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THE EFFECTS OF THE PARASITIC PLANT *CUSCUTA GRONOVII* ON THE
MATING SYSTEM OF ITS HOST PLANT, *IMPATIENS CAPENSIS*

By

Katherine Margaret Lander

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ABSTRACT

THE EFFECTS OF THE PARASITIC PLANT *CUSCUTA GRONOVII* ON THE MATING SYSTEM OF ITS HOST PLANT, *IMPATIENS CAPENSIS*

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Parasitic plants attach to other plants and obtain water, nutrients, and/or carbon from their vascular systems, causing a variety of effects at the individual, population, and community levels. These effects have been hypothesized to be similar to those of insect herbivores, but few studies have tested this idea. In this study, I investigated the effects of the parasitic plant *Cuscuta gronovii* on the growth, fitness, and mating system of one of its host plants, *Impatiens capensis*. I also attempted to compare the effects of the parasite to the effects of insect herbivores, but the herbivory levels in the experiment were too low to make a valid comparison. Plants infested with *C. gronovii* were 21% shorter than plants that were not infested, produced 27% fewer seeds, and produced a greater proportion of self-pollinated seeds (0.95 compared to 0.84). Instead of comparing their effects to those of all insect herbivores, parasitic plants might more appropriately be compared to other organisms that also act as physiological sinks, such as gall-forming insects and sap-sucking insects.

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INTRODUCTION

Parasitism is ubiquitous in plant communities (Dobson and Hudson 1986).

Though they are often overlooked in ecological theory and practice, parasites have been shown to have large effects on communities and ecosystems by influencing the course of succession (Van der Putten et al. 1993), altering host life history traits (Clay 1986), and altering species composition in communities (West and Marks 1987). While the effects of some groups of parasites on plant communities have been well-studied, (e.g., nematodes [De Rooij-Van der Goes 1995], viruses [Malmstrom et al. 2005], and fungi [Holah and Alexander 1999]), the ecological effects of parasitic plants on other plants in the community have not received as much attention (Marvier 1998).

Parasitic plants have been hypothesized to have similar effects on host plants and communities as those of herbivorous insects (Atsatt 1977, Pennings and Callaway 2002). Like insect herbivores, parasitic plants have host preferences, alter host physiology and morphology, and can reduce host fitness by reducing survival or reproductive output. In a recent review, Pennings and Callaway (2002) compared the effects of parasitic plants with herbivores. They reported that there are similarities in the effects of parasitic plants and insect herbivores on host communities, including evidence that herbivores and parasitic plants both can alter the competitive hierarchy of a plant community. There are also important differences between parasitic plants and insect herbivores that may impact how they affect plant communities. One important difference is that many insect herbivores are mobile and parasitic plants are not. Mobile insects are able to move about the landscape to find high quality food, while parasitic plants are more restricted in space, with many species being confined to the same host plant throughout their entire life cycle

(i.e., mistletoes). While insect herbivores are more common across the landscape, parasitic plants can have significant effects on plant population- and community-level processes where they are found. Many questions about the similarities and differences between insect herbivores and parasitic plants still remain unanswered and unstudied.

For instance, a plant's mating system, the proportion of self-fertilized to outcrossed seeds produced, is one of its important life history characteristics. A shift in the mating system of a population of plants can affect the fitness of individuals (Charlesworth and Charlesworth 1987) and the genetic variation within the population (Hamrick and Godt 1990). A plant can be highly outcrossing, highly selfing, or have a mixed mating system that produces both selfed and outcrossed seeds. In a survey of 345 plant species, Goodwillie et al. (2005) reported that 42% have a mixed mating system, which they defined as having an outcrossing rate between 0.2 and 0.8. Plants achieve a mixed mating system by self-pollinating ovules by anthers in the same flower, by receiving pollen that was distributed by a pollinator from another flower on the same plant (geitonogamy), or by producing heteromorphic flowers (some that are cross-pollinated and some that are self-pollinated).

While several studies have reported the effects insect herbivores can have on a plant's mating system (Elle and Hare 2002, Steets and Ashman 2004, Cole and Ashman 2005, Ivey and Carr 2005), there are no reported studies of the effects of a parasitic plant on its host's mating system. Herbivory has been shown to impact a plant's mating system in several ways. Herbivores can directly impact plants by reducing their size or the resources available for reproduction (Koptur et al. 1996), or indirectly affect a plant's

fitness by causing it to produce smaller flowers that are less attractive to pollinators (Strauss et al. 1996), resulting in a greater proportion of flowers being self-pollinated.

Study system

The *Impatiens capensis*-*Cuscuta gronovii* host-parasite system was used in this study to compare the impacts of parasitic plants and insect herbivores on the growth, fitness, and mating system of the host. *Impatiens capensis* is a native annual that is commonly found in mesic habitats at the edges of wetlands, alongside rivers and lakes, in moist woods, and in roadside ditches throughout the Midwestern and Eastern United States. It produces both chasmogamous (CH) flowers that are open and cross-pollinated, and cleistogamous (CL) flowers that are closed and self-pollinated. The dimorphic flowers can be distinguished from each other as buds, flowers, fruits, and pedicels. Taller plants produce significantly fewer CL flowers than shorter plants, but biomass has been reported to have no effect on the proportion of CL flowers produced (Lu 2002). Seeds from CH flowers require 1.5 to 2 times the investment of energy and resources as CL seeds (Waller 1979), but seedlings germinated from CH seeds are competitively superior to seedlings from CL seeds (Waller 1984).

Environmental conditions, such as light availability and soil moisture, can alter the number and proportion of CH and CL flowers produced by an individual plant (Schemske 1978, Waller 1980). Biotic factors can influence the mating system of *I. capensis* as well. Steets and Ashman (2004) and Steets (2005) showed that herbivory affects the mating system of *I. capensis* by reducing the resources available for reproduction, shifting the proportion of CL to CH flowers in favor of the less expensive CL flowers. CL flowers are also advantageous in an uncertain environment because it

generally takes less time for a CL flower to complete development from a bud to a fruit than it takes a CH flower (Schemske 1979).

A biotic factor that affects *I. capensis* that has not yet been studied in the context of its mating system is the parasitic plant *Cuscuta gronovii*, which is commonly a parasite of *I. capensis*. While *C. gronovii* is not a specialist on *I. capensis*, Schoolmaster (2005) reported that in some habitats *C. gronovii* must infect *I. capensis* as a seedling before it can infect any other host species. In Michigan, *C. gronovii* germinates from seeds in the soil in early June, but withers and dies within a few days if it does not make contact with a suitable host plant. Once its haustoria penetrate a host plant, the connection to the soil withers, and *C. gronovii* grows entirely aboveground for the rest of its life cycle, sinking coils of haustoria into the stem and petioles of the host plant. The more coils the parasite produces around a plant, the more severely the fitness of the plant is affected. In one study in which individuals of the host plant *Hormathophylla spinosa*, a woody shrub, with 10%, 30%, 60% and 100% of the canopy covered with *Cuscuta epithymum* were surveyed, host plants with more than 60% of their surface covered with produced significantly fewer seeds than host plants with less than 30% covered (Gómez 1994).

The *Impatiens capensis*-*Cuscuta gronovii* host-parasite system is an ideal system to investigate parasitic plant-host plant interactions and compare the effects of a parasite with the effects of insect herbivores for several reasons. First, *I. capensis* and *C. gronovii* commonly co-occur in wetlands and disturbed mesic habitats in southwest Michigan. Second, it is simple to distinguish self-pollinated fruits from cross-pollinated fruits in *I. capensis*. Third, *I. capensis* is fed upon by a variety of herbivorous insects. Fourth, it is easy to quantify parasitism by *C. gronovii* because it is a shoot parasite and grows

entirely aboveground. In addition, because *I. capensis* is an annual and does not have a seed bank in the soil (Leck 1979), it is possible to determine the fitness effects of herbivory and parasitism in a single growing season

I used this system to address two questions: 1. Does the parasitic plant *C. gronovii* alter the growth, fitness, and mating system of its host *I. capensis*? and 2. How do the effects of the parasite compare to the effects of insect herbivores? I hypothesized that parasitic plants would have more severe effects on the host plants in terms of growth, fitness, and mating system than herbivores because parasitic plants are constantly associated with a host throughout the season and as a consequence may reduce resources to the host more than herbivores do.

METHODS

I conducted two experiments to compare the effects of insect herbivores and parasitic plants on the mating system of *I. capensis*: a field experiment to examine the effects of herbivory and parasitism in a natural population, and a more controlled pot experiment using transplanted seedlings grown within a fence to exclude deer, which often feed on and trample *I. capensis* plants (personal observation). Both experiments were designed to test the direct effects of herbivory and parasitism independently, but not their interaction, and included three treatments: herbivory, parasitism, and control. The plants assigned to the herbivory treatment were subjected to natural levels of insect herbivory and no parasite was introduced. The plants assigned to the parasitism treatment were sprayed with insecticide and one parasite individual was introduced per plot or group of plants. The plants assigned to the control treatment were sprayed with insecticide and no parasite was introduced.

Kellogg Forest field experiment

I established the field experiment in an area of the Kellogg Forest along the bank of Augusta Creek in Kalamazoo County, Michigan (Figure 1, Site A) with a relatively uniform distribution of *I. capensis* in the understory. I selected fifteen 1 m² plots in an area where the dominant vegetation was comprised of *I. capensis* and randomly assigned each plot to one of three experimental treatments (herbivory, parasitism, or control) with 5 plots per treatment. I selected thirty *I. capensis* plants in each plot and monitored them for growth and reproductive characteristics (see Data collection, below).

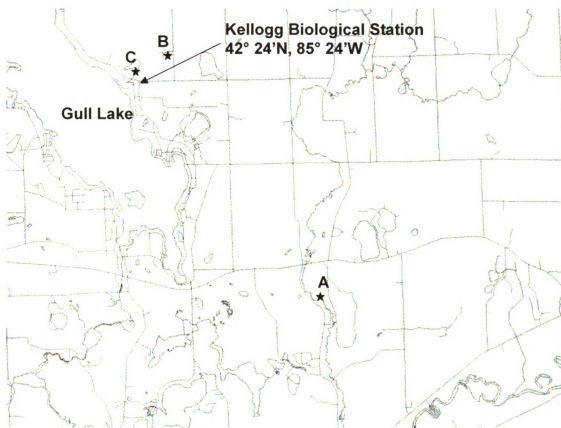


Figure 1. Research sites and surrounding area near the Kellogg Biological Station in Kalamazoo County, Michigan. Site A: Kellogg Forest (field experiment); Site B: Field Lab (pot experiment); Site C: Turkey Marsh (*I. capensis* collection site). Scale: 1 cm = 0.72 km.

The plots were established in a location where none of the *I. capensis* plants growing in this area in the previous year had been parasitized by *C. gronovii*, although patches of *C. gronovii* were located nearby. To introduce the parasite to the plants in the parasitism treatment, I collected seeds from the Kellogg Forest in fall 2005, germinated them in the greenhouse and then added them to the parasitism treatment plots in early June when *C. gronovii* was observed germinating naturally in the Kellogg Forest. To stimulate germination, I soaked the seeds in concentrated sulfuric acid for 30 minutes, rinsed them under running water for 5 minutes, and then placed them on damp filter paper in Petri dishes that were kept in the greenhouse for two weeks. Within a few days of germination, I tied one *C. gronovii* individual with cotton thread to an *I. capensis* individual at the center of each parasitism treatment plot. Several failed to establish within a week, so I replaced them with cuttings from *C. gronovii* individuals growing naturally in the Kellogg Forest.

I attempted to reduce insect herbivory in the control and parasitism treatments by spraying the plots assigned to those treatments with insecticide every 7-14 days as needed. I used two insecticides in combination: Conserve (Dow AgroSciences, 5 mL per gallon of water) to reduce herbivory by caterpillars and Endeavor (Syngenta, 1 gram per gallon of water) to reduce herbivory by aphids and whiteflies. These two insecticides have been shown to have no impact on *I. capensis* growth or reproduction (Steets 2005). I sprayed the herbivory treatment with water at the same time to control for the addition of water to the control and parasitism plots.

There was a great deal of mortality of the *I. capensis* plants in the field experiment due to deer herbivory and trampling. Only 50% of the Kellogg Forest plants

survived to the end of July. The parasitic plant *C. gronovii* also failed to establish in all but one of the plots at the Kellogg Forest. As a result, I did not analyze data from this experiment, but instead used the observed biotic and abiotic characteristics as a comparison for the plants grown in pots at the Field Lab. Data from the Kellogg Forest plants are summarized in Appendix A.

Field Lab pot experiment

To establish the pot experiment at the Field Lab (Figure 1, Site B), I collected *I. capensis* individuals from a natural population growing at the edges of Turkey Marsh, a wooded wetland area at the Kellogg Biological Station (Figure 1, Site C). Seedlings were collected when they were 15 to 25 cm tall and transplanted into pots (diameter: 16 cm, height: 14 cm) filled with potting soil. I planted a single individual in the center of each pot and arrayed them in groups of nine pots inside a fenced deer-exclosure at the Kellogg Biological Station's Terrestrial Plant Ecology Field Lab. The pots were placed under a shade cloth that was open at the sides to allow insect (pollinator and herbivore) access. The shade cloth reduced the photosynthetically active radiation levels from $1778 \mu\text{E}/\text{m}^2/\text{s}$ in full sun to a mean of $600 \mu\text{E}/\text{m}^2/\text{s}$, which is similar to the light availability in some areas of the Kellogg Forest.

I used groups of 9 pots to create conditions more similar to the natural conditions that would allow the parasite to spread from the center plant in the group to the other plants in the group. It was necessary to have several pots in a group because the parasite *C. gronovii* needs to have access to several host individuals as it matures or it drains too many resources from one plant and kills it (personal observation). Groups of pots were 1 meter apart from each other to prevent the parasite from spreading to adjacent groups.

Once the experiment was established, I could not move the pots again because the parasitic plant grew across individuals in the groups. As a consequence I could not randomize effects of environmental variation that occurred under the canopy. I randomly assigned the groups of pots to the three treatments (control, herbivory, or parasitism), with 6 replications per treatment. To maintain soil moisture at levels similar to those in natural populations, the plants were watered every morning by a sprinkler for 20 minutes.

I introduced the parasite in the parasitism treatment by tying one individual of *C. gronovii*, germinated as described above, to the center plant in the group of 9 pots. The parasite eventually established in all of the parasitism treatment replications at the Field Lab. I reduced herbivory in the control and parasitism treatments using insecticides as described above.

Data collection

I monitored growth, reproduction, and herbivory and parasitism levels on all plants in both experiments at weekly intervals for 12 weeks. I measured growth as height and number of leaves. I measured the percent herbivory by scoring the proportion of area missing from each leaf to the nearest 10%, and then calculated the mean percent herbivory for the entire plant. I measured parasitism levels as the number of coils of *C. gronovii* around each *I. capensis* plant. At the height of fruiting, CH and CL fruits were collected from a subset of the plants so that the mean number of seeds per fruit could be calculated, and then for each plant multiplied by the number of fruits produced. In late September, the aboveground biomass of all surviving plants were harvested, dried at 60 °C for 5 days, and weighed. Before I harvested each plant, I counted the number of fruits

still on the plant and the number of pedicels remaining from fruits that had already dehisced to determine the total fitness of each plant.

Light and soil moisture levels were determined in both experiments at the beginning of September. I measured the photosynthetically active radiation (PAR) at solar noon $\pm$ 1 hour on successive cloudless days using a Sunfleck PAR Ceptometer (Decagon) at the top of the *I. capensis* canopy. I calculated the percent water content as the mean of three measurements taken in the center of each plot or pot using a TDR probe (Trime).

Data analysis

To test the effects of the treatments (parasitism, herbivory, and control) on the dependent variables height, biomass, total seed production, and proportion CL seed production, I conducted a single-factor ANOVA on the group means of all surviving plants using SAS (Version 9.1). Because not all nine plants in the parasitism treatment groups became parasitized during the season, non-parasitized individuals were excluded from the group mean of this treatment.

All plants in the herbivory treatment experienced some level of herbivory during the season. To test for differences in the weekly estimates of herbivory level among the three treatments, I used a repeated measures test in SAS (Version 9.1) using PROC GLM.

Because the groups of pots could not be moved once the experiment was established, the variation in light availability due to proximity to the edge of the shade cloth could not be controlled. To model the relationships of the effects of the parasitic plant and the effects of light availability on *I. capensis* reproduction, a path analysis using AMOS (Version 6.0) was conducted on data from the control and parasitism treatments.

From a review of the literature, I expected that light availability would be important in determining the amount of reproduction and the balance between CH and CL reproduction (Schemske 1978, Waller 1980). I used light level (PAR) recorded over the canopy of each group of 9 pots and the means of height, biomass, CH seeds, and CL seeds for all surviving plants of the groups of 9 pots measured at the end of the season for the path analysis. CH and CL seeds were calculated by collecting a subset of mature fruits from all treatments, then multiplying the numbers of fruits and pedicels from dehiscent fruits to obtain an estimate of total seed production over the season for each plant. Parasitism was included in the model as the mean total number of coils per group per week.

I included several correlations in the model. I expected plant height and biomass to be correlated because taller plants would have more leaf nodes and branches and thus more mass. I included both height and biomass in the path analysis because *I. capensis* plants need to achieve a certain height before they are able to produce CH flowers (Lu 2002), regardless of biomass. I also expected a correlation between CH and CL seeds; it could be a positive correlation because larger plants produce more of each seed type, or it could be a negative correlation if larger plants switch to producing primarily CH seeds.

Many indices can be used to evaluate the fit of the model for a path analysis. I looked at the following: the goodness of fit index (GFI), the comparative fit index (CFI), and the root mean square of error approximation (RMSEA). All three indices indicated the same results, so I only report the GFI.

RESULTS

Herbivory and parasitism levels

Several orders of insects were observed feeding on *I. capensis* over the course of the experiment, including Lepidoptera (caterpillars), Coleoptera (beetles), Homoptera (aphids), and Hemiptera (planthoppers). In this study, I only quantified the amount of herbivory done by the chewing insects (Lepidoptera and Coleoptera), not the sucking insects (Homoptera and Hemiptera). However, herbivory levels by chewing insects were low (on average less than 1% of each plant was damaged) in the experiment. Only during one week were herbivory levels significantly higher in the herbivory treatment than in the control and parasitic treatments (Figure 2).

In the parasitism treatment, the mean number of coils per parasitized plant per group increased throughout the season (Figure 3a). The number of plants that were parasitized in each experimental unit ranged from 3 to 9, with a mean of about 5 plants by the end of the season (Figure 3b). By the end of the season, the number of coils per parasitized plant ranged from 2 to 107.

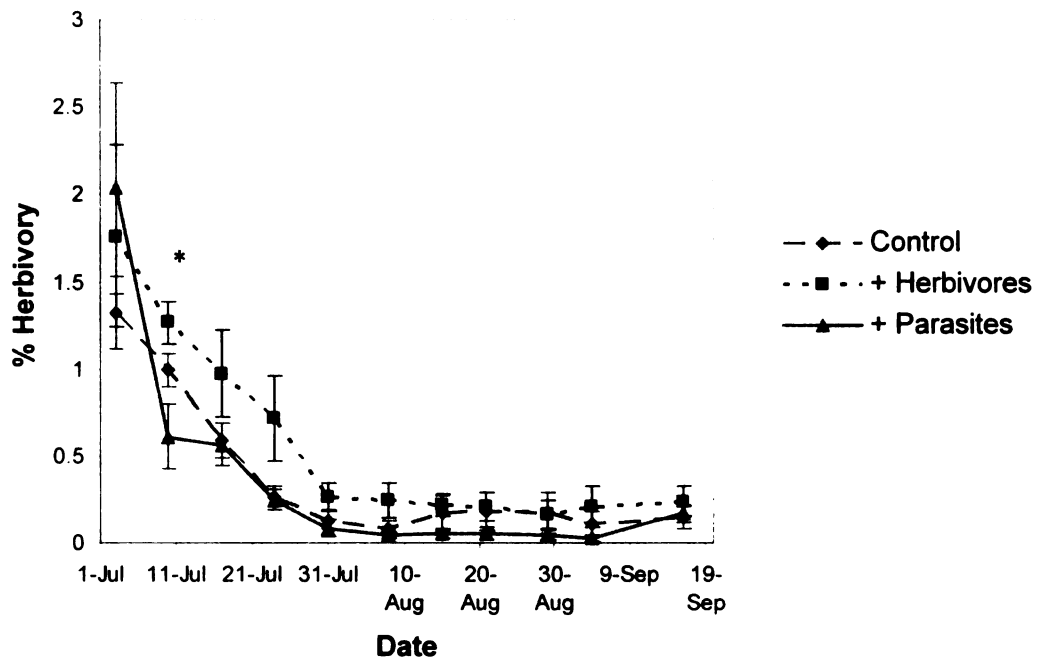


Figure 2. Weekly estimates of % leaf area consumed by insect herbivores (mean $\pm$ standard error, $n = 6$ groups of 9 plants per treatment) for *I. capensis* plants grown in pots at the Field Lab. The three treatments were significantly different from each other in the second week, as indicated by the asterisk (*).

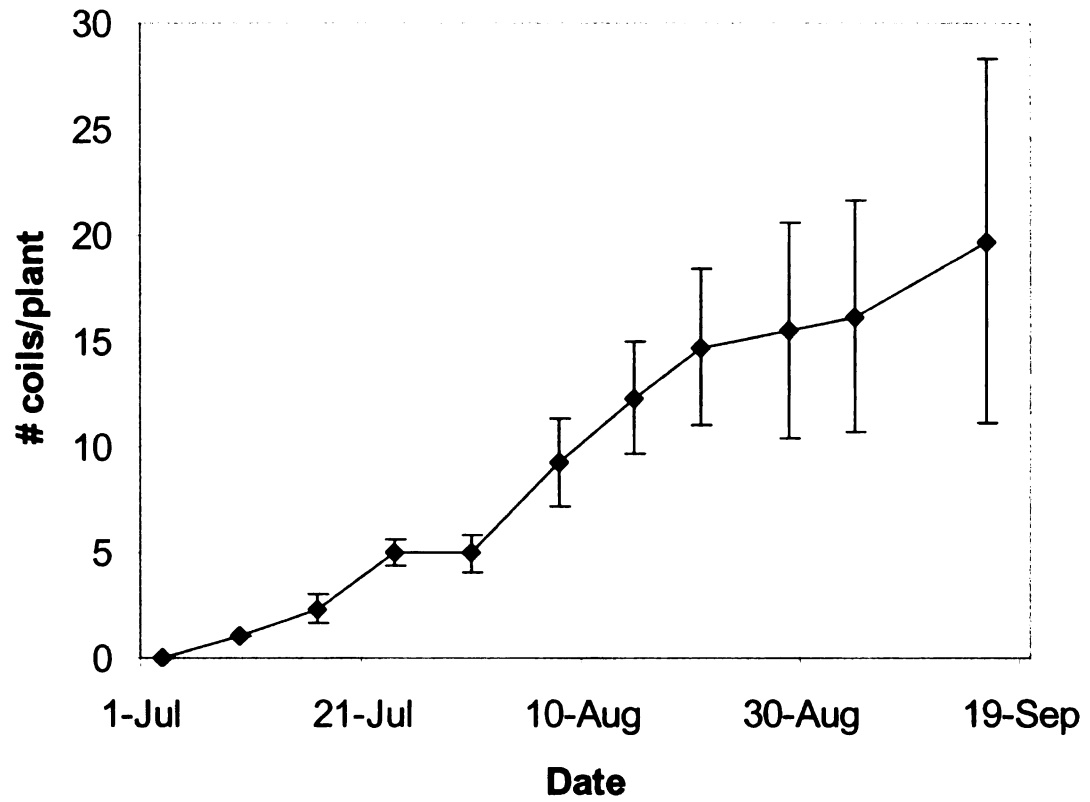


Figure 3a. Weekly estimates of the number of coils of *C. gronovii* on the stem of parasitized *I. capensis* plants grown in pots at the Field Lab in the parasitism treatment (mean $\pm$ standard error, $n = 6$ groups).

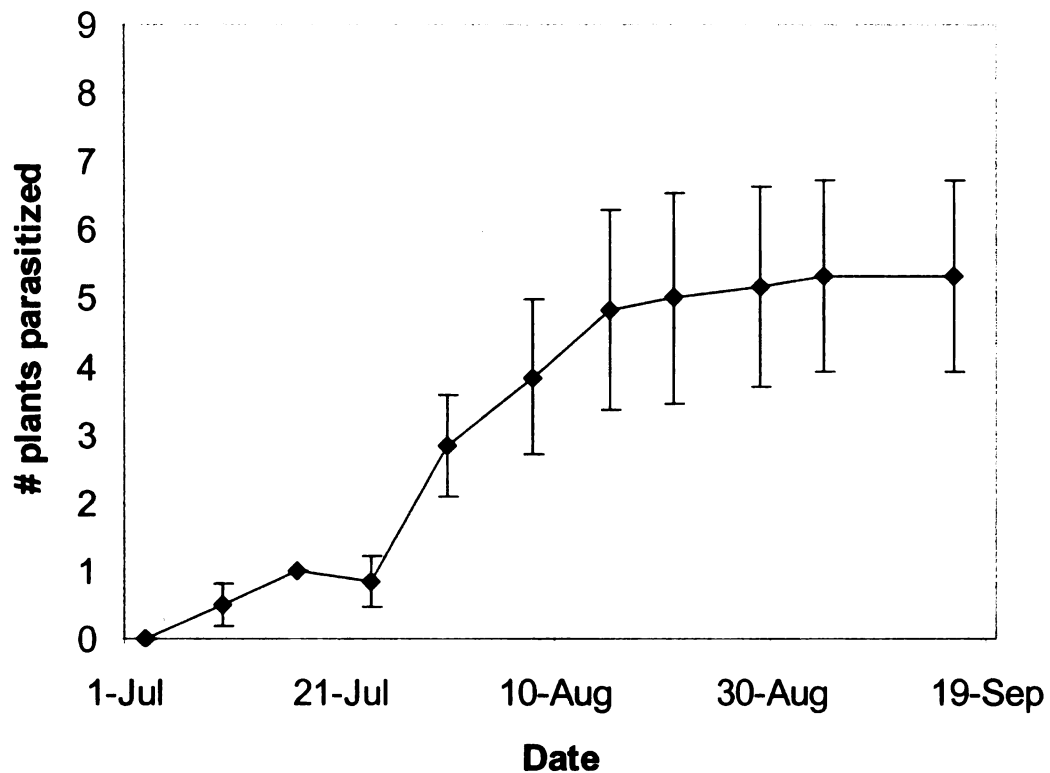


Figure 3b. The number of *I. capensis* plants parasitized by *C. gronovii* at the Field Lab in the parasitism treatment over the growing season (mean $\pm$ standard error, $n = 6$ groups).

Effects of parasitism and herbivory

Parasitism by *C. gronovii* had significant effects on several attributes of *I. capensis* growth and reproduction, but herbivory did not have a significant impact on any of these characteristics (Figure 4). Significant treatment effects were found for height ($F_{2,15} = 9.03, p = 0.003$), biomass ($F_{2,15} = 3.87, p = 0.044$), seed production ($F_{2,15} = 4.01, p = 0.040$), and proportion of CL reproduction ($F_{2,15} = 18.52, p < 0.0001$). Fisher's LSD test showed that in all cases the parasitism treatment was significantly different from the control and herbivory treatments, which did not differ from each other.

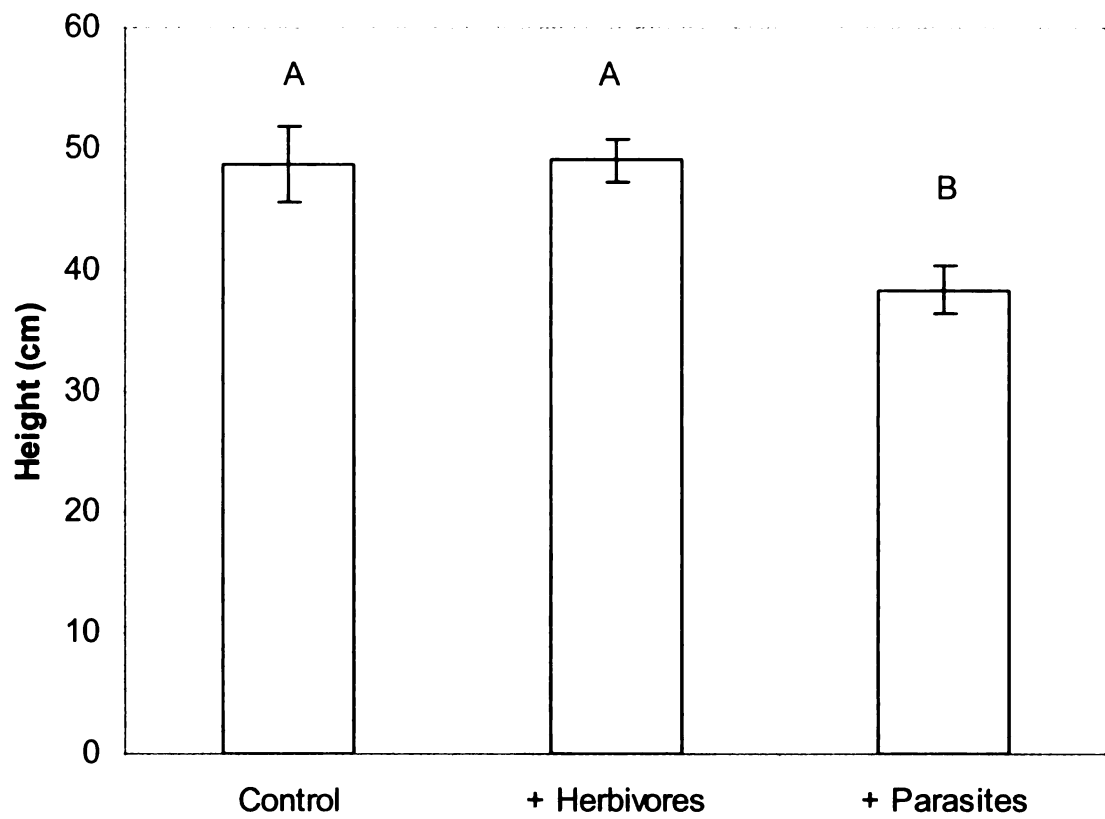


Figure 4a. Final height (mean $\pm$ standard error, $n=6$) of *I. capensis* plants measured at the end of the season (September). Treatments with different letters are significantly different at $\alpha=0.05$ using Fisher's LSD test.

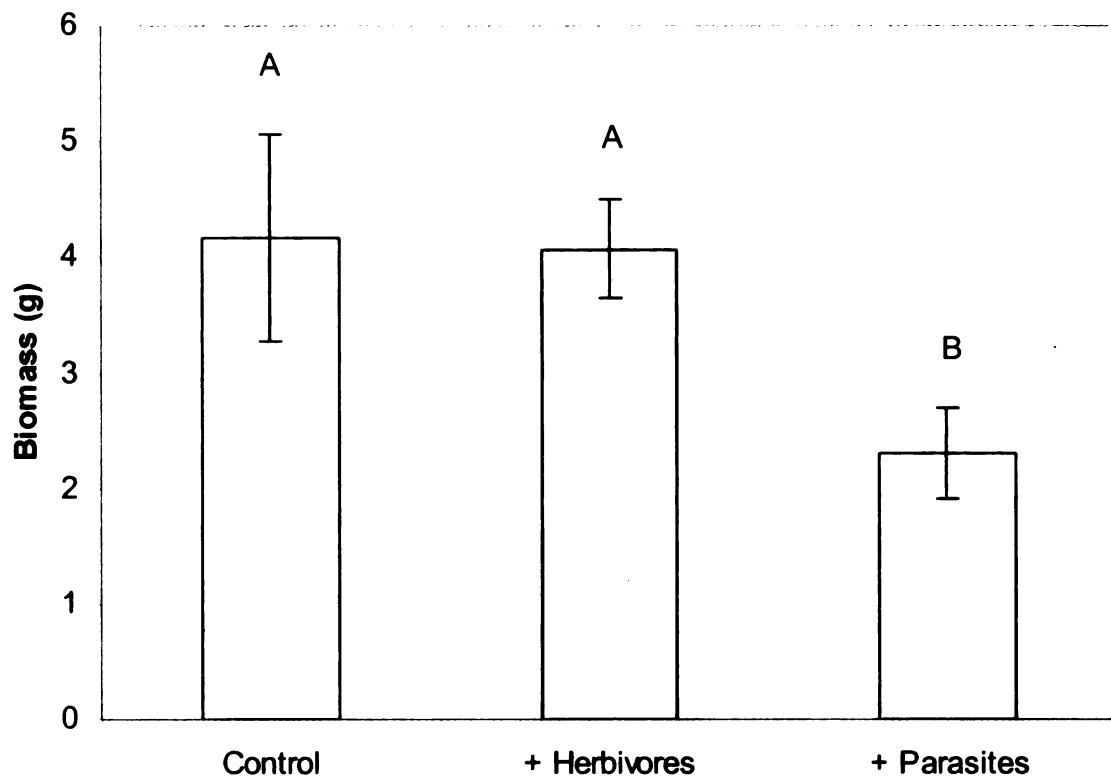


Figure 4b. Final biomass (mean $\pm$ standard error, n=6) of *I. capensis* plants measured at the end of the season (September). Treatments with different letters are significantly different at $\alpha=0.05$ using Fisher's LSD test.

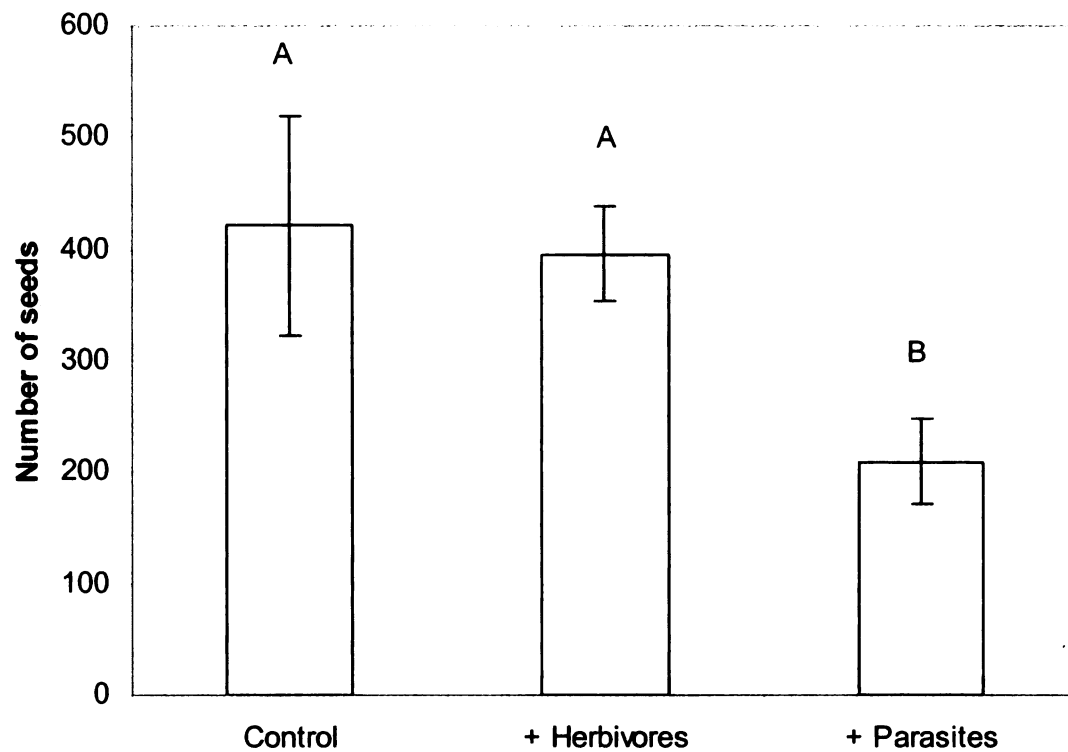


Figure 4c. Total number of seeds produced (mean $\pm$ standard error, $n=6$) by *I. capensis* plants measured as the number of fruits and pedicels remaining on the plants at the end of the season multiplied by the mean number of seeds per fruit. Treatments with different letters are significantly different at $\alpha=0.05$ using Fisher's LSD test.

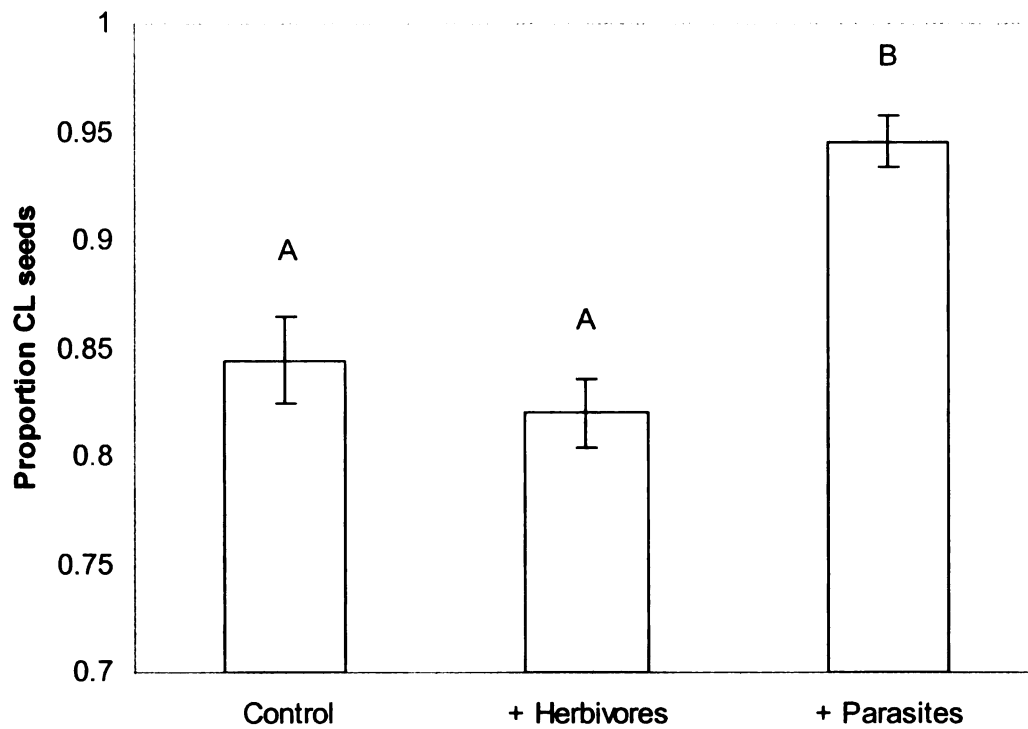


Figure 4d. Proportion of cleistogamous (self-pollinated) seeds produced (mean $\pm$ standard error, $n=6$) by *I. capensis* plants measured as the number of CH and CL fruits and pedicels remaining on the plants at the end of the season multiplied by the mean number of seeds per each type of fruit and converted to a proportion. Treatments with different letters are significantly different at $\alpha=0.05$ using Fisher's LSD test.

Path analysis

The path analysis model (Figure 5) was consistent with the data ($\chi^2 = 0.576$, $df = 1$, $p = 0.448$, $n=12$). This model was constructed such that the arrows leading directly from light and parasitism to CH and CL seeds represent any effects that are not mediated through height and biomass.

This model explains 98% of the variation in CL seeds and 97% of the variation in CH seeds. The effect on reproduction is mediated by height and biomass, of which 41% and 11% respectively of the variation is explained by light and parasitism (Figure 6). CH and CL seed production were affected to similar degrees by parasitism (Table 1). Height affected CH seeds more strongly than CL seeds, as expected.

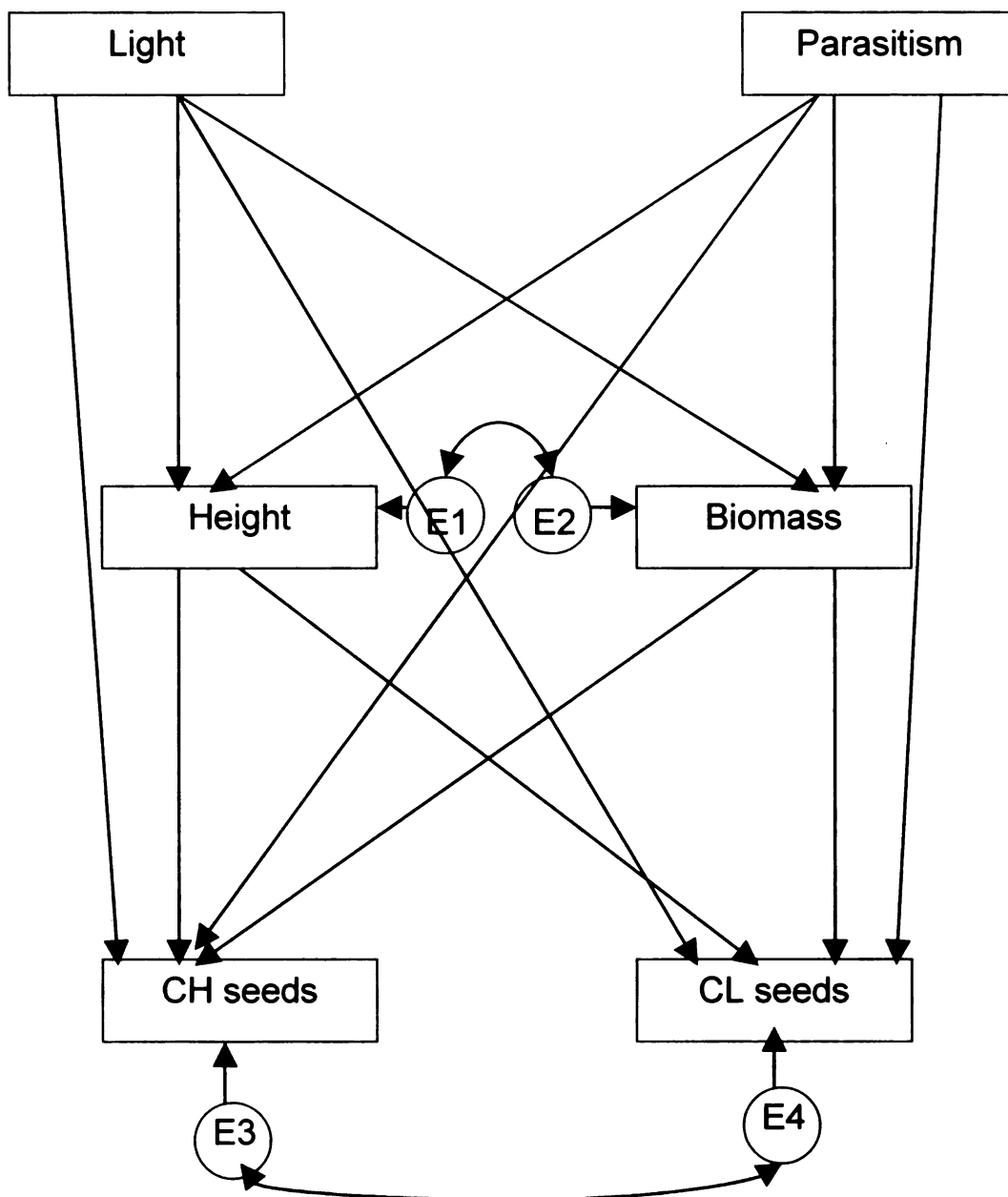


Figure 5. Initial path analysis model showing the hypothetical relationships between biotic and abiotic factors, vegetative plant characteristics, and reproductive characteristics of the host plant *I. capensis*. The arrows leading directly from light and parasitism to CH and CL seeds represent any effects that are not mediated through height and biomass. The correlations between the dependent variables are through their residual error terms (E1-E4).

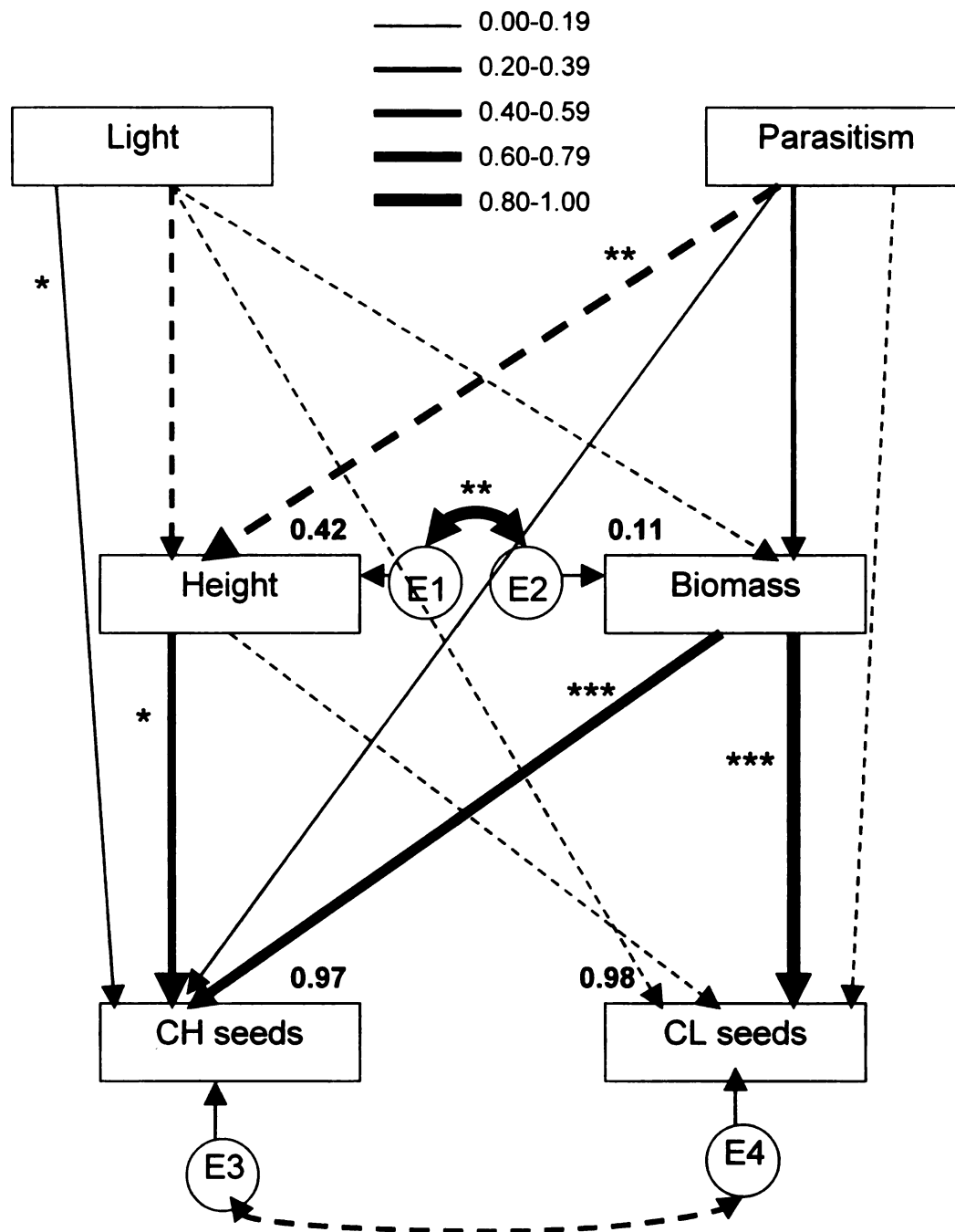


Figure 6. Path analysis model showing the hypothetical relationships between biotic and abiotic factors, vegetative plant characteristics, and reproductive characteristics of the host plant *I. capensis*. Line thickness represents the standardized regression weights. Dashed lines indicate negative regression weights; solid lines indicate positive regression weights. The proportion of variation in each variable explained by the model is indicated by the numbers on the tops of the boxes of the dependent variables. The asterisks to the left of the lines represent the significance level: *** $p < 0.01$, ** $0.01 < p < 0.05$, * $0.05 < p < 0.1$. GFI = 0.982.

Table 1. Standardized total, indirect, and direct effects of variables used in the path analysis on CH and CL seed production.

Variable	Total effects	Indirect effects	Direct effects
On CH seeds			
Height	0.427		0.427
Biomass	0.601		0.601
Parasitism	-0.432	-0.436	0.004
Light	-0.047	-0.179	0.132
On CL seeds			
Height	-0.131		-0.131
Biomass	1.084		1.084
Parasitism	-0.325	-0.261	-0.064
Light	-0.115	-0.064	-0.052

Environmental conditions

Although the shade treatment reduced light availability in the pot experiment to levels similar to those in the Kellogg Forest and the pots were watered daily, the Kellogg Forest was both wetter and shadier than the Field Lab site. Soil moisture levels ranged from 16.3% to 26.2% in the pots at the Field Lab with a mean of 21.9%, which were well below levels at the Kellogg Forest (44.0% to 91.6% with a mean of 70.0%).

Photosynthetically active radiation (PAR) ranged from 149 to 727 $\mu\text{E}/\text{m}^2/\text{s}$ at the Field Lab under the shade cloth with a mean of 608.7 $\mu\text{E}/\text{m}^2/\text{s}$; one group of 9 pots (at the edge of the shade cloth) received close to full sunlight at noon (1741 $\mu\text{E}/\text{m}^2/\text{s}$). At the Kellogg Forest, PAR ranged from 20 to 659 $\mu\text{E}/\text{m}^2/\text{s}$, with a mean of 209.5 $\mu\text{E}/\text{m}^2/\text{s}$.

DISCUSSION

The results of this experiment show that parasitism by *C. gronovii* negatively affects the growth, fitness, and mating system of its host *I. capensis*. However, I was not able to compare the effects of parasitism to that of insect herbivores as initially proposed

due to low levels of insect herbivory at the Field Lab and high levels of deer herbivory and lack of parasite establishment at the Kellogg Forest.

While the insect herbivory levels observed in this study were low, they were not unprecedented for woodland herbaceous plants. Steets and Ashman (2004) surveyed 10 populations of *I. capensis* in Pennsylvania during one season and found that the mean proportion of leaves damaged (leaves with any herbivore damage/total leaves) ranged from about 0.15 to 0.45. When calculated this way, the herbivory levels of the plants in the herbivory treatment at the Field Lab ranged from 0.009 to 0.11 across the season. The number of leaves damaged each week stayed fairly constant (mean = 2 leaves), but these plants produced so many leaves (more than 1000 leaves for some plants by the end of the season) that the herbivory levels were nearly undetectable. The herbivory levels in the Kellogg Forest ranged from 0.13 to 0.37 over the season, with a mean of 0.26, which is consistent with the levels reported by Steets and Ashman (2004).

Insect populations have been observed to be extremely variable through time (Turchin 1990) and many species experience episodic outbreaks following years of low abundance. These outbreak cycles have been shown to affect reproductive output in populations of perennial plants (Carson and Root 2000). In annuals, an episodic outbreak could cause a complete reproductive failure and in a species like *I. capensis*, with no seed bank, this would result in local extinction. It is unclear if the low levels of insect herbivory observed at the Field Lab are typical of this site.

Mediators of parasitic plant impacts

In this study, parasitism of *Impatiens capensis* by *Cuscuta gronovii* resulted in a significant reduction in total reproduction, and in the proportion of outcrossed (CH,

chasmogamous) seeds produced. In addition, the path analysis revealed that these reductions in host plant fitness were mediated through the effects of parasitism on plant height and biomass. There was no significant direct effect of parasitism on CH and CL seed production, indicating that there was no additional effect of parasitism on fitness beyond the effects mediated through the reductions in height and biomass. The model explained less of the variation in height and biomass, indicating that factors other than parasitism and light are involved in determining these traits (e.g., unmeasured environmental or soil factors).

Parasitic plants vs. insect herbivores

The extremely low levels of herbivory in this experiment prevent direct comparisons of the effects of parasitism and herbivory on *I. capensis*. However, the magnitude of the parasitism effects I measured is higher than those reported by Steets and Ashman (2004). I found that the parasitic plant *C. gronovii* reduced height by 21%, compared to the 10% reduction by insect herbivores found by Steets and Ashman (2004). The reduction in total reproduction was also stronger (27% by the parasite, compared to 14% by insects [Steets and Ashman 2004]). In this study, parasitism increased the proportion of CL seeds from 0.84 to 0.95; in Steets and Ashman (2004), herbivory increased the proportion of CL seeds from 0.57 to 0.70.

Based on these comparisons, parasitism had stronger effects on plant growth and reproduction than insect herbivory did, contrary to some of the predictions of Pennings and Callaway (2002). While both herbivory and parasitism levels are likely to vary spatially and temporally, once an area has been colonized by a parasite I would expect that the effects would be strong and consistent across years (unless the parasite or host go

locally extinct). Thus the abundance of the host and parasite are more likely to be coupled in time. Predictions of the effects of parasitic plants on host plants will need to incorporate these differences in spatial-temporal dynamics.

The mobility and mode of feeding of an insect herbivore may also impact its effects on fitness. Sap-sucking insects (e.g., aphids) that tend to colonize a host at low numbers, increase over time, and stay on the host for a long time may have comparable effects on fitness to parasitic plants. The aphid stylets might function similarly to parasitic plant haustoria and cause a physiological drain on the host. Gall-forming insects, such as the gall fly *Eurosta solidaginis* which produces galls on goldenrod, could also act as physiological sinks and would be expected to have effects comparable to those of parasitic plants. I have compiled a bibliography of research papers with data on the impacts of different types of insects on host plants that could be used to explore these effects (Appendix B).

Future research

Research in this area could have several possible future directions. One possible approach would be to repeat this study in a year or across sites with higher levels of insect herbivory. Treatments in which herbivores were intentionally introduced could also be used to better quantify the effects of varying levels of herbivory on plant fitness and then used to compare to a range of parasitism levels.

To investigate the long-term effects that *C. gronovii* has on *I. capensis* populations, communities with *C. gronovii* could be surveyed over several years to determine whether *C. gronovii* always parasitizes plants in the same spatial areas, as I have observed, or whether it follows plants around the habitat (Callaway and Pennings

1998). Genetic analyses could also be done to determine if *C. gronovii* prefers to parasitize inbred plants derived from CL seeds or plants from outcrossed CH seeds. It would be interesting to know whether populations of *I. capensis* that are consistently parasitized by *C. gronovii* have different outcrossing rates than populations that have not been recently parasitized. I would expect that because *C. gronovii* increases the proportion of selfed (CL) seeds produced by *I. capensis* that parasitized populations would have a lower outcrossing rate. However, if *C. gronovii* prefers to parasitize plants from outcrossed CH seeds, spatial cycles could result.

Finally, Schoolmaster (2005) observed that *C. gronovii* uses *I. capensis* as a nurse plant, meaning that the parasite needs *I. capensis* to establish, but it conducts most of its reproduction on nearby perennial plants. In this experiment, the parasite did not have the option of parasitizing other species of plants, and so this may have magnified the impacts on *I. capensis* reproduction. In natural populations of *I. capensis*, the parasite may move onto other species (e.g., *Onoclea sensibilis*, *Solidago patula*, *Eupatorium maculatum*) as it grows and this may limit (or reduce) its impact on *I. capensis*. Thus the impact of the parasite on *I. capensis* populations may vary more in sites with alternative hosts (e.g., diverse wetlands) than where *I. capensis* forms a monoculture (e.g., the Kellogg Forest site).

APPENDIX A: SUPPLEMENTAL DATA

This appendix contains data on vegetative characteristics of *I. capensis* populations from the Kellogg Forest field experiment and Field Lab pot experiment (see Methods and Data collection, above). Seeds were not counted from *I. capensis* fruits harvested in the Kellogg Forest, so there are no data on total reproduction for plants from this site. Data for the Kellogg Forest plants are presented as mean values per plot of the surviving plants (see Table 2 for population density data). Plants whose tops were eaten by deer but still survived with some leaves lower on their stems are excluded from the graphs because they would skew the measurements of height and numbers of leaves. Data for the Field Lab plants are presented as mean values per group of 9 plants. The graphs are plotted with the same scale on the y-axes for the Kellogg Forest and the Field Lab.

The treatments are defined as follows: The plants assigned to the herbivory treatment were subjected to natural levels of insect herbivory and no parasite was introduced. The plants assigned to the parasitism treatment were sprayed with insecticide and one parasite individual was introduced per plot or group of plants. The plants assigned to the control treatment were sprayed with insecticide and no parasite was introduced.

Table 2. Number of surviving *Impatiens capensis* plants per week per treatment at the Kellogg Forest (mean $\pm$ standard error, $n=5^a$). Surveys were initiated on June 21; no surveys were done on August 2 or between September 5 and October 1.

Week	Date	Control	Herbivory	Parasitism
1	June 21	30 $\pm$ 0	30 $\pm$ 0	30 $\pm$ 0
2	June 28	29.2 $\pm$ 0.2	29 $\pm$ 0.45	29 $\pm$ 0.45
3	July 5	19.8 $\pm$ 3.2	22.4 $\pm$ 2.18	20.2 $\pm$ 1.93
4	July 12	17.2 $\pm$ 3.60	20 $\pm$ 2.59	18.8 $\pm$ 1.74
5	July 19	17.5 $\pm$ 2.72	18 $\pm$ 2.51	16 $\pm$ 1.97
6	July 26	17.25 $\pm$ 2.87	17.4 $\pm$ 2.42	15.4 $\pm$ 2.16
8	August 9	15.25 $\pm$ 3.54	15.4 $\pm$ 1.81	14 $\pm$ 2.35
9	August 16	15.25 $\pm$ 3.54	15.4 $\pm$ 1.81	13.2 $\pm$ 2.52
10	August 23	14.75 $\pm$ 3.82	14.4 $\pm$ 1.86	12.8 $\pm$ 2.56
11	August 30	14.75 $\pm$ 3.82	13.4 $\pm$ 1.63	12.2 $\pm$ 2.18
12	September 5	14 $\pm$ 3.56	12.2 $\pm$ 1.66	11.6 $\pm$ 1.66
15	October 1	6 $\pm$ 1.96	5.8 $\pm$ 1.62	5.4 $\pm$ 0.93

^a $n=4$ for the control treatment after July 12 due to destruction of one plot by deer.

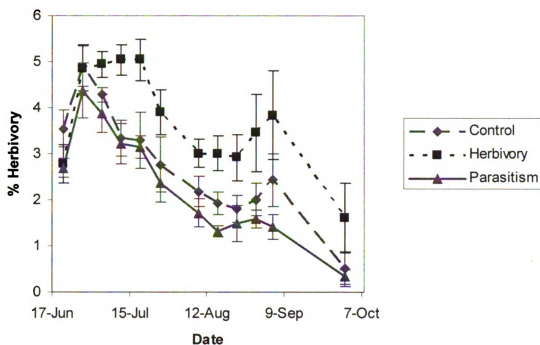


Figure 7. The % leaf area consumed by insect herbivores per plot per week (mean $\pm$ standard error, $n=5$) for *I. capensis* plants grown in the Kellogg Forest.

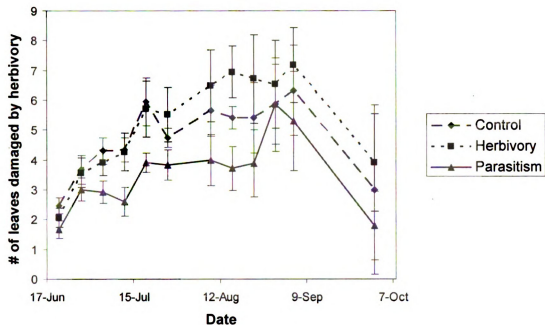


Figure 8a. The number of leaves with damage from insect herbivores per group per week (mean $\pm$ standard error, $n=5$) for *I. capensis* plants grown in the Kellogg Forest.

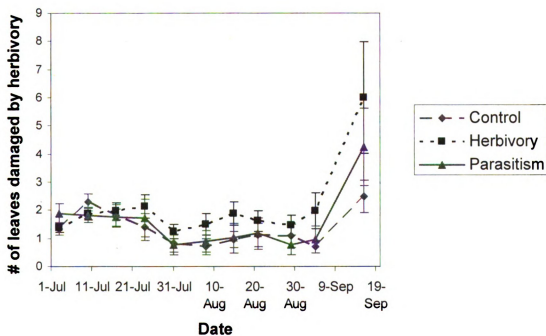


Figure 8b. The number of leaves with damage from insect herbivores per group per week (mean $\pm$ standard error, $n=6$) for *I. capensis* plants grown at the Field Lab.

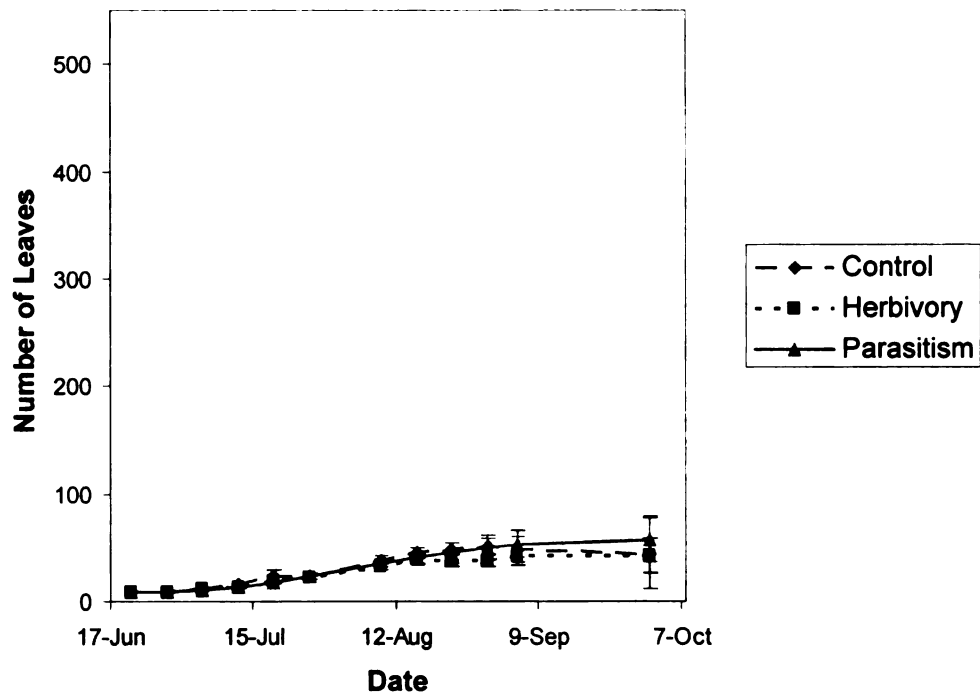


Figure 9a. The number of leaves per plant per plot per week (mean $\pm$ standard error, $n=5$) for *I. capensis* plants grown in the Kellogg Forest.

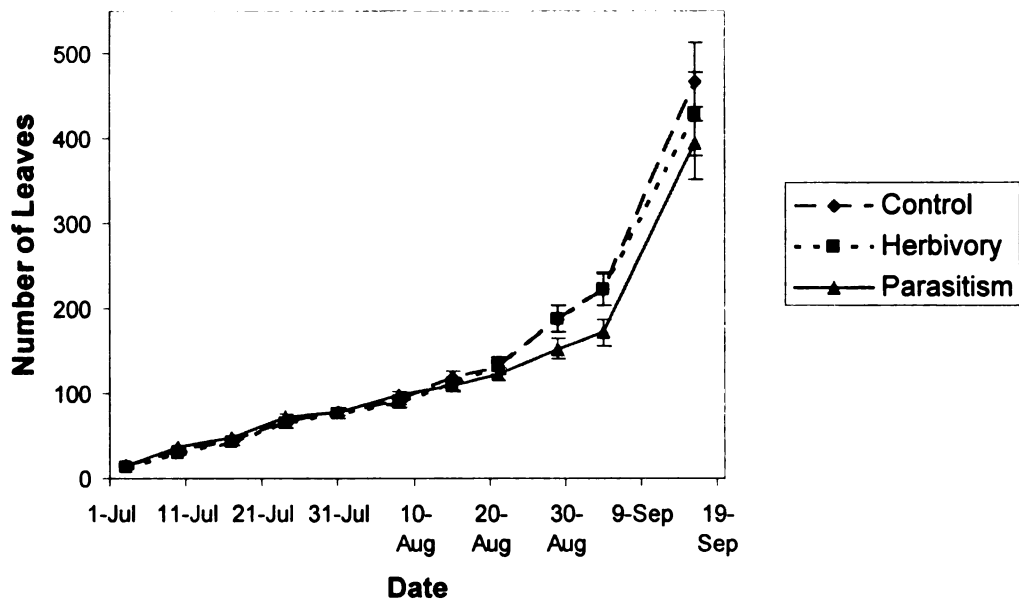


Figure 9b. The number of leaves per plant per group per week (mean $\pm$ standard error, $n=6$) for *I. capensis* plants grown at the Field Lab.

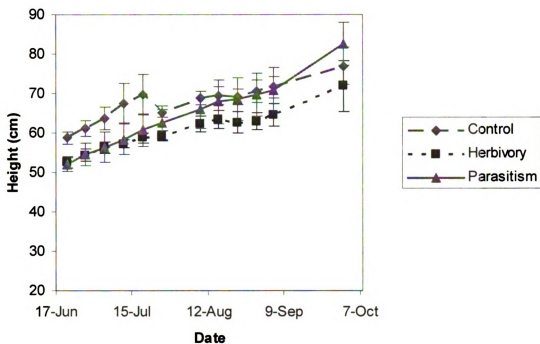


Figure 10a. The height per plant per plot per week (mean $\pm$ standard error, $n=5$) for *I. capensis* plants grown in the Kellogg Forest.

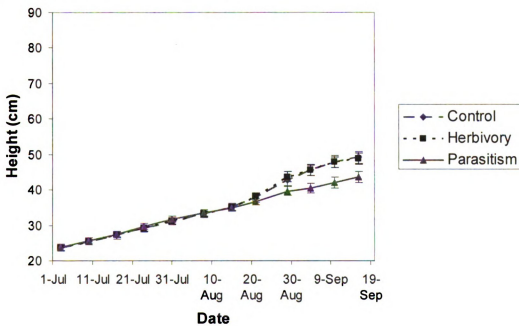


Figure 10b. The height per plant per group per week (mean $\pm$ standard error, $n=6$) for *I. capensis* plants grown at the Field Lab.

APPENDIX B: SUPPLEMENTAL BIBLIOGRAPHY

Pennings and Callaway (2002) hypothesized that parasitic plants are similar to insect herbivores in their effects on plant populations and communities. However, many insects chew the leaves of plants and then move on to new hosts, whereas parasitic plants tap into the xylem and phloem of a plant and so act as continual physiological sinks on the host plants. These two types of organisms might be expected to have different effects on plant survival and reproduction because they operate in fundamentally different ways. It is also likely that the way in which an herbivore feeds on a host plant would affect its effect on plant growth and fitness. Based on this, I proposed that instead of comparing parasitic plants to all insect herbivores, the effects of parasitic plants should be compared to those groups of organisms that also act as continual physiological sinks on plant resources: sap-sucking insects (Hemiptera), gall-forming insects (larvae of several orders), and fungal endophytes and pathogens.

I compiled literature containing data of the effects of these organisms on their host plants by using the following search string in ISI Web of Science in July 2006: (sap-sucking OR sap-feeding OR parasitic plant* OR galls OR galling OR gall OR fungus or fungal) AND (host OR biomass OR growth OR reproduction OR herbivory) NOT genetic. I added papers that contained data in graph or tabular form to the bibliography. To obtain any papers that I missed in this search, I looked through each paper's literature cited section to obtain older papers, and I found newer papers that cited each paper using ISI Web of Science. In the end, I compiled 26 papers on arthropod galls, 11 papers on fungal endophytes, 24 papers on fungal pathogens, 26 papers on parasitic plants, and 28 papers on sap-sucking insects. Several papers contain data from more than one species

within a taxa (i.e., two species of aphids were studied) or measure the effects on more than one species of host plant, so these papers would generate multiple data points in a meta-analysis.

The following list of papers contains data in tables or graphs of the effects of the above-listed taxa on host plant growth or reproduction. This data could be used to conduct a meta-analysis to determine whether parasitic plants have similar effects on their hosts as any of the other taxa.

Arthropod galls

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