

INSECT HERBIVORES INCREASE THE SPATIAL AGGREGATION OF A CLONAL PLANT

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Premise of research. In a plant population, the pattern of spatial dispersion from uniform to strongly aggregated can influence the intensity of ecological interactions, including those between plants and their consumers, such as herbivorous insects. Whether insect herbivores also contribute to the generation of dispersion patterns within plant populations, however, is not well understood. We investigated how insect herbivory and plant density interact to influence the degree of aggregation of stems in experimental plots of the clonal perennial herb *Solanum carolinense*, a noxious weed in the southeastern United States and invasive in other parts of the world.

Methodology. We planted *S. carolinense* in 40 experimental plots at five densities and maintained each plot at one of two herbivory levels. Stems in every plot were initially planted in a uniform dispersion pattern. For 3 yr, we quantified the dispersion of clonal recruits in each plot at six spatial scales.

Pivotal results. At larger spatial scales, we found significant interactions between plant density and insect herbivory. In plots with herbivores, spatial aggregation increased as plant density decreased, but this relationship was weak or nonexistent in plots where herbivores were excluded (herbivore-excluded plots exhibited random dispersion of stems across all densities). *Solanum carolinense* in plots exposed to herbivores were on average twice as aggregated as those that had herbivores excluded.

Conclusions. These results suggest that insect herbivores can influence clonal growth or ramet survival in ways that increase population-level aggregation of *S. carolinense*. Our findings also imply that *S. carolinense* populations in its invasive range may have increased spatial spread and decreased intraspecific competition when herbivory is low. We discuss the potential for specific types of feedbacks between insect damage and plant dispersion, highlighting important targets for future research.

Keywords: density effects, dispersion, herbivory, population dynamics, Ripley's *K*, *Solanum carolinense*.

Online enhancements: appendix figures and tables.

Introduction

The pattern of spatial dispersion (i.e., uniform, random, or aggregated) of plants within a population is first generated through seed or propagule dispersal and establishment (e.g., Levine and Murrell 2003), with aggregated patterns often arising from limited dispersal (e.g., Prentice and Werger 1985; Barot et al. 1999). The initial dispersion may then be modified by biotic interactions, such as intraspecific competition (e.g., King and Woodell 1973; Stoll and Bergius 2005), facilitation (e.g., Muller 1953; Haase et al. 1996), or mortality from natural enemies (e.g., Louda 1982; Real and McElhany 1996; Gomez 2005). It is important to understand the factors that influence plant aggregation because the dispersion of individual plants

within a population plays a key role in determining the ecological interactions they experience. In particular, plant dispersion patterns can influence the presence and intensity of intra- or interspecific competition (e.g., Phillips and MacMahon 1981; Stoll and Prati 2001; Eccles et al. 2002), effective pollinator visits (e.g., Rasmussen and Brodsgaard 1992; Kunin 1993), and attack by herbivores (e.g., Root 1973; Kareiva 1985; Turchin 1987).

Despite a large literature studying the causes and consequences of plant spatial dispersion (e.g., Murrell et al. 2001; Stoll and Prati 2001; Law et al. 2009; McIntire and Fajardo 2009), there is neither a consensus nor a clear predictive framework for how plant dispersion will change under various biotic conditions. Herbivory is one factor that has been considered potentially important for modifying plant aggregation, but there is not a consistent message from previous studies about how herbivores actually influence plant dispersions. For example, grazing by mammals has been found to increase spatial heterogeneity of vegetation in some studies (e.g., Belsky 1986; Hart-

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nett et al. 1996; Rietkerk et al. 2000) and to decrease heterogeneity in others (e.g., Adler et al. 2001; Deleglise et al. 2011). In one of the few studies to attempt a predictive framework, Adler et al. (2001) predicted (through literature review and a simulation model) that mammalian grazers may increase or decrease aggregation depending on both the spatial pattern of grazing and the prior spatial dispersion of vegetation. This confounding effect of prior dispersion is a common challenge for studies, which tend to compare differences in plant aggregation between areas that vary in herbivory history without controlling for other differences between sites. The dearth of well-controlled, multiple-year experiments exploring how plant dispersions are generated and modified is one important reason why it has been difficult to reliably connect dispersion patterns with the processes that create them.

Whether insect herbivores can contribute to within-population dispersion patterns has not been thoroughly examined experimentally, despite their potential to alter plant dispersion through density-dependent mortality (e.g., Janzen 1970; Louda 1982) or by altering plant reproduction (Herrera 1991; Buckley et al. 2003; Underwood and Halpern 2012). Prior studies of natural enemies modifying plant dispersion have focused mainly on large, grazing mammals (reviewed in Adler et al. 2001), seed predators (e.g., Louda 1982; Silman et al. 2003), or pathogens (e.g., Real and McElhany 1996). This gap in our knowledge of how insect herbivores may affect plant dispersion patterns is important because the mechanisms by which insects alter plant dispersion may differ from those of mammals. For example, repeated trampling of seedlings and propagules emerging between vegetation patches is an important mechanism influencing plant spatial heterogeneity that is specific to large mammals (e.g., Gomez 2005; Rayburn and Monaco 2011). Moreover, whether grazing herbivores affect plant dispersion depends on the scale of investigation (e.g., Komac et al. 2011), and the scale and selectivity of herbivory are likely different between vertebrate and invertebrate herbivores (e.g., Piqueras 1999) and among insect life stages. For example, defoliating larvae are usually restricted to movement on their natal host or its close neighbors (unlike mammals; e.g., McCauley 1992), whereas adult insects may choose plants on which to feed or oviposit at the patch level (e.g., Kareiva 1985). As the distance between plants increases, limited movement by insects may restrict their options to plants in the immediate surroundings (e.g., Viswanathan et al. 2008), creating areas of intense damage where stem density is low and areas of diluted damage where stem density is high (Otway et al. 2005).

How dispersion patterns are generated may be particularly important in clonal plants because clonal dispersal distances are often short relative to sexual dispersal (Winkler and Fischer 2002), which may lead to greater aggregation. Dispersion patterns of clonal plants are largely a product of vegetative growth, which can be influenced by a variety of factors. Rhizome, stolon, or root length can change with environmental stress (Sakai 1995), density (Meyer and Schmid 1999), and pathogen pressure (D'Hertefeldt and van der Putten 1998). While rhizome length is known to be affected by manual defoliation (Benot et al. 2010) and insect damage (Cain et al. 1991; Wise et al. 2006), which should thus influence the dispersion of stems within populations, no study to our knowledge has experimentally shown differences in the population-level dispersion patterns of clonal plants with different histories of herbivore pressure.

We experimentally test the hypothesis that insect herbivores will affect the degree of spatial aggregation in replicate populations of the clonal plant *Solanum carolinense*. Our experimental plots were originally established for a study of density-dependent demography of *S. carolinense* (Underwood and Halpern 2012); these plots thus allowed us to examine both the effects of herbivores on the dispersion of stems and how plant density may interact with herbivory to affect the dispersion of clonal recruits. We might expect the effects of herbivores on plant dispersion to vary with density because, for example, some insects are attracted to and/or retained in high-density patches (e.g., Janzen 1970; Root 1973; Shea et al. 2000) while others prefer to feed on plants at low densities (e.g., Fagan et al. 2005; Viswanathan et al. 2008; Halpern et al. 2014). Plant density can also decrease plant size and performance (e.g., Weiner 1985; Underwood and Halpern 2012), and smaller plants may experience reduced survival or asexual reproduction (e.g., Piqueras and Klimes 1998; Buckley et al. 2003). In our study, replicate plots were cleared and *S. carolinense* stems were initially planted in a uniform dispersion pattern at one of five density levels. Plots were then consistently exposed to high or low herbivory levels for 4 yr while plants grew and recruited naturally. Because we minimized the effects of prior plant spatial pattern and environmental heterogeneity in our design, differences in aggregation of clonal recruits among treatments provide evidence that insect herbivores and plant density are important drivers of plant spatial dispersion and reveal the scales and conditions under which aggregation of plant stems is more likely.

Material and Methods

Study System

Solanum carolinense L. is an herbaceous clonal perennial native to the southeastern United States and is considered invasive elsewhere (Illick and Fertig 1962; Follak and Strauss 2010). In northern Florida, where this study took place, the growing season for *S. carolinense* typically begins in April and ends in October. *Solanum carolinense* is not a dominant plant in old-field habitats; natural densities of *S. carolinense* vary between 0 and 22 stems/m² (S. Halpern, unpublished data). *Solanum carolinense* has bee-pollinated flowers and plastic self-incompatibility (Travers et al. 2004), but seed germination and seedling establishment are vanishingly rare in established undisturbed populations (S. Halpern, personal observation; M. Wise, personal communication). In contrast, clonal reproduction is extensive. New ramets typically occur less than 1 m from the center of the root system (Miyazuki 2008). Physiological integration of clones is unlikely to persist for long periods of time; in a study conducted in large plastic pools, roughly half of all ramets produced from single genets planted the previous year were already disconnected by midseason excavation (A. S. Hakes, unpublished data). In our experimental populations, *S. carolinense* recruited exclusively via clonal reproduction, so the spatial structure documented here can be attributed solely to this mode of reproduction.

Solanum carolinense hosts a diverse community of insect herbivores in its native range (Wise 2007). Dominant herbivores of *S. carolinense* in northern Florida include *Leptinotarsa juncta* and *Epitrix fuscula* (Coleoptera: Chrysomelidae) as well as *Manduca sexta*. Many of its herbivores also damage economically important crops, such as *Solanum melongena*, making it difficult

to approve biocontrol agents for this and other invasive *Solanum* plants in their introduced ranges (Olckers and Hulley 1995). Insect herbivores cause high damage levels in natural populations, with documented effects on plant performance. In the plots of *S. carolinense* used in this study, an average of 12% of all leaf area is removed by insect herbivores, with some plots receiving up to 37% damage and some individuals up to 75% damage (Underwood and Halpern 2012). Herbivore damage has been shown to negatively affect the growth and reproduction of *S. carolinense* ramets (Wise and Sacchi 1996; Underwood and Halpern 2012). The density of *S. carolinense* can also influence herbivore behavior (Halpern et al. 2014), so we included plant density as a covariate when examining the effect of herbivore damage on plant spatial patterns.

Experimental Design

Forty experimental plots of *S. carolinense* were established in 2007 in cleared sites of natural, old-field plant communities at the North Florida Research and Education Center in Quincy, Florida. Prior to our experiment, *S. carolinense* was a minor component of the plant community at this site (S. Halpern, personal observation). Although planted *S. carolinense* represented the sole species in each newly created plot at the start of the experiment, within a few months of planting grasses (such as *Digitaria ciliaris* and *Paspalum notatum*) and forbs (such as *Sida spinose*, *Commelina communis*, and *Cassia obtusifolia*) reestablished within the plots. A thorough description and analysis of the plant communities within each of our plots in 2011 (the year following this study) is provided in Kim et al. (2015).

Within each plot, *S. carolinense* stems were planted in a uniform distribution at one of five initial densities (0.65, 2.8, 11.1, 22.7, and 30.9 stems/m²). Plot size ranged from 1.6 to 98 m², with larger plots being associated with lower densities for logistical reasons (table A1; tables A1–A7 are available online). Due to constraints on the number of plants available for this very large experiment, the lowest-density plots were larger than the highest-density plots. However, each density was planted in two different-sized plots to partially separate the effect of plot size and density, which are often confounded in studies of plant density (see fig. A1 for a diagram of the plot design; figs. A1–A4 are available online). Within each density class, smaller plots had one row of buffer stems surrounding the 25 central stems, while larger plots had up to four rows of buffer plants (total number of *S. carolinense* per plot ranged from 49 to 144 in the year of planting). Initial planting density was the same across the whole plot (buffer and central area).

Within each plot, we collected data only in the area defined by the 25 central plants in the initial planting. The one to four rows (depending on plot size) of plants surrounding the central area provided a buffer to avoid edge effects on plant dispersion in the central area where data were taken (i.e., to assure that the assumptions of isotropy and stationarity are met). To partially control for potential variation in growth patterns among plant genotypes, the representation of plant genotypes in the central area was kept similar across plots. The 25 central plants included one plant each from 20 genets clonally propagated from root cuttings (source genets were collected from populations in northern Florida and southern Georgia and propagated in a greenhouse for multiple generations) and five plants that were seedlings from various maternal families. The same 20 clonal

genets were used in all plots, but the genetic identity of seedlings varied among plots. The buffer plants were randomly selected from a collection of about 15 additional clonal genotypes. See Underwood and Halpern (2012) for more details about the experimental design.

Half of the plots in each of the five density treatments were assigned to an herbivory-reduced treatment. In these plots, each individual *S. carolinense* stem (including those in the buffer area) was sprayed biweekly during the growing season with a 0.13% carbaryl insecticide, while stems in the control plots were sprayed with an equivalent amount of water. Carbaryl reduced damage 3.5–4.5-fold (Underwood and Halpern 2012) but did not affect pollinator visits or pollen viability in *S. carolinense* (A. Winn, unpublished data). Carbaryl has been shown to not affect plant growth in a variety of herbaceous plants (e.g., Stinchcombe and Rausher 2001; Meyer et al. 2005). By selectively spraying *S. carolinense* stems, herbivores were permitted to feed on other plant species within plots; however, because the dominant herbivores to *S. carolinense* are specialists (Wise 2007; Underwood and Halpern 2012), it is unlikely that spraying increased damage to neighboring plants (Kim et al. 2015).

Each June from 2008 to 2010, we marked every live *S. carolinense* stem in each central area of the plot. Spatial coordinates for each stem were determined using a laser measurement system that measures interplant distances (~3 cm accuracy); we converted these distances to coordinates using triangulation. We focus on the distribution of stems present in June, when annual population surveys occurred. This survey timing corresponded with herbivore activity and when most new ramets had emerged. Although some stems do not persist throughout the growing season (32% of stems marked in June 2010 could not be relocated in September), herbivore effects on spatial patterns did not differ between June and September for the one year (2010) when we collected late-season data (data not shown). The comparison with 2010 late-season data shows that data from June likely provide a conservative estimate of herbivore effects on plant spatial patterns because the index of aggregation was strongly correlated between June and September 2010 ($r = 0.93$) and the effect size for differences in aggregation between herbivore and sprayed plots was greater in September (A. S. Hakes, unpublished data).

Data Analysis

We used Ripley's K function, $K(t)$, to describe the degree of aggregation of *S. carolinense* stems within our plots. Ripley's K is a measure of the average number of points (i.e., stems) located within a set distance (t) from each sampled point, divided by the mean intensity (i.e., total number of points per area) of the pattern. If the distribution of the points is Poisson random, $K(t)$ is expected to equal πt^2 . To attain constant variance and easier interpretation, we linearized $K(t)$ to the function $L(t)$:

$$L(t) = t - \sqrt{K(t)/\pi},$$

which is expected to equal zero for any distance t when dispersion is random (Dale 1999; Fortin and Dale 2005). When the equation is written this way, $L(t)$ values less than zero indicate aggregation, and values greater than zero indicate uniform dispersion (e.g., fig. A2).

We conducted Ripley's K analyses using PASSaGE software (ver. 2; Rosenberg and Anderson 2011). We corrected for edge

effects by weighing each count by the inverse of the proportion of the circle of radius t centered on point i that falls within the study plot, $w_{ij} = 1/p_{ij}$ (Haase 1995; Perry et al. 2006). Dispersion patterns may vary depending on the spatial scale of investigation, so we calculated $L(t)$ separately at incremental 0.105-m radii (t) within each plot. This radius size was chosen because it represents the midpoint between planted stems in the second-highest density plots. Other studies of perennial herbs have shown that clonal dispersal distances occur within this range of scales (e.g., D'Hertefeldt and Jonsdottir 1999). Because our experimental plots varied in size, this radius distance allowed us to calculate $L(t)$ values for at least two spatial scales in the smallest plots (two scales fit within even the smallest plots) and $L(t)$ values at between four and six different scales for the remaining plots (which were large enough to encompass more spatial scales). Consequently, the number of data points included in each analysis varies by spatial scale.

We used repeated-measures analysis of covariance (ANCOVA) to examine the effect of herbivore damage (whether plots were exposed to herbivores or sprayed with an insecticide), plant density (cumulative average of each plot's density from 2008 to the current census year; within-plot density was highly correlated among years; $r > 0.90$), year of census (2008, 2009, and 2010), and their interactions on the index of aggregation at a given scale, $L(t)$. To linearize the relationship between stem density and $L(t)$, which was initially asymptotic (see fig. A3), we first di-

vided individual density values by the inflection point of the curve and then natural log transformed the data. We conducted a separate repeated-measures analysis for each of the six spatial scales at which we calculated $L(t)$ (within a 0.105-, 0.210-, 0.315-, 0.420-, 0.525-, and 0.630-m radius surrounding each plant). Separate analyses for each spatial scale were necessary because the scales are not independent of one another and thus could not be included as a factor in the model. We made Bonferroni corrections to α to account for multiple tests. We used the SAS PROC MIXED procedure to conduct repeated-measures analyses (SAS Institute 2003). We specified a Toeplitz covariance structure and restricted maximum likelihood estimation method to account for our repeated-measures design and change in sample size across spatial scales.

Results

All 40 experimental plots of *Solanum carolinense* were planted in a uniform dispersion when established in 2007. In the following 3 yr, differential mortality and new clonal recruits altered the dispersion of *S. carolinense* stems within each plot to a random or aggregated pattern, as indicated by the index of spatial aggregation (Ripley's $L(t)$ values; see fig. A2 for an example). In general, aggregation increased ($L(t)$ became more negative) as the scale of investigation surrounding each point increased (fig. 1). At smaller spatial scales, plots exposed to her-

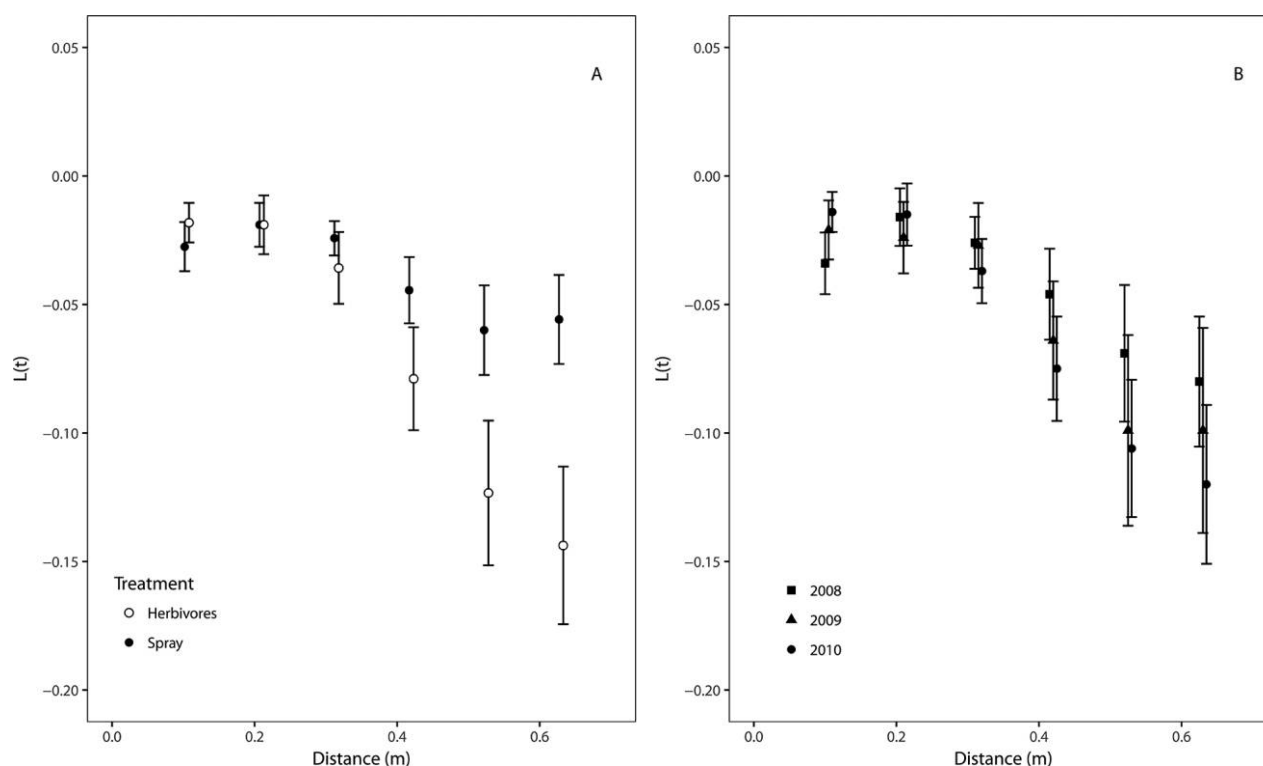


Fig. 1 Average index of aggregation \pm SE of *Solanum carolinense* plots at each of six 0.105-m scales of investigation (i.e., radius at which Ripley's $L(t)$ values were calculated). Negative $L(t)$ values indicate an aggregated distribution. A compares plots with herbivores and those sprayed with an insecticide averaged across years, while B compares plots censused in 2008, 2009, and 2010 averaged across treatments. Means \pm SE are calculated with $N = 60$ (A) and $N = 40$ (B) plots at the two smallest scales and with fewer plots for larger scales (e.g., $N = 24$ [A] and $N = 16$ [B] at the 0.630-m scale) because experimental plots varied in size and smaller plots could not be examined at larger spatial scales.

bivores and those sprayed with insecticide both developed nearly random spatial distributions (fig. 1A). However, at the two largest spatial scales (0.525 and 0.630 m), *S. carolinense* plots that were exposed to herbivores were on average 2.1 and 2.6 times more aggregated than those without herbivores, respectively (fig. 1A).

There was a marginally significant effect of year (our repeated-measures variable) at spatial scales 0.105, 0.315, 0.420, and 0.525 m after adjusting α for multiple ANCOVA tests (tables A2–A6). At these spatial scales, mean spatial aggregation increased slightly in each of the three years of census (fig. 1B).

We found that herbivores influenced the degree of aggregation, but this effect differed with density. After Bonferroni corrections to α , we found a significant interaction between herbivore damage and *S. carolinense* density at the two largest spatial scales (0.630 m: $F_{1,22} = 12.07$, $P = 0.002$; 0.525 m: $F_{1,23} =$

8.96, $P = 0.007$) and a marginally significant interaction at the third largest scale (0.420 m: $F_{1,37} = 5.33$, $P = 0.027$, $\alpha = 0.0125$; tables A5–A7). By examining separate regressions between $L(t)$ and density in herbivore plots and herbivore-free plots, we can visualize this interaction (fig. 2). At each of the three largest distances, there was a significant relationship between $L(t)$ and density (i.e., greater aggregation at lower density) in the presence of herbivores ($r = 0.73$, $P < 0.001$, fig. 2D; $r = 0.72$, $P < 0.001$, fig. 2E; $r = 0.74$, $P < 0.001$, fig. 2F), but this relationship was weaker or nonsignificant in populations without herbivores ($r = 0.53$, $P < 0.001$, fig. 2D; $r = 0.28$, $P = 0.162$, fig. 2E; $r = -0.06$, $P = 0.78$, fig. 2F). At the next smaller distance (0.315 m), there was a significant effect of density on the degree of aggregation ($F_{1,66} = 19.52$, $P < 0.001$), but this was not influenced by herbivores. In general, low-density populations were aggregated, and populations exhibited a more random dis-

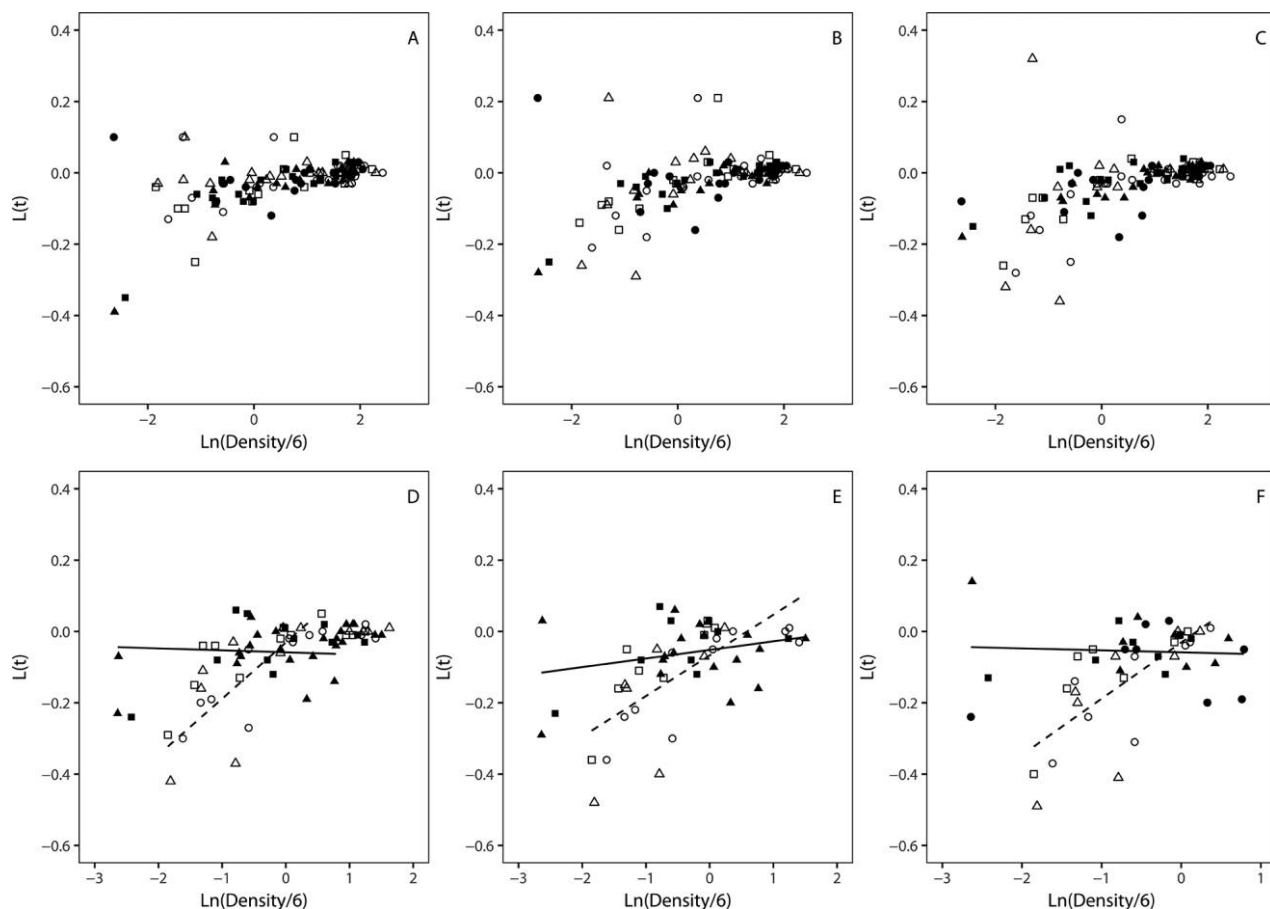


Fig. 2 Relationships between average density and the index of spatial aggregation (Ripley's $L(t)$ value) of *Solanum carolinense* in 40 experimental plots sprayed with an insecticide (black shapes) or exposed to natural herbivory levels (white shapes) and censused in 2008 (squares), 2009 (triangles), and 2010 (circles). Average ramet density was transformed ($\ln(\text{density}/6)$) to linearize its relationship with $L(t)$ (see fig. A2 for untransformed data). Spatial aggregation was determined at six scales of investigation (i.e., radius [t] surrounding each data point): A, 0.105 m; B, 0.210 m; C, 0.315 m; D, 0.420 m; E, 0.525 m; and F, 0.630 m. Negative $L(t)$ values indicate an aggregated distribution. There was a significant interaction between density and herbivore presence (white shapes, dashed lines) or absence (black shapes, solid lines) on the index of spatial aggregation at the three largest scales of investigation (see also fig. A3). Note that for smaller scales (0.105 and 0.210 m), each of the 40 plots has three data points ($N = 120$), but there are fewer data points for larger scales (0.315 m: $N = 116$; 0.420 m: $N = 72$; 0.525 m: $N = 53$; 0.630 m: $N = 48$) because experimental plots varied in size and smaller plots could not be examined at larger spatial scales. Note also that X-axis ranges differ by scale.

persion as average density increased (fig. 2C). There was a significant three-way interaction among herbivores, density, and year at the two smallest scales (0.105 and 0.210 m; tables A2, A3). This pattern is likely driven by the 2010 insecticide-sprayed plots, which were random across all densities at these scales and deviated from the general trend of decreasing aggregation with increasing density (fig. A4).

Discussion

Our study provides experimental evidence that insect herbivores together with plant density can shape the within-population spatial dispersion of stems of a clonally reproducing plant. Over the course of our 3-yr study, low-density plots of *Solanum carolinense* that were exposed to herbivores were on average over twice as aggregated as those where herbivores were excluded; these effects occurred at the two largest spatial scales, 0.525- and 0.630-m radii. At these larger spatial scales, plants became more aggregated as density decreased, but only in the presence of herbivores. At the smallest spatial scales, however, plant stems were not aggregated in either herbivore treatment. Overall, our results suggest that insect herbivores can influence clonal growth or ramet survival in ways that increase the aggregation of stems. These changes in plant dispersion may, in turn, modify the impact of subsequent herbivores through reciprocal effects.

Herbivores may promote aggregation through direct and indirect mechanisms. Herbivore damage can affect plant survival (e.g., Guretzky and Louda 1997), which could translate to direct changes in plant dispersion. In particular, negative density-dependent mortality may increase aggregation when isolated stems receive more damage from herbivores. When insect search distances are shorter than interplant distances, insect larvae may be less likely to leave and/or more likely to return to isolated plants (e.g., Jones 1977). For density-dependent mortality to account for the spatial patterns documented in this study, herbivores would need to be most attracted to low-density plots, and within these plots stems emerging farther away from parents (i.e., more isolated) should be more susceptible to mortality from damage than those emerging close to the parent. Both at this field site and in a separate greenhouse experiment, there is evidence that a key herbivore for *S. carolinense* at our site, the specialist *Leptinotarsa juncta*, prefers to oviposit on *S. carolinense* stems at low rather than high density. During the first year of our study, *L. juncta* egg and clutch number were ~90% reduced in the highest-density plots compared with the lowest-density plots (Halpern et al. 2014). Plants with higher egg and clutch number may face a higher risk of mortality because *L. juncta* larvae usually stay on their natal plant until they are adults (McCauley 1992). Oviposition choice by *L. juncta* is mediated by density-induced changes in plant traits (i.e., plants grown at higher densities are less preferred even when neighbors are removed prior to herbivore introduction; Halpern et al. 2014), although it is unclear what specific plant traits drive oviposition behavior in our system. Together, these results suggest that *L. juncta* prefers *S. carolinense* plants grown at low densities and that this preference may lead to increased aggregation of stems over time, possibly through negative density-dependent mortality.

Herbivores may also indirectly increase the aggregation of stems in low-density plots by altering clonal growth patterns. For example, herbivore damage may reduce overall plant size, leaving fewer resources available for sexual (e.g., Marquis 1992; Wise and Sacchi 1996; Underwood and Halpern 2012) or asexual (e.g., Cain et al. 1991) reproduction. Fewer clonal offspring and shorter clonal connections between parent and offspring should promote greater aggregation. If herbivore effects on plant size or reproduction are the mechanism generating the effects we observed, patterns of aggregation would be most pronounced in low-density plots because at high densities clonal recruits may intermix and obscure clumping of offspring around parents. Several observations from our system are consistent with herbivores indirectly influencing clonal growth through reductions in plant size. *Solanum carolinense* total aboveground stem and branch length, a strong correlate of biomass (Spearman's $\rho = 0.935$, $N = 25$, $P < 0.001$), was 25% lower in plots where herbivores were present, and damage by herbivores can decrease *S. carolinense* asexual reproduction by reducing plant size (Underwood and Halpern 2012). We were not able to determine the genetic identities of clonal recruits, so we cannot infer whether differences in aggregation were the result of shorter clonal dispersal distances. However, in other systems defoliation has been shown to reduce the distance between clones, increasing ramet density and limiting the area occupied (e.g., Cain et al. 1991; Benot et al. 2010). Determining how herbivores and plant density influence clonal growth will be a crucial step in understanding the ecological and evolutionary causes and consequences of clonal growth in plants.

Negative density-dependent mortality and changes in clonal growth are not mutually exclusive mechanisms; both may be acting concurrently in our system to mediate effects of herbivores on plant spatial patterns, and both may be mediated by the size of the plant. At our study's conclusion in 2010, there were 44% fewer stems in plots with herbivores than without herbivores, but it is difficult to determine whether this difference is mainly driven by greater stem mortality or reduced asexual reproduction in herbivore plots. It is reasonable to suspect that when stems are small, herbivore attack is more likely to translate to mortality (e.g., Canham et al. 1999), directly affecting dispersion patterns. When stems are large, herbivore damage may reduce the size and reproduction of stems rather than causing outright mortality. Smaller stems will have fewer resources for clonal growth and produce fewer propagules at shorter distances from the parent (e.g., Cain et al. 1991), indirectly promoting aggregation. Additional experiments are needed to determine how these mechanisms contribute to the effects of herbivores on plant spatial patterns observed in this study.

Changes in plant aggregation like those documented here may have important implications for the rate of spatial spread of invasive clonal plants. Our results suggest that release from natural enemies in the introduced range may allow invasive clonal *Solanum* species to grow larger and produce more clonal propagules that establish at farther distances from the parent plant compared with plants in the native range with their herbivores. Thus, release from herbivores may increase the spatial spread of invasive populations. Moreover, a random dispersion of larger plants when released from herbivores may reduce intraspecific competition.

Our finding that insect herbivores can interact with stem density to influence the spatial dispersion patterns of a clonally reproducing plant invites further research into whether there are positive or negative feedbacks between plant spatial patterns and herbivore damage that may affect the population dynamics and spatial spread of plants (including weedy and invasive plants of applied importance). For example, our study shows that herbivores can increase the aggregation of plant stems. If herbivores avoid plants that are in dense patches (e.g., Fagan et al. 2005; Halpern et al. 2014), then this decreased herbivore preference of aggregated plants may lead to greater survival and reproduction of ramets in patches, which could increase aggregation further. A similar result may be expected if areas of aggregation receive less damage per stem because of dilution effects (e.g., Solomon 1981; Otway et al. 2005). However, the benefit of reduced herbivory with increased aggregation may be counteracted by a greater intensity of intraspecific competition as belowground plant connections dissolve, which could promote a decrease in aggregation if stems farther from intraspecific competitors perform better. Thus, populations could oscillate between clumped and random patterns and high and low intensities of herbivory and intraspecific competition, especially if the

timescale at which density affects herbivory differs from the timescale at which density affects competition. Alternatively, if aggregation increases herbivore attraction and retention, as has been shown in other systems (e.g., Root 1973), and if damage decreases clonal dispersal distances (promoting aggregation), then feedbacks between herbivore damage and plant aggregation may intensify damage and clumping. A scenario where insect damage promotes aggregated stems that are small in size and produce few clonal propagules that emerge close to the parent plant would be ideal for biocontrol.

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