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# Nitrogen Pulses and Competition between Native and Invasive Plant Species

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NITROGEN PULSES AND COMPETITION BETWEEN NATIVE AND INVASIVE PLANT SPECIES

By

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**ABSTRACT**

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Variation in the timing and size of resource fluctuations can influence how plants grow, allocate biomass, and reproduce. Resources are sometimes made available in relatively continuous, reliable pulses while other times they are temporally separated and unpredictable. Native and invasive plant species are thought to respond differently to resource fluctuations, or pulses, which can influence competitive outcomes. The “Fluctuating Resource Hypothesis” predicts that resource fluctuations benefit invasive species more than native species, potentially because many invaders are highly effective at rapidly capturing resources. In a field setting, we examined the effects of varying nitrogen pulses on competition between exotic invasive and native species that are common in the intermountain prairie. We planted pairs of two native and two invasive plant species alone and in competition, and these groups of species received one of three treatments: no nitrogen at all (control), one large pulse of nitrogen (0.31 g N), or three smaller pulses equaling the total amount of nitrogen in the large pulse. The total amount of nitrogen added in the treatments was quite small in an attempt to mimic what these plants would be more likely to experience in nature. Invasives competitively suppressed natives regardless of the pulse treatment. Conversely, natives did not influence invasives and there was no effect of nitrogen addition or pulses on natives or invasives. Our results provide relatively limited insight into the impact of nitrogen pulses on plant interactions because the total amount added was low, and did not stimulate growth relative to controls. However, in that context we did not find evidence for any influence of fluctuating resources on the growth or competitive interactions of invasive or native plants.

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## Introduction

Resources fluctuate in nature, and their patterns of fluctuation can vary drastically across micro-habitats and ecosystems. In some places, resource pulses are steady and predictable, while in others they are rare and stochastic (Noy-meir 1973). Since plants are sessile and cannot readily move to utilize resources, they are especially sensitive to the nature of these resource fluctuations. Variability in resource supply and demand creates a dynamic environment that favors different plants at different times, promoting coexistence and increasing diversity.

Resource pulses vary in their *timing* and *size*. The *timing* of when resources become available has been shown to affect the rate at which plants uptake and utilize resources for growth and allocation among roots, shoots, and reproduction (Farley and Fitter 1999, Chesson et al. 2004, Hodge 2004). This is due to the phenology of plant life stages (i.e. timing of germination, maximum growth rate, setting seed, etc…) which can affect resource demand over time (Bilbrough and Caldwell 1997, Gebauer and Ehlringer 2000, Chesson et al. 2004). Along with timing, plants can respond differently to the *size* of a resource pulse. Some species only uptake resources once a minimum quantity is reached in their environment, while others may continuously acquire resources (Fig. 1, Chesson et al. 2004). For example, deciduous trees break from dormancy and grow leaves when resources in their environment reach a certain availability, while evergreen trees continually capture resources, potentially even during small pulses that do not trigger deciduous trees to break from dormancy (Noy-meir 1973, Chesson et al. 2004). The variation in supply of resources and demand by the plants creates an environment that favors different plants at different times, and permits their coexistence.

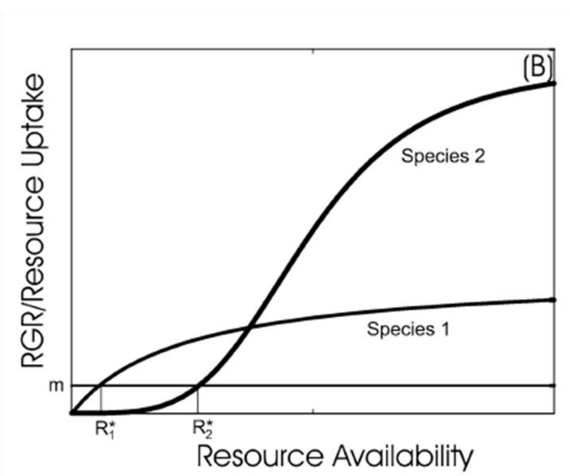


**Fig 1.** *From (Chesson 2004)* The resource uptake rates of two species in response to resource availability. Species 1 has a low threshold requirement to initiate resource uptake, but has a low saturation level. Species 2 only begins resource uptake when availability reaches a threshold that is higher than that of species 1 and also saturates at a much higher level, meaning that it can take up more resources overall.

The timing of resource delivery directly influences resource availability. Pulsed resources are inconsistent and lead to periods where resources are available (during the pulse), inter-pulse periods where resources are no longer available, and a gradient in between these times (Ostfelt and Keesing 2000, Novoplansky and Goldberg 2001, Chesson et al. 2004). Competition between plants for available resources should be strongest during the time of greatest resource availability (Goldberg et al. 1999). These effects may be most pronounced in arid and semi-arid environments where resource pulses are rare and the timing and size of these pulses have been found to play an important role in determining community composition (Bilbrough and Caldwell 1997, Chesson et al. 2004, Schwinning et al. 2004, Funk and Vitousek 2007)

Coexistence theory generally assumes that trade-offs between growth and survival limit species from being the best at utilizing resources under all environmental conditions (Tilman 1982, 1988, Hodge 2004, Funk and Vitousek 2007, Angert et al. 2009). For example, plants often exhibit a trade-off between water use efficiency and nitrogen use efficiency, where species that are particularly drought tolerant are less able to assimilate nitrogen, and species that are less drought tolerant can better assimilate nitrogen (Field et al. 1983, Gong et al. 2011, Patterson et al. 1997, Dijkstra et al. 2016). While these tradeoffs have been shown for native species, the response of exotic invasive species to resource heterogeneity is not so clear. Many examples exist where exotic invasive species have been able to out-compete natives and reach disproportionately large abundances (reviewed in Stachowicz and Tilman 2005). These scenarios have led many to ask whether exotic invasive species might possess a fundamental advantage that has led to their competitive success. Some meta-analyses have found that exotic invasive species might be more plastic or somehow better able to avoid the trade-offs that native species are subject to (Thompson 1995, Funk 2008, Davidson et al. 2011). Conversely, others have found that exotic invasive species are not more plastic than native species (Palacio-López and Gianoli 2011). The Fluctuating Resource Hypothesis (FRH) and Stochastic Niche Theory (SNT) posit that exotic invasive species may become established by utilizing resources not used by the native plant community and that exotic species do not posses any fundamental advantage over native plant species but that environments with fluctuating resources are inherently more invasible because of their resource stochasticity (Davis et al. 2000, Tilman 2004). However, even in low-resource, long-lived environments where one would expect the native community to be highly adapted to fill resource niches and excess resources are unlikely, invaders have been successful and even show a better ability than natives at capturing resources (Funk and Vitousek 2007).

In semi-arid ecosystems, nitrogen (N) is a limiting resource that becomes available immediately following precipitation events and often only for very short windows of time (Noy-Meir 1973). Plants and microbes rapidly assimilate recently mineralized N, often lowering available N to pre-pulse levels in just a few days (Cui and Caldwell 1977, Hodge et al. 1999). These precipitation induced N pulses have been shown to affect individual growth and competitive interactions in plant communities (Bilbrough and Caldwell 1997, Lamb et al. 2007, James and Richards 2005, 2006, Gebauer et al. 2002). James et al. (2006) compared the growth and interactions of two native shrubs and an invasive annual grass to different sized resource pulses applied at different times and found that the response of native and exotic species varied with the timing and magnitude of resources. In this case, however, the exotic grasses may have benefited from smaller more frequent resource pulses that did not reach the deeper roots of the native shrubs but instead created resource niches that may have reduced actual direct competition (James et al. 2006). Davis and Pelsor (2001) explored resource addition in a field experiment and found that increased resource availability had large impacts on the survival and abundance of encroaching species. However, the effects of pulses *per se* were not tested, thus limiting the scope of inference in this study to the effect of *increased* resources in general and not resource fluctuations. In this context, we experimentally examined the growth of exotic invasive and native species to ask: 1) across species, how does pulse frequency and total resource quantity influence plant performance? And 2) is competition intensity affected by pulse frequency and/or total pulse quantity?

**Methods**

In the spring of 2016, we grew two exotic invasive forb species (*Centaurea stoebe* (CM) and *Linaria dalmatica* (Linaria)) and two native grass species (*Poa secunda* (PSAND) and *Pseudoroegneria spicata* (BB)) alone and in combination to assess the influence of resource fluctuations on growth in and out of competition. All species are perennials and are commonly found growing together in the intermountain/foothill grasslands of the northern Rocky Mountains. Seeds were sown in a greenhouse in early February 2016 and then transplanted on May 28 and 29 in the University of Montana's Experimental Gardens at Fort Missoula

(Missoula, Montana, USA) into 10 $cm^2$ plots (240 total). Within each plot, we planted either an exotic or native species alone (control) or combined (paired native and exotic). Each plant combination was replicated 10 times. In order to be sure that these plants only experienced one pulsed resource, the plots were not allowed to dry out. Automated sprinklers were adjusted seasonally to avoid overwatering and in the height of summer watered up to four times a day to maintain soil saturation. All plots were hand weeded regularly.

Once established, each planting treatment received one of three N pulse treatments: control (no pulse), one large pulse or a series of three small pulses that delivered the same total amount of N as the large pulse over the duration of the experiment. We applied N to each plot using a 20-0-0 liquid fertilizer (Vigoro®) containing 17.5% N in the form of Urea (quickly available N) and 2.5% triazone (slowly-available N), diluted in water. On June 22, we applied a large pulse of 0.31g N and a small pulse of 0.103g N. The small pulses were applied two subsequent times in one week intervals.

Plants were harvested on July 28, dried and weighed. We tested the effects of competition and pulse treatments on aboveground biomass for each species in ANOVAs with competition and pulse treatments as fixed factors and biomass as a dependent variable. The strength of interaction was also analyzed with a relative interaction intensity index (RII; Armas et al. 2004).

## Results

There was no effect of nitrogen pulses on the biomass of native or exotic invasive plants when grown alone ($P = 0.50$) or in competition ($P = 0.39$; Figure 2). Exotic invasive species competitively suppressed native species regardless of the pulse treatment ($P < 0.001$; Figure 3). Conversely, native plants did not influence the growth of exotic invasive species ($P = 0.41$; Figure 3).

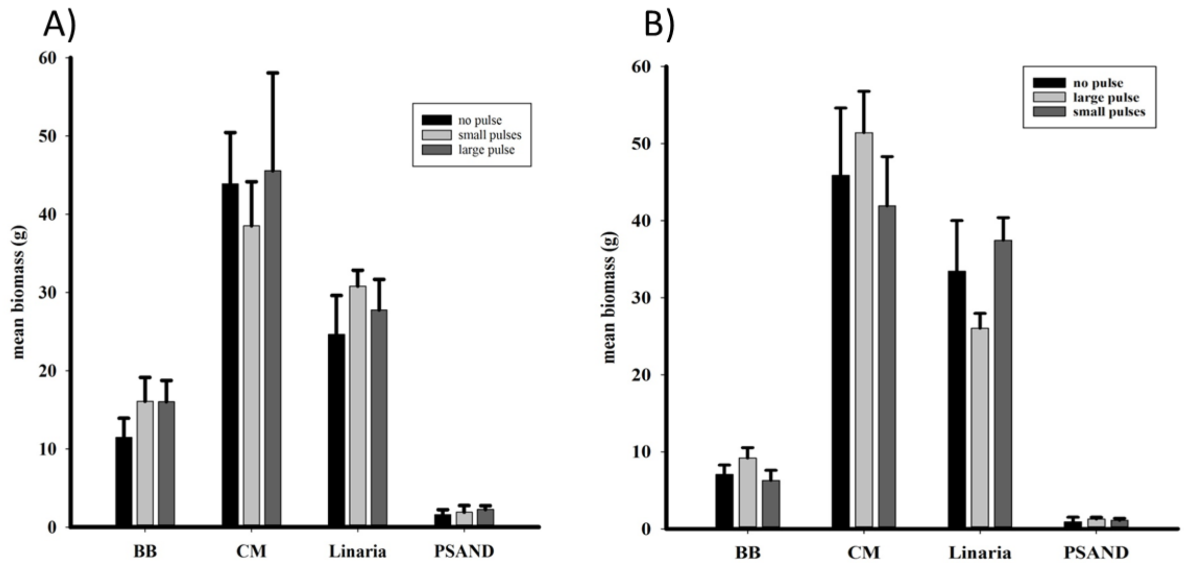


**Figure 2.** Mean biomass of BB (*P. spicata* ), CM (*C. stoebe*), Linaria (*L. dalmatica*), and PSAND (*P. secunda*) when in grown A) alone (no competition) or B) in competition. Error bars are + 1 SE.

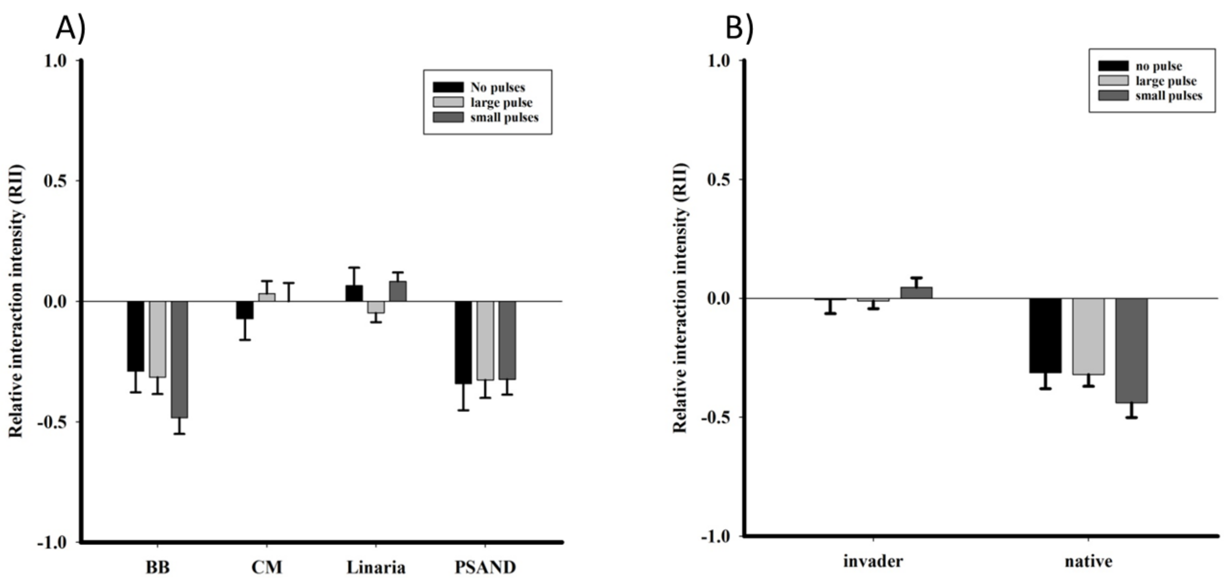


**Figure 3**: Relative interaction intensity (RII) for: A) BB (*P. spicata* ), CM (*C. stoebe*), Linaria (*L. dalmatica*), and PSAND (*P. secunda*) when in grown in competition with natives (in the case of invaders) or invasives (in the case of natives). B) Pooled RII for invaders and natives demonstrate the clear negative effect that invasive plants had on native species ($P < 0.0001$). Nitrogen pulses did not have a significant effect on plant biomass when plants were grown in competition or alone ($P = 0.39$). Error bars are + 1 SE.

## Discussion

The timing by which resources become available to plants varies a great deal between environments. In some cases this timing appears to be continuous, whereas in other systems, for instance, arid and semi-arid regions, resources are delivered in unpredictable pulses. Previous research has suggested that native and exotic invasive plant species may differentially access resources and these differences might help exotic species gain large competitive advantages (Thompson 1995, Davidson et al. 2011). We varied the timing and quantity of N added to native and exotic plant species in a field setting. We found no effect of fluctuating resource pulses on plant growth for any of our study species (Figure 2). Additionally, resource fluctuations did not influence competitive interactions between native and exotic species in this study (Figure 3).

It is possible that while we tried to mimic a natural N pulse for this system the amount of N added in this experiment was too small to have an influence. Nitrogen capture may also have been influenced by soil phosphorus availability and/or water availability. Phosphorus is a limiting nutrient that has been shown to affect N uptake (Schjorring 1986, James and Richards 2005) and could have limited the effect of the N pulses in our study. Additionally, it is possible that the natural soil N levels at this site were high enough to meet plant demands. Soil moisture levels were kept constant throughout the experiment. Since N typically becomes available during water pulses in semi-arid environments (Noy-meir 1973), constant watering may have facilitated N mineralization and kept N levels high enough to meet plant demands (Austin et al. 2004). Future research should control for P availability, and provide N in larger pulses in order to incite a measureable response.

Finally, the exotic and native species chosen for this study, while abundant on the landscape, do not share growth forms or root growth strategies. The invasives in our study (*C. stoebe* and *L. dalmaticus*) have taproots that can access deeper nutrient pools, while the natives in our study (*P. spicata* and *P. secunda*) have shallow, fibrous roots that mainly capture nutrients from the upper parts of the soil. In an environment where the upper soil is nutrient poor, we would expect tap-rooted invasives to an have advantage over shallow-rooted natives. A connected study is currently underway to examine these same questions in a new field experiment with higher nitrogen levels and lower water levels. Understanding how resource fluctuations influence plant interactions in grasslands is fundamental to predicting and hopefully preventing exotic species from proliferating in a changing climate where precipitation patterns will likely become unpredictable.

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