The Effects of Soil Volume and Soil nutrients on Competition between Native and Invasive species

Persus O. Akowuah '18 and Edward Lowry

Department of Biology, Hampden-Sydney College, Hampden-Sydney, VA 23943

Studies of competitive interactions have been performed over wide arrays of species in plant ecology. While invasive species are frequently presumed to be effective competitors in environments where they successfully invade, the mechanisms by which they out-compete natives with is often unknown. *Centaurea stoebe,* commonly known as knapweed, is a flowering plant native to Europe that has colonized the East Coast of North America and has been dubbed a noxious weed efficient at displacing native plants. Numerous competition studies have examined on *C. stoebe* in western regions but largely focus on threatened natives and rangeland grasses. This study represents the first examination of the invader in competition with an eastern North American native that shares growth characteristics and resource requirements with *C. stoebe*. Our competition study uses a native forb *Lespedeza Capitata,* the bush clover. Our experiment aims to test whether soil volume and nutrient composition affect competition methods used by the invader *C. stoebe* with the native *L. capitata*. An intraspecific and interspecific greenhouse competition was performed over the course of 56 days. The results indicate that resource availability plays a significant role in determining outcomes of *C. stoebe* competition with the native. The results also suggest a significant negative effect of intraspecific competition on *C. stoebe* plants when grown in a restricted soil volume.

Resource availability is an important factor that determines community structure and biodiversity. The order in which species arrives in a community can play an important role in species diversity and biodiversity (Kardol, Souza and Classen 2012). While the timing with which an invasive species arrives at a community may have a significant role in community structure and biodiversity, any arrival of an invasive species in a native community can be expected to have a negative impact on existing community structure and function. Invasive plants are by definition species that have disruptive population expansion, spread and displace native plants and alter existing community functions and relationships. Invasive plants do not only displace native plants, but they cause some degree of damage to an environment and endanger ecosystems and decreases biodiversity. Plants that have invaded a given environment are referred to as weed pest. One of these invaders that have been well studied is *Centaurea stoebe*, the spotted knapweed. It is a flowering plant native to Eastern Europe that is now a weed pest widely found in Northern America. It is a prime example of an invasive species that is excelling outside of its habitat. *C. stoebe* utilizes different methods to out-compete native species in Northern America, the species is efficient at seed production making it spread easily and abundantly in each area. Its tap root system allows it to uptake water faster than any competing and neighboring plants, and due to its allelopathic abilities and low palatability, it can outcompete native species all around the east coast. Competition is not the only factor that makes invasive species important to study, but also the threat they pose to the environment when they outcompete native plants over a given area. When invasive species out-competes native species like grass in an area, soil erosion and runoffs are increased which decreases soil nutrients and soil resources. Examining the methods used by *C. stoebe* in competition is an important step in decreasing its spread in the East Coast and eliminating the negative effects it has on local biodiversity. *C stoebe* competition with native plants has greatly been studied by many researchers, but most of them were performed in competition with native grass which is poor competitors to *C. stoebe* and shares no characteristics. In order to effectively examine the methods used by *C. stoebe* to out-compete native, a native plant with similar growth pattern and root characteristics that also compete with *C. stoebe* is an ideal choice.

Previous work by Sean Kellogg '15 at Hampden-Sydney College has established that an efficient native competitor of *C. stoebe* is the Bush Clover, *Lespedeza capitata*. *L Capitata* is a perennial forb native to the East Coast of the United States and is a known competitor of *C. stoebe* with apparently similar habitat needs and population structure based on field observations of our lab group. We selected it as a promising candidate-species for analyzing the methods used by *C. stoebe* in competition. *L. capitata* has a taproot type growth form and a population density similar to that of *C. stoebe*. *Lespedeza* is in the family *Fabaceae* and is typical in that it supports nitrifying bacteria and is likely to augment nutrient availability of nitrogen in the soil. Nitrogen fixation by species in the family *Fabaceae* occurs in root nodules produced by the plant. The root nodules contain bacteria known as *Rhizobium spp*. that take atmospheric nitrogen and assimilate them into the soil providing nutrients for the plant. It is a viable hypothesis that nitrogen fixation by *L. capitata* enables *C. stoebe* to thrive in the areas where they co-occur, and could enable them to out-compete the native plants in the area even under stressful our otherwise low nutrient conditions. Field observations indicate that both species thrive in areas with disturbed sandy, and rocky soils with varying low nutrient and moisture levels (He et al. 2012, authors' personal observations locally). Our observation of *C. stoebe* and *L. capitata* populations in Farmville Virginia shows that the population of *C. stoebe* are high in areas where the soil has been highly disturbed. *C. stoebe* and *L. capitata* species were both observed in the same disturbed areas but wherever there was an abundance of *L. capitata* the *C. stoebe* population tended to be lower but with bigger stem and higher in stem count and intricate root system. In areas where *C. stoebe* were the dominant species, the stems and stem count were significantly lower. This observation made us propose an experimental design to test whether soil volume and nutrient availability affected the competitiveness of *C. stoebe* in a given environment. A greenhouse experiment was conducted over the course of 56 days in one season to test the proposed hypothesis above. The greenhouse experiment addressed two main questions: does soil volume favor competition? And are there are distinct differences between the effects of interspecific competition and intraspecific competition under the same conditions.

Seedlings of the study species *C. stoebe* were germinated from seeds collected from local populations in Farmville, VA. and were transplanted at the earliest viable stages to pots placed in arrays in the greenhouse. *L. capitata* seedlings were collected at the earliest stages of growth from local wild populations and similarly transplanted. The soil substrate was commercial grade sand and pots were in two sizes, large pots with a volume of 2.5 L and small pots of 1L. For intraspecific competition treatment groups, two of the invader, *C. stoebe* were planted in a small 1L pot and another two were planted in a large 2.5L. For the second treatment, the same steps for the invader were followed for the native *L. capitata*. For the third interspecific treatment group, one invader and one native were planted together in a small 1L pot and another set was planted in a large 2.5L pot. In addition, a set of control plants each growing alone in a pot were prepared, five natives in small pots, five in large pots, and the same for the invader. A total of 128 pots were used for the experiment The plants were placed in the greenhouse under an automated watering system that watered every other day and allowed to grow for 56 days. Conditions were hot, ranging from 25 to 45 degrees Celsius from night to day. Positions of the plants were shifted periodically to reduce possible micro-climate effects within the greenhouse. A weekly addition of dilute (1/10th strength) Hoagland's solution (Hoagland and Arnon 1950) was applied to reduce potential effects of nutrient differences across soil types. Plants were measured weekly for the length of the longest leaf (*Centaurea*) or stem (*Lespedeza*) and the number of leaves on each plant was recorded. We chose this metric over total leaf area for *C. stoebe* as young leaves rapidly develop and senesce in a dynamic process from week to week as seedlings grow; young seedlings may often support only one or two fully developed leaves while old leaves slowly wither. Based on our field observations we associate the largest leaf currently developed by the seedling as a good predictor of overall plant vigor and likelihood of survival.

Species	**Pot size**	**Control**	**Inter-specific**	**Intra-specific**
Centaurea stoebe	Large	17.7± 0.1	8.5 ± 0.4	8.9 ± 0.3
	Small	12.5 ± 0.4	8.2 ± 0.4	6.3 ± 0.3
Lespedeza capitata	Large	13.3 ± 0.6	7.9 ± 0.7	12.3 ± 0.5
	Small	11.1±1.8	10.8 ± 0.7	11.9 ± 0.5

Table 1: Mean values ± S.E. for plant treatment groups at eight weeks of growth.

This table, shows the average growth values at the end of eight weeks. The invasive *C. stoebe* appeared to grow larger given the greater soil volume in the large pots. Competition, on the other hand, appeared to have a negative impact on the invader's growth where no plant under intra or interspecific competition regimes appeared to grow as large as the controls. Growth rates are displayed in Figures 1-4 and in Table 2.

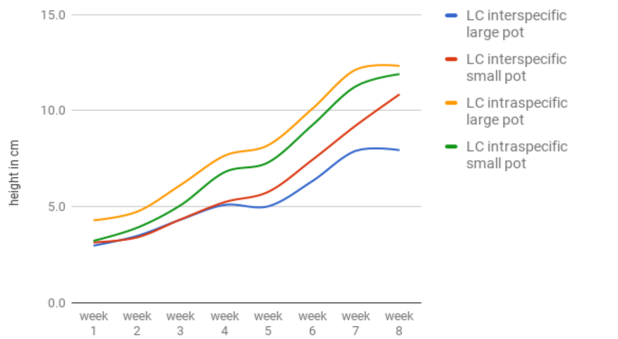

Figure 1: shows the Centaurea plants in the big pots were higher in height compared to the ones in the small pots, which was expected.

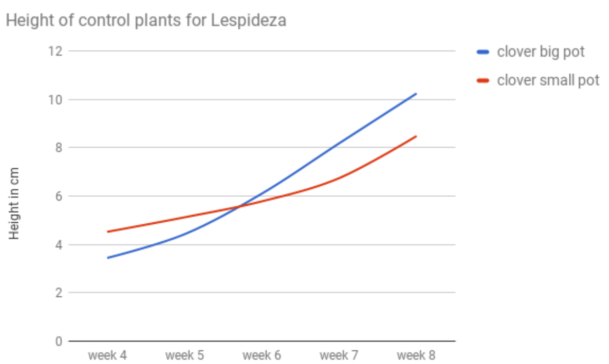

Figure 2: Growth curves for competition treatments of *Centaurea stoebe*

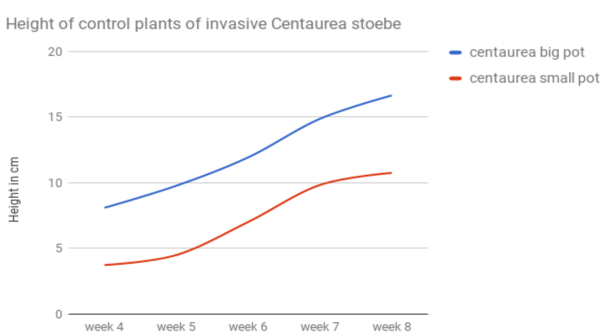

Figure 3: Control values for *Lespedeza capitata*

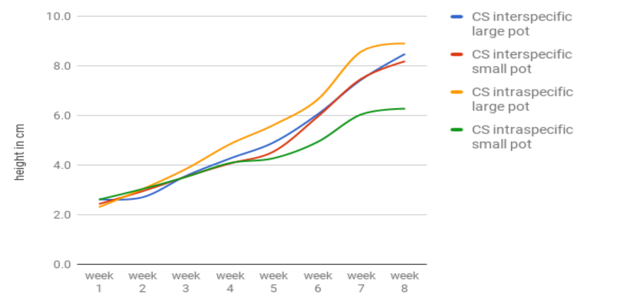

Figure 4: Growth curves for competition treatments of *Lespedeza capitata*

Species	**Pot size**	**Control**	**Inter-specific**	**Intra-specific**
Centaurea stoebe	Large	2.22	0.87	0.99
	Small	1.94	0.84	0.54
Lespedeza capitata	Large	1.74	0.75	1.26
	Small	0.95	1.10	1.31

Table 2: Growth rate as indicated by the slope of the line from figures 1-4. The values indicate the cm of height gained per week on average over eight weeks.

Species	**Pot size**	**Interspecific**	**Intraspecific**
Centaurea stoebe	Large	-0.35 ± 0.10	-0.34 ± 0.08
	Small	-0.16 ± 0.10	-0.32 ± 0.09
Lespedeza capitata	Large	-0.28 ± 0.17	0.01 ± 0.11
	Small	-0.06 ± 0.17	0.00 ± 0.12

Table 3: Mean values for Relative interaction intensity (RII) in competition treatments for the invasive and native species.

RII = (βi- βc) / (βc+ βi) where βi is an individual plant in competition and βc is the mean value for control plants not subject to competition. Values range from a minimum of -1 indicating a high level of competition to a maximum of 2 indicating a high level of facilitation (i.e. a positive value indicates more growth with another plant present).

Resource availability plays an important role in the functioning of a community and the richness of biodiversity it supports. The resources available to a species depends in part on how effective the species compete with neighboring species. The experiment I performed sought to find whether soil volume affected the competitiveness of a widely known European invader found in eastern North America. *C. stoebe* is a well-studied invader that is thriving outside of its native habitat and frequently co-occurs in its eastern North American habitat with a native plant, *Lespedeza capitata*. The greenhouse experiment I carried out examined the effects of intraspecific and interspecific competition between the two species. Based on the growth of the plants after eight weeks of competition in the various treatments, as shown in *Figure 1*, *C. stoebe* appeared on average to grow larger in the 2.5L pots given the greater soil volume. Competition appeared to have a negative impact on the invader's growth although it is worth noting that average values under both and intra or interspecific competition regimes appeared to be significantly smaller than plants grown alone as the controls. These results show that under competition both species tend to perform less since both species are competing for the same resources. Fig 1-2 are the plotted data of the *C. stoebe.* In fig 1, the control group, the *C. stoebe* in the larger volume pots grew substantially more on average than the ones in the smaller volume pots. Invasive plants were grown under intra- versus interspecific competition yielded apparently opposing results. The growth curve for the *C. stoebe* in competition with *L. capitata* in both the small 1L and the larger 2.5 L pots were closer in height with no apparent significant difference. On the other hand, the *Centaurea* in intraspecific competition in the small 1L pot showed an effect of competition not observed in other treatments. For the *C. stoebe* in these smaller pots, the growth curve was much lower compared to the other treatments, especially plants in the 2.4L pots. These results indicate that in competition, or low resource availability as defined by soil space, interactions appear to have a negative impact on *C. stoebe* individuals in competition with each other.

L. capita display competitive interactions largely in line with our expectations based on their empirical status when found at field sites with the invader. As indicated in Figure 3, the average growth curve of *L. capitata* plants in the larger 2.5L pots is somewhat steeper compared to the ones in the 1L pots. As seen in Figure 4, in the interspecific competition treatments, the clover in the small 1L pots had a significantly higher growth curve compared to the ones in the larger 2.5L pots. The clovers in competition with each other and had similar growth curve with no significant difference. Based on these results, it appears likely that resource availability does play an important role in the competitiveness of *C. stoebe* populations. In competition with each other, *C. stoebe* individuals tend to be more negatively impacted than the ones in competition with the native *L. capitata* species. We can also safely assume that invasive plants in competition with each other have a greater negative impact on the species' population growth rates compared to the ones on interspecific competition.

Relative interaction intensity (RII) was measured for both species in intraspecific and interspecific treatments groups. The RII values range from a minimum of -1 indicating a high level of competition and +1 indicating facilitation, where one or both species positively benefit from the interaction (Cristina Armas et. al 2004). From the data presented in Table 3 the RII values indicate that the for the *C. stoebe* population in intraspecific competition ranged from -0.32 to -0.34 which compared to the *L. capitata* population in the intraspecific competition which had an RII value of 0.00 to 0.01 indicating little to no competition. Based on this analysis we find a relatively high level of competitive effect within the interspecific competition treatment for *C. stoebe*. These results agree favorably with the analysis base on the growth curve plots and lend further credibility to the theory that *C. stoebe,* while likely to be a good competitor generally, is particularly effective in competition under stressful conditions i.e. in disturbed, low nutrient levels or under limited soil volumes per individual. When conditions are favorable, and resources are abundant, its impact on native species may be relatively lower until conditions become stressful or limiting, but under normal conditions, as the results indicate, *C. stoebe* competition with itself has always had a negative.

REFERENCES

Armas C, Ordiales R, Pugnaire FI (2004) Measuring plant interactions: A new comparative index. Ecology 85:2682–2686.

Blicker, P.S., Olson, B.E. & Engel, R. (2002) Traits of the invasive *Centaurea maculosa* and two native grasses: Effect of N supply. Plant and Soil 247, 261-269.

Callaway RM, Waller LP, Diaconu A, Pal R, Collins AR, Mueller-Schaerer H, Maron JL. Escape from competition: neighbors reduce *Centaurea stoebe* performance at home but not away. Ecology. 2011 Dec 1;92(12):2208-13.

Callaway, R.M., DeLuca, T.H. and Belliveau, W.M. (1999) Biological-control herbivores may increase competitive ability of the noxious weed *Centaurea maculosa*. Ecology 80:

1196-1201.

Emery, S.M. and Rudgers, J.A. (2012) Impact of competition and mycorrhizal fungi on growth of *Centaurea stoebe*, and invasive plant of sand dunes. American Midland Naturalist 167:213-222.

He WM, Montesinos D, Thelen GC, Callaway RM (2012) Growth and Competitive Effects of *Centaurea stoebe* Populations in Response to Simulated Nitrogen Deposition. PLOS ONE 7(4): e36257

He, W.-M., Feng, Y., Ridenour, W.M., Thelen, G.C., Pollock, J.L., Diaconu, A. and Callaway, R.M. (2009) Novel weapons and invasion: biogeographic differences in the competitive effects of *Centaurea maculosa* and its root exudate -catechin. Oecologia 159: 803-815.

Herron, G. J., Sheley, R. L., Maxwell, B. D., & Jacobsen, J. S. (2001). Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. Restoration Ecology, 9(3), 326-331.

Hill, J. P., Germino, M. J., Wraith, J. M., Olson, B. E., and Swan, M. B. (2006). Advantages in water relations contribute to greater photosynthesis in *Centaurea maculosa* compared with established grasses. International Journal of Plant Sciences, 167(2), 269-277.

Jacobs, James S.; Sheley, Roger L. 1999. Competition and niche partitioning among Pseudoroegneria spicata, Hedysarum boreale, and *Centaurea maculosa*. The Great Basin Naturalist. 59(2): 175-181. [37465]

Kedzie-Webb, S. A., Sheley, R. L., Borkowski, J. J., and Jacobs, J. S. (2001). Relationships between *Centaurea maculosa* and indigenous plant assemblages. Western North American Naturalist, 43-49.

Knochel, D. G., Flagg, C., and Seastedt, T. R. (2010). Effects of plant competition, seed predation, and nutrient limitation on seedling survivorship of spotted knapweed (*Centaurea stoebe*). Biological invasions, 12(11), 3771-3784.

Marshall, J. M. (2011). Tanacetum bipinnatum germination and competitive interaction with *Centaurea stoebe* seedlings. The Michigan Botanist, 50.

Muller-Scharer H. The impact of root herbivory as a function of plant density and competition: survival, growth and fecundity of *Centaurea maculosa* in field plots. Journal of Applied Ecology. 1991 Dec 1:759-76.

Olson, B.E. & Blicker, P.S. (2003) Response of the invasive *Centaurea maculosa* and two native grasses to N-pulses. Plant and Soil 254, 457-467.

Reinhart, K. O., and Rinella, M. (2011). Comparing susceptibility of eastern and western US grasslands to competition and allelopathy from spotted knapweed [*Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek]. Plant ecology, 212(5), 821-828.

Ridenour, W.M. and Callaway, R.M. (2001) The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126: 444-450.

Thorpe, A. S., & Callaway, R. M. (2011). Biogeographic differences in the effects of *Centaurea stoebe* on the soil nitrogen cycle: novel weapons and soil microbes. Biological Invasions, 13(6), 1435-1445.