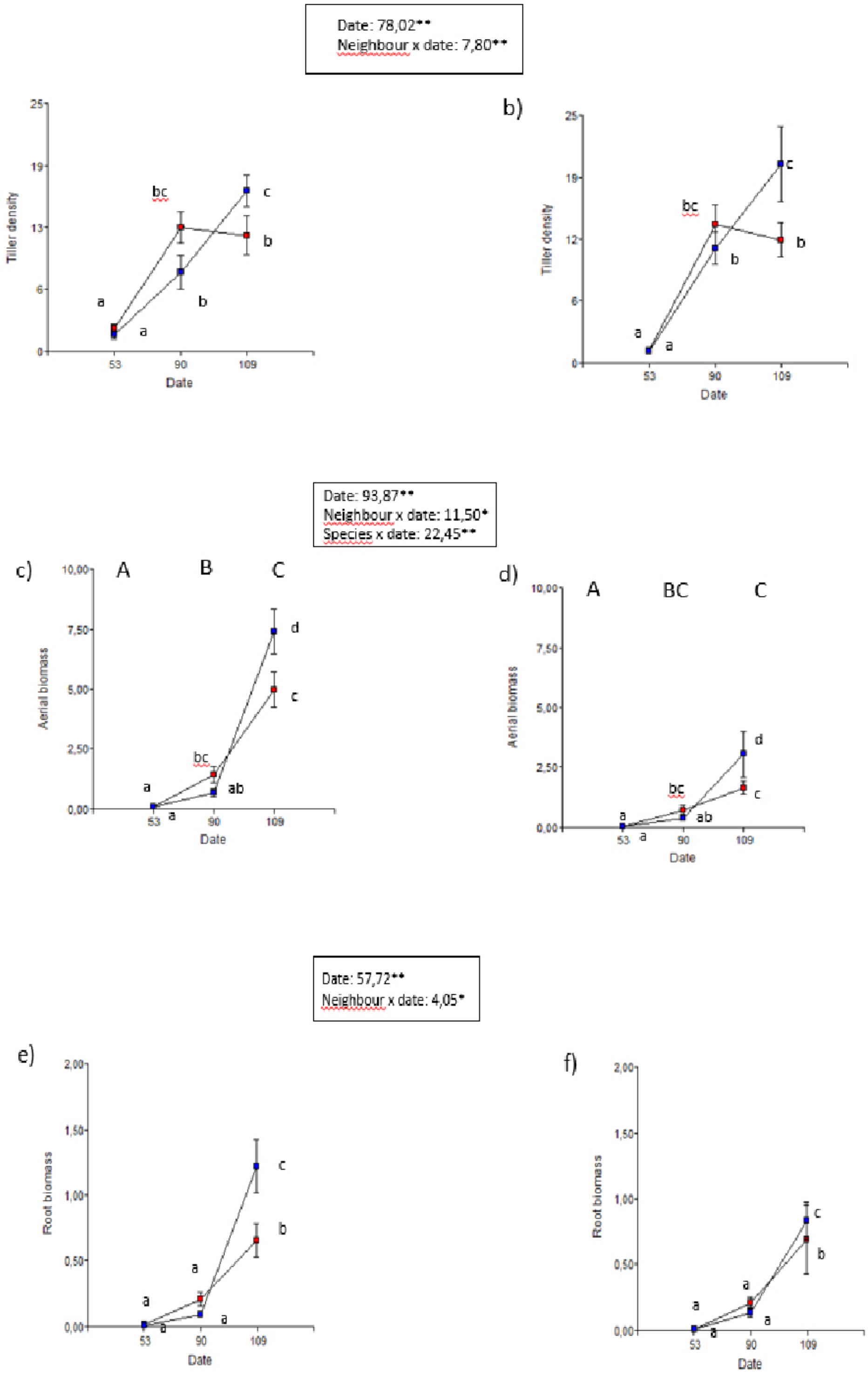

Figure 2. Tiller density (g.plant^{-1}) (a, b), aerial biomass (g.plant^{-1}) (c, d), and root biomass (g.plant $^{-1}$) (e, f) along days after sowing in target plants of Bw (squares; left panels: a, c, e) and Dg (circles; right panels: b, d, f) with different neighbors (red: Bw; blue: Dg). For each variable, we inserted the values of F only for the factors with significant effects (**: $p<0.01$; *: $0.01<p<0.05$). Different lowercase letters within each graph indicate significant differences among the 12 means represented in both panels of each variable ($p< 0.05$; Tukey's test). Different capital letters over the panel indicate significant differences between species for each date ($p< 0.05$; Tukey's test).

Competition intensity

We found a significant species × date interaction for all the variables we studied. At the beginning of the establishment phase (53 and 90 das), Bw presented negative RII values, and Dg showed positive RII values. This indicated that both Bw and Dg produced more when they were surrounded by Bw than when they were accompanied by Dg neighbors. These positive effects of Bw on aerial biomass (at 90 das; Figure 3c) and root biomass (at 53 das; Figure 3d) were significant and tended to be significant for the other two variables analyzed (root biomass and aerial biomass). In contrast, at the end of the establishment phase, the annual neighbor tended to have the expected negative effect on both species for all the variables studied. This last effect was more significant for tiller density and aerial biomass than for total biomass and root biomass (Bw-positive vs. Dg-negative RII values; Figure 3). In all cases, we refer to a tendency when statistical analysis went through "a" to "ab" instead of those variables that went from "a" to "b" (or vice versa).

Discussion

As formerly shown by Gatti et al. (2013, 2015), toward the end of the early establishment period (109 days after sowing), the more competitive annual neighbor tended to have negative effects on the growth of both species. However, unexpectedly, the more competitive annual neighbor had no effect—and even had some beneficial effects—at the earliest moments of the establishment phase. These results suggest that while plants grow in an open canopy, i.e., with minimal competition, an annual neighbor could promote an increase in the tiller density and growth of plants, regardless of their identity. However, after this early stage, as resources become scarce, the competitive effects of annual neighbors predominate. This effect may suggest a temporal change in the effect of the annual species, from a facilitative to a competitive effect.

In natural herbaceous communities, sometimes there is facilitation during the establishment phase because vegetation generates a favorable

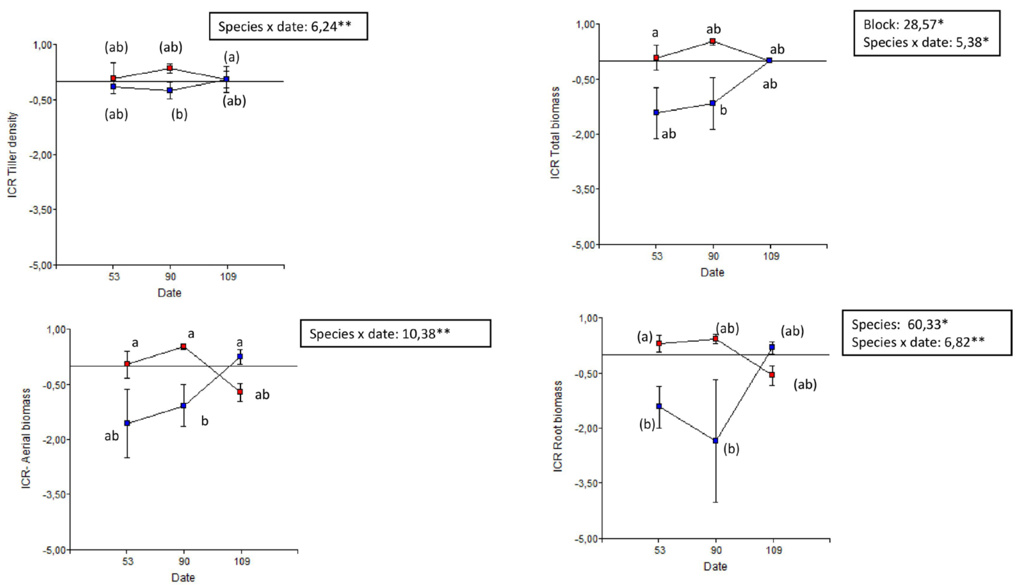

Figure 3. Relative intensity index (RII) for a) tiller density, b) total biomass, c) aerial biomass and d) root biomass for the annual (red symbol: Bw) and perennial (blue symbol: Dg) species. For each variable, we inserted the values of F only for the factors with significant effects (**: p<0.01; *: 0.01<p<0.05). Different letters indicate significant differences among the 12 means represented in both panels for each variable (p< 0.05; Tukey's test). For each variable, the RII was calculated as (mixture-monoculture)/(mixture + monoculture) (Armas, 2004).

microclimate for the germination and establishment of new seedlings (Ganade & Brown, 2002). However, as time progresses, the recruitment of new individuals tends to cease because the availability of resources is reduced, in part by the resource consumption of formerly facilitative individuals (Ganade & Brown, 2002). This would imply a change in the role of facilitation along a stress gradient (Scheffer, 2009; D´Odorico et al., 2007). However, only a few experiments have shown the existence of these patterns, in which "a competitive enemy becomes a friend" (Levine, 1999) or vice versa, as occurred in our study.

Few antecedents of such facilitative effects were found between cultivated grass forage species. One of the exceptions was the study conducted by Skinner (2005), who examined the emergence, mortality, and early growth of four forage species commonly found in temperate northeastern U.S. pastures: two drought-tolerant species ['Penlate' orchard grass (*Dactylis glomerat*a L.) and 'Viking' birdsfoot trefoil (*Lotus corniculatus* L.)] and two drought-sensitive species ['Basion' perennial ryegrass (*Lolium perenne* L.) and 'Will' white clover (*Trifolium repens* L.)]. In most cases, there was a negative effect of neighbors on survival, as evidenced by a negative relationship between mortality rate and distance to the nearest neighbor. However, in a dry year, perennial ryegrass mortality decreased as the distance to the nearest neighbor decreased, suggesting that survival was facilitated by the presence of neighbors.

Although our results cannot be extrapolated to all the annual/perennial pairs of forage species or even to all the environmental conditions, they show a potential very early facilitation effect of annual grasses in the establishment phase of pastures. We hypothesize that this slight facilitative early effect of annual perennial grasses would be related to the reduction in the minimal temperatures generated by a canopy higher and denser than that of perennial species (Benech-Arnold et al., 1988). In the future, it could be interesting to evaluate what happens with other pairs of annual and perennial species that are commonly used in humid regions, such as annual ryegrass (*Lolium multiflorum*) and tall fescue (*Festuca arundinacea*), respectively.

Conclusions

This work suggests that when designing pastures, a moderate initial density of annual species, according to the densities used in the present study, not only increases the production in the first cold season but could also have an initial facilitating effect. However, more research should be conducted to analyze the grade at which the initial density of annuals must be decreased to minimize the subsequent inhibitory effect on perennials.

Conflict of interest statement

We confirm that there are no conflicts of interest among the authors.

Data Availability Statement (DAS)

The data that support this study will be shared upon reasonable request to the corresponding author.

Declaration of Funding

This work resulted from the grade thesis of Agustina Lavarello Herbin. We would like to thank grants UBACyT-G0005 and PICT-2007-00463 for providing the funds needed for developing this research.

Acknowledgments

We would also like to thank Mario Suarez for the manual help provided during field work and Alejandra Ayala Torales and Gabriela Abeledo, who evaluated the grade thesis that resulted in the present article.

Resumen

A. Lavarello Herbin, M. L. A. Gatti, y R. Á. Golluscio. 2024. ¿Cómo afecta la vecindad de especies anuales o perennes a los primeros cien días del establecimiento de las gramíneas? Int. J. Agric. Nat. Resour. 57-67. Las gramíneas anuales y perennes pueden desempeñar un papel estratégico en el aumento de la sostenibilidad de los sistemas ganaderos de zonas templadas. Sin embargo, el impacto de la competencia entre especies forrajeras genéticamente mejoradas anuales y perennes en los pastos apenas ha sido estudiado. En este trabajo evaluamos la dinámica temprana del macollaje y la partición de carbono y la competencia intraespecífica e interespecífica en, o entre, una especie de pasto C_3 anual (*Bromus willdenowii*; pasto de la pradera; Bw) y perenne (*Dactylis glomerata*; pasto de huerto; Dg). Sembramos 24 microparcelas de 0,18 m^2 en mayo de 2008. Cada microparcela constituyó una unidad experimental y contenía cinco líneas de siembra espaciadas 0,175 m entre sí. En tres de las líneas sembramos diferentes combinaciones de las gramíneas mencionadas, mientras que en las dos líneas intermedias sembramos trébol rojo (*Trifolium pratense*). Aplicamos aleatoriamente un conjunto factorial de ocho tratamientos: 2 especies (Dg vs. Bw) × 2 tipos de competencia (intra vs. interespecífica) × 2 niveles de fertilización con nitrógeno invernal (0 vs. 170 kg de N ha^{-1}), diseñado en tres bloques completos al azar. La fertilización no tuvo ningún efecto significativo en ninguna especie. El período de evaluación tuvo una duración de 109 días después de la siembra (dds), separados en tres fases (0-53 dds, 59-90 dds y 90-109 dds). Las variables registradas fueron biomasa aérea (hojas, láminas y material senescente), biomasa de raíces y densidad de macollos por especie. Como se esperaba, Bw inhibió el crecimiento de Dg en la última etapa de establecimiento, pero sorprendentemente lo promovió en la etapa más temprana. Este trabajo sugirió que una baja densidad inicial de una especie anual debería optimizar el efecto facilitador inicial de la especie anual sobre la especie perenne con su posterior efecto inhibidor.

Palabras clave: *Bromus willdenowii*, cebadilla criolla, competencia, *Dactylis glomerata*, facilitación, pasto ovillo.

References

Armas, C., Ordiales, R. & Pugnare, F.I. (2004). Measuring plant interactions: a new comparative index. *Ecology, 85*(10), 2682-2686. https://doi.org/10.1890/03-0650

Begon, M. & Harper, L. (1996). Ecology: individuals, populations and communities. 3rd Edition. BlackWell Science. 876 pp.

Benech-Arnold, R. B., Ghersa, C. M., Sanchez, R. A. & Fernandez, A. G. (1988). The role of fluctuating temperatures in the germination and establishment of *Sorghum halepense* (L.) Pers. Regulation of germination under leaf canopies. *Functional Ecology,* 311-318. https://doi.org/10.2307/2389403

Berardo, A. (1996). La fertilización fosfatada y nitrogenada de las pasturas y sus efectos en distintos sistemas de producción. Fertilización de cultivos extensivos y forrajeras. Seminario de Actualización Técnica, CPIA y SRA. Buenos Aires. pp 173-182.

Capdevielle, B. (2020). Transformaciones en la ganadería vacuna Argentina y la cuestión agraria actual, ¿qué culpa tiene la vaca? *Revista Interdisciplinaria de Estudios Agrarios, 53*, 24-49. https://www.ciea.com.ar/web/wp-content/uploads/2021/11/capdevielle.pdf

Connell, J.H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat., 12*, 661-696. https://doi.org/10.1086/284165

Di Rienzo J.A., Casanoves F., Balzarini M.G., Gonzalez L., Tablada M. & Robledo C.W. (2008). InfoStat, versión 2008. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.

Fang, S., Clark, R. & Liao, H. (2012) 3D Quantification of Plant Root Architecture In Situ. In: Mancuso S. (Ed), *Measuring Roots, An Updated Approach* (pp. 135-148). Springer-Verlag.

Fernández Greco, R., Mazzanti, A. & Echevarría, H. (1995). Efecto de la fertilización nitrogenada sobre el crecimiento de forraje de un pastizal natural de la pampa deprimida bonaerense. *Revista Argentina de Producción Animal, 15*, 173-176.

Ganade, G. & Brown, V.K. (2002). Succession in old pastures of central Amazonia. Role of soil fertility and plant litter. *Ecology, 83*(3), 743-754. https://doi.org/10.1890/0012-9658(2002)083[0743:SIOPOC]2.0.CO;2

Gatti, M.L., Ayala Torales, A.T., Cipriotti, P.A. & Golluscio, R.A. (2013). Leaf and tiller dynamics in two competing C3 grass species: influence of neighbours and nitrogen on morphogenetic traits. *Grass and Forage Science, 68*, 151-164. https://doi.org/10.1111/j.1365-2494.2012.00881.x

Gatti, M.L., Ayala Torales, A.T., Cipriotti, P.A. & Golluscio, R.A. (2015). Dynamics of structural traits in two competing C3 grass species: influence of neighbours and nitrogen. *Grass and forage Science, 70*,102-115. https://doi.org/10.1111/gfs.12099

Guaita, S., Vivas, H. & Quaino, O. (1999). Fertilización fosfatada y encalado sobre la producción de alfalfa en el departamento las Colonias. INTA EEA Rafaela. Actualización técnica Nº231. 4pp.

Hume, D.E. (1991). Effect of cutting on production and tillering in Praire grass (*Bromus willdenowi* Kunth) compared with Ryegrass (*Lolium sp.*) species. *Annals of Botany, 68*(1), 1-11. https://doi.org/10.1093/oxfordjournals.aob.a088211

Islam, M.A. & Ashilenje, D.S. (2018). Diversified forage cropping systems and their implications on resilience and productivity. *Sustainability, 10*(11), 3920. https://doi.org/10.3390/su10113920

Lemaire, G. & Millard, P. (1998). An ecophysiological approach to modelling resource fluxes in competing plants. *Journal of Experimental Botany 50* (330), 15-28. https://doi.org/10.1093/jxb/50.330.15

Levine, J. M. (1999). Indirect facilitation: evidence and predictions from a riparian community. *Ecology, 80*, 1762-1769. https://doi.org/10.1890/0012-9658(1999)080[1762:IFEAPF]2.0.CO;2

Nurjaya, I.G.M.O. & Tow, P.G. (2001). Genotype and environmental adaptation as regulators of competitiveness. In: Tow, P.G. & Lazenby, A. (Eds), *Competition and succession in pastures*. (pp 43-32). AB International Publishing.

Paruelo, J.M., Guerschman, J.P. & Verón, S.R. (2005). Expansión agrícola y cambios en el uso del suelo. *Ciencia Hoy, 15*(85), 14-23.

Ries, R.E. & Svejcar, T.J. (1991). The grass seddling: when it is established? *Journal of range management 44*(6), 574-576. https://doi.org/10.2307/4003038

Sanderson, M.A., Archer, D., Hendrickson, J., Liebig, M., Nichols, K., Schmer, M., Tanaka, D. & Aguilar, J. (2013). Diversification and ecosystem services for conservation agriculture: outcomes from pastures and integrated crop-livestock systems. *Renewable Agriculture and Food systems*, *28*(2), 129-144. https://doi.org/10.1017/S1742170512000312

Sanderson, M.A., Skinner, R.H. & Elwinger, G.F. (2002) Seedling development and field performance of prairiegrass, grazing bromegrass and orchardgrass. *Crop Science, 42*, 224–230. https://doi.org/10.2135/cropsci2002.2240

Scheffer, M. (2009). *Critical transitions in nature and society*. Princeton University Press, Princeton, NJ.

Scheneiter, O., Mattew, C. & Rimieri, P. (2008). The effect of defoliation management on tiller dynamics of praire grass. *Revista Argentina de Producción Animal, 28*(1), 7-20.

Scheneiter, O. & Rimieri, P. (2001). Herbage accumulation, tiller population density and sward components of praire grass under different nitrogen levels. *New Zealand Journal of Agricultural Research, 44*, 13-22. https://doi.org/10.1080/00288233.2001.9513457

Skinner, R. H. (2005). Emergence and survival of pasture species sown in monocultures or mixtures. *Agronomy Journal, 97*(3), 799-805. https://doi.org/10.2134/agronj2004.0211

Sugiyama, S. (1999) Genetic variation in the relative dominance of mixed swards: potential influence and its mechanism. *Grassland Science*, *44*, 303-309.

Thom, E.R., Fraser, T.J. & Hume, D.E. (2011). Sowing methods for successful pasture establishment- a review. *Pasture Persistence-Grassland Research and Practice Series*, *15*, 31-38. https://doi.org/10.33584/rps.15.2011.3217

Wilson, S. D. & Tilman, D. (1993). Plant competition and resource availability in response to disturbance and fertilization. *Ecology, 74*(2), 599-611. https://doi.org/10.2307/1939319