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Inter- and intraspecific competition and shade avoidance in the carnivorous pale pitcher plant in a nutrient-poor savanna

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PREMISE OF THE STUDY: Ecologists generally agree that weak interspecific competition for light contributes to high plant species diversity in ecosystems with nutrient-poor soils. However, the role of competition for light in such ecosystems that are also maintained by fire is poorly understood. I quantified intra- and interspecific competition for light in a fire-maintained nutrient-poor pine savanna by contrasting the effects of conspecific and heterospecific neighbors of the pale pitcher plant, *Sarracenia alata*.

METHODS: Accounting for initial neighbor abundance/aboveground production and initial transplant size, I measured growth and survival of small and large pitcher plant ramets of *Sarracenia alata* transplanted to the vicinity of natural, undisturbed mixtures of large pitcher plants and their heterospecific neighbors in the field. I tested competition for light and nutrients by clipping conspecific neighbors and by excluding prey from unclipped neighbors of transplants. I tested interspecific competition by uprooting heterospecific neighbors.

KEY RESULTS: Plant survivorship increased when conspecific neighbors were clipped and/or starved but not when heterospecific neighbors were uprooted. Small pitcher plants benefited from clipping large conspecific neighbors, suggesting that competition for light was important. Large pitcher plants benefited from excluding prey from their neighbors, with no additional benefit of clipping, suggesting that competition for prey limited their survival. Transplants produced new pitchers that were taller with narrower openings (i.e., shade avoidance) when heterospecific neighbors were left intact but not when conspecifics were unclipped.

CONCLUSIONS: Results demonstrate size-dependent intraspecific competition for light and nutrients and interspecific shade avoidance in *Sarracenia alata*, which could be important to understanding species coexistence in fire-maintained nutrient-poor ecosystems.

KEY WORDS carnivorous plant; competition for light; competition for nutrients; niche partitioning; phenotypic plasticity; Sarraceniaceae; size-dependent competition; species coexistence.

The processes responsible for plant species coexistence in nutrient-poor ecosystems remain poorly understood. Although ecologists generally agree that interspecific competition for light can lead to reductions in plant species diversity in nutrient-rich ecosystems, the role that competition for light plays in nutrient-poor systems is generally dismissed as being relatively inconsequential (Tilman, 1988; Huston and DeAngelis, 1994; Rajaniemi, 2003; DeMalach et al., 2016). The potential for interspecific competition for light to result

in mortality and thus species loss increases with increasing soil nutrient supplies (Huston and DeAngelis, 1994; DeMalach et al., 2016). Hence, reduced competition for light has been proposed as a contributing factor explaining the high plant species diversity seen in moderately nutrient-poor ecosystems (Rajaniemi, 2003; DeMalach et al., 2016).

Although competition for light may be weaker in nutrient-poor ecosystems than in nutrient-rich ecosystems, it can nonetheless

be important in nutrient-poor ecosystems that are maintained by frequent fires. Low-intensity fires in fire-maintained savannas with nutrient-poor soils are frequently cited as being necessary for maintaining herbaceous species diversity (Folkerts, 1982; Walker and Peet, 1984; Gilliam and Christensen, 1986; Provencher et al., 2001; Glitzenstein et al., 2003, 2012; Palmquist et al., 2014; Brewer, 2017). Because such fires typically reduce aboveground biomass without dramatically changing belowground biomass, one might assume that the positive responses to fire are largely due to reductions in aboveground competition (i.e., increased light). Furthermore, the rapid regrowth of vegetation to pre-burn levels suggests that many plants must be able to endure or avoid shade during years without fire (e.g., via persistent seed and bud banks, reduced flowering, morphological shade avoidance; Brewer and Platt, 1994; Brewer, 1999a, b; Hinman and Brewer, 2007). In particular, shade avoidance plasticity (e.g., altered stem or leaf morphology or allocation) in response to imminent shade has the potential to prevent competitive displacement (Brewer, 1999b; Callaway et al., 2003; Dybzinski and Tilman, 2007).

Despite the fact that numerous studies have examined morphological shade avoidance plasticity (e.g., Dudley and Schmitt, 1996; Callaway et al., 2003; Casal, 2013), very little is known about differences between conspecific and heterospecific neighbors. Species coexistence may not occur if shade avoidance is greater between conspecifics than between heterospecifics (Turcotte and Levine, 2016). Shade avoidance plasticity has previously been demonstrated in nutrient-poor savannas (Brewer, 1999b, 2003b; Abbott and Brewer, 2016), but these studies did not specifically examine whether it was more effective in the presence of heterospecific relative to conspecific neighbors. To my knowledge, there are no field studies conducted in nutrient-poor ecosystems that have specifically contrasted intraspecific and interspecific competition for light and shade avoidance.

Carnivorous pitcher plants (e.g., *Sarracenia* L. spp.), many of which are associated with nutrient-poor soils and fire (Brewer and Schlauer, 2018), offer a promising system for examining mechanisms of resource competition because of the ease by which both light and nutrient availability can be manipulated. Previous competition studies with pitcher plants in fire-prone savannas, however, have not contrasted the strength of intra- and interspecific competition or the effect of competition for light with the effect of competition for nutrients (Brewer, 1999b, 2003b; Abbott and Brewer, 2016). Shade avoidance plasticity in pitcher plants (i.e., producing taller pitchers with greater investment in pitcher support) may come at the expense of prey capture, due to the production of smaller openings and reduced pitcher volume (Brewer, 1999b, 2003b), which could then compromise their ability to compete for nutrients. If intraspecific competition for prey is stronger than interspecific competition for nutrients, then shade avoidance is likely to be more adaptive in the presence of heterospecific neighbors than in the presence of conspecific neighbors.

In this study, I examined growth, survival, and shade avoidance responses of the pale pitcher plant, *Sarracenia alata* Alph. Wood, to conspecific and heterospecific neighbors intraspecific and interspecific competition. I measured competition (a negative non-trophic interaction between neighbors) by quantifying growth and survival, whereas I considered shade avoidance to be a type of phenotypic plasticity. Specifically, I transplanted small and large pitcher plant ramets to the vicinity of natural, undisturbed mixtures of large pitcher plants and their heterospecific neighbors in

the field. Accounting for initial neighbor abundance/aboveground production (i.e., leaf area index, pitcher production) and initial transplant size, I tested the hypothesis that competition was greater with conspecific neighbors than with heterospecific neighbors in part because of more effective interspecific shade avoidance. In addition, I tested the importance of two different mechanisms of intraspecific aboveground competition (competition for prey and competition for light) by excluding prey from unclipped neighbors of the transplants (reduction in competition for prey but no reduction in competition for light) and by clipping the conspecific neighbors of the transplants (reduction in both competition for prey and light). It was not possible to implement a treatment that reduced competition for light without also reducing competition for prey. Nevertheless, large transplants were less likely than small transplants to be shaded from above by large conspecific neighbors. Hence, the control (no prey exclusion of unclipped neighbors) for large transplants was assumed to be more-or-less equivalent to a treatment in which there was little or no overhead shading at the time of planting. In contrast, the control for small transplants was assumed to be equivalent to a treatment in which there potentially was shade from larger neighbors at the time of planting. I was therefore able to indirectly assess a possible size-dependent interaction between competition for nutrients and competition for light in pitcher plants. Competition with heterospecific neighbors was manipulated by uprooting them, which potentially reduced competition for light and nutrients simultaneously. Because these are wetland systems and because *S. alata* produces small root systems compared to most of its heterospecific neighbors (Brewer, 2003b), I assumed intraspecific belowground competition for nutrients or water was minimal (see Abbott, 2017, for empirical support) and thus did not include a conspecific uprooting treatment.

I hypothesized that competition for light would be stronger with conspecifics, especially between large and small plants, than with heterospecifics. I further hypothesized that shade avoidance responses would be more beneficial and thus apparent in the presence of heterospecifics than in the presence of conspecifics because: (1) shade avoidance plasticity is not likely to be effective in small pitcher plants when located adjacent to large pitcher plants; (2) shade avoidance is likely to be constrained to a greater extent by intraspecific competition for prey between equal-sized (i.e., large) pitcher plants than by interspecific competition for soil nutrients; and/or (3) fitness of pitcher plants may be increased more by competing with unrelated conspecifics than by avoiding competition with them (Gersani et al., 2001).

METHODS

Study site and experimental design

This study was conducted in a ~4-ha open wet pine savanna in Desoto National Forest in southeast Mississippi, USA (Sandy Creek; 30°43' N, 88°58' W) (Brewer, 2017). The savanna contained a sparse overstory of *Pinus elliottii* Engelm., mixed with rare individuals of *Pinus palustris* Mill., and has been historically maintained by regular (once every 3-5 years) fires since 1982 (Brewer, 2017). Poor drainage, low pH (~4.3), nutrient-poor soils [25.5 ± 0.5 ppm (s.e.) surface water nitrate], periodic fires, and a lack of cultivation combine to produce an "old-growth" groundcover community dominated by perennial grasses and sedges (Brewer, 1998; Hinman

et al., 2008; Brewer et al., 2011). Although light levels experienced by large adult groundcover herbs are typically high away from trees (>90% gap fraction), in years without fire, overhead canopy gap fraction at ground level in these areas can be less than 1%, and thus light availability to seedlings and juveniles can be quite low.

Sarracenia alata co-occurs with a variety of carnivorous and non-carnivorous species in the savanna studied here (Brewer, 2003b). Although *S. alata* tends to be less common near trees and in associated shrub thickets, there is no evidence of either favored or forbidden combinations of *S. alata* with other herbaceous species (Brewer, 1998, 2017). Accordingly, the focus of the current study was to contrast the strength of intraspecific competition with that of interspecific competition in the aggregate, under natural field conditions, and without regard to the specific identities of the heterospecific neighbors of *S. alata*.

On May 28 and 29, 2017, I established 120 15 × 15 cm plots, each located around a single clump of mature *Sarracenia alata* ramets (hereafter, in situ pitcher plants) and away from trees and associated shrub thickets. All in situ pitcher plants occurred adjacent to established herbaceous plants, the most common of which were clumps of large grasses [e.g., *Muhlenbergia expansa* (Poir.) Trin., *Ctenium aromaticum* (Walter) Alph. Wood], smaller grasses [*Dichantheium ensifolium* (Baldw. ex Elliott) Gould & C.A. Clark], cespitose sedges (e.g., *Rhynchospora oligantha* A. Gray), and the small carnivorous herb, *Drosera capillaris* Poir.). These species were also among the most common herbaceous species within the savanna as a whole (Brewer, 1998; Hinman and Brewer, 2007). One hundred and twenty target ramets of *S. alata* (60 small and 60 large) were located and identified for transplanting. Each ramet contained 1 to 3 live pitchers and was size-standardized within each of the two size categories. For small transplants (post-seedling juveniles), the dorsoventral diameter at the lip of the largest pitcher of a ramet (a reliable indicator of ramet size [Brewer, 1999b, 2003b]) was less than 1 cm and the tallest pitcher was less than 20 cm. For the large transplants, the dorsoventral diameter was greater than 2 cm and the tallest pitcher was greater than 30 cm (comparable in size to the in situ pitcher plants). Large transplants were adult ramets of a size large enough to flower (although I avoided sampling flowering ramets). The 120 target ramets were carefully excavated, minimizing damage to roots and rhizomes, and then randomly assigned to a 3 × 2 × 2 factorial arrangement of conspecific, heterospecific, and transplant size treatments, respectively. Hence, there were 10 replicates for each of the 12 treatment combinations. The target ramets were taken from areas within the same site that were environmentally similar to the 15 cm × 15 cm plots. The conspecific competition treatment consisted of an unmanipulated control and two neighbor manipulation levels: (1) starving all in situ neighbor pitchers (prey exclusion); and (2) clipping all in situ neighbor pitchers to the ground (clipping). Prey was excluded by inserting cotton batting into the live in situ pitchers in May and was intended to reduce intraspecific nutrient competition. Previous observations of these species have revealed that inserting cotton batting into pitchers reduces prey capture (but not the height or shading capacity) of the treated pitchers and reduces pitcher volume of new pitchers and their ability to capture prey (Brewer, 2003b). In contrast, the clipping treatment was intended to reduce both prey capture and light capture by treated pitchers and thus reduce intraspecific competition for prey and light. The heterospecific competition treatment was represented by an unmanipulated control and a single treatment level. For the

treatment, all heterospecific plants within a 10-cm radius of the transplant were carefully uprooted, minimizing disturbance to the in situ pitcher plants. Soils were moderately wet and loose, which facilitated uprooting. Soil associated with the transplant was used to fill the resulting holes. The heterospecific neighbor reduction treatment was intended to reduce above- and belowground competition from heterospecifics without reducing intraspecific competition. Each transplant was rooted within 3 cm of the in situ pitcher plant clump and adjacent heterospecific plants. Planting was done in such a way that pitchers of the transplants were interspersed among the aboveground parts of both conspecific and heterospecific neighbors.

Accounting for initial transplant size and neighbor density/size

Although I attempted to size-standardize transplants within each size category, I nonetheless accounted for initial size as a possible covariate in the analysis of growth and survival (see *Data Analysis*). Initial target plant size was estimated by locating the tallest pitcher that showed no signs of senescence, recording diameter and height of this pitcher, and calculating the log product of these measurements. Groundcover plant communities of wet pine savannas are dominated by perennials, many of which are rhizomatous (e.g., *Sarracenia alata*) and/or bunch forming (e.g., the dominant grasses and sedges). Therefore, there is no straightforward way to count individuals and thus account for neighbor density, per se, in this system. Nevertheless, estimates of both intraspecific and interspecific competition could be biased by significant spatial variation in neighbor biomass and the relative abundance/biomass of conspecific and heterospecific neighbors. For these reasons, immediately before treatment application, initial groundcover canopy leaf-area index (LAI) at ground level was measured with a LI-COR plant canopy analyzer (LI-COR, Lincoln, Nebraska, USA). LAI at ground level in May was highly negatively correlated with ground-level canopy gap fraction (gap fraction) as an exponential function (gap fraction = $1.15 \cdot e^{-0.85 \cdot \text{LAI}}$; $R^2 = 0.99$) and provided a good estimate of aboveground biomass of neighboring groundcover aboveground biomass. In addition, I measured the dorsoventral aperture diameter and the height of the largest pitcher of in situ pitcher plants within a 15-cm radius of the target and estimated pitcher volume, assuming it approximated that of a right circular cone: $\frac{1}{3} \text{height} \times \pi \frac{1}{2} \text{diameter}^2$. Initial target size, ground-level LAI, neighbor volume, and their interactions with the treatments were considered as possible covariates in the statistical analyses, which are described in detail in the *Data analysis* section.

Growth and survival measurements

On September 7, 2017 (100 to 101 days after transplantation), I measured the height and the dorsoventral diameter of the largest pitcher that emerged since the initial census. No pitchers that were measured in May (most of which were senescent by September) were re-measured. Hence, growth was estimated by measuring final size of target pitcher plants corrected for their initial size. Final size was estimated by taking the log product of height and the dorsoventral diameter at the lip of the tallest non-senescent pitcher in September. Likewise, initial ramet size was accounted for by taking the log product of height and diameter of the tallest non-senescent pitcher derived from the same rhizome in May. In some cases, no new pitchers were produced on the ramets since the initial census. Because it was not always obvious how to distinguish between

ramets that were dead and those were still alive but failed to produce new live ramets since the May census, a ramet was assumed to be “alive” only if at least one new pitcher was present during the September 2017 census. Strictly speaking, “dead” ramets were those that either were truly dead or those that lacked new pitchers in the September census.

Shade avoidance measurements

Shade avoidance and/or increased light capture effort of the transplants relative to prey capture effort was estimated by calculating the log ratio of pitcher height and aperture diameter, specifically, $\log(\text{pitcher height}) - \log(\text{aperture diameter})$. Unlike some other *Sarracenia* species [e.g., *S. purpurea* (Gotelli and Ellison, 2002)], *Sarracenia alata* does not produce phyllodia (decumbent, flattened leaves that do not capture prey). However, *S. alata* can produce upright pitchers that fail to open, thus precluding prey capture (Brewer, 2003b). Hence, aperture diameter was assumed to be the same as the dorsoventral diameter at the lip of the pitcher except in those cases in which transplants produced pitchers that failed to open, in which cases, the aperture diameter was assumed to be zero. A value of 1 was thus added to all length and diameter measurements before calculating log ratios to deal with these zero values. Higher pitcher height to aperture diameter ratios indicated that the plants were investing more resources into light capture at the expense of prey capture (i.e., shade avoidance), while lower pitcher height to aperture diameter ratios indicated that the plants exhibited a greater potential for prey capture at the expense of light capture (Brewer, 2003b).

During the September census, I discovered that one of the transplants designated to be a small transplant was in fact a large transplant (based on the measurement of size in May). In addition, I was unable to locate two of the small transplants (i.e., the numbered tags could not be found). Hence, there were three missing observations (each from a different treatment combination) for the analyses of small transplants (57 instead of 60) and one additional observation for the analyses of large transplants (61 instead of 60).

Data analysis

Because responses to neighbor manipulations were potentially contingent upon initial neighbor LAI, initial *in situ* neighbor pitcher volume, and the initial size of the transplants, I systematically examined relationships between all response variables and each of these three covariates and their interactions with the treatments. Statistical models (linear models for final size and height to aperture ratio and nominal logistic models for survival) were subsequently simplified, removing all non-significant interactions. General linear models including the covariates, the treatments, and each covariate's interactions with the treatments were used to test effects on log final size of targets and the log change in the height to aperture ratio. Because of unbalanced data and to preserve statistical power, all non-significant interactions were dropped from the reported statistical models. Transplant survival in response to the covariates, the treatments, and each covariate's interactions with the treatments was initially analyzed using a generalized linear model assuming a binary response (i.e., a nominal logistic model), but the analysis failed to provide a stable iterative solution. As a result, survival of small transplants in response

to conspecific and heterospecific treatments was analyzed using chi-square tests of independence. Two tests of conspecific treatment effects were clipped vs. non-clipped pitcher plant neighbors and starved vs. control neighbors. Survival of large transplants in response to treatments was analyzed using a nominal logistic model that initially included all covariates, the treatment factors, treatment interactions, and each covariate's interactions with the treatment factors. All non-significant interactions were subsequently dropped from the model. The nominal logistic model that ultimately was used and reported compared conspecific controls with those transplants with treated pitcher plant neighbors, as well as a test for differences between the starved and clipped treatments, accounting for all covariates. Tests designed to examine mechanisms of competition (i.e., prey, light) were a priori orthogonal contrasts using the mean square error. All analyses were conducted using JMP (version 5.0; SAS Institute, Cary, North Carolina, USA).

RESULTS

Growth of transplants

Log final size, adjusted for log initial size, ground-level LAI, and initial neighbor pitcher volume were not significantly affected by the conspecific treatment ($F_{2,87} = 0.48$; $P = 0.62$), the heterospecific treatment ($F_{1,87} = 0.73$; $P = 0.40$), transplant size category ($F_{1,87} = 0.10$; $P = 0.76$) or any interaction. Although log final size was positively correlated with initial log size ($t_{87} = 2.60$; $P = 0.01$), it was not correlated with ground-level LAI or initial neighbor pitcher volume ($F_{1,87} = 0.07$; $P = 0.77$ and $F_{1,87} = 0.49$; $P = 0.63$, respectively).

Survival of small transplants

The survival (i.e., incidence of new pitcher production) of small *Sarracenia alata* transplants was negatively affected by competition for light with large *in situ* *S. alata* ramets. Survival of small transplants was significantly higher in the clipped treatment (19 of 19) than in the starved treatment or the control combined (27 of 38; Pearson chi-square = 6.82, $df = 1$; $P < 0.01$; Fig. 1). Survival did not, however, differ significantly between the starved treatment (13 of 19) and the control (14 of 19; Pearson chi-square = 0.13, $df = 1$, $P = 0.72$; Fig. 1). In contrast to the conspecific treatment, uprooting heterospecific neighbors had no effect on the survival of small *S. alata* transplants (survival Pearson chi-square = 0.16, $df = 1$, $P = 0.69$). Among observations in which pitcher plant neighbors were not clipped, survival was negatively associated with initial ground-level LAI (Likelihood ratio chi-square = 4.39; coefficient = -0.99 ; $df = 1$, $P = 0.04$, $n = 38$), but not with initial neighbor pitcher volume nor log initial transplant size ($P > 0.45$). There was, however, no significant interaction between initial ground-level LAI and the heterospecific treatment or between initial neighbor pitcher volume and the heterospecific treatment ($P > 0.22$).

Survival of large transplants

The survival of large *Sarracenia alata* transplants was moderately negatively affected by competition for prey with large *in situ* *S. alata* ramets (Fig. 2). Survival of large transplants was significantly higher

in the starved and clipped treatments combined (36 of 41) than in the control (13 of 20; Likelihood ratio chi-square = 4.82, $df = 1$; $P = 0.03$; Fig. 2). Survival did not, however, differ significantly between the starved treatment (19 of 21) and the clipped treatment (17 of 20; Likelihood ratio chi-square = 1.43, $df = 1$; $P = 0.23$; Fig. 2), indicating a lack of competition for light between large transplants and their large conspecific neighbors. Survival of large transplants was positively (not negatively) related to the initial in situ neighbor pitcher volume (coefficient = 0.42; Likelihood ratio chi-square = 6.43, $df = 1$; $P = 0.012$). On the other hand, the volume of new pitchers produced by in situ neighbors was negatively affected by starving and clipping ($F_{2,105} = 4.21$, $P = 0.02$; Fig. 3). Neither initial ground-level LAI nor initial size was a significant predictor of survival of large transplants (Likelihood ratio chi-square = 0.15 and 0.04, respectively, $df = 1$; $P > 0.70$). In contrast to the conspecific treatment, uprooting heterospecific neighbors had no effect on the survival of large *S. alata* transplants (Likelihood ratio chi-square = 0.54, $df = 1$, $P = 0.46$).

Shade avoidance responses

Both small and large *Sarracenia alata* transplants appeared to show a shade avoidance response to heterospecific neighbors but not to conspecific neighbors (Fig. 4A, B). Shade avoidance, indicated by the change in the log ratio of pitcher height to aperture diameter, was highly significantly affected by the heterospecific treatment ($F_{1,87} = 13.52$, $P < 0.01$), such that transplants produced taller pitchers with reduced aperture diameters when heterospecific neighbors were left intact (Fig. 4A). There was no significant effect of the conspecific treatment on shade avoidance ($F_{2,87} = 1.13$, $P = 0.33$; Fig. 4B). None of the covariates or factors or their interactions were statistically significant ($P > 0.32$).

DISCUSSION

Intraspecific competition was greater than interspecific competition

Despite considerable attention paid to competition and coexistence in nutrient-poor systems (reviewed in Rajaniemi, 2003; Craine and Dybzinski, 2013), debate continues over how competition affects species coexistence in these systems (Rajaniemi, 2003; Pärtel and Zobel, 2007; Brewer, 2011; Craine and Dybzinski, 2013). I suggest that one contributing factor to the continued debate is the lack of field studies that contrast intraspecific with interspecific competition for light in nutrient-poor ecosystems.

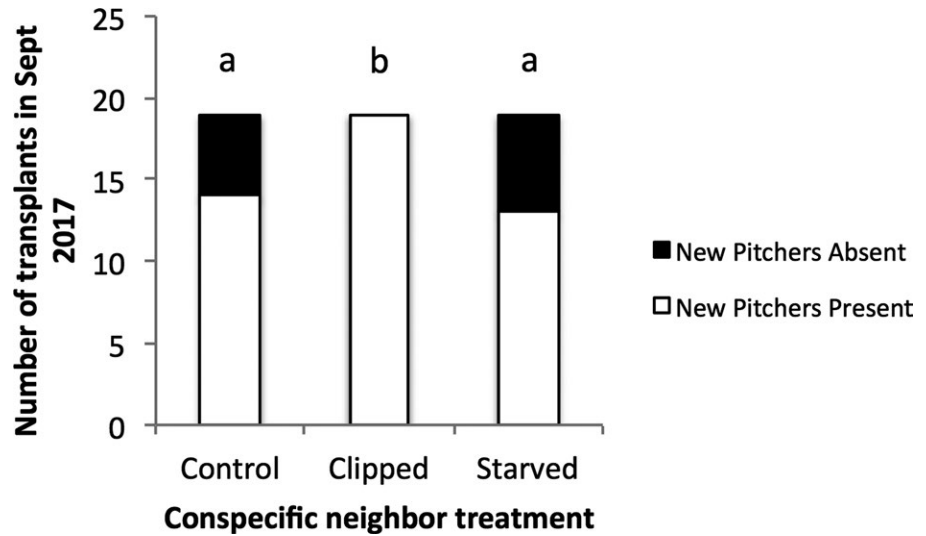


FIGURE 1. Survival responses of small *Sarracenia alata* transplants to starving or clipping of large in situ neighboring *S. alata* ramets. Shared letters above stacked bars represent a lack of statistically significant ($P < 0.05$) differences in the proportion of transplants that survived until September 7, 2017, based on planned orthogonal chi-square tests of independence (clipped vs. control and starved, then control vs. starved).

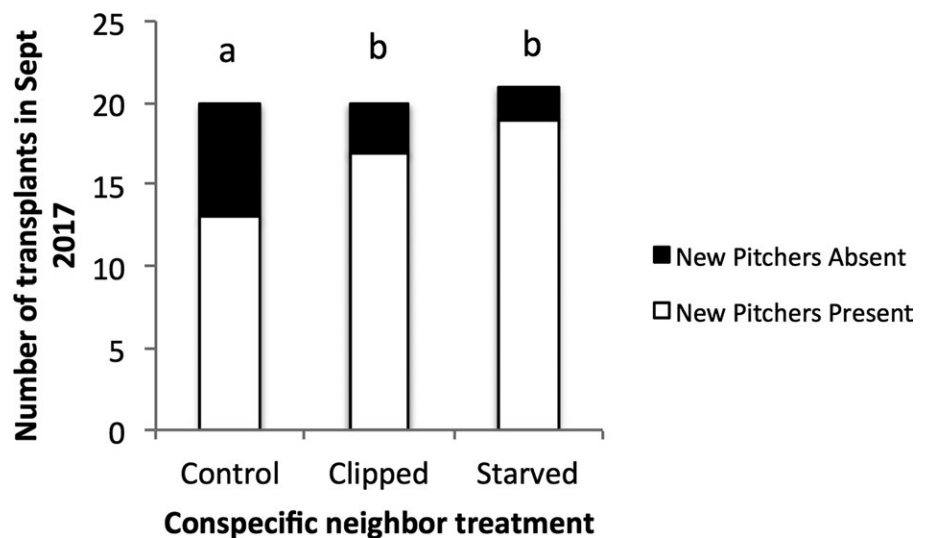


FIGURE 2. Survival responses of large *Sarracenia alata* transplants to starving or clipping of large in situ neighboring *S. alata* ramets. Shared letters above stacked bars represent a lack of statistically significant ($P < 0.05$) differences in the proportion of transplants that survived until September 7, 2017, based on planned likelihood ratio chi-square tests of the conspecific treatments (control vs. clipped and starved, then clipped vs. starved), correcting for initial size, ground-level LAI, and initial neighbor pitcher volume.

I believe this is the first field experiment to show that competition for light with conspecifics was greater than interspecific competition in a moderately nutrient-poor ecosystem. Because interspecific competition for light is generally hypothesized to be relatively weak in nutrient-poor ecosystems (Tilman, 1988; Huston and DeAngelis, 1994; Rajaniemi, 2003; DeMalach et al., 2016), one might reasonably assume that intraspecific competition for light must be weak also. The results of the current study contradict that assumption for *Sarracenia alata*, however. Although

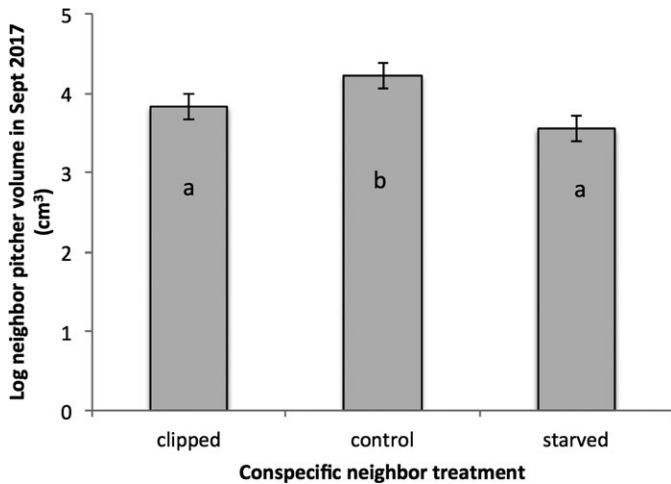


FIGURE 3. Neighbor pitcher volume in September 2017, corrected for initial neighbor pitcher volume in May 2017, initial ground-level LAI, and initial transplant size, in response to conspecific treatments. Neighbor pitcher volume was estimated from the height (cm) and dorsoventral diameter at the lip (cm) of the largest pitcher using the formula of a right circular cone. Values are least squares means plus or minus 1 standard error derived from the mean squared error for the analysis. Shared letters on bars represent a lack of statistically significant ($P < 0.05$) differences in post-treatment (September 2017) neighbor pitcher volume, based on planned orthogonal contrasts for all observations (control vs. clipped and starved, then clipped vs. starved). $N = 40, 37,$ and 37 for clipped, control, and starved neighbors, respectively.

there were no effects of neighbors on pitcher plant growth (i.e., the sizes of new pitchers), competition for light between small transplants and large in situ pitcher plants resulted in the former having a reduced incidence of new pitcher production during the growing season. In contrast, I found no evidence of significant competition for light (or belowground competition) between pitcher plants and their heterospecific neighbors. Although different methods of manipulation were implemented for conspecific and heterospecific neighbors in this study, if anything, the current study overestimated the effects of heterospecific neighbors, given that they were completely removed rather than clipped. Previous field experiments in this system showed significant positive effects of neighbor removal on pitcher plant growth (Brewer, 1999b, 2003b). Those studies, however, removed *all* neighbors (including conspecifics), and thus did not provide unequivocal evidence of interspecific competition. Furthermore, an experiment in the same system that manipulated the aboveground effects of heterospecific neighbors using clipping and belowground effects of heterospecific neighbors using trenching found no evidence of significant above- or belowground competition between *S. alata* and its neighbors (Abbott, 2017). Taken together, these results demonstrate a lack of (or very weak) competition above- or belowground for resources between *S. alata* and its heterospecific neighbors in this system. More generally, they demonstrate that field competition experiments that involve the removal of neighbors from the vicinity of small transplanted targets (without regard to whether neighbors are the same or a different species from the target plant) can provide a misleading picture of the role of competition.

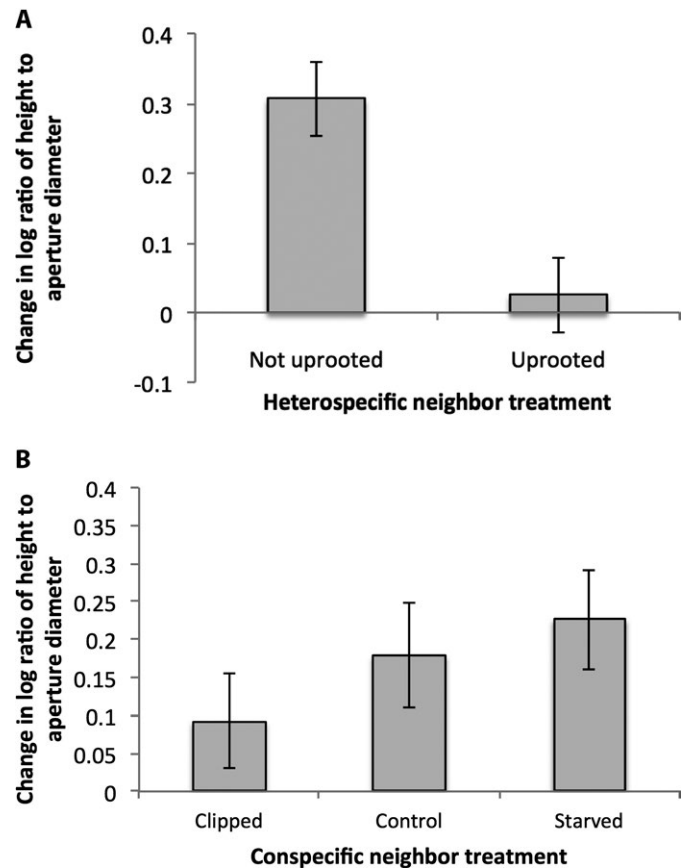


FIGURE 4. Shade avoidance responses of small and large *Sarracenia alata* transplants to: (A) the removal of heterospecific neighbors; and to (B) starving or clipping of large neighboring in situ *S. alata* ramets. Shade avoidance was estimated as the change in the log ratio of the height (cm) and dorsoventral aperture diameter (cm) of the largest pitcher between May and September, corrected for initial size, ground-level LAI, and initial neighbor pitcher volume. Values of log ratios of height to diameter are least squares means plus or minus 1 standard error derived from mean squared error for the analysis. $N = 49$ and 46 for the control and the uprooted heterospecific treatments, respectively, and $28, 35,$ and 32 for the control, the clipped, and the starved conspecific treatments, respectively.

The relative intensity of competition for light and prey in *Sarracenia alata* depended on plant size

In contrast to responses by small pitcher plants, large pitcher plants showed evidence of intraspecific competition for prey (for another example with a carnivorous plant, see Gibson, 1991). Both starving and clipping in situ pitcher plant neighbors appeared to release large transplants from competition, increasing the incidence (but not the size) of new pitchers during the growing season. In the current study, I found evidence that both starving and clipping reduced the size of new pitchers in the in situ neighbor pitcher plants. Hence, when their neighbors were starved or clipped, large transplants were competing with neighbors that produced smaller new pitchers than those produced by untreated neighbors. In contrast, small transplants were likely still shaded by large in situ neighbors that had not been clipped, regardless of whether they had been starved.

The size-dependent responses of pitcher plants to aboveground competition for light and prey found in the current study suggest that shading of small pitcher plants by large pitcher plants reduced the effect of competition for prey between large and small pitcher plants.

The size-dependent competitive responses of pitcher plants have important implications for understanding the relative intensity of competition for light and for nutrients and their interaction. Several attempts to partition the effects of above- and belowground competition in non-carnivorous plants lack a treatment in which aboveground competition is retained but belowground competition is reduced (e.g., Wilson and Tilman, 1991; Twolan-Strutt and Keddy, 1996; Emery et al., 2001). Hence, these studies assumed there was no interaction between aboveground and belowground competition. Such an assumption is not always valid (Wilson, 1988; Cahill, 2002). Previous studies have shown that a negative interaction between above- and belowground competition can be expected in about half of the cases (Wilson, 1988; Cahill, 2002). If the performance of small individuals of a species is limited more by light than by soil resources (e.g., nutrients) because of a high likelihood of being shaded by larger neighbors, then competition for light may reduce competition for nutrients (Wilson, 1988; Cahill, 2002). The removal or reduction of aboveground parts of large neighbors of small plants, however, could make the performance of the latter more limited by nutrients (Brewer, 2003b), thus resulting in greater competition for nutrients. In contrast, larger (i.e., taller) plants are less likely to be shaded by their neighbors and thus might be expected have their performance limited more by nutrients, regardless of whether the aboveground parts of their neighbors are reduced or removed.

Pitcher plants avoided shade with their heterospecific neighbors but not with their conspecific neighbors

The lack of competition between pitcher plants and their heterospecific neighbors may have resulted from effective heterospecific shade avoidance plasticity combined with the lack of belowground competition for nutrients. Shade avoidance (in this case, the production of taller pitchers with smaller aperture diameters) was evident in both small and large pitcher plants when heterospecific neighbors were left intact. For such a strategy to be effective, belowground competition for nutrients between pitcher plants and their heterospecific neighbors must be weak or absent. Otherwise, shade avoidance plasticity could place pitcher plants at a disadvantage to non-carnivorous plants when competing for nutrients. Although the lack of competition for nutrients between pitcher plants and their non-carnivorous neighbors could be caused by specialization on different sources of nutrients (prey vs. soil), previous experiments in this system found no evidence of pitcher plants being at a belowground competitive disadvantage when denied prey (Brewer, 2003b; Abbott, 2017). I suggest that belowground competition between pitcher plants and their heterospecific neighbors likely does occur in this system, but the mechanism is more likely related to belowground preemption of space and/or nutrient supplies than to nutrient concentration reduction (Brewer, 2003a; Myers and Harms, 2009; Craine and Dyzinski, 2013) or water reduction (Brewer et al., 2011). Because this was a transplant experiment (and not a seed addition experiment) and because transplants were not

placed directly on clumps of heterospecific plants, belowground preemptive competition could not be quantified in the current study.

The occurrence of heterospecific shade avoidance combined with the lack of conspecific shade avoidance suggests that pitcher plants respond differently to the light environments created by conspecific and heterospecific neighbors. Although the physiological mechanism is not known and has not been investigated in pitcher plants, the shade avoidance response is likely mediated by light quality (e.g., red-far red ratios or blue light) (Casal, 2013). It is possible that conspecific and heterospecific neighbors have different effects on light quality (Crepey and Casal, 2015), which in turn may affect the shade avoidance response. Regardless of the mechanism involved, the ability of plants to distinguish between conspecific and heterospecific neighbors with regard to shade avoidance responses has important implications for species coexistence theory. Recognition of heterospecific and conspecific neighbors in a way that results in greater competition with the latter could enable stable species coexistence without there being differences in mechanisms of resource use or capture (Chesson, 2000) or species-specific soil community-mediated feedbacks (Bever, 2003).

Caveats

This study demonstrates the importance of size-dependent intraspecific competition for light and interspecific shade avoidance in the carnivorous pale pitcher plant in a nutrient-poor system. Large pitcher plants shaded small pitcher plants but competed with one another more strongly for prey. Greater per capita intraspecific competition compared to per capita interspecific competition is a contributing factor to stable species coexistence (Volterra, 1926). In the current field study, however, although I accounted for initial size and cover of neighbors, I did not manipulate neighbor densities as per an additive-series experiment (e.g., Brewer et al., 1998) and thus did not explicitly quantify per capita effects. Furthermore, I only examined competitive responses of *Sarracenia alata* and thus do not know whether the responses observed here apply to any species other than *S. alata*. Hence, it is premature to conclude that the responses observed in the current study are sufficient to promote stable coexistence between pitcher plants and their heterospecific neighbors. The potential for competition for light and shade avoidance to mediate species coexistence in nutrient-poor ecosystems deserves additional study.

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DATA ACCESSIBILITY

Data used in the analyses for this manuscript are provided in a supplemental file Appendix S1 in a table entitled “Data for each

individual pitcher plant including height, diameter, survival, and their conversions for statistical analyses.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Data for each individual pitcher plant including height, diameter, survival, and their conversions for statistical analyses.

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