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The Effect of Self-Recognition in the Competition Between Genets of Solidago altissima

Charles Jaques
Eastern Illinois University
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Biology
Graduate Degree Program

Please submit in duplicate.
THE EFFECT OF SELF-RECOGNITION IN THE COMPETITION BETWEEN GENETS OF SOLIDAGO ALTISSIMA

BY

CHARLES JAQUES

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE – BIOLOGICAL SCIENCES

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY

CHARLESTON, ILLINOIS

2018

I HEREBY RECOMMEND THAT THIS THESIS BE ACCEPTED FULLFILLING THIS PART OF THE GRADUATE DEGREE CITED ABOVE
ABSTRACT

Competition is a major driving force in the abundance, distribution, and diversity within any biological system. Plants are more likely to suffer reductions in fitness as a consequence of competition, as they typically occur in dense communities. Individuals within these populations must respond to both inter- and intraspecific competition. Recent studies suggest that the ability to distinguish kin from non-kin may play an integral role in the success of individuals within different plant populations and communities. However, a less known interaction is that between individual clones within a genet as they grow, spread, and begin to interact with nearby rival genets.

This study focused on the ability of Solidago altissima ramets to differentiate between self and non-self interactions, and the role that these responses have in mitigating competition. Plant samples were obtained from wild populations occurring at the Douglas-Hart Nature Center, Mattoon, Illinois. Rhizomes from five different genets were harvested and grown in no competition (rhizome grown singly), self, and non-self treatments. Rhizomes were cut to 10 cm for standardization and allowed to grow for 18 weeks. Leaves were collected after approximately 6 weeks for leaf area analysis, aboveground biomass was harvested after 15 weeks, and rhizome biomass was harvested after 18 weeks. All harvested samples were placed in an oven and allowed to dry at 60 °C for a minimum of two weeks before mass determination. These data were then used to evaluate competitive responses for each measurement by genotype and competitive interaction (self/non-self).

Controls (no competition) were used to establish a baseline for growth and demonstrated no significant variation inherent to the different genotypes used in the experiment. In contrast, all measurements taken from the competition treatments showed
significant variation by genotype. However, the results for aboveground and rhizome biomass were indicative of a general competitive response, as responses to both self and non-self interactions were identical. Leaf area, on the other hand, demonstrated both a significant variation by genotype and by competitive interaction, where-in self treatments produced smaller leaves than non-self treatments.

Changes in leaf structure would be correlated with direct competitive responses both above and below ground. Variation in leaf area between self and non-self treatments is indicative of differing competitive responses; however, many of the mechanisms and consequences for this particular change in responses have yet to be identified. Future work should focus on root interactions, potential chemical signals, and the role that red:far-red ratios may play in clonal communication and competition.
DEDICATION

I would like to dedicate my thesis manuscript to my father, David Jaques, for always supporting me in my endeavors, my friend, Kaylin Smith, who assisted me in the lab while I collected and analyzed my data, and my professors, Dr. Meiners, Dr. Carlsward, Dr. Hung, and Dr. Havercroft, who have pushed me and encouraged me to succeed. Without all of you, I would not be who I am today, and I thank you for your parts in my journey.
ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Meiners, and my committee members, Dr. Carlsward and Dr. Canam, for their time and patience while I worked to complete my degree. Their guidance has been greatly appreciated and valued, as I worked to complete my degree while also working full time outside of the university. Without them, I would have never been able to accomplish my goal of obtaining a master’s degree in biological sciences.

I also want to thank these individuals for assisting me with formatting and critiquing my thesis document to ensure it was of the highest caliber it could be before submission.

Finally, I would like to thank my friends and students who helped me with the harvesting of my samples and those that kept me company in the lab during the many hours of data analysis. Kaylin Smith, Zane Smith, Joe Perez, and Noah Blatnik. Thank you all for the help you provided me during my time as a graduate student at EIU.
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Values plotted are mean ± 1 SE.
INTRODUCTION

Plants are often viewed as much less dynamic than their animal counterparts. However, these organisms are far from being passively engaged with their environment. Plants have developed complex means to respond to the various biotic and abiotic stressors in their environments (Biedrzycki and Bais, 2010). Certain responses such as the release of volatile organic compounds are used as a means of defense (Kessler and Baldwin, 2001). Other mechanisms allow plants to detect herbivory and communicate (Heil and Karban, 2010). This signaling increases the ability for non-attacked plants to defend themselves (Biedrzycki and Bais, 2010; Heil and Karban, 2010). Plants have also been found to use similar chemical queues in their environments to detect competitors in their surroundings (Baldwin, 2010). Not only do these signals to indicate the presence of competitors but may also identify the degrees of relatedness of the neighboring plants (Callaway and Mahall, 2007; Biedrzycki and Bais, 2010; Chen et al., 2012). Similarly, mounting research suggests that self/non-self recognition may play a significant role in competition (Mahall and Callaway, 1991; Biedrzycki and Bais, 2010; Chen et al., 2012).

Competition is a ubiquitous ecological process where individuals struggle to capture limiting resources such as nutrients, space, reproductive partners, and light (Depuydt, 2014). It is also viewed as one of the most influential factors in determining the composition and structure of an ecosystem (Aerts, 1999; Novoplansky, 2009; Baron et al., 2015; Aschhough et al., 2016). Evolutionarily, plants have developed two major competitive behaviors when interacting with neighbors – responses that increase their overall competitive abilities and those that minimize competitive interactions (Falik et al., 2003; Novoplansky, 2009). The mechanisms plants use to respond to their neighbors
include aggressive above and belowground growth (Aschehoug et al., 2016). This growth may be to maximize nutrient uptake in a given location or to produce new growth away from a competitive interaction (Falik et al., 2005; File et al., 2012). Plants have also been documented as producing below ground chemical signals (File et al., 2012) and inhibitory allelochemicals (Callaway and Aschehoug, 2000; Novoplansky, 2009; Aschehoug et al., 2016), as well as altered leaf allocation (Dudley and File, 2007; Aschehoug et al., 2016) in response to competition.

The biological costs of these mechanisms vary depending on the type of interaction taking place. In situations of interspecific competition, it is likely that adaptations favoring increased competitive behaviors will emerge (Falik et al., 2003); however, in communities involving large populations of closely related individuals, such as with clonal organisms, it seems likely that natural selection would emphasize the ability for plants to minimize competitive interactions to increase relative fitness (Falik et al., 2003; Gruntman and Novoplansky, 2004; Novoplansky, 2009; Dudley and File, 2007; Karban et al., 2013). If this is the case, then it is important to determine the extent that such selective pressure influences plants that occur in dense, closely related patches, such as in the case of ramets within a clonal genet. Ultimately, the recognition of neighbors and self should improve a clonal species’ ability to grow and compete in its environment.

Communities have various forms of competitive interactions depending on their composition. Interspecific competition occurs between all co-occurring species and generally results in a reduction of plant fitness for both competitors (Tilman, 1997; Molles, 2012). When it comes to fitness costs, intraspecific competition is more likely to reduce the overall fitness of an organism, as there will be minimal niche differentiation.
with competitors (Molles, 2012). Within clonally expanding species, there may be an additional level of intraspecific competition. Since clonal species can reproduce both sexually and asexually, intraspecific competition not only occurs at the population level between genets, but it also occurs intraclonally between ramets (Kleunen et al., 2001). While interclonal competitive interactions may be critical to the ecological sorting of genotypes within a habitat, these interactions would presumably have entirely negative consequences for the plant and may inhibit the plant’s ability to compete interclonally (Karban and Shirojiri, 2009).

Although there have been many recent studies into the ability for plants to recognize their neighbors on the grounds of relatedness and identity (see Gruntman and Novoplansky, 2004; Callaway and Mahall, 2007; Dudley and File, 2007; Biedrzycki and Bais, 2010), commonly referred to as kin recognition (Mateo, 2004; Mehils et al., 2008), the impacts on genetic relatedness on competition is far less understood (Biedrzycki and Bais, 2010; Chen et al., 2012; Depuydt, 2014). Mounting research suggests that kin-recognition plays some role in the competitive strategies of many plant species. Being able to identify kin may allow an organism to reduce competitive behaviors with related individuals and increase competition with non-related individuals (Waldman, 1988) increasing their inclusive fitness (Hamilton, 1964).

As an example, the annual plant *Cakile edentula* has been shown to have the ability to distinguish between kin and non-kin and alter root allocation patterns in response. This species, similar to other annual plants, occur in dense clusters often comprised of closely related individuals (Vekemans and Hardy, 2004). It is in these environments, where individuals will not only compete with unrelated organisms but related organisms, that a
kin recognition response is expected to be observed. Indeed, when growing with related individuals, *C. edentula* allocated fewer resources to the production of fine root mass than it did when grown with a non-related individual (Dudley and File, 2007). In a similar experiment conducted by Donohue (2003), competition that involved siblings resulted in higher reproductive rates and higher rates of overall fitness when compared to nonsiblings.

Self-recognition in plants is not as well documented as kin-recognition (Karban and Shirojiri, 2009). Examples of this behavior were seen in clonal plants such as *Ambrosia dumosa* (Mahall and Callaway, 1991) and *Artemisia tridentata* (Karban and Shirojiri, 2009). When *A. dumosa* roots made contact with another nonrelated *A. dumosa* the rates of root elongation drastically reduced; however, this behavior was not observed when roots of one plant made contact with other roots on the same plant (Mahall and Callaway, 1991). In this experiment, some sort of physiological connection was required for the behavior to occur. In the experiment involving *A. tridentata*, the impacts of herbivory and the influence of communication through volatiles from self/non-self individuals were measured. The results showed that cloned specimens responded more positively to volatile queues. Thereby acquiring less natural damage than plants who received signals from non-self plants (Karban and Shirojiri, 2009). Here the response was triggered by above ground volatiles and did not require any form of contact between the individual plants.

The research in this study will focus on the clonal plant *Solidago altissima*, and its potential for individuals within a genet to self-recognize and mediate the impact of intraspecific competition. Growth and resource allocation between clones collected from
a local nature preserve will be analyzed to determine the growth when not in competition, when grown with other individuals of the same genet, and when clones are grown with individuals from another genet. Analyzing patterns in these three scenarios will allow for the assessment of whether or not self-recognition takes place in *Solidago altissima* and to what extent it plays in the mitigation of competitive effects.
METHODS

Model System

The focus of this study was to analyze the ability for clonal herbaceous species to differentiate between self and non-self-interactions. *Solidago altissima* (synonymous with *S. canadensis*) was selected due to its prevalence in early successional and prairie restoration ecosystems, as well as its aggressive rhizomatous growth patterns (Walck *et al.*, 2001; Sakata *et al.*, 2015).

*Solidago altissima* is a native to North America; however, it has become a wide spread invasive in habitats ranging from Europe to East Asia (Meyer and Schmid, 1999b; Walck *et al.*, 2001; Sakata *et al.*, 2015;). This species of goldenrod is characterized by its more extensive rhizome allocation, more expansive leaf area, and a greater average height when compared to other *Solidago* species (Schmid *et al.*, 1988; Walck *et al.*, 2001). *S. altissima* is typically introduced to new habitats through seed dispersal (Meyer and Schmid, 1999b). Although the plants continue to produce seeda once established, they begin to spread almost exclusively through their rhizomatous growth (Hartnett and Bazzaz, 1985; Eriksson, 1993; Meyer and Schmid, 1999a; Sakata *et al.*, 2015). More importantly, competition results in the loss of distinct genotypes as clonal interactions develop over time (Hartnett and Bazzaz, 1985). This shift would indicate that as these plants mature they will be exposed to various degrees of intra and interspecific competition. There is indication that ramets of *S. altissima* has the ability to share and partition resources (Walck *et al.*, 2001; Yv *et al.*, 2001). Being able to self-recognize in the early colonization process would enable these organisms to effectively partition...
resources minimizing self-competition and increasing their overall fitness within the environment.

Study Site

All goldenrod plants were collected from the Douglas-Hart Nature Center in Mattoon, Illinois, USA (39.4925° N, 88.3109° W). This site is comprised of 29.9 hectares including three prairies, a woodland, a pond, and a wetlands habitat. The prairies are located in the South East, the North, and along the Western edge of the property. The nature reserve is surrounded by agricultural fields on all sides. Douglas-Hart Nature Center was repurposed from agricultural use to a 13.4-hectare nature reserve in the mid 1960’s (Douglas-Hart Nature Center, www.dhnature.org). Since the 1960’s the additional prairie restorations have been added to expand the biodiversity of the site. Plant assemblages in prairie restorations have been added through scheduled plantings and natural succession and have been managed with fire at least once every five years contingent on local weather patterns. Restoration plantings have never included *S. altissima*, so all populations are natural colonizations.

*Solidago altissima* plants were collected from the Western edge prairie. This location was chosen because it is the youngest of the three prairie restorations where *S. altissima* genets were more likely to occur in discreet patches. The edge prairie is boarded by woodlands to the East, agricultural fields to the West, wetland habitat to the North, and a parking lot to the South. There is also a packed dirt path that separates about a quarter of the prairie from the rest of the field.
Specimen Collection

Rhizomes of *S. altissima* were collected in late May from five genets located at various locations throughout the prairie. Genets were selected to be a minimum of 40 meters from other collections to ensure discreet, homogeneous patches. From each clone, 40-45 rhizome segment, each with a single aboveground stem were collected. These rhizomes were marked to associate them with a corresponding clone ID (A-E). This level of replication accommodated for any mortality between collection and potting. Samples were placed into a large trash bag to preserve moisture and transported from the collection site to the experiment site at Eastern Illinois University in Charleston, Illinois, USA (39.4780° N, 88.1759° W).

Experimental Design

To ensure similar size among replicates, all rhizomes within a clone were separated and cut to a uniform 10 cm rhizome length with all above ground biomass removed at the first above ground node. These rhizomes were then planted into treatments which included plants grown by themselves, with another genetically identical individual (self-competition), and specimens grown with one of every other phenotype combination (non-self-competition; e.g. clone A with clone B or clone A with clone E etc.). Labels were physically attached to each stem in order to identify them properly later on in the experiment.

Plants were grown in standard 15.24 cm (6in) azalea pots with a volume of 206.15 cm³ that were placed outside into wooden frames for support at the green house at Eastern Illinois University. The pots were filled with soil that was obtained from
farmland in Casey, Illinois, USA to ensure appropriate microbial populations and abiotic conditions to the field. Pots were covered with 50% shade cloth in order to reduce water loss while growing. Plants had to be watered once every other day at the beginning of the experiment in late May, which was later increased to once or twice a day by mid-June due to increased temperatures and low rainfall.

Leaf samples were collected mid-July after approximately 6 weeks of growth. One fully expanded leaf from each plant were removed at the node. This resulted in a sample size of 5 leaves per genotype per treatment. All leaves were obtained from a height of two-thirds to total plant height to ensure that only mature, fully expanded leaves were included. These leaves were put measured individually for leaf area (LI-3100, Li-Cor Inc., Lincoln, NE) and dried at 60 °C for mass determination. Above ground biomass was collected in late September at around 15 weeks of growth. Stems were removed from their point of growth on the original stem with pruning shears, dried as above, and biomass measurements were taken.

Below ground biomass was harvested in early October after 18 weeks of growth. As a result, some samples had resprouted. This vegetation was harvested along with the below ground biomass as primarily a reallocation of resources from the rhizome to the stem. In order to collect the samples, pots were submerged in water and allowed to soak for 1-2 minutes. After the pots soaked, they were gently compressed to loosen the soil and the root systems gently washed to remove excess dirt. Once belowground biomass was sufficiently cleaned, roots were removed and preserved in a solution of FAA and ethyl alcohol for evaluation of mycorrhizal colonization. The remaining rhizome tissue
and any above ground re-growth was dried at 60 °C and mass determined to the nearest 0.1 mg.

Data Analyses

All analyses were conducted using R software (R Core Team, 2017). Response ratios, \( \ln[\text{sample}/(\text{sample} - \text{control mean})] \), were generated to assist in the detection of relationships among the different competitive responses. ANOVA models were initially constructed to describe variation among the clones included in the experiment. To assess the experimental comparison of self vs non-self competition, ANOVA models included plant genotype and competition treatment (self vs. non-self).
RESULTS

Data were collected from plants grown without competition (controls), self competition, and non-self competition. These were also separated among all genotype combinations. All samples from the self and non-self competition treatments were analyzed for differences in aboveground biomass, rhizome biomass, and leaf area. Control data were used as a baseline measurement for growth (Figure 1) and to check for any inherent differences among the five genotypes in the experiment. Although all of the genotypes grown without competition had some variation in growth during the experiment, there were no significant differences among genotypes in aboveground biomass, rhizome biomass, or leaf area values when grown in isolation (Table 1, Figure 1).

In order to assess *S. altissima*’s response to the different competitive treatments, data were evaluated for their overall self/non-self competitive responses and the self/non-self competitive responses among genotypes. In addition to these measurements, individual response ratios were generated using the self competitive treatments as a reference to explore results that showed significance. Genotypes differed strongly in aboveground biomass, rhizome biomass, and leaf area with all three showing significant differences among genotypes (aboveground $P = 0.0016$; rhizome $P < 0.0001$; leaf area $P < 0.0001$; Table 2). Response ratios generated from genotype competition for aboveground biomass and rhizome biomass (Figures 3 and 4) indicate that the differences arose from a general competitive response, rather than any inherent variation between self and non-self competition.
In contrast to the biomass measurements, leaf area response ratios also indicated a general trend for plants in non-self competition to produce larger leaf areas with the exception of genotype D (Figure 5). Leaf area data were then further analyzed using response ratios for the reactions of individual genotypes (Figure 6). This was used to evaluate whether the patterns indicated by self/non-self genotype response ratios were the result of consistent competitive responses across genotypes. These values highlighted the tendency for genotypes to produce larger leaf area values when grown with non-self competitors. It is worth noting that the individual response ratios for genotype B show that the trend of producing more leaf area in the non-self treatments was skewed by one large positive response in the genotype B with genotype C combination (Figure 6). Genotype B with D and B with E both showed positive growth, but they had values close to zero.

The conclusion that aboveground and rhizome biomass results were generated as a consequence of a general competition effect was further supported by the analysis of the overall self/non-self competition response. Both of these measurements indicated no significant results among the various genotypes (Table 2). However, leaf area was much more useful in establishing an overall self/non-self response showing a small, but significant, effect between competition types ($P = 0.0314$; Table 2).
Table 1: Variation among *S. altissima* genotypes in aboveground biomass, rhizome biomass, and leaf area when grown as controls without competition.

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<td></td>
<td>Error</td>
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Table 2: Variation in response ratios among *S. altissima* genotypes in aboveground biomass, rhizome biomass and leaf area as a result of genotype competition and competition type (self vs. non-self). Values in bold indicate a significant ($P \leq 0.05$) model effect.

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Figure 3: Influence of genotype and competitive type on growth of aboveground biomass with associated response ratios using self competition as a reference. Values plotted are mean ± 1 SE.
Figure 4: Influence of genotype and competition type on growth of rhizome with associated response ratios using self competition as a reference. Values plotted are mean ± 1 SE.
Figure 5: Influence of genotype and competition type on allocation of leaf area with associated response ratios using self competition as a reference. Values plotted are mean ± 1 SE.
Figure 6: Individual genotype response ratios for influence of genotype and competitive type on allocation of leaf area. Genotype D is excluded as it did not show significant variation between self and non-self competition. Values plotted are mean ± 1 SE.
DISCUSSION

One of the major goals throughout the course of this experiment was to induce a competitive signal between rival genets of *S. altissima*. Competition in plant communities is a symphony of inter- and intraspecific interactions orchestrated by both physiological and biochemical responses (Kong *et al.*, unpublished; Novoplansky, 2009). In a traditional model, competition results in a change in fitness as one species or individual begins to outcompete another (Fowler, 1986; Tilman, 1997). Changes in competitive responses were used in this experiment to identify variation between self and non-self response between rival genets and ramets.

Kin recognition studies (see Dudley and File, 2007; Murphy and Dudley, 2009; Biedrzycki *et al.*, 2010; Karban *et al.*, 2013; Marler, 2013) demonstrate that many species of plants have a certain level of phenotypic plasticity that allows them to alter their competitive strategies based on neighbor identity (Murphy and Dudley, 2009; Dudley *et al.*, 2013). By communicating and interacting, closely related individuals can minimize impacts on one another, while simultaneously competing heavily with non-related individuals (Waldman, 1988; Falik *et al.*, 2003). This ability should maximize the fitness of related individuals.

Clonal organisms offer a chance to test for relatedness recognition in a unique ecological setting. Organisms such as *S. altissima* typically occur in dense populations of genetically identical individuals (ramets), which may or may not maintain physiological connections. Applying the same principles used in studying kin recognition, we expect that the plants should receive an evolutionary advantage from distinguishing self from non-self and altering their interactions based on this. This is especially true for young
populations of clonal species, which are often competing for similar resources with rival genets during early successional stages (Hartnett and Bazzaz, 1985). Any changes as a result of neighbor recognition should be identifiable as an alteration in the traits linked to competitive ability, including changes in allocation to root, stem, and leaf development (Murphy and Dudley, 2009).

Changes in these three foundational traits were collected in response to all treatments within this experiment. Data for rhizome biomass were used as a surrogate for root data, as disentangling individual roots was problematic. There is a direct relationship shared between rhizome mass and root mass (Manning et al., 1989), justifying this substitution. If a strong self versus non-self signal were present, it would be expected that self treatments allocate fewer resources to the development of one or more of these structures to minimize competition. Therefore, non-self interactions would result in significantly higher biomass and leaf area production values if competition were predominately aboveground, rhizome mass if competition were primarily belowground. The data collected showed that regardless of competition treatment, significant changes occurred in the production of aboveground biomass, rhizome biomass, and leaf area relative to control plants (Figure 1, Figure 3, Figure 4, Figure 5). Aboveground and rhizome biomass only varied by genotype and did not differ significantly between self and non-self treatments (Table 2; Figure 2). Previous studies on self interactions in roots (Mahall and Callaway, 1991; Chen et al., 2012) indicate that some form of physical proximity between roots is needed before a change in allocation could be observed. It is possible that the duration of this experiment was not long enough for such an interaction.
to occur. However, the clear signal of competition in this study would argue the interaction should have been sufficient to induce a response for these two traits.

In contrast to aboveground and rhizome biomass, leaf area not only showed significant variation across genotypes ($P<0.0001$; Table 2) but also slight, yet significant, variation ($P=0.0314$) between self and non-self competition. When placed in competition with genetically identical individuals, the plants grew smaller leaves than they did when grown with non-self competitors. Reduced leaf area means a decrease in the photosynthetic capabilities of individual leaves. Conversely, smaller leaves will also allow for deeper light penetration within a stand, which in turn increases the photosynthetic activity at lower regions of the plants. This could lead to an increase in the overall fitness for the organism, as more of the plant maintains photosynthetic activity. It is also likely that plants use these light signals to influence root-root communication and to guide the development of new growth (Grundel et al., 2014). In clonal plants, this could lead to higher densities within genets, as new growth is likely to be produced in conjunction with queues from light signals (Grundel et al., 2014). Therefore, this growth strategy could make it more difficult for weaker rival genets to penetrate and outcompete larger and more fit genets.

Although the mechanism that would generate this leaf response is not currently known, Karban and Shiojiri (2009) show that genetically identical individuals respond to volatile cues passed through the air, rather than the rhizosphere. It is also not completely clear how to interpret the change in leaf area whether it should be considered an altruism or a consequence of increased competition between genetically identical individuals. Smaller leaves could result from less water or other resources available to the plants for
light acquisition. More closely related plants are expected to compete more strongly (Valiente-Banuet and Verdú, 2008) supporting this interpretation. However, neither aboveground or rhizome biomass was altered significantly by competitor identity, arguing against stronger competition as a driver of smaller leaves. Therefore, the data from this experiment more so supports reduced leaf area in self competition as an altruistic trait.

Several studies have demonstrated that plant species can have the ability to distinguish self versus non-self in some capacity (see Mahall and Callaway, 1990, 1996; Falik et al., 2003; Gruntman and Novoplansky, 2004; Karban and Shiojiri, 2009; Chen et al., 2012). Despite these studies spanning the better part of three decades, the possible mechanisms behind these unique competitive interactions remain mostly conjecture. One likely mechanism is light signaling from neighbors (Crepy and Casal, 2015), particularly mediated by changes to the R:FR ratio (reviewed in Grundel et al., 2014). The ability to capture and harness light is vital to the success of all photoautotrophic organisms. This energy can not only be used to generate carbon compounds essential to various biological functions, but can also be used to generate signals indicating unwanted reductions in light (Holmes and Smith, 1977) and nearby competitors (Ballaré et al., 1990). The latter of which occurs when light is reflected off nearby plants (Grundel et al., 2014) and is detected by photoreceptors, such as phytochromes (Chen et al., 2004; Franklin, 2008; Ballaré, 2009). As competitors encroach upon the space occupied by a rival plant, they reduce the R:FR ratio. Low R:FR ratios have been documented to significantly influence a plant's secondary chemistry (Tegelberg et al., 2004; Izaguirre et al., 2006; Cerrudo et al. 2012), as well as the release of compounds both above and belowground (Finlayson
et al., 1998; Pierik et al., 2004; Izaguirre et al., 2013). Whether light signals can differentiate self from non-self competition is not clear.

Another of the more commonly hypothesized mechanisms is the release of soil-mediated chemical signals that can be transferred from one plant to another (Mahall and Callaway, 1990; Falik et al., 2003; Falik et al., 2005; Callaway and Mahall, 2007; Chen et al., 2012). Some studies suggest that these signals are used to regulate communication between individuals (Chen et al., 2012), possibly through enzymes or other chemicals located on the surface of root cells (Callaway and Mahall, 2007). Other arguments have included allelopathic chemicals (Mahall and Callaway, 1990; Falik et al., 2005) where a plants’ sensitivity to its own allelochemicals regulate self/non-self signaling (Falik et al., 2005). Response to allelochemicals may be of interest to this model system, as goldenrod are frequently shown to produce allelochemicals in laboratory and field experiments (Abhilasha et al., 2008; Pisula and Meiners, 2010). Unfortunately, as cited by Chen et al. (2012) there is very little understanding or documentation of such individual-specific chemicals.

Another often discussed chemical mechanism is the use of various volatile molecules (Callaway and Mahall, 2007; Karban and Shiojiri, 2009), commonly employed as a defense signal to induce defenses against herbivory or parasitism (Karban and Shiojiri, 2009). However, the effect of these volatiles varied depending on whether they were perceived as from self (genetically identical cuttings) or non-self (different genetic individuals; Karban and Shiojiri, 2009). Many other possible mechanisms have been posed such as electrical signals or oscillations generated by plants may play (Falik et al., 2005; Callaway and Mahall 2007; Chen et al. 2012), plant hormones (Falik et al, 2005;
Grundel et al., 2014), and internal synchronization (Chen et al., 2012). Although the exact signaling mechanism is not known, the signal should be detectable from the external environment to induce a response (Chen et al., 2012). If this holds true, then further experimentation incorporating mechanistic elucidation will be needed demystify the source of these unique interactions.
CONCLUSIONS

Competition is often discussed in relation to populations of organisms; however, such interactions are a summation of responses generated between individuals (Weiner, 1990). In such circumstances, there is an expected evolutionary advantage for organisms to distinguish between competitors based on relatedness (Karban et al., 2013). There have been several studies demonstrating that at least some plants have this ability (see Dudley and File, 2007; Murphy and Dudley, 2009; Biedrzycki et al., 2010; Karban et al., 2013; Marler, 2013). Plants have also been shown to have the capability to discern between various degrees of self and non-self signals (see Mahall and Callaway, 1991, 1996; Falik et al., 2003; Gruntman and Novoplansky, 2004; Karban and Shiojiri, 2009; Chen et al., 2012).

In clonal species, it is likely that the ability to discriminate between self and non-self plays a critical role during the competitive sorting of genets in early successional communities. The most frequent measure of this interaction has been to study root growth, and its impact on biomass. Here rhizome, used as a surrogate for root analysis, and aboveground biomass demonstrated no significant signal, but the leaves in self treatments produced significantly smaller leaves than those in non-self treatments. A plant's ability to absorb light has been shown to influence its competitive ability (reviewed in Gundel et al., 2014) suggesting this may in fact be an altruistic alteration in plant morphology.

Understanding how plants are able to communicate and what drives their competitive responses is essential to understanding how plant populations and communities develop. Even though the signals driving such interactions are predominately unknown, further efforts to identify self/non-self responses and signals may be critical to
understanding the invasiveness of clonal species, as well as successional patterns following disturbance.


