Competition affects clonal traits in rhizomatous grasses to favor an invasive species over a native species

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Abstract

Competitive effects on biomass and vegetative reproduction can be especially strong when plants are young and establishing their clonal network of ramets. Invasive clonal plants may mitigate the effects of competition better than native clonal plants. We evaluated the competitive effects on the propagule supply and the number and biomass of tillers and rhizomes of invasive (*Bromus inermis*) and native (*Pascopyrum smithii*) perennial grass seedlings. Competition reduced aboveground biomass and the number of tillers for both species in most competitive scenarios, except for *B. inermis* under inter-specific competition. While intra-specific competition had similar reductions for each species in the number of belowground propagules (buds, juvenile tillers and rhizomes) that produce the next generation of ramets, inter-specific competition did not impact belowground propagule production of the invasive species but negatively impacted the native species. Belowground rhizome production and lateral spread of both species were less affected by competition enabling plants to successfully establish belowground clonal networks that will potentially foster physiological integration and future clonal plant success. Invasion by *B. inermis* may be facilitated by clonal traits, such as its ability to maintain larger tiller and propagule production than the native when under competition. Plant invasions involving clonal species would benefit from considering the role of clonal traits in their success.

Keywords Bud bank, *Bromus inermis*, Invasion, *Pascopyrum smithii*, Northern Great Plains

竞争通过影响克隆性状增强根茎型禾草入侵种的优势地位

摘要：在植物生长早期及克隆分株网络建立阶段，竞争对生物量积累和营养繁殖的影响尤为显著。与本地克隆植物相比，入侵克隆植物可能更能缓解竞争带来的不利影响。本研究以入侵种无芒雀麦(*Bromus inermis*)和本地种西方偃麦草(*Pascopyrum smithii*)幼苗为研究对象，评估竞争对其繁殖体供给以及分蘖和根茎数量与生物量的影响。结果表明，在多数竞争情境下，竞争均降低了两物种的地上生物量和分蘖数量，但在种间竞争条件下光果早熟禾未表现出这一趋势。在种内竞争条件下，两物种地下繁殖体(芽、幼分蘖和根茎)数量的降低幅度相似；而在种间竞争条件下，地下繁殖体的产生对入侵种影响不显著，但对本地种产生明显抑制作用。竞争对两物种地下根茎产生及其侧向扩展的影响较小，使其能够建立地下克隆网络，从而有利于后续的生理整合与种群扩展。光果早熟禾在竞争条件下仍能维持较高的分蘖和繁殖体产生能力，这一克隆性状可能促进其入侵成功。上述研究表明，在克隆植物入侵研究中，应重视克隆性状在入侵过程中的作用。

关键词：芽库，无芒雀麦(*Bromus inermis*)，入侵，西方偃麦草(*Pascopyrum smithii*)，北部大平原

Introduction

Biological invasions currently threaten terrestrial, marine and freshwater function and biodiversity around the globe (Dukes and Mooney 1999; Pimentel *et al.* 2005; Vitousek *et al.* 1996). Introduced species that become invasive and start expansion into native plant communities need to be good competitors with the dominant species (Richardson *et al.* 2000; Vilà and Weiner 2004). Many invasive plant species are clonal which can enhance their performance through physiological integration (Estrada *et al.* 2020; Liu *et al.* 2016; Pyšek and Richardson 2007), but invasive clonal plants often invade systems dominated by clonal plants which would have similar benefits from clonality (e.g. Otfinowski and Kenkel 2008). Therefore,

invasive clonal species potentially exhibit different clonal traits than their competitors or inhibit the clonal trait expression of their competitors enabling them to be competitively superior to co-occurring native clonal plants (e.g. Wang *et al.* 2019).

Perennial grassland ecosystems offer an excellent system to compare differences between native and invasive clonal grass species. In perennial grasslands, seedling recruitment of perennial grasses is often rare, as most of the tillers are recruited from vegetative belowground buds (Rogers and Hartnett 2001; Benson and Hartnett 2006; Ott *et al.* 2019). For example, in some undisturbed tallgrass prairie, >99% of tiller recruitment occurs from belowground buds rather than seed (Benson and Hartnett 2006). In the northern Great Plains of North America, the invasion of non-native *Bromus inermis* into tallgrass and mixed-grass prairie is a growing concern, as *B. inermis* invasion rapidly displaces the dominant native species and homogenizes the plant community and modifies the soil (Jordan *et al.* 2008; Piper *et al.* 2015; Stotz *et al.* 2019) causing loss of species diversity and reduced habitat use by native ungulates (Dillemuth *et al.* 2009; Trammell and Butler 1995). The success of *B. inermis* may be due to subtle but important differences in clonal traits (Klimešová *et al.* 2019). For example, compared to the native perennial grass *Pascopyrum smithii*, *B. inermis* recruited a greater proportion of its buds to vegetative tillers and had greater tiller establishment except when precipitation was intermittent (Bam *et al.* 2022; Ott *et al.* 2017). However, these clonal traits could shift outcomes when these species are placed in direct competition with one another. For example, inter-specific competition rather than intra-annual precipitation variability and clipping shifted spatial bud placement in both these species with the invasive species locating more buds further away from the parent plant and the native species placing more buds closer to the parent plant (Bam et al. 2023).

Although there are many clonal traits, such as ramet longevity, the persistence of clonal connections, degree of physiological integration, and carbohydrate supply in the clonal growth organ (Klimešová *et al.* 2019), clonal traits related to plant demography, such as ramet multiplication rate and bud bank size, can provide insight into the immediate and potential competitive effects on the biomass and number of ramets. Competition studies often focus on the responses of aboveground productivity and flowering effort to determine competitive effects (Aschehoug *et al.* 2016; Corbin and D'Antonio 2010; Nernberg and Dale 1997; Ulrich and Perkins 2014). Nevertheless, reductions in aboveground biomass due to competition are often correlated with declines in the population demography of stems (i.e. the number of aboveground ramets recruited in clonal species; Cheplick and Gutierrez 2000). On the other hand, these aboveground reductions may or may not be mirrored in belowground biomass responses to competition. Many clonal plants invest significant resources in belowground clonal organs, such as rhizomes and tubers, that may provide resource storage and a reservoir of future ramets in the form of buds (i.e. bud bank; Klimešová 2025; Ott *et al.* 2019). Moreover, competition experienced by clonal plants can shift biomass allocation from aboveground organs to belowground organs (Cheplick and Gutierrez 2000; Dietz *et al.* 2002) or can reduce both above- and below-ground biomass (Schmidt *et al.* 2008).

In clonal species, plant architectural development of seedlings through vegetative reproduction (i.e. clonal growth via the addition of new ramets) is key to continued growth and expansion (Speek *et al.* 2011). Young clonal plants need to create this extensive integration, which, in the case of invasive species, can be used to facilitate their invasion (Maurer and Zedler 2002). However, competition during plant establishment may greatly influence the invasion trajectory at a site (Gioria and Pyšek 2017).

The main scientific question of this study is:

Do the clonal traits of establishing perennial grass plants of the dominant native *P. smithii* and the invasive *B. inermis* differ under competition? Specifically, Is the

1) production of aboveground and belowground ramets (i.e. ramet multiplication rate)
2) lateral spread via rhizomes
3) vegetative reproductive potential (i.e. supply of propagules)

of the native species more greatly impacted by inter-specific competition than the invasive species?

In order to examine the competitive effects on the clonal development of invasive and native seedlings, vegetative reproduction of *B. inermis* and *P. smithii* experiencing intra- and inter-specific competition were examined during their first growing season using a temperature-controlled greenhouse. Both aboveground and belowground demographic clonal traits and plant biomass were measured by evaluating belowground bud production, propagule development, tiller and rhizome recruitment, and biomass. This study complements Bam *et al.* (2023), which examined changes in propagule and tiller spatial placement in response to competition, but did not examine changes in propagule numbers, propagule development, and tiller and rhizome production. We hypothesize that competition will decrease total tiller and rhizome recruitment and biomass in seedlings of both species. Competition will also reduce the propagule supply of both species. Because *B. inermis* successfully invades *P. smithii* dominated grasslands, we hypothesize that inter-specific competition will have a greater negative effect on the propagule supply, lateral spread, and tiller and rhizome production of the native *P. smithii* than the invasive *B. inermis*.

Methods

Experimental Overview

Competition effects on the vegetative reproduction of the invasive *B. inermis* and native *P. smithii* were examined following a 3-month simulated growing season in a temperature-controlled greenhouse at South Dakota State University in 2017. *Pascopyrum smithii* (western wheatgrass) and *B. inermis* (smooth bromegrass) are both strongly rhizomatous, perennial C_3 grasses that begin flowering in late May (USDA 2006). *Pascopyrum smithii* is native to North America and the dominant species in northern mixed-grass prairie. In contrast, *B. inermis* was introduced from Eurasia in the late 1880s for forage and has made an extensive impact on the grasslands of North America by invading disturbed prairies from its repeated introductions for soil retention and livestock grazing (Cully *et al.* 2003; DeKeyser *et al.* 2013; Grant *et al.* 2020; Otfinowski *et al.* 2007; Stotz *et al.* 2019).

Bromus inermis and *P. smithii* seeds were respectively obtained from local suppliers (Dakota's Best Seed LLC, Platte, South Dakota, USA; Golden Willow Seeds, Inc., Midland, South Dakota, USA). Seeds were germinated in a commercial potting mix soil (Miracle-Gro) with a temperature regime of 16 °C night/ 22 °C day. Due to the slower germination of *P. smithii*, *P. smithii* seeds were sown five days earlier than *B. inermis* seeds to obtain the same growth stage at the time of transplant. When seedlings reached the two-leaf developmental stage in late May, seedlings of similar size were transplanted into pots (16.5 cm dia. x 10 cm depth) filled with 600 g of potting-soil (PRO-MIX® BX). Seedlings were randomly assigned to one of three treatments: no competition, intra-specific competition (competition with a conspecific neighbor), or inter-specific competition (competition with a heterospecific neighbor; Fig. 1). For each species, there were 30 plant replicates for each treatment. Because the plants of the two species shared the same pot for the inter-specific competition treatment, the experiment consisted of 150

pots. Seedlings were used in this experiment to examine clonal traits at the plant establishment phase when the newly established genet starts producing its first clonal ramets.

Immediately after transplant, pots were watered to field capacity (44–45% Volumetric Water Content (VWC); Decagon Devices, Soil Moisture Sensor: Model EC-5 calibrated to the potting soil). Soil moisture levels dropped down to 25–28% VWC two weeks post-transplant and were maintained throughout the experiment by watering each pot every other day with 72 mL of water. Total water received was consistent across treatments and simulated average growing season precipitation of 51 mm per month (based on 1981–2010 March–August precipitation recorded at Rapid City Regional Airport, South Dakota; https://climate.sdstate.edu, Accessed 27 May 2016). The greenhouse daylength and temperature regime mimicked mixed grass prairie field conditions during the growing season (June–August; Supplementary Table S1).

Plants were harvested 12 weeks after treatment initiation. A plant is considered an entire clone (i.e. genet) within a pot. One plant from each pot of the intraspecific competition treatment was randomly chosen for analysis using a random number selection process. Plants were washed free of soil and sorted. All adult aboveground tillers and belowground rhizomes of each plant were counted and rhizome lengths were measured. Rhizomes were defined as belowground stems at least 0.5 cm in length with elongated internodes. Adult tillers had vertically elongated aboveground beyond their bud's prophyll and had reached >9% of the recorded vegetative tiller height for each species, which is 3.6 cm and 4.5 cm for *B. inermis* and *P. smithii* respectively (Table 1; Great Plains Flora Association 1986; Ott *et al.* 2017). Three generations of tillers occurred during the experiment. Therefore, tillers and rhizomes were classified by generation following Ott and Hartnett (2015); (see Fig. 6 in Bam *et al.* 2022). Using random numbers assigned to plants, aboveground and rhizome biomass were measured based on ten randomly

selected plants of each species from each treatment. Biomass was oven-dried for 72 h at 60 °C and then weighed.

Using random numbers, a random sub-sample of up to three adult tillers and three adult rhizomes from each tiller generation were selected from each plant to assess bud production and bud development stages. This sub-sample size enabled a majority of tillers and rhizomes per plant undergoing competition to be counted while maintaining even sampling effort across treatments. This enabled between six and nine adult tillers and rhizomes to be sampled per plant. Each adult tiller/rhizome was examined using a dissecting scope (Olympus® Stereo Microscope) with magnification between 6.7x and 45x. Basal/belowground buds, juvenile rhizomes, and juvenile tillers were counted, assessed to be living or dead, and classified by their size (Table 1; Ott *et al.* 2017). Dead buds and juvenile tiller and rhizomes were identified by their desiccated interiors lacking membrane integrity. Collectively, live buds, small juvenile tillers and rhizomes, and large juvenile tillers and rhizomes were called live propagules.

Statistical Analysis

Linear mixed models were used to analyze the effect of competition and species on propagule development, live propagule supply, new tillers established per tiller of each generation, and overall plant establishment measured by total tillers, total rhizomes, total rhizome length, aboveground biomass, and rhizome biomass per plant (PROC GLIMMIX; SAS Institute 2017). The residual method was used to approximate the denominator degrees of freedom. Multiple pairwise comparison between treatments were significant at $P < 0.05$.

For each plant, live propagules per plant was calculated by summing the number of propagules belonging to each of the three generations of adult tillers and rhizomes. The number

of propagules for each generation of tillers within a plant was obtained using the propagule count per adult tiller of each generation (e.g. primary tiller, secondary tiller, etc.) multiplied by the total adult tillers for each generation. Similarly, the number of propagules for each generation of rhizomes within a plant was obtained by multiplying the propagule count per rhizome length of each rhizome generation multiplied by the total rhizome length of that rhizome generation. The total number of live propagules per plant was analyzed using a gamma distribution in a two-way factorial treatment structure with the factors of competition and species in a complete randomized design (CRD).

The number of live propagules per plant belonging to each propagule development stage (Table 1) was analyzed using a gamma distribution in a three-way factorial treatment structure with the fixed factors of competition, species, and development stage in a randomized split-plot design. Competition and species were analyzed at the whole-plot of plant while developmental stage was analyzed at the sub-plot of a portion of the plant.

Both total adult tillers and total adult rhizomes per plant were analyzed using a negative binomial distribution in a two-way factorial treatment structure with the factors of competition and species in a CRD. Total rhizome length per plant was analyzed using a gamma distribution in a two-way factorial treatment structure with the factors of competition and species in a CRD. Tiller replacement (i.e. the number of new tillers established per tiller in each generation) was analyzed using a negative binomial distribution in a three-way factorial treatment structure with the factors of competition, species, and generation in a randomized split-plot design. Competition and species treatments were applied to the experimental unit of plant (whole-plot) and the generation factor was applied to the experimental unit of tiller (sub-plot). Aboveground biomass and rhizome biomass per plant were analyzed using a normal distribution and a gamma

distribution respectively in a two-way factorial treatment structure with the factors of competition and species in a CRD.

The relative interaction index (RII) was used to assess the intensity of the intra-specific and inter-specific interactions for each species. RII is calculated as follows:

$$RII = \frac{B_w - B_O}{B_w + B_O}$$

where B_O is the measured response of the target plant growing in absence of inter- or intra-specific interactions and B_W is the measured response of the target plant growing with another conspecific (intra-specific interaction) or heterospecific (inter-specific) plant (Armas *et al.* 2004). When RII values are significantly different from zero, a positive value indicates a positive response to competition while a negative value indicates a negative impact from competition. RII values were assessed for six response variables, including total tillers, total rhizomes, total rhizome length, aboveground biomass, rhizome biomass, and total live propagules per plant. To calculate intra-specific RIIs, a plant of *B. inermis* or *P. smithii* grown without competition were randomly paired with a conspecific plant that had experienced intra-specific competition. Calculation of inter-specific RIIs was similarly completed by pairing plants grown without competition with conspecific plants that had experienced inter-specific competition. RII values for each response variable were analyzed using a normal distribution in a two-way factorial treatment structure with the fixed factors of competition and species in a CRD.

Results

Aboveground competitive effects

For both species, intra- and inter-specific interactions had a competitive effect on aboveground tiller numbers and biomass as almost all RII values were negative and significantly different from zero (Fig. 2a, d). Therefore, neighbor presence resulted in aboveground response

to competition. However, each species differed in their response to intra- and inter-specific competition. Tiller production and biomass of *P. smithii* declined to a similar extent under the two types of competition. However, *B. inermis* tiller numbers and aboveground biomass had greater reductions when competing with a conspecific plant rather than with a *P. smithii* plant (Fig. 2a, d). Without competition, *B. inermis* and *P. smithii* produced similar aboveground biomass per plant (Supplementary Fig. S1a), but *P. smithii* produced more tillers per plant than *B. inermis* (Fig. S2a). This indicates that *B. inermis* tillers tend to be larger than *P. smithii* tillers.

Three generations of tillers occurred in each species over the 12 weeks of the study. Tiller replacement values (no. of adult tillers produced per parent tiller) were greatest for primary tillers followed by secondary tillers (Fig. 3). The tertiary tiller generation made up a small component of the overall tiller population of each species. *Pascopyrum smithii* had greater tertiary tiller replacement values than *B. inermis* which demonstrated *P. smithii*'s ability to quickly produce the next tiller generation. For each species, both types of competition reduced tiller replacement values within each tiller generation except *B. inermis* experiencing inter-specific competition and tertiary *P. smithii* experiencing intra-specific competition (Fig. 3).

Belowground competitive effects

Competition, either intra- or inter-specific, did not affect the belowground rhizome number, rhizome length and rhizome biomass of *B. inermis* (Fig. 2b, c,e). Belowground rhizomes of *P. smithii* were significantly negatively affected by intra- and inter-specific competition but were not statistically different from *B. inermis*' belowground response to competition (Fig. 2bc, e; Supplementary Figs S1b and S2b, c). In general, *P. smithii* produced more rhizomes of greater length and had greater total rhizome biomass than *B. inermis* (Supplementary Figs S1b and S2b, c).

Competitive effects on the propagule bank

Competition reduced the number of live propagules per plant for both species except for *B. inermis* experiencing inter-specific competition (Supplementary Fig. S3). Intra-specific competition yielded similar reductions in the propagule bank size for both species (Fig. 2f). Inter-specific competition showed divergent effects on the two species with *B. inermis* maintaining a propagule bank similar in size to when it grew in the absence of competition while *P. smithii* saw an even greater reduction in propagule numbers than under intra-specific competition (Fig. 2f). Propagule development into juvenile tillers and rhizomes within the propagule bank was limited as a large proportion of propagules were maintained as buds (~80%; Fig. 4). *Pascopyrum smithii* maintained ~10% more propagules as juvenile tillers than *B. inermis* but competition did not affect propagule development (Fig. 4).

Discussion

As hypothesized, inter-specific competition had a greater negative effect on the clonal traits of the native *P. smithii* than the invasive *B. inermis*. However, contrary to the hypothesis, this negative effect was limited to the clonal traits of tiller multiplication (i.e. tiller production and biomass) and propagule supply whereas lateral spread and rhizome multiplication were unaffected. Competition in plant invasions can focus on both the ability of the invader to grow when in the native plant community and the native plant community's tolerance to the invasive species (Vilà and Weiner 2004). When comparing the aboveground and belowground tolerance of the native to the invasive, *P. smithii* tolerated the invasive *B. inermis* as the competitive response of the native *P. smithii* did not differ between intra- and inter-specific competition indicating that the native species exerted similar effort of competing against itself as it did against the invasive *B. inermis*. When considering the invasive species' ability to grow in the

presence of the native, the invasive *B. inermis* had better aboveground stem and biomass production when competing against the native. However, the invasive did not alter its allocation to belowground rhizomes or biomass when competing against the native.

Aboveground ramet multiplication (i.e. tiller production and biomass) may be more responsive to competition than belowground ramet multiplication and lateral spread (i.e. rhizomes). Both intra- and inter-specific competition from the native and invasive rhizomatous grasses negatively affected aboveground tiller recruitment and biomass with little effect on belowground rhizome recruitment and biomass. The similar effect of intra- and inter-specific competition on the belowground growth of both species could indicate belowground growth priorities of these individual plants or their ability to evade belowground competition. Due to the rhizomatous growth form of these species, rhizomes may have been able to spread out their resource use throughout the pot preventing intense competition for belowground resources. Alternatively, competition may initially affect aboveground growth and only affect belowground growth as competitive intensity increases. Aboveground growth is often seasonal in herbaceous plants with their perennating organs residing belowground for multiple years (Klimešová and Klimes 2007). Therefore, a plant may continue investment in long-term carbohydrate storage and organs supporting a belowground bud bank while reducing aboveground short-term investments in tillers used for carbon capture. Competition experienced by clonal plants can reduce overall above- and below-ground biomass (Schmidt *et al.* 2008) or shift biomass allocation from aboveground organs to belowground organs (Cheplick and Gutierrez 2000; Dietz *et al.* 2002). Belowground competitive effects may only become apparent after a longer period of competition than this twelve-week experiment.

The aboveground response of *B. inermis* to competition with *P. smithii* may be a result of changes in the light environment. Competitor species can create different light environments that vary in intensity and heterogeneity which in turn can alter the aboveground morphological response of clonal species (Bittebière *et al.* 2012). *Bromus inermis* maintains leaf widths that can be two to four times wider than *P. smithii* (Great Plains Flora Association 1986). The self-shading effect may be greater with *B. inermis* than for *P. smithii* because of its larger leaf surface area as observed in other perennial grasses (Jurik and Kliebenstein 2000). In its native range, *B.inermis* seedlings had lower biomass and height with increased competition (Liu *et al.* 2008), which may indicate that a competitor with equivalent leaf surface area may be a better aboveground competitor with *B. inermis* than *P. smithii*.

Tillers and rhizomes both grow from the same pool of belowground axillary buds. Therefore, a tradeoff can exist between using a bud for tiller or rhizome outgrowth (e.g. McIntyre 1970). When in competition with *P. smithii*, *B. inermis* invested more into additional tillers rather than into rhizomes indicating it valued monopolizing aboveground canopy space over belowground soil area. *Bromus inermis* prioritization of aboveground carbon capture can potentially convert into belowground gains in the future as well-established tillers could support belowground expansion (Song *et al.* 2013).

Because vegetative reproduction via belowground buds is the primary source of tiller recruitment in perennial grasses (Benson *et al.* 2004; Dalgleish and Hartnett 2009; Ott *et al.* 2019), negative effects on the belowground bud bank of the native *P. smithii* in the presence of invasive *B. inermis* may be a mechanism through which non-native perennial grasses displace native perennial grasses (Schmidt et al. 2008; Wilson and Pärtel 2003). Although both intra- and inter-specific competition reduced the bud bank of *P. smithii*, only intra-specific competition

reduced the bud bank of *B. inermis*. *Bromus inermis* was able to produce more tillers when competing with *P. smithii* than itself. Buds are produced at the base of each leaf on a tiller (Evert 2006). Therefore, bud production is likely to increase concurrently with increased tiller production (Ott *et al*. 2019). Although rhizome number and length did not change significantly in this study, they also would be source of increased bud production at their nodes. *Bromus inermis* bud development, as shown by increased bud transitions into juvenile tiller and rhizome stages, was only reduced during intra-specific competition but maintained regular development during inter-specific competition. As the propagule bank represents the potential future growth of these species, *P. smithii* may be at a disadvantage in future generations when competing with *B. inermis*.

Conclusion

Clonal traits in newly establishing plants can be affected by competition and may provide insight into the mechanisms behind successful plant invasions. Clonal traits, such as lateral spread and the multiplication rates of tillers and rhizomes, demonstrate the current effects of competition on space occupancy and clonal expansion while clonal traits related to the bud bank or propagule supply indicate future impacts of competition on the vegetative reproductive potential. Although the lateral spread and rhizome production of the invasive *B. inermis* and native *P. smithii* did not shift when in competition with one another, *P. smithii* experienced greater reductions in both its propagule supply and tiller production than *B. inermis*. This clonal superiority of the invasive species could enable it to outcompete the native as their clones age. Plant invasions involving clonal species would benefit from considering the role of clonal traits in their success.

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Authors' Contributions

Conceptualization, JPO, JLB, and LX; methodology, JPO, JLB, and LX; investigation, SB and LX; formal analysis, JPO and SB; writing—original draft preparation, JPO, SB, and LX; final draft preparation, JPO and LX; funding acquisition, JPO, JLB, and LX.

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Tables

Table 1. Bud, rhizome, and tiller developmental stages

Developmental Stage	Description
Buds	Contained within the prophyll
Small juvenile tillers/rhizomes	Apex elongated <3.0 mm beyond prophyll
Large juvenile tillers/rhizomes	Elongated >3.0 mm beyond prophyll AND <4.5 cm in total height or length (*P. smithii*) < 3.6 cm in total height or length (*B. inermis*)

Adult tillers/rhizomes	≥4.5 cm in total height or length (*P. smithii*) ≥3.6 cm in total height or length (*B. inermis*)

Tillers were considered adult tillers when ≥9% of the recorded vegetative tiller height for each height for each species (Great Plains Flora Association 1986; Ott *et al.* 2017).

Figure Captions

Figure 1 Conceptual diagram of experiment from Bam et al. 2023. Treatments include the pots with solitary *B. inermis*, and *P. smithii* individuals, conspecific neighbors (intra-specific competition), and heterospecific neighbors (inter-specific competition).

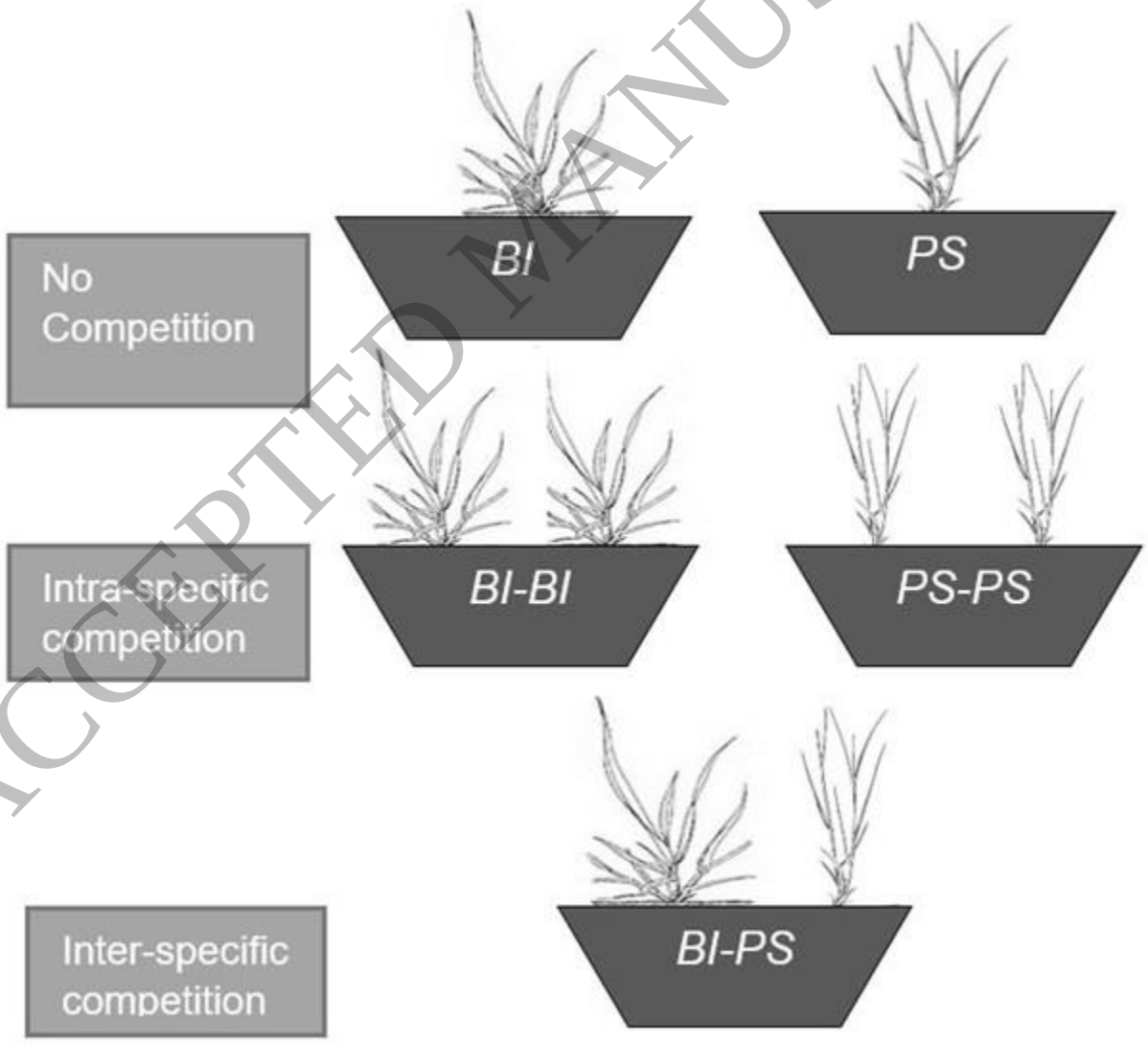


Figure 2 Effect of competition on RII values of *Bromus inermis* and *Pascopyrum smithii* based on total tillers, total rhizomes, total rhizome length, aboveground biomass, rhizome biomass, and total propagules per plant. Values are mean RII ± SE based on the statistical model. Different letters above bars indicate significant difference among the combinations of competition and species within a response variable at $P < 0.05$. Statistical interaction results are not shown when $P > 0.05$. Positive RII values indicate a facilitative interaction and negative RII values indicate a competitive interaction. RII values that are significantly different from zero are indicated with an asterisk (*).

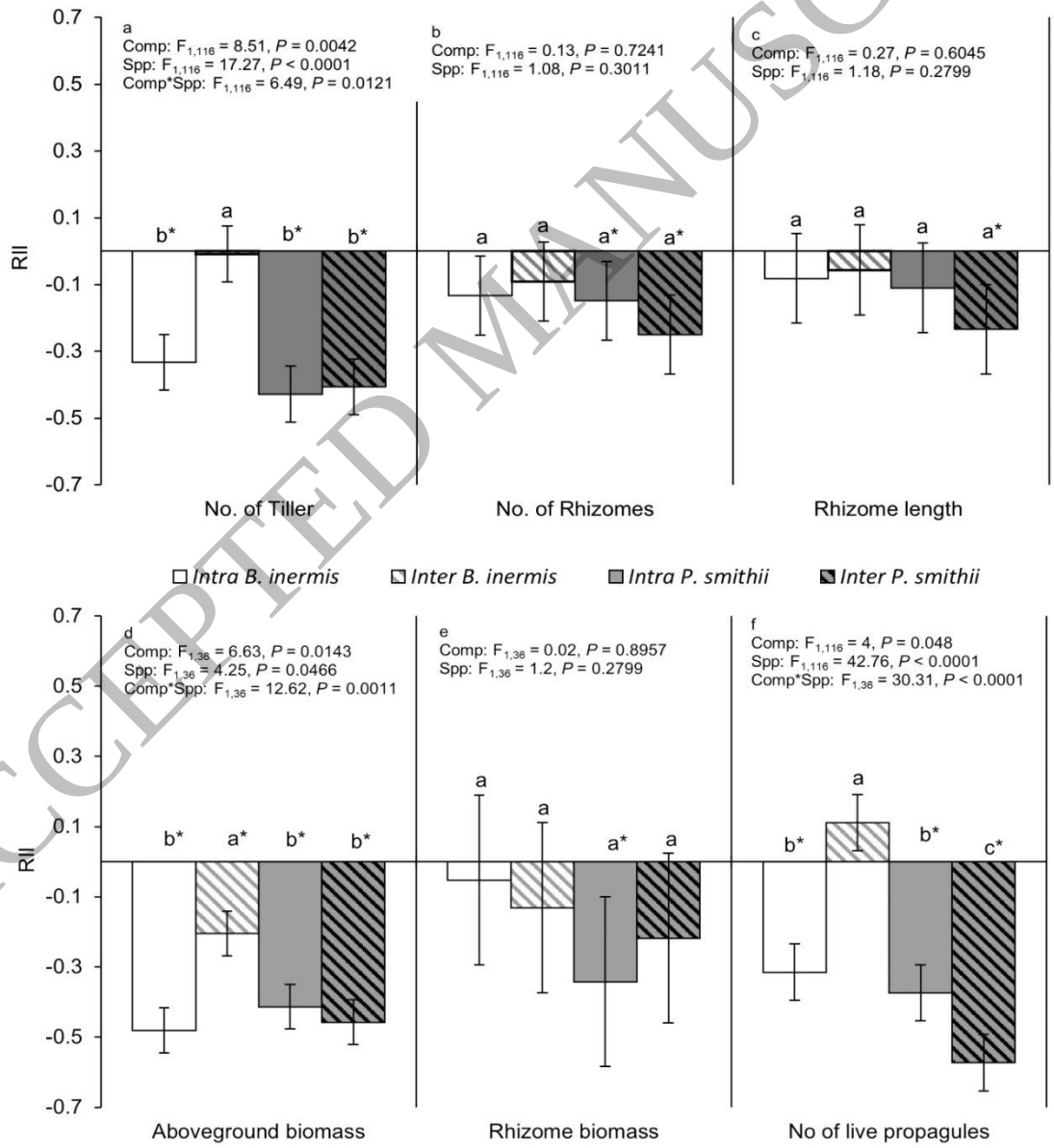


Figure 3 Effect of competition on generational tiller replacement of *Bromus inermis* and *Pascopyrum smithii*. Three daughter tiller generation cohorts were produced for each species and defined as primary, secondary, and tertiary tiller generation. Values indicate the number of tillers per the number of previous generation tillers (i.e. tiller replacement). Values are mean ± SE based upon the statistical model. Different letters above bars indicate significant difference across treatment at *P*-value < 0.05. Interaction results are not shown when *P*-value > 0.05.

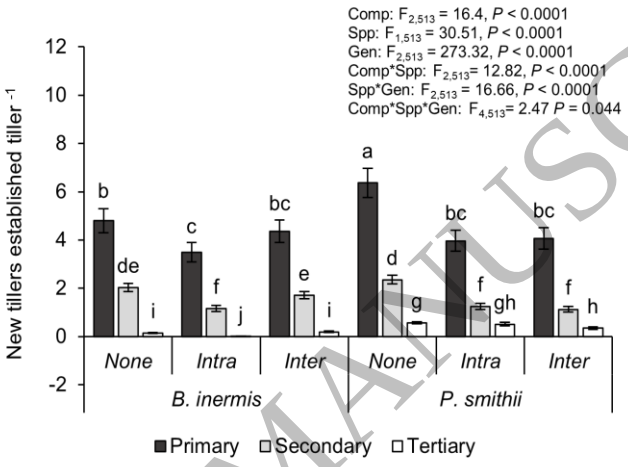
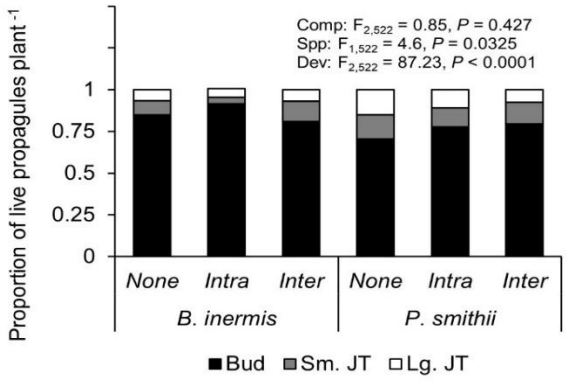
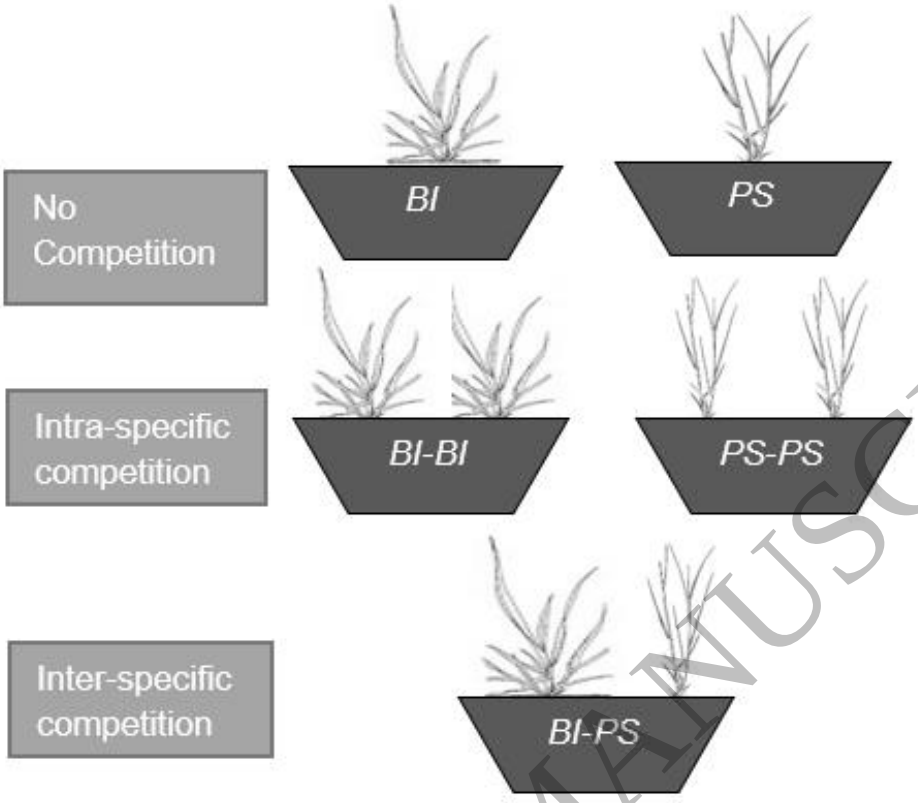


Figure 4 Effect of competition on the proportion of live propagules at each development stage per plant of *Bromus inermis* and *Pascopyrum smithii*. Live propagules were classified into three developmental classes including buds, small juvenile tillers/rhizomes (Sm. JT) and large juvenile tillers/rhizome (Lg. JT). Interaction results are not shown when *P*-value > 0.05.





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2 Graphical Abstract

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