

Competitive Ability of Native and Non-Native Prairie Species in Response to Soil Nitrogen and Density

A Senior Honors Thesis

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By

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Abstract

The objective of this paper is to determine how competitive response varies between the prairie native *Solidago rigida* and the closely related *Solidago canadensis*, an invasive prairie species. I tested the idea that invasive species would exhibit greater biomass under increased nitrogen levels, while native species would not show significant difference across differences in nitrogen. I tested to see if variations in plant density changed how both of these plants respond to increased and ambient nitrogen levels.

I found the invasive *S. canadensis* to have significantly higher biomass than the native *S. rigida* at high nutrient availabilities (total biomass: $F_{1,1} = 15.34$, $p = .0002$). I also found that biomass for *S. canadensis* decreased as soil nitrogen levels decreased, while biomass for *S. rigida* did not decline from high to ambient nitrogen and at some densities it increased. While change in biomass from high to ambient nitrogen decreased at all densities for *S. canadensis*, the highest four densities for *S. rigida* demonstrated an increase in biomass.

Our findings suggest that that as soil nutrients decrease, competitive dynamics between native and invasive species change. The results show that when grown under lower soil nitrogen conditions, *S. rigida* may be able to outcompete invasive neighbors, particularly when local densities are high. The findings also show the importance of considering density when comparing invasive and native responses to soil nitrogen, since *S. rigida* only exhibits a higher level of competitive ability at high densities and low levels of nitrogen.

Introduction

Restoration of human altered landscapes into more diverse, functionally intact ecosystems has been receiving increased attention and efforts in recent years. One subject of restoration has been tallgrass prairies throughout the Midwest, including Ohio. Many restoration sites have been located in agricultural fields or other areas that significantly differ from natural prairies, and consequently may favor invasive plant species that are not typically found in natural prairies. The study of characteristics of native and invasive tallgrass prairie species can allow us to determine methods for better preparing restored prairies for native species, as well as determining traits for invasiveness in prairie invasive species.

Native prairie soils have limited available soil nitrogen, and prairie plants have evolved to do well under these conditions (Morgan 1997). However, soils of prairie restoration sites generally contain high amounts of inorganic nitrogen due to fertilizer use. This provides an ideal environment for nitrophilic species, which are exotic to native grasslands (Wedin and Tilman 1996, Green and Galatowitsch 2002, Baer *et al.* 2003).

According to competition theory, superior competitors are those which are best able to utilize available habitat resources, and thus should have greater population growth than inferior competitors. Thus, in high nitrogen soils we would expect prairie invasives to be competitively dominant over prairie natives (Bear *et al.* 2003, 2005, Burns 2004, Rickey and Anderson 2004, Suding *et al.* 2004). In a study by Green and Galatowitsch (2002) the invasive grass *Phalaris arundinacea* suppressed the shoot and root biomass of the native community under all nitrogen levels, but suppression was greatest under the highest levels of nitrogen. However, in a situation where nitrogen is removed from the soil, we would expect prairie natives, which can tolerate decreased resources, to be more competitive. A study by Perry *et al.* (2004) showed that the

sedge *Carex hystericina* was a superior competitor for nitrogen and under reduced nitrogen conditions it was able to outcompete *P. arundinacea*. However, other studies show that low resource availability does not increase the relative competitive ability of native plants to compete with invasives when nitrogen levels decrease (Maillet and Lopez-Garcia 2000, Kolb and Alpert 2003, Burns 2004). These studies suggest that preventing resource enrichment will not suffice to control invasion by non-native plant species.

Studies of competitive ability across nutrient gradients predict contrasting results. Grime (1979) and Huston (1979) suggest that the intensity of both root and shoot competition increases along nutrient gradients and that competition is most intense in productive habitats because these habitats support high growth rates. However, Wilson and Tilman (1991, 1995) suggest that unproductive habitats should have the most intense competition for soil resources. They have also found that as soil fertility increases there will be an increase in shoot competition and a decrease in root competition.

One approach to plant competition is to distinguish two distinct aspects: competitive effect, the negative effect an individual has on its neighbor; and competitive response, a plant's ability to tolerate suppression from neighbors (Goldberg and Fleetwood 1997, Howard 2001). The project I present looks at the competitive response of a pair of native and invasive *Solidagos* under seven different densities and two nitrogen levels, ambient and increased. The invasive *Solidago canadensis* was planted among native species while the native *Solidago rigida* was planted among invasive species. As such, I am interested in how the competitive response of our focal species permits them to invade the contrasting habitat type. I expect that, as an invasive species, *S. canadensis* will exhibit greater biomass under increased nitrogen levels, while *S. rigida*'s biomass will not vary between nitrogen levels. I expect the competitive response of both

species to decrease as plant density increases. I also expect that the density at which biomass significantly increases will suggest critical densities at which competitive suppression is released.

Methods

Study Species

The study species I used were two native goldenrods, *Solidago canadensis* and *Solidago rigida* (Asteraceae). *S. canadensis* is a clonal herbaceous perennial that is dominant in midsuccessional old fields throughout much of the northeastern and midwestern United States and is not native to tallgrass prairies (Goldberg 1987, see Werner et al. 1980 for discussion of taxonomy and general ecology). *S. rigida* is an herbaceous fall-flowering perennial that is a common component of native tallgrass and mixed grass prairies in the midwest (Brown 2002). *S. rigida* has very limited vegetative reproduction and adventitious buds that do not usually spread far from the plant. *S. rigida* is easily distinguished by its stiff, short, ovate leaves, its yellow flat-topped inflorescence, and its relatively large flower heads.

Soil Nutrient Treatments

For this experiment there were two levels of soil N: high, in which the soil was enriched with N and ambient, where the soil was left alone. N availability was increased by addition of NH_4NO_3 to a total rate of $50 \text{ g N m}^{-2}\text{y}^{-1}$ prior to planting. In addition, I applied N fertilizer twice, once in July and once in August to the high N plots. The high nitrogen levels were realistic for old agricultural sites, while the ambient nitrogen levels were slightly higher than native prairie soils.

The Garden Experiment

I established four experimental plots in Columbus, Ohio at the Ohio State University Waterman Farm. I applied one of the nitrogen soil treatments to each of the two 8 x 4 m main

treatment plots. I divided each main treatment plot into two 2 x 4 m subplots that each contained one hexagonal fan array (Figure 1. Howard 2001, see Antonovics and Fowler 1985 and Kunin 1993 for discussion of hexagonal fan arrays and geometry). The arrays utilized an additive design of 7 densities in modified hexagonal fans that efficiently used neighbor individuals. In this paper I will refer to each density by their number, with one being the farthest from the center with the lowest density and seven being the closest to the center with the highest density. Each fan array includes ten replicates at each density.

I planted each target or focal plant in the middle of six neighbors that encircled the target in the shape of a hexagon. When the non-invasive *S. rigida* was the target, it was surrounded by the invasive species *Phalaris arundinacea*, *Bromus inermis*, and *S. canadensis*. When the prairie-invasive *S. canadensis* was the target, it was surrounded by the non-invasive *Calamagrostis canadensis*, *Elymus canadensis*, and *S. rigida*. These species were chosen as a representative sample of grasses and forbs typically found to be native and invasive to tallgrass prairies.

While each target-neighbor combination had seven densities, these densities were planted with a specific pattern, and were not randomly dispersed throughout the plot. Thus, comparisons at the individual species level for both targets and neighbors are autocorrelated and violate the assumption of independence. However, since I am only looking at the target species in terms of how they respond to the neighbors as a whole (as natives or invasives and not individual species) I do not feel that this will introduce too much bias into the results of this experiment.

I germinated the seeds for all the species at the Ohio State University Biological Sciences Greenhouse from May 16 to May 24, 2005, with the timing of planting staggered to ensure similar emergence times. Between June 13 and June 25, 2005 I planted the seedlings (n = 2604) in the garden plots. I weeded the plots throughout the summer to eliminate outside species. I

harvested the plants from October 9 to November 3, 2005. I harvested the root and shoot mass for all living focal species and neighbors and noted mortality. I clipped the shoots from the roots at ground level and dried them. Roots were washed and dried. All plants were dried at 60.0°C and weighed to the nearest 0.001g.

Root, shoot, and total biomass for high and ambient nitrogen treatments were analyzed as a function of species, treatment, density and their interactions using analysis of variance (JMP Ver. 5.1.2, SAS Institute). To normalize variances, all biomasses were transformed using the base-10 logarithm.

Results

When I combined data for both nutrient treatments, there were no significant differences between the two species for root, shoot, or total biomass (Table 1, 2 and 3). However, when species were compared at the two nutrient levels, both species increased biomass with increased nitrogen. When the species were grown in high nitrogen *S. canadensis* had an overall higher shoot and total biomass than *S. rigida* at all densities. Root biomass for *S. canadensis* was higher at all but the fourth and sixth densities (Figure 2). Overall, it is evident that *S. canadensis* was a better competitor at all densities when grown in high nitrogen. However, when both species were grown in ambient nitrogen there was a significant difference in root, shoot, and total biomass between the two species (root: $F_{1,1} = 3.03$ $p = .0007$; shoot: $F_{1,1} = 18.16$, $p < .0001$; total: $F_{1,1} = 15.34$, $p = .0002$). Root, shoot, and total biomass were higher for *S. rigida* in all but two of the three outer densities (Figure 3). This shows that *S. rigida* was a better competitor than *S. canadensis* at lower nitrogen levels, especially in more dense conditions.

When I combined data for both species there was a significant difference in shoot and total biomass between the two treatments (Table 2 and 3). I observed that the root biomass for

the lowest four densities all declined in ambient compared to high nitrogen, while the highest three densities all increased in root biomass as soil nitrogen decreased (Figure 4). Total biomass declined for all but the fifth and sixth densities as nitrogen levels decreased. Shoot biomass remained the same or declined.

At all density levels shoot and total biomass of *S. canadensis* significantly decreased with a decrease in nitrogen (shoot: $F_{1,1} = 24.07$, $p < .0001$; total: $F_{1,1} = 15.03$, $p = 0.0002$). Root biomass also demonstrated a decrease at all densities, although it was not significant (Figure 5). For *S. rigida*, there was no significant difference between high and ambient nitrogen for any of the biomasses. It did, however, experience an increase in root, shoot, and total for the highest four densities when soil nitrogen decreased (Figure 6).

Discussion

I conducted this experiment to test the competitive response of a pair of prairie native and prairie invasive species of *Solidago* at two levels of soil nitrogen. In agreement with my expectations, I found higher performance of the invasive *S. canadensis* than the native *S. rigida* at high nutrient availabilities. I also found that biomass for *S. canadensis* decreased as soil nitrogen levels decreased, while biomass for *S. rigida* did not decline from high to ambient nitrogen and at some densities it increased. These results suggest that *S. canadensis* had a greater opportunistic response to resource availability than *S. rigida*, and that when grown under lower soil nitrogen conditions *S. rigida* may be able to outcompete invasive neighbors, particularly when local densities are high.

The experimental design of this experiment had the invasive *S. canadensis* invading a plot of native species and had the native *S. rigida* invading a plot of invasive species. These results show that *S. rigida* had a higher competitive response at lower nitrogen levels compared

to higher nitrogen. If neighbors of *S. rigida* had been analyzed we would expect them to have a lower biomass at ambient nitrogen, and thus a higher competitive response at high nitrogen level compared to the ambient nitrogen level.

I also observed that when each species was planted at varying densities, not all densities had the same response to the treatment. While all densities of *S. canadensis* showed a decrease in biomass as nitrogen decreased, *S. rigida* showed an increase in biomass for all but the first and third lowest densities. Analysis also showed that *S. rigida* showed an increase in growth from high to ambient nitrogen for the highest densities. Both these results show that decreased soil nitrogen did not aid *S. rigida* unless it is planted at high densities. In the highest four densities *S. rigida* showed the greatest competitive suppression while in high nitrogen. Once it reached the critical density at the fourth density level, ambient nitrogen no longer aided in the competitive ability of *S. rigida*.

I also found that *S. canadensis* and *S. rigida* suppressed neighbors in opposite ways. *S. canadensis* suppressed natives, which typically have slower above ground growth, by having early and rapid shoot growth, which permitted it to limit light available to neighboring native plants. *S. rigida*, however, suppressed invasive plants such as *S. canadensis* below ground by investing more in root growth. As we have seen, *S. rigida* was able to make larger roots in soils with reduced nutrients, and it was in these soils that *S. canadensis* decreased both its root and shoot biomass.

Taken together, these findings support the observation that as soil nutrients decrease, competition increases between native and invasive species (Wilson and Tilman 1991, 1995, Perry *et al.* 2004). Our results also support studies that show that unproductive habitats have

more intense competition for soil resources and as soil fertility decreases there is a decrease in shoot competition and an increase in root competition (Wilson and Tilman 1991, 1995).

I have shown density to be an important factor that influences competitive ability in response to soil nutrients. Other studies have shown that lower resource availability alone does not increase the relative competitive ability of the native to compete with the invasive species (Maillet and Lopez-Garcia 2000, Kolb and Alpert 2003, Burns 2004). While I have observed *S. rigida* to have a higher competitive ability than invasive species at high densities and lower levels of nitrogen, I also show that when grown in less dense patches *S. rigida* does not increase its competitive ability at lower nitrogen levels. Previous studies that measured the responses of natives and invasives to reduced soil nutrients did not take into consideration density related factors. Further studies on other closely matched native and invasive plant species should also incorporate density factors into their studies to determine if competitive ability at different nitrogen levels varies at different densities.

Based on this study I recommend that if tallgrass prairies are restored, reducing soil nitrogen and growing plants at a high density provides a mechanism for reducing the establishment of invasive species. It is important that managers understand that the performance of invasive species in tallgrass prairies depends on nitrogen availability and density. Knowing this can help them predict what species will become invasive by measuring relative performance of potential invaders under a range of nitrogen availabilities and densities.

It is important to realize that this study was only conducted over one growing season with plants starting out at relatively the same size and in the seedling stage. Further growing seasons may have led to different interactions between the focal species and the respective neighbors. Studies over the lifetime of the plant including survival, germination characteristics, and

fecundity are necessary to determine if lower nitrogen levels and specific density planting will allow for the long-term decline of invasive species within tallgrass prairies.

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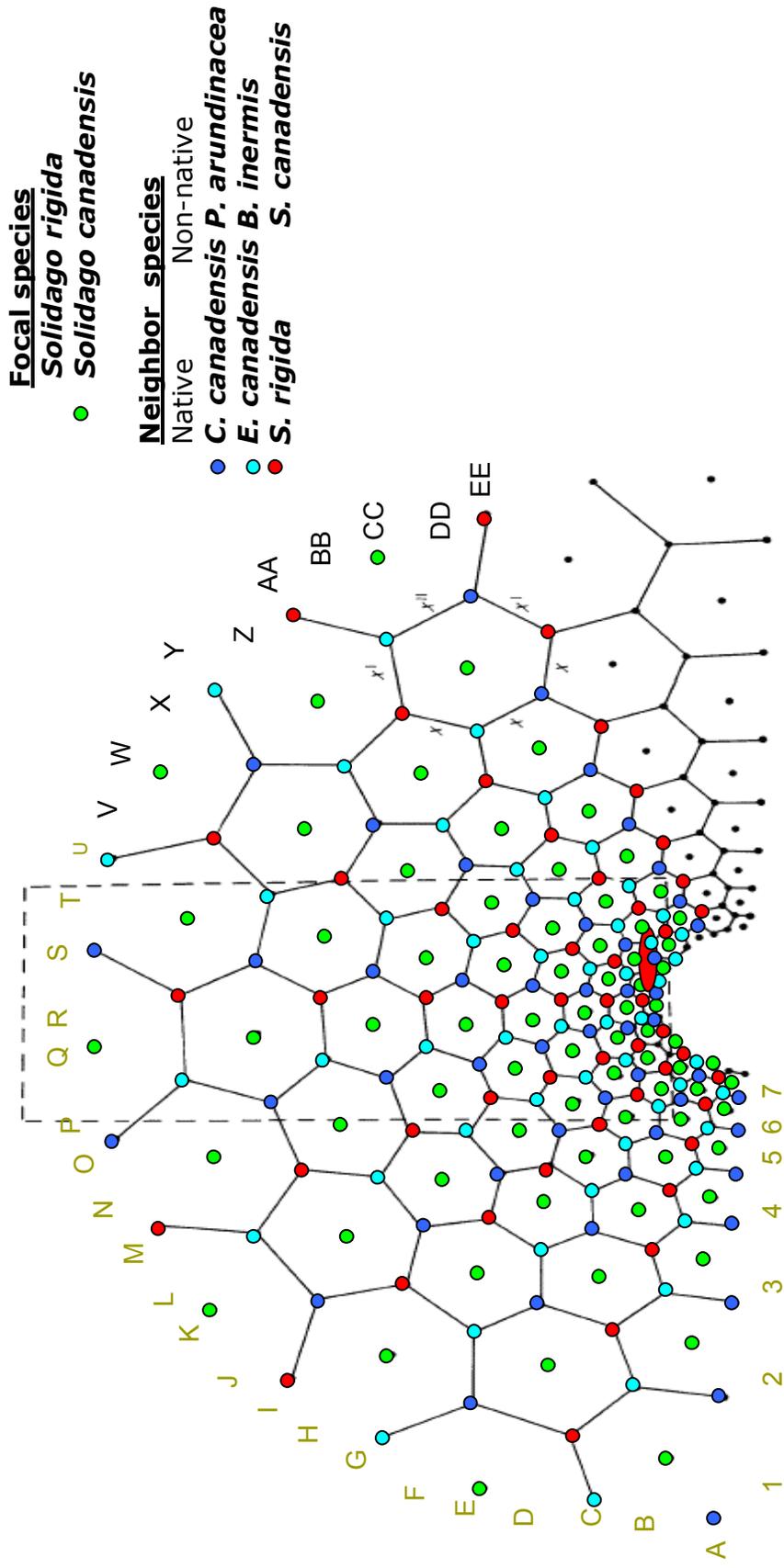


Figure 1 Graphical Representation of the Hexagonal Fan Array. The numbers along the bottom (1-7) signify the numerical representation for the density at that arc. The letters along the arcs (A-EE) signify rays of plants that include all 7 densities. Each ray is a replicate, so there are 10 replicates of the focal species at each density.

Table 1. ANOVA for transformed root biomass across seven densities and two nutrient levels for *S. canadensis* and *S. rigida* (JMP Ver. 5.1.2, SAS Institute).

Source	DF	F-ratio	P-value
Density	6	31.26	<.0001
Nutrient treatment	1	0.33	.56
Species	1	3.21	.07
Density x Treatment	6	2.22	.04
Density x Species	6	1.94	.08

Table 2. ANOVA for transformed shoot biomass across seven densities and two nutrient levels for *S. canadensis* and *S. rigida* (JMP Ver. 5.1.2, SAS Institute).

Source	DF	F-ratio	P-value
Density	6	31.04	<.0001
Nutrient treatment	1	10.80	.001
Species	1	2.92	.09
Density x Treatment	6	2.81	.01
Density x Species	6	2.12	.05

Table 3. ANOVA for transformed total plant biomass across seven densities and two nutrient levels for *S. canadensis* and *S. rigida* (JMP Ver. 5.1.2, SAS Institute).

Source	DF	F-ratio	P-value
Density	6	62.32	<.0001
Nutrient treatment	1	6.04	.01
Species	1	3.28	.07
Density x Treatment	6	2.76	.01
Density x Species	6	2.28	.04

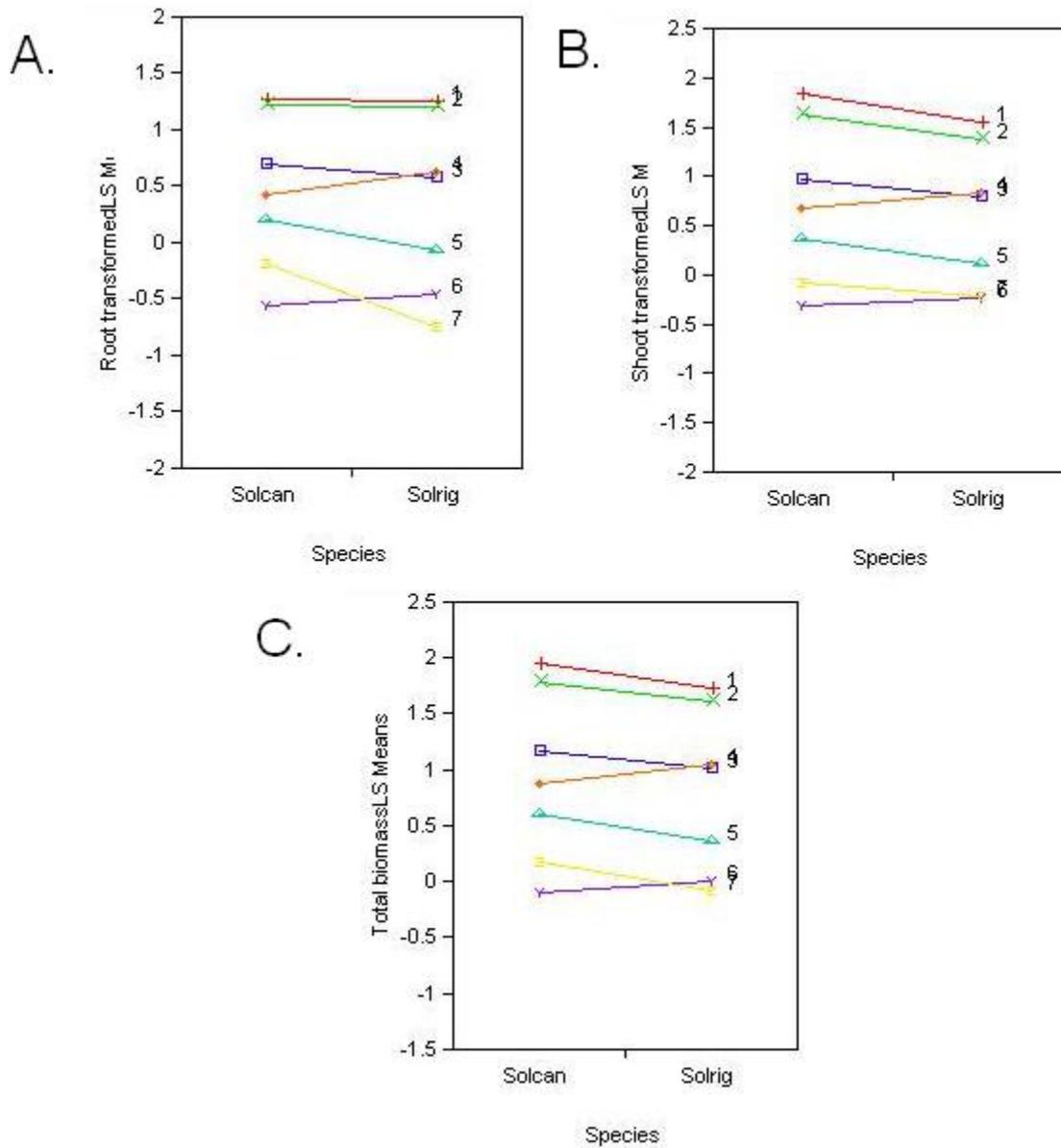


Figure 2 Difference in Root (A, n=103), Shoot (B, n=103) and Total (C, n=103) biomass for *S. canadensis* and *S. rigida* in the high nitrogen treatment over the seven densities, with density increasing from 1 to 7. (LSM = Least Squares Means)

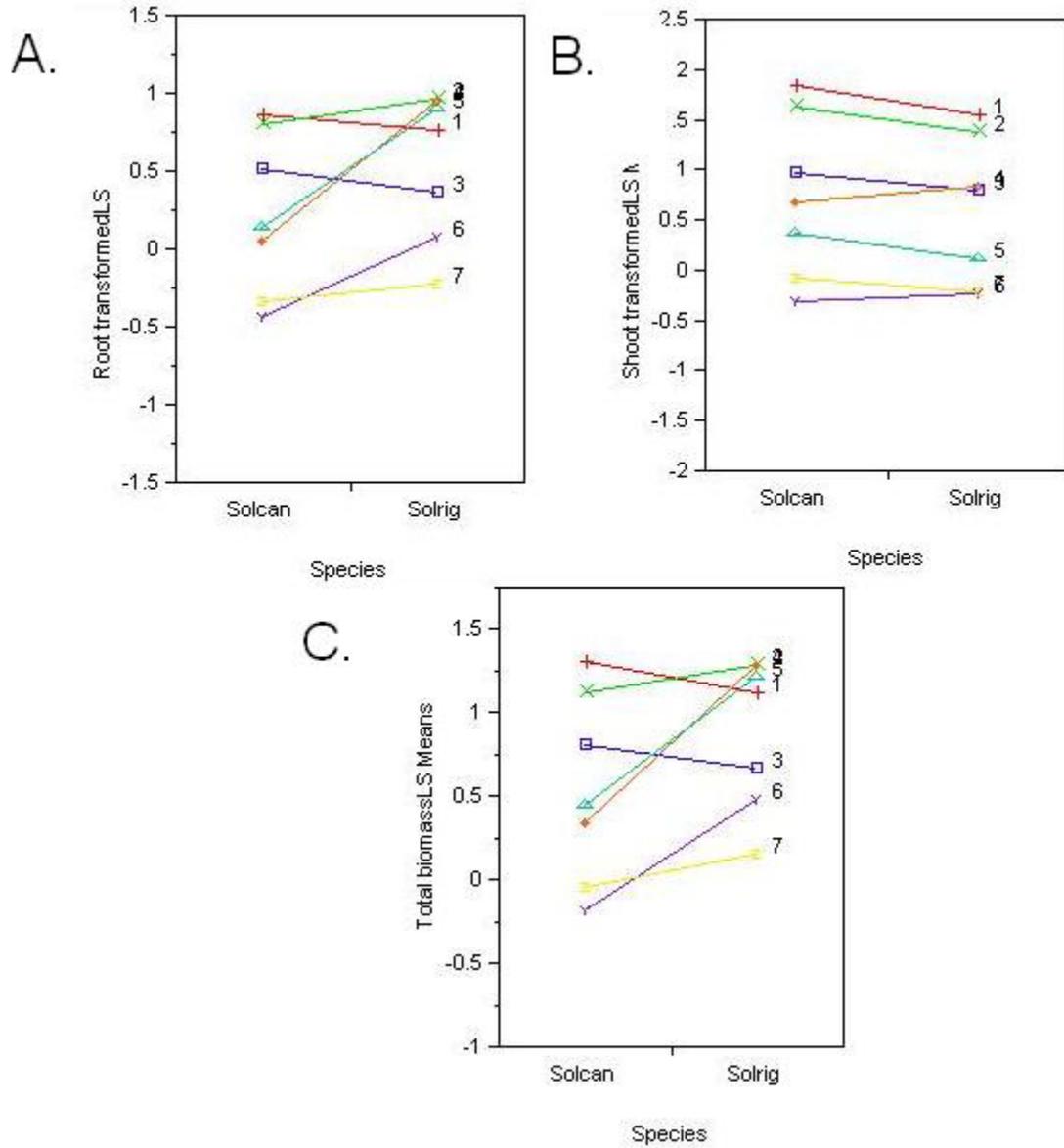


Figure 3 Difference in Root (A, n=117), Shoot (B, n=117) and Total (C, n=117) biomass for *S. canadensis* and *S. rigida* in the ambient nitrogen treatment over the seven densities, with density increasing from 1 to 7. (LSM = Least Squares Means)

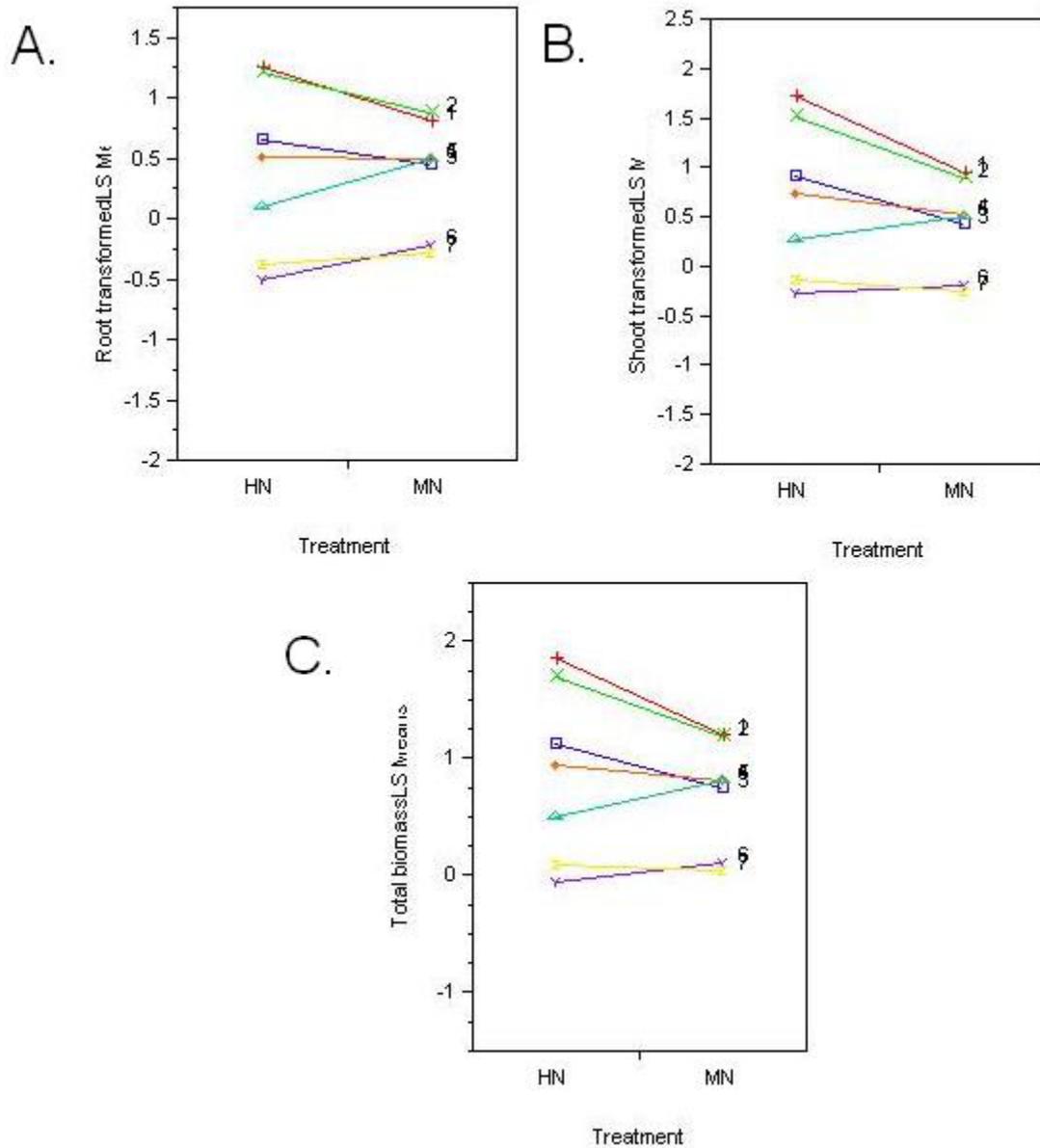


Figure 4 Difference in Root (A, n=201), Shoot (B, n=201) and Total (C, n=201) biomass for high and ambient nitrogen treatments for both species combined across seven densities, with density increasing from 1 to 7. (LSM = Least Squares Means, HN = High Nitrogen Treatment, MN = Ambient Nitrogen Treatment)

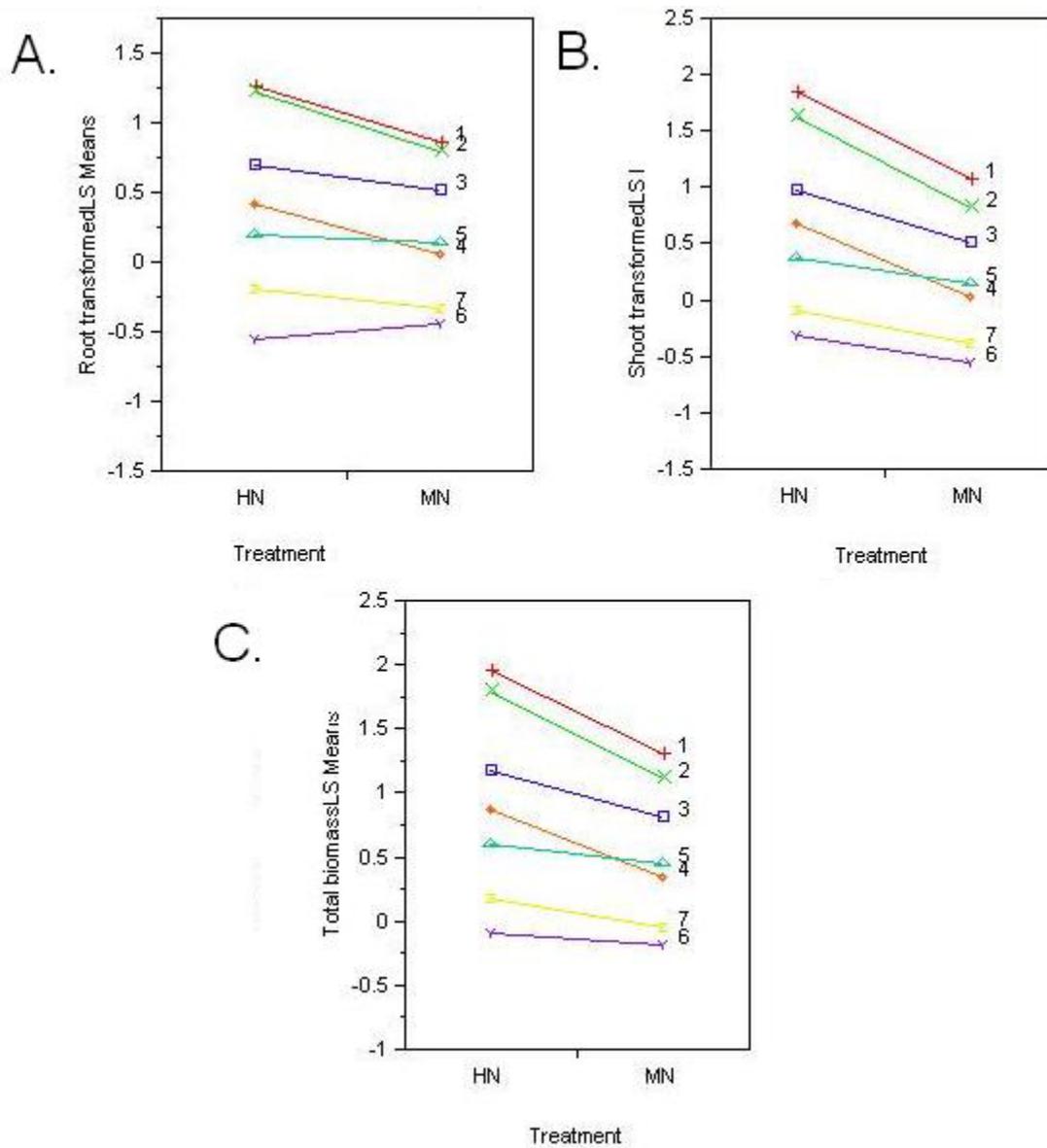


Figure 5 Difference in Root (A, n=123), Shoot (B, n=123) and Total (C, n=123) biomass for high and ambient nitrogen treatments in *S. canadensis* over the seven densities, with density increasing from 1 to 7. (LSM = Least Squares Means, HN = High Nitrogen Treatment, MN = Ambient Nitrogen Treatment).

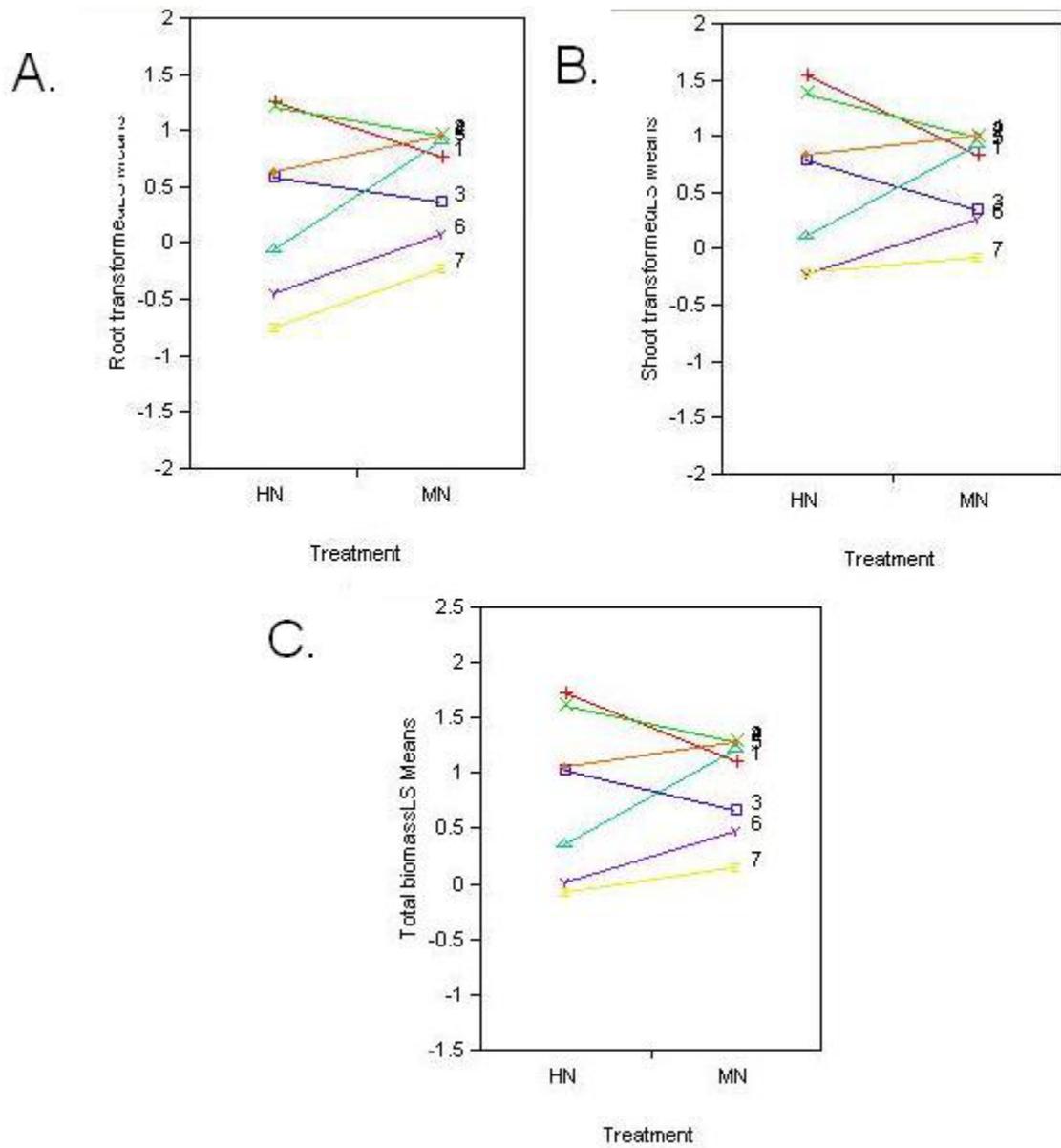


Figure 6 Difference in Root (A, n=97), Shoot (B, n=97) and Total (C, n=97) biomass for high and ambient nitrogen in *S. rigida* over the seven densities, with density increasing from 1 to 7. (LSM = Least Squares Means, HN = High Nitrogen Treatment, MN = Ambient Nitrogen Treatment).