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Coming undone: hemiparasite presence and effects in a prairie grassland diminish over time

Victoria A. Borowicz[1] · **Morgan R. Walder**[1] · **Joseph E. Armstrong**[1]

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Abstract

Root hemiparasites acquire resources from neighboring plants' vascular systems and can limit host growth, depress community productivity, and exert keystone effects. The strength of these effects is posited to be greater where hosts are nutrient-stressed but studies of annual hemiparasites show effects to be short-lived and variable. We conducted a 10-year experiment testing whether fertilizer addition alters the impact of the clonal, perennial hemiparasite *Pedicularis canadensis* on a prairie community and examine whether short-term trends reflect longer-term effects on community dynamics. Hemiparasite removal in 1-m^2 plots increased productivity over the first three field seasons, but later the difference between removal and non-removal plots diminished as *P. canadensis* disappeared from 24 of the 48 non-removal plots. Effects of hemiparasite removal were context independent relative to fertilizer and shade treatments, but fertilizer initially increased, and then subsequently suppressed *P. canadensis* biomass. In non-removal plots, hemiparasite biomass was negatively associated with total community dry mass, which was greater in fertilized plots. Initially, fertilizer promoted graminoids, but after seven more field seasons, non-legume forbs responded most strongly. Measures of biodiversity tended to increase with hemiparasite cover. Demographic data collected at two different times for *P. canadensis* show high survivorship of established plants, high seed input, with seedling survival greater in taller vegetation. Unlike annual hemiparasite populations, well-established *P. canadensis* buffer populations against large demographic swings. At the scale of a few square meters, this keystone species produces significant heterogeneity in a prairie, but its presence at that scale is transient over approximately one decade.

Keywords Clonal growth · Heterogeneity · Keystone effect · *Pedicularis canadensis* · Perennial

Introduction

Grasslands cover more than 30% of the Earth's surface and perform vital ecosystem services, including livestock forage, carbon storage, wildlife habitat, climate regulation, and water and nutrient cycling (White et al. 2000; Carlier et al. 2009). Grasslands are also among the most threatened biomes (Hoekstra et al. 2005). Temporally dynamic, grasslands may persist as shifting mosaics of vegetation due to "pyric herbivory" (Fuhlendorf et al. 2008). This interaction of discrete fire and patchy grazing by ungulates (Fuhlendorf and Engle 2001) produces landscape-level effects that encompass factors operating at finer spatial scales. Local differences in productivity and consumption affect abundances and competition among plant species, alter structural heterogeneity (Veldhuis et al. 2016), and contribute to resource partitioning by consumers (Cromsigt and Olff 2006). Together, these large- and small-scale causes of spatial and temporal heterogeneity in vegetation drive diversity across trophic levels (Fuhlendorf and Engle 2004; Joern and Laws 2013; Hovick et al. 2015; Myers et al. 2015).

Studies of grassland consumers focus on animals, but parasitic plants can be important consumers. Most grassland parasites are generalist root hemiparasites, which photosynthesize but also acquire water, minerals, and in some cases metabolites, from neighbors via vascular links ("haustoria") between roots (Press et al. 1999; Irving and Cameron 2009). Root hemiparasites can profoundly impair host

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✉ Victoria A. Borowicz
vaborow@ilstu.edu

[1] School of Biological Sciences, Illinois State University, Normal, IL 61790-4120, USA

growth, physiology, and reproduction, and exert keystone effects on the structure of microbial (Bardgett et al. 2006), plant (Cameron et al. 2005; Phoenix and Press 2005; Press and Phoenix 2005), and invertebrate (Hartley et al. 2015) communities. When they reach high densities, hemiparasites may be important sources of heterogeneity.

Hemiparasitism frequently reduces productivity (Davies et al. 1997; Marvier 1998; Joshi et al. 2000; Pywell et al. 2004; Bao et al. 2015) and can shift relative biomass or cover. Local change in community composition may be magnified if susceptibility to hemiparasitism affects competitive relations among species (Gibson and Watkinson 1991) or if there is a tradeoff between competitive ability and vulnerability to hemiparasites. Evenness, species richness, or other measures of diversity should increase when hemiparasites more strongly suppress dominant species. These community responses to hemiparasites have been observed in field and greenhouse studies (Bardgett et al. 2006; Decleer et al. 2013; Bao et al. 2015; DiGiovanni et al. 2017; Fibich et al. 2017; Těšitel et al. 2017). However, some cases of no hemiparasite effect (Mudrák and Lepš 2010; Těšitel et al. 2017) or reduced evenness (Joshi et al. 2000) and diversity (Gibson and Watkinson 1992; Fibich et al. 2017) with hemiparasites have also been observed.

Hemiparasites may affect individual hosts more strongly in nutrient-poor soils, where nutrient limitation further reduces host growth, diminishing competition with the hemiparasite for light (Těšitel et al. 2015; Matthies 2017). If so, their impact on competitive relations between host species varying in susceptibility to hemiparasitism should also be stronger when nutrients are limiting. Support for the hypothesis that hemiparasite effects on the community are context dependent is mixed. Pot culture experiments with *Rhinanthus* spp. (Gibson and Watkinson 1991; Matthies and Egli 1999) show stronger effects on competition between host species in nutrient-poor soils but a manipulative field experiment with *R. minor* in a semi-natural meadow (Mudrák and Lepš 2010) indicated effects of nutrients and hemiparasitism are additive. So too did a manipulative field experiment with the clonal, perennial hemiparasite *Pedicularis canadensis* L. on a restored tallgrass prairie (Borowicz and Armstrong 2012). After three field seasons, hemiparasite removal, fertilizer addition, and artificial shade in 1-m^2 plots produced visible effects. Removal of *P. canadensis* increased total biomass in plots by > 50%, but the impact of hemiparasite removal was consistent across levels of soil fertility and light, i.e., it was not context dependent.

While field experiments have demonstrated the impact of annual (Ameloot et al. 2005; Mudrák and Lepš 2010), biennial (Decleer et al. 2013; Bao et al. 2015), and perennial hemiparasites (Borowicz and Armstrong 2012) on community productivity and composition, the temporal nature of these effects are less well studied. Short-term experiments with hemiparasites quantify the direction and magnitude of hemiparasite effects but may fail to capture parasite-host dynamics and the broader community response (Ameloot et al. 2006). For example, in brief experiments, *Rhinanthus* species strongly affected community productivity (reviewed in Ameloot et al. 2005), but over 25 years, *R. angustifolius* (= *R. serotinus* (Schönh.) Oborny) had no persistent impact on aboveground productivity (Ameloot et al. 2006). Stochastic variation within individual *R. angustifolius* populations indicate the absence of persistent equilibrium, and widespread collapse among grassland plots suggested drought to be a particularly important driver of the hemiparasite's population dynamics (Ameloot et al. 2006).

Drought probably strongly affected *R. angustifolius* population dynamics and impact because it is an annual hemiparasite without a persistent seed bank (Ameloot et al. 2006). By contrast, *P. canadensis* is a clonal perennial hemiparasite with thick storage roots and access to drought-tolerant hosts. Resilient, established *P. canadensis* should have persistent local populations even if seedling mortality is high. However, depletion of hosts could cause local extinction or clonal growth away from a location. After reporting results following three field seasons (Borowicz and Armstrong 2012), we continued to manipulate fertilizer and hemiparasite presence for seven additional years. In addition, we gathered demographic data on *P. canadensis*. We had two goals: (1) to determine whether our conclusions, i.e., effects of hemiparasitism and fertilizer on the community are additive, continue to be true over a longer period; and (2) to provide an overview of how the life history of *P. canadensis* may produce population dynamics distinct from more commonly studied *Rhinanthus* species. We show that *P. canadensis* can be a significant source of heterogeneity in a restored prairie as its spatial distribution slowly changes.

Materials and methods

Hemiparasite. Pedicularis canadensis (Orobanchaceae) is a rosette-forming root hemiparasite found in dry to mesic grasslands and open woodlands from the Eastern US to the Great Plains (Gleason and Cronquist 1991; USDA, NRCS 2018). Yellow, bumble bee-pollinated flowers are arranged on spikes that are very visible in the spring, often revealing dense patches or rings of this clonal species. After the first year, a plant may remain a single vegetative crown, produce rhizomes and multiple crowns, or produce a single inflorescence. Seedlings and networks of interconnected crowns produce expanding patches. *Pedicularis canadensis* produces numerous thick storage roots and tiny haustoria on very fine roots. In central Illinois, *P. canadensis* flowers as early as April through May, and remains green until a hard frost. Inspection of roots for the presence of haustoria indicate that *P. canadensis* can parasitize > 100 species in 35 families (Piehl 1963; JE Armstrong, unpub. data).

Field site. The John English Prairie is a 3.6 ha reconstructed tallgrass prairie in Comlara Park, McLean Co., IL, USA (40.621388, − 89.014729). It was established over 45 years ago on former agricultural land, by seeding native grasses, herbaceous legumes, and non-legume dicots (henceforth "forbs"). The prairie is burned routinely in the early spring, including the years in which we harvested biomass. The area has a gentle slope with moderately well drained silt loam soil (USDA websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx).

When we started our experiment in 2006, we detected *Lespedeza cuneata* (Dum. Cours.) G. Don (= *L. juncea* var. *sericea* (Thunb.) Lace & Hauech), an herbaceous but brushy exotic legume, in 29 of the 96 plots. Elsewhere we report what this experiment indicates about *L. cuneata* invasion at this site (Walder et al. 2019). Here we focus on the response of the community to the manipulations of hemiparasite presence and fertilizer addition.

Experiment After an early spring burn in 2006, we established 96, 1-m^2 plots distributed in 12 spatial blocks. Each plot was > 1 m from the nearest neighbor and most were several meters apart. We placed plots so that *P. canadensis* was present in all plots within blocks at similar abundance. Within blocks, plots were randomly assigned one of eight treatments that were combinations of three factors: *P. canadensis* removal (no/yes), fertilizer (not added/added), and shade (full sun/50% shade). Except in 2013, when no eradication took place, we removed *P. canadensis* from assigned plots annually in April-early May using a narrow tool ("dandelion digger") to pry up or sever the roots of *P. canadensis* within plots as well as a 0.5-m buffer zone around the plot. Previous observations indicate that 96% of *P. canadensis* haustoria are within 20 cm of the crown (J. E. Armstrong, unpubl. data). The first year we sham-disturbed control plots and repeated this the second year in control plots of blocks that required much removal. Thereafter most removal plots required little disturbance and no sham-removal was applied. We spread 70 g of 10–10–10 (N–P–K) granular fertilizer over assigned plots in mid-May, and in the first year we repeated this in July. Growth enhancement each year was visible up to the perimeter of plots, suggesting little movement of fertilizer beyond the area of application. We placed 50% shade cloth over assigned plots starting in mid-June when the canopy closes and throughout the summer cut slits in the cloth to allow taller vegetation to grow into full sun. This treatment was discontinued after 5 years, following the 2010 season, and these plots continued to receive fertilizer or removal treatments as originally assigned.

In October of 2006, 2008, and 2015 we harvested all vegetation 2 cm aboveground from a 0.25 m^2 portion of each plot. We selectively harvested *L. cuneata* and *P. canadensis* in 2009, and *L. cuneata* in 2010. Harvests were from the center of the plot for all years except 2015, when the northwest corner was harvested. Except for *L. cuneata*, which was somewhat green, most vegetation had begun to senesce. Vegetation was sorted into graminoids, forbs, *L. cuneata*, remaining legumes, and *P. canadensis*, dried, and weighed.

Demography In April 2008, we tagged 92 isolated *P. canadensis*. We were unable to relocate seven tags the following spring and so eliminated these plants from the data set. The remaining 85 plants were originally in these six size classes: non-reproductive small (single crown without cotyledons, < 4 pairs of leaves, $n = 17$); non-reproductive large (single crown, > 4 pairs of leaves, $n = 13$); non-reproductive multiple (> 1 crown, $n = 13$); reproductive small (single inflorescence, $n = 13$); reproductive medium (2-10 inflorescences, $n = 15$); and reproductive large (> 10 inflorescences, $n = 14$). To evaluate seed production, we selected one well-developed inflorescence on each reproductive plant before seed dispersal began. We measured inflorescence length from bottom-most to top-most opened flower, bagged the inflorescence, and later retrieved it after fruits matured. After fruits had dried, we counted the number of fertile fruits and seeds to determine mean seeds cm^{-1}. Average fecundity for reproductive small individuals was simply the average of total seed production in bagged inflorescences for this size class. Average fecundity for medium and large reproductive individuals was calculated by multiplying average seeds cm^{-1} from bagged inflorescences (across both size classes) times the total length of all inflorescences on an individual. The average fecundity was then determined for medium and large reproductive size classes. To evaluate mortality and development, we returned the following May and recorded the developmental stage of each survivor.

To estimate seedling mortality, we established 19, 20 × 20 cm plots in early June 2008, each with at least two seedlings, identifiable by the presence of persistent cotyledons. Seedlings were marked with color-coded pins and recorded as they appeared within plots over several weeks. 114 seedlings were followed, with half located in nine plots within short, open vegetation, and half in ten plots heavily shaded by *Coreopsis tripteris* L., which grow to 1.5 m. These 19 plots were representative of the area in which the other size classes were evaluated. We counted seedlings weekly through mid-September, and the following year counted survivors in early June and in mid-September.

In June 2013 we set up and photographed two, 20 × 20 cm subplots in 36 of the 48 non-removal plots in our main experiment to determine seedling mortality. These subplots were placed to include as many *P. canadensis* seedlings as possible. The other 12 non-removal plots were excluded because we were unable to locate > 1 seedling in these plots. We re-photographed the plots and made a final count the following May. In July 2014, we determined cover of *L.*

cuneata in the plots using a 1-m frame strung with wire at 10-cm intervals. Using the interior 7 × 7 intersections, we recorded the number of intersections out of 49 that were above *L. cuneata*.

In spring and summer 2014, we selected 177 *P. canadensis* representing the seven size classes. As with the 2008–2009 observations, these plants were not within experimental plots but this time we sampled a broader area of the prairie. We photographed most of the plants, enabling us to identify confidently the plants associated with 156 tags relocated in 2015. We counted the number of inflorescences on each reproductive plant and multiplied this by the estimated number of seeds per inflorescence from the size categories in 2008.

Statistical analysis—Experiment We used SAS/STAT ® software, version 9.4 (SAS Institute Inc) to perform all analyses. The effect of fertilizer on the hemiparasite in non-removal plots over time was tested with two-way mixed effects analysis of variance (ANOVA), with the difference in log-transformed dry shoot mass of *P. canadensis* between 2008 and 2015 as the response variable, and fertilizer and block as main effects. In this and all other analyses, spatial block was a random effect. Two of the original 48 non-removal plots were omitted because *P. canadensis* was no longer in them in 2008. Between 2008 and 2015, *P. canadensis* disappeared from a number of plots. We used a generalized linear model to test the effect of fertilizer on the probability of extinction, treating extinction as a binary variable.

We conducted a doubly multivariate repeated measures analysis of variance (PROC GLM, SAS 9.4) to determine how the three functional groups of plant species responded to the fertilizer and hemiparasite removal treatments across years. Although present in 2008, *P. canadensis* had disappeared from many non-removal plots by 2015, and, therefore, would not have been a continuously applied treatment. We re-assigned these plots to a third category, resulting in three *P. canadensis* treatments: (1) continuously present, (2) continuously absent due to removal, and (3) extinct from the plot between 2008 and 2015. We used this assignment for both harvest years (2008 and 2015). Log-transformed total dry shoot mass of graminoids, forbs, and all legumes (including *L. cuneata*) from each of the 94, 1-m^2 plots were the multiple response variables. Year of harvest (2008 and 2015) was the within-subjects repeated factor. Block, fertilizer, and removal were the between-subjects factors. Block was included to account for spatial variability, but non-significant interactions involving block were omitted from the final model.

Shade was a factor in the original 2008 analysis but was discontinued after 2010. To explore the possibility that reduction in light during a portion of the experiment affected the outcome, we first included shade as an independent variable, but found it was not significant. We then conducted the statistical analysis omitting shade as a factor but retaining all plots, using their assignments to the fertilizer and removal treatments. Results were qualitatively the same for both analyses, and so we report results from the latter analysis, excluding shade as a factor. Because we already reported the effects of treatments on biomass harvested in 2008 (Borowicz and Armstrong 2012), we next conducted MANOVA on just the 2015 harvest data to understand better the more recent responses of functional groups to treatments. We followed this with ANCOVA of the total dry mass in non-removal plots with dry mass of *P. canadensis* as the covariate and fertilizer and block as explanatory variables to determine whether there is a significant association between growth of the hemiparasite and standing biomass of the community.

Community indices are used sometimes to assess quality of a prairie. From our vegetation survey in 2015, we calculated Shannon's H, evenness, and floristic quality index (FQI) for each of the 48 plots originally assigned the non-removal treatment in 2006. Shannon's H accounts for both abundance and evenness of species in a community, with evenness being a measure of the relative abundance of species, measured as percent cover. FQI, which reflects the "floristic integrity" of a site, is a weighted index of species richness (Taft et al. 1997). This value takes into consideration the association of a species with disturbance and assigns high values to species restricted to high-quality natural areas and low values to species adapted to severe disturbance. We used values assigned by Taft et al. (1997) for vegetation in Illinois. Fertilizer treatment and spatial block were main effects, the percent cover of *P. canadensis* was the covariate, and the community indices were response variables in MANCOVA (PROC GLM, SAS 9.4). The square of evenness was used to meet assumptions of the model.

Demography For 2008–2009, we summed seedlings by vegetation type (short vs. tall) and tested for a difference in seedling survival between 2008 and 2009 using a Kruskal–Wallis test (McDonald 2014). For 2013–2014, we summed the seedlings in subplots within plots, and tested the effect of fertilizer treatment on the proportion of seedlings in 2013 that survived to 2014 with PROC GLIMMIX using a binomial error distribution and logit link function. This analysis included spatial block as a main effect and cover of *L. cuneata* in 2014 as a covariate.

For demographic data from 2008 to 2009, and separately 2014–2015, we calculated survival and transition to other stages of development and expressed these in stage-structured demographic matrix models (Caswell 2001). Limitations in the numbers of plants and transitions observed, and absence of estimates of germination rates preclude formal demographic analysis of population growth rate, λ, and elasticities. However, these data provide the first population-level estimates for development and mortality of a perennial hemiparasite in a prairie ecosystem.

Results

Biomass Although *P. canadensis* biomass increased over the first 3 years of fertilizer addition (Borowicz and Armstrong 2012), that trend was reversed thereafter. Between 2008 and 2015, *P. canadensis* biomass declined overall, but especially in fertilized plots ($F_{1,22}=10.89$, $P=0.0033$, Fig. 1), and this effect varied among blocks ($F_{11,22}=10.89$, $P=0.0219$). Part of this reduction in the hemiparasite's mass was due to extinction of *P. canadensis* in 24 of the 48 non-removal plots. However, probability of extinction of the hemiparasite did not differ significantly between fertilizer treatments ($F_{1,33}=2.26$, $P=0.1419$).

Overall, dry masses within plots (exclusive of *P. canadensis*) varied among blocks ($F_{11,77}=3.21$, $P=0.0012$) and increased where *P. canadensis* was removed ($F_{2,77}=6.76$, $P=0.0020$) or fertilizer was added ($F_{1,77}=7.15$, $P=0.0091$; Fig. 2). Growth of the three functional groups in plots from which *Pedicularis canadensis* had been removed differed significantly from growth in plots where the hemiparasite was still present or had gone extinct ($F_{3,75}=7.42$, $P=0.0002$). Responses of the plant groups to these two categories of non-removal did not differ ($F_{3,75}=0.12$, $P=0.9458$), indicating a persistent effect following extinction. The lack of a significant removal x fertilizer interaction ($F_{2,77}=0.15$, $P=0.8600$) indicates that the impact of *P. canadensis* removal was consistent across levels of fertilizer. Functional groups differed over time with forbs and legumes exhibiting large gains in mass ($F_{3,75}=5379.68$, $P=0.0001$; Fig. 2). Graminoids and forbs increased with *P. canadensis* removal or fertilizer addition but fertilizer depressed growth of legumes (Fig. 2). By 2015, *P. canadensis* treatment no longer affected growth of the three plant groups significantly ($F_{6,156}=1.24$, $P=0.2873$; Fig. 2c). A significant fertilizer effect ($F_{3,77}=5.90$, $P=0.0011$) was primarily due to increased growth of forbs ($P=0.0002$; Fig. 2d). The standardized canonical coefficients indicated the opposite trend for legumes (Graminoids = 0.2986, Forbs = 1.884, Legumes = − 0.4711), but fertilizer did not significantly affect dry mass of legumes ($P=0.1200$) or graminoids ($P=0.9347$). Although the *P. canadensis* removal did not significantly affect growth of the functional groups in 2015, ANCOVA of masses from non-removal plots in 2015 shows *P. canadensis* mass was negatively associated with total dry mass ($P=0.0010$, slope = − 26.61, se = 6.97). Fertilizer significantly increased total mass ($F_{1,21}=17.26$, $P=0.0004$).

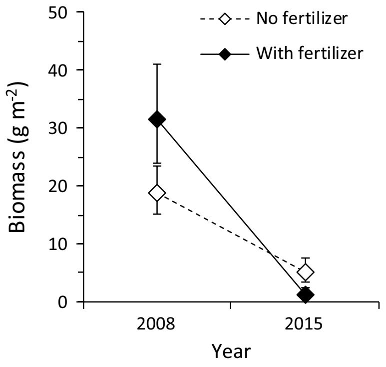

Fig. 1 Mean ± SE dry mass of *P. canadensis* from non-removal plots that were never fertilized or fertilized annually. 2008 was 3 years into the study and 2015 was after an additional 7 years. Means (upper, lower standard errors) were back-transformed. Statistical analysis was performed on the difference between years in log-transformed values

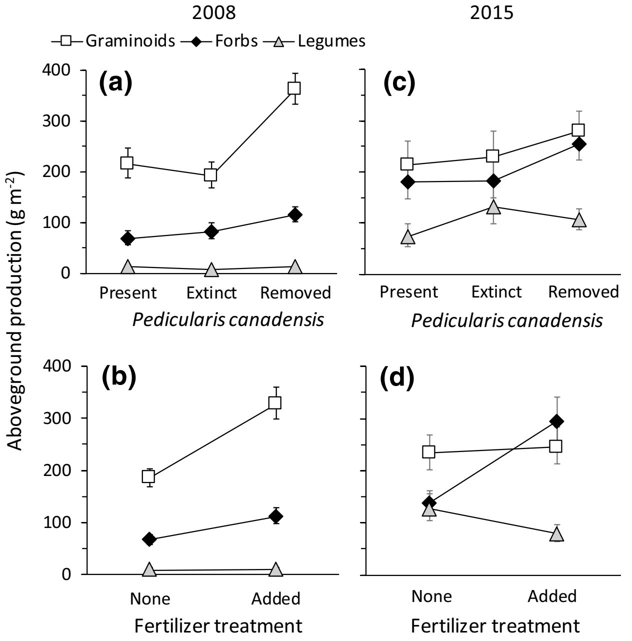

Fig. 2 Effects of **a** *Pedicularis canadensis* removal and **b** fertilizer addition on total aboveground dry mass after three summers in 2008, and **c**, **d** after an additional seven summers of treatments in 2015

Cover. Measures of diversity and community composition calculated for the non-removal plots varied spatially but were not affected by fertilizer treatment (Table 1). Increasing *P. canadensis* cover significantly affected the pattern of community response, with Shannon's H and squared evenness responding in opposite directions (lower H associated with greater evenness; see standardized canonical coefficients, Table 1). In individual linear models, biodiversity, as measured by Shannon's H ($y=0.007x+0.957$, se of the slope = 0.003, $P=0.0361$) and FQI ($y=0.032x+3.981$, se of the slope = 0.015, $P=0.0470$) increased with *P. canadensis* cover, whereas squared evenness was not affected ($y=-0.001x+0.547$, se of the slope = 0.002, $P=0.4548$).

Table 1 MANOVA results for the effects of *P. canadensis* abundance measured as % cover (Pc cover), fertilizer application, and spatial block on Shannon's Index of Diversity (H), Floristic Quality Index (FQI), and Evenness

Source	*df*	*F*	*P*	Standardized canonical coefficients		
				H	FQI	Evenness
Pc cover	3, 21	4.10	0.0195	− 2.0362	0.0912	1.1227
Block	33, 69	2.32	0.0016	0.3191	1.6959	0.0572
Fertilizer	3, 21	0.62	0.6095	0.8947	1.2263	− 0.6907
Fertilizer x block	33, 69	1.18	0.2797	1.5821	0.5817	− 0.8177

The square of evenness was analyzed to meet the assumptions of the model

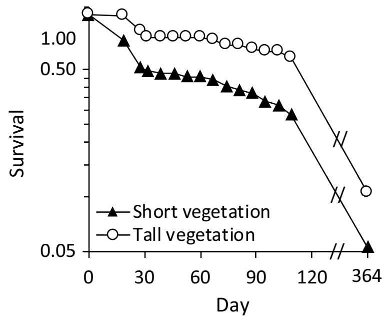

Fig. 3 Log-transformed survivorship curve for *Pedicularis canadensis* seedlings in short vs. tall vegetation between June 2008 and June 2009. 57 seedlings were in each group

Demography 2008–2009 Seedling survival in the low vegetation dropped more rapidly than did survival in taller vegetation and half as many plants were alive after one winter in these more exposed areas ($H = 12.08$, 1 *df*, $P = 0.0005$; Fig. 3). Out of the 57 seedlings in each vegetation type, three survived the winter in the low vegetation and six survived in the tall vegetation for an overall survival rate of 7.9%. Compared to seedlings, survival of older plants was quite high. Except for transitions to seedlings and to small non-reproductive plants, almost every possible transition between size classes occurred (Table 2; see Electronic Supplemental Material ESM1 for loop diagram showing observed transitions between 2008 and 2009). All but the seedling stage were observed to transition to the multi-crown (non-reproductive) class, and plants in this stage either remained vegetative or became medium or large reproductive plants. In 2009, medium reproductive plants averaged 5.8 (sd = 2.6) inflorescences and large reproductive plants averaged 20.6 (sd = 8.9) inflorescences (maximum = 43).

Demography 2013–2015 In May 2014, 13.1% of the seedlings from the previous June were still alive. Seedling survival was not significantly associated with *L. cuneata* cover measured in 2014 ($F_{1,23} = 1.71$, $P = 0.2041$, slope = − 0.11, se = 0.08), fertilizer treatment ($F_{1,23} = 1.53$, $P = 0.2288$), or location in the field ($F_{8,23} = 1.10$, $P = 0.4000$). Non-reproductive single-crown plants and small reproductive plants remained in the same size category (except seedlings), transitioned to one or two size-categories larger, or remained non-reproductive but invested in multiple crowns (Table 3; see Electronic Supplemental Material ESM1 for loop diagram showing observed transitions between 2013 and 2014). Multi-crown non-reproductive remained in that stage or became reproductive, although one regressed to a vegetative single crown. Reproductive medium plants averaged 4.9 (sd = 2.4) inflorescences and large reproductive plants

Table 2 Transition matrix for 2008–2009 population of *Pedicularis canadensis*

	Vegetative					Reproductive		
	Seeds	Seedling (SDL)	Single small (VSS)	Single large (VSL)	Multi-crown (VMC)	Small (RS)	Medium (RM)	Large (RL)
Seeds						128	1016	2783
SDL	ne							
VSS		0.0526	0.3529					
VSL			0.0588				0.0625	
VMC			0.1765	0.1538	0.1538	0.1538	0.2500	0.1429
RS			0.1176	0.0769	0	0	0.0625	0
RM			0.2941	0.4615	0.3850	0.5384	0.3750	0.4286
RL				0.1538	0.0770	0	0.1875	0.3571

Numbers are probabilities for transitioning from a category in 2008 (columns) to a category in 2009 (rows). Seeds refers to the average number of seeds produced annually by a small, medium, or large plant

ne No estimate available

Table 3 Transition matrix for 2014–2015 population of *Pedicularis canadensis*

	Vegetative					Reproductive		
	Seeds	Seedling (SDL)	Single small (VSS)	Single large (VSL)	Multi-crown (VMC)	Small (RS)	Medium (RM)	Large (RL)
Seeds						181	994	3795
SDL	ne							
VSS		0.2105	0.1395					
VSL		0.1053	0.3488	0.2778	0.0400			
VMC		0.0526	0.1860	0.4444	0.3600	0.1765	0.1111	0
RS			0.0233	0.1389	0.0800	0.1765	0	0
RM				0.0278	0.2400	0.4705	0.6667	0
RL					0.1600	0.1765	0.2222	1.0000

Numbers are probabilities for transitioning from a category in 2014 (columns) to a category in 2015 (rows). Seeds refers to the average number of seeds produced annually by a small, medium, or large plant

ne No estimate was made

averaged 28.1 (sd = 22.8) inflorescences (maximum of 76 inflorescences).

Discussion

After ten field seasons of treatments, hemiparasite removal and supplemental nutrients increased biomass of plots, but these two factors did not interact, indicating that *P. canadensis*'s effect was not context dependent for soil nutrients. This is consistent with our original conclusion after three field seasons (Borowicz and Armstrong 2012) and with the results of a factorial experiment with fertilizer and another hemiparasite, *R. minor* (Mudrák and Lepš 2010). The impact of *P. canadensis* on the aboveground biomass of the community was greatest in 2008 when our measures of the average mass of *P. canadensis* in non-removal plots peaked, providing the starkest illustration of the hemiparasite's impact on community productivity. Diminishing impact from *P. canadensis* over the next 7 years was associated with decline in *P. canadensis* mass, indicating that at the scale of one m^2, this hemiparasite can have strong effects that wax and wane as the hemiparasite's dynamics produce increases and declines. The dynamic nature of *P. canadensis* abundance was especially striking in fertilized plots, where initially the hemiparasite mass increased along with the community biomass, but then declined below that observed in unfertilized plots (Fig. 1). In contrast to our results, fertilizer application did not initially increase mass in *Pedicularis kansuensis* Maxim., an annual/biennial hemiparasite of sub-arctic grasslands in China (Liu et al. 2017). In that study, addition of low [N], high [N], or P fertilizer to 4 × 3 m plots depressed *P. kansuensis* biomass by the second season of treatment, whereas the control plots showed no evident trend. In both these studies, relatively constant average presence across control plots, but also decline or extinction from individual plots, suggests *Pedicularis* spp. do not reach a stable equilibrium at the scale of one or a few m^2, but can be a persistent member of a grassland community over a larger spatial scale.

Relationships between *P. canadensis* and community metrics in this study were weak but significantly positive for Shannon H and FQI. Density of this hemiparasite was significantly and positively associated with species richness in an observational study elsewhere on this site (Hedberg et al. 2005), and positively associated with floristic quality on several prairies elsewhere in Illinois (DiGiovanni et al. 2017). Perennial plants dominate tallgrass prairies, and we assume hemiparasites initially alter relative abundances by differentially reducing growth of susceptible species rather than affecting recruitment. If *P. canadensis* impairs growth of aggressive dominants, opportunities for rarer species to establish may increase. However, in the non-removal plots, *P. canadensis* tended towards a positive association with abundance of *L. cuneata*, a non-native legume (Walder et al. 2019), suggesting that hemiparasites could raise diversity by making sites more vulnerable to invasion by exotic species. This should be of special concern to managers wishing to use hemiparasites to reduce dominant species (Pywell et al. 2004; Bullock and Pywell 2005; DiGiovanni et al. 2017).

In short-term experiments with annuals and biennials, community biomass generally increases when hemiparasites are removed, but change in community composition has been less consistently observed (review by Ameloot et al. 2005; Mudrák and Lepš 2010; Demey et al. 2015). We found that as *P. canadensis* declined and disappeared, its influence waned, but a strong negative relationship between current mass of *P. canadensis* and dry mass of all other vegetation was evident in the non-removal plots. Because vegetation increased in removal plots, we can feel confident that the abundance of the hemiparasite was a cause of the negative relationship rather than a response to a shading effect of denser vegetation.

Hemiparasite seedlings may be especially vulnerable to shading because they require energy to locate and parasitize hosts (Těšitel et al. 2011). Species of *Rhinanthus* do not appear to establish in grasslands in which aboveground biomass production exceeds a threshold of about 5 T/ha (Ameloot et al. 2006; Mudrák and Lepš 2010; Hejcman et al. 2011). Because ours was a removal experiment, we did not follow recruitment into experimental plots, but even in our fertilized plots, dry mass of vegetation did not reach this threshold. In greenhouse experiments, shading increased mortality of second-year *P. canadensis* plants (Mardoian and Borowicz 2016) and reduced root growth of first-year plants paired with *Andropogon gerardii* Vitman (Borowicz and Armstrong 2012), raising the possibility that the presence of this hemiparasite would be more limited in more productive grasslands. Nonetheless, we observed that seedling survival from 2008 to 2009 dropped significantly sooner in open, shorter vegetation than in the shade of tall plants, and *L. cuneata* cover did not affect seedling survival in 2013–2014. On the prairie, direct sun dries the top layer of the soil rapidly, stressing young plants, whereas established *P. canadensis* have access to roots of neighbors with extensive, deep root systems. Well before surrounding vegetation shades them, established *P. canadensis* grow rapidly and flower, and during this early part of the season, potentially access carbon translocated in the xylem stream of perennial herbaceous hosts. Thus, older plants are resilient against drought and shade.

In 2006, we placed plots where *P. canadensis* was densest, but by 2015 the hemiparasite had disappeared from half of these plots. *Pedicularis canadensis* continues to be very dense in some areas of the site. Based on our observation of individual plants, we suspect that the hemiparasite moved out of some plots via underground, rhizomatous growth. Ten years before the onset of this experiment, the John English Prairie included two very large rings of *P. canadensis* and several smaller patches spreading outward (Armstrong et al. 1996), and arcs of yellow inflorescences are still visible during flowering in the spring. Elsewhere, we have observed isolated but discrete patches develop a ring structure that is dense at the leading edge and progressively less organized towards the center. These observations, coupled with *P. canadensis* effects on growth of hosts and the community, indicate that this hemiparasite is a significant source of spatial heterogeneity. Clonal hemiparasites such as *P. canadensis* can contribute on a local scale to the shifting mosaic on tallgrass prairies produced at the landscape level by pyric herbivory (Fuhlendorf and Engle 2004).

As a clonal perennial, *P. canadensis* has a growth pattern and population dynamics very different from short-lived hemiparasites. For annual hemiparasites with no persistent seed bank, years with poor seed set or unsuccessful germination can produce rapid decline in population size and local extinction (Svensson and Carlsson 2004; Ameloot et al. 2006). We suspect that *P. canadensis* also has a short-lived seed bank. Poor seed set occurs in years when cold, wet weather in the spring deters bumble bee pollination, and these years are followed by springs with strikingly few *P. canadensis* seedlings (Borowicz and Armstrong, pers. obs.). However, compared to demographic variation of short-lived species, low mortality and clonal growth of well-established *P. canadensis* seem to buffer the population against annual variation in density. Another perennial hemiparasite, *Pedicularis furbishiae* S. Watson is not clonal, lacks a seed bank, and is restricted to the banks of the St. John River in Maine and New Brunswick, Canada. For *P. furbishiae*, stochastic disturbance from ice scouring and bank erosion causes frequent patch extinction, and such volatile metapopulation dynamics endanger persistence of this species (Menges 1990).

Study of clonal plant demography is challenging (de Witte and Stöcklin 2010). Our depiction of population dynamics represents an initial description showing areas most in need of additional data. We do not have a good estimate of germination of these very small seeds, but anecdotal observation argues against long dormancy. Seed input can vary dramatically between years because of weather and bumble bee activity. However, high survivorship of older stages moderates population dynamics and lifetime fecundity is potentially very high. A combination of empirical research and modeling are required to explore more fully the responses of hemiparasite populations to the environment and to predict their impact on the community.

Conclusion

Long-term ecological studies help quantify the processes underlying community change and the scale over which these processes act, both of which are important for natural resource management (Lindenmayer et al. 2012). Long-term studies of root hemiparasite population dynamics are rare, and our study of a clonal perennial shows important differences in comparison to annual *Rhinanthus* spp. (Ameloot et al. 2006). High survival of older plants buffers the population against annual variation in environmental factors such as precipitation, and clonal growth results in increasing and then declining densities at the local scale of 1 m^2. Consequently, *P. canadensis* can significantly reduce productivity locally and affect community composition, but this effect changes over time and space as *P. canadensis* depresses growth of the most susceptible or least tolerant hosts and opens opportunities for less susceptible species. In this way, hemiparasites can promote or suppress spatial heterogeneity, depending on the competitive relations and differences among species in susceptibility to parasitism. This includes potentially opening the community to invasion by exotic species.

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Author contribution statement VAB and JEA designed and conducted the experiment. All authors gathered new data. VAB analyzed the data and wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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