The ecology of invasions in a Minnesota grassland: characteristics of invasive species and invaded communities and the effects of global change

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Abstract

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Biological invasions are causing dramatic changes in the distribution and abundance of species around the world. Invasions are one of the leading threats to conservation of native species, yet our ability to predict which species will be aggressive invaders and where they will invade is unreliable at best. Using both experiment and observation, I examine the characteristics of invasive species and invaded communities in an effort to improve predictive ability for invasions.

One particularly aggressive invader in much of North America, *Hieracium aurantiacum*, has invaded areas occupied by a rare, native congener *H. longipilum*. Using these species as a model system, I compare the traits of the native and invasive congeners, testing for differences in competitive ability under ambient and enhanced nitrogen conditions (greenhouse competition experiments), differences in response to herbivores and pathogens (field exclosure experiments), and differences in morphology (field observations) that might contribute to the success of the invasive species. The results indicate that *H. aurantiacum* is not a superior competitor to *H. longipilum*, but its

success in invasion may be explained partly by enemy escape through invasion of a new range and partly by its unique morphological traits.

Biological invasion requires not only a successful invader but also a susceptible community. I report the results of an observational study, in which I examined the characteristics of the plant neighborhoods where invaders were successfully established. Invaders achieved greater sizes in neighborhoods with less crowding (fewer neighbors of smaller size) and lower species diversity.

Global change may further exacerbate the problem of biological invasions by creating conditions that are favorable for invasive plants. I report the results of a study that examined the effects of co-occurring changes in atmospheric carbon dioxide, nitrogen deposition, and species richness. This experiment indicated that different invaders may have distinct responses to global change factors, with some species benefiting from global change and others showing a negative response.

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Barbara Cox Diller

(July 21, 1909 – July 18, 2002)

in memory of her scientific curiosity and

in thanks for her loving support.

OVERVIEW

In ecosystems around the world today, exotic species are ubiquitous and often highly problematic. In North America, more than 10% of the plant species present are exotic (Vitousek et al. 1997b); in Canada, the percentage of plants that are exotic is greater than 22%. In the Hawaiian Islands, the most invaded region of North America, there are at least 4,598 exotic species, posing a serious conservation threat to the native Hawaiian flora and fauna. Indeed, exotic species are the second leading cause of endangerment of native species in North America (Wilcove et al. 1998).

The most aggressive exotic species become invaders in native habitats, often having extensive impacts on native species and ecosystem processes. Impacts range from population-level impacts, such as predation (Baker 1965, Savidge 1987, Grosholz et al. 2000, Martin et al. 2000), herbivory (Louda and Potvin 1995, Fajvan and Wood 1996), hybridization (Ayres et al. 1999, Perry et al. 2001), or competition (Huenneke and Thomson 1994, Petren and Case 1996, Kupferberg 1997, Meekins and McCarthy 1999), to community-level impacts in which species composition is drastically altered (Human and Gordon 1997, Lambrinos 2000), to ecosystem-level impacts, such as changes in hydrology (Busch and Smith 1995), nutrient cycling (Vitousek et al. 1987, Scott et al. 2001), or disturbance regimes (D'Antonio and Vitousek 1992).

While it is apparent that invasive species are having dramatic impacts on native ecosystems, it still remains unclear why they are so successful in native ecosystems. Developing the capacity to understand and predict the dynamics of invasions is important for conservation and management, yet our knowledge about what makes an invasion successful is remarkably deficient. Until recently, the primary approach to understanding the traits of invaders was purely observational. In 1965, Baker compiled a list of traits that seemed to be common among invasive plants, and this study was widely cited in the literature. Thirty years later, Lodge (Lodge 1993b, Lodge 1993a) used the same approach in compiling a list of traits mentioned in the literature as traits related to invasiveness, yet most of the evidence available at that time was anecdotal, rather than empirical. The primary benefit of Lodge's study was to point out areas in need of further research in order to gain a better general understanding of the traits associated with invasiveness.

One way to identify the traits responsible for invasibility is to compare invaders to co-occurring, closely-related, native species, often species in the same genus, with similar growth forms. Congeners are likely to share many or most of their traits, thus by comparing them it is possible to isolate their differences. Among those differences is the reason that the exotic species has become a successful invader in a habitat already occupied by a closely-related native species.

I used the congener comparison approach to try to identify traits associated with invasion success of *Hieracium aurantiacum* in Minnesota grasslands by comparing it to a co-occurring native species, *Hieracium longipilum*. Chapters I & II examine characteristics of these two species and provide a detailed comparison of their ecologies.

In Chapter I, I report the results of two greenhouse competition studies using *H. aurantiacum* and *H. longipilum*. I discuss plant success (growth and reproduction) at different densities and proportions of species planted, as well as how those patterns are affected by increased nitrogen availability.

Chapter II reports the results of field observations and experiments performed to test the natural enemies hypothesis as a possible explanation for the invasion success of *H. aurantiacum*. Differences in morphological characters between the invader and its native congener are also discussed, as well as their possible importance for differences in performance between the two species.

Reasons for invasion success can also be examined from a community perspective. A successful invasion requires not only a successful invader, but also a susceptible community. In particular, I have focused on the effects of changes in species richness and other global change factors on the success of invasive species.

Experimental studies (Knops et al. 1999, Levine 2000, Naeem et al. 2000, Kennedy et al. 2002) have indicated that invaders are more successful (i.e. achieve greater biomass) in areas with lower resident plant species richness. However, it is not known if these same patterns hold for natural, unmanipulated systems. In Chapter III, I report the results of an observational study that explored the role of the composition of an invader's immediate plant neighborhood in determining the success of that invader. The importance of species richness, diversity, and neighborhood crowding are discussed.

Finally, in Chapter IV I discuss the potential effects of multiple, co-occurring global change factors on the success of invasive plants. I address this question by reporting the results of a large-scale factorial experiment in which atmospheric CO_2, nitrogen deposition, and resident plant species richness were manipulated simultaneously; the effects of these treatments and their interactions on the two most common invaders in the experimental plots, *Crepis tectorum* and *Conyza canadensis*, are disucussed.

CHAPTER I

COMPETITIVE INTERACTIONS BETWEEN A NATIVE PLANT AND ITS INVASIVE CONGENER

INTRODUCTION

Invasive species can have dramatic impacts on ecosystems by causing the extirpation of native species (Savidge 1987, Smith 2000) or by substantially altering ecosystem processes (Vitousek *et al.* 1987; D'Antonio and Vitousek 1992; Sala 1996; Scott *et al.* 2001). The effects of invasive species on native ecosystems, however, are often more subtle on short time scales in ecosystems subject to natural variability in species abundances (Mack 2000). Though many invasive species have impacts that are harder to detect than those of the most visible invaders, their influence in natural systems may still be quite large. This is particularly true of invasive plant species that may have slow but steady impacts on soil or native plant community composition that are not readily apparent until the invader reaches some threshold population size (Mack et al. 2000). Furthermore, altered resource availability resulting from human activities, such as increased atmospheric nitrogen deposition, may favor invasive species and exacerbate their impacts on native ecosystems (Dukes and Mooney 1999, Scherer-Lorenzen et al. 2000). In this chapter, I will experimentally examine the potential for resource competition between a native and an invasive species under ambient conditions and with enhanced nitrogen availability.

Competition between native and exotic plant species is one of those subtle impacts that is often difficult to distinguish without careful observation and experimentation. Several studies have demonstrated that invasive species can be successful because they are able to outcompete native species for resources. Walck *et al.* (1999) showed, in both greenhouse and field studies, that two introduced plant species, *Coronilla varia* (purple crownvetch) and *Festuca arundinacea* (tall fescue), caused significant reductions in the growth of *Solidago shortii* (Short's goldenrod), an endangered forb endemic to northeastern Kentucky. Similarly, Huenneke and Thomson (1994) found that *Cirsium vinaceum*, a threatened species endemic to the Sacramento Mountains in New Mexico, had reduced growth when *Dipsacus sylvestris* (teasel), an invasive species, was present. The growth of *Dipsacus*, however, was unaffected by the presence of *Cirsium*. A study examining the interactions between *Alliaria petiolata* (garlic mustard) and three plant species native to northeastern U. S. forests found that *Alliaria* was able to outcompete some, but not all, of the native species (Meekins and McCarthy 1999). The competitive success of *Alliaria* was greatest when grown at high densities, suggesting that once an invader reaches some critical population size, its effects on native species may increase markedly.

Other studies have shown that exotic species that are competitively inferior to native species can successfully invade communities where an extrinsic factor favors the exotic. *Tamarix ramosissima* (salt cedar), for example, has been successful in invading floodplains in the southwestern United States that were historically dominated by *Populus deltoides* subsp. *wislizenii* (cottonwood). In a field pot experiment, Sher *et al.* (2000) demonstrated that *Populus* seedlings were more limited by intraspecific than interspecific competition. These results suggest that *Tamarix* may be a successful invader because of its ability to tolerate human-modified flow regimes, rather than having the ability to outcompete the dominant native species.

The outcome of competition between a native and an invasive species may potentially differ with changing nitrogen availability (Tilman and Wedin 1991, Wedin and Tilman 1993, Navas et al. 1999). Increasing atmospheric nitrogen deposition is expected to favor invasive species by making more nutrients available for growth and reducing competition with native species (Dukes and Mooney 1999). A few studies have shown that growth of an invasive species increases when nitrogen is enhanced (Tilman 1993, Maron and Jeffries 1999), however few experimental studies have specifically examined resource competition between native and exotic species under increased levels of nitrogen. One study examined the effect of reduction in density of neighbors on the growth of an exotic species, *Hieracium floribundum*, under both enhanced nitrogen and ambient conditions (Reader 1990). The results showed that vegetative reproduction of *H. floribundum* increased when fertilizer (NPK) was added, but only when neighbors were removed, suggesting that *H. floribundum* is not a strong competitor for nitrogen. On the other hand, a greenhouse study comparing competition between *Protea repens*, a native South African shrub, and *Acacia saligna*, an invasive shrub, found that *Acacia* grew rapidly under high nitrogen conditions, leading to decreased growth in *Protea* (Witkowski 1991). For many invasive species, we have little or no information about their abilities to outcompete co-occurring native species under ambient or enhanced nitrogen conditions.

One rapidly spreading and potentially problematic invader is *Hieracium aurantiacum*, also known as orange hawkweed or devil's paintbrush. *H. aurantiacum* was introduced to North America by 1875 for use as a garden ornamental (Voss 1996), and it has become a widespread invader across North America, with its presence confirmed in 31 of the 50 U.S. states (http://www.csdl.tamu.edu/FLORA/b98/check98.htm) and across Canada (Royer and Dickinson 1999). In some areas, *Hieracium aurantiacum* is a relatively recent invader. One such place is Cedar Creek Natural History Area (hereafter referred to as Cedar Creek), in Bethel, Minnesota, a 2200-acre scientific and natural area in the east central part of the state. *H. aurantiacum* was first recorded in one old field at Cedar Creek in 1975, and had spread to a second area at Cedar Creek by 1984 (Delaney 1989).

Cedar Creek is also home to four native species in the genus *Hieracium*. One of the native species, *Hieracium longipilum*, has a similar growth form to the invader; both species are rosettes that flower once a year, have dense trichomes on their leaves and flowering stalks, and have apomictic, ligulate flower heads. Both species are found in many of the same old fields at Cedar Creek, often growing side by side. *H. longipilum* has a more restricted range than *H. aurantiacum*, being predominantly found in sandy prairies in the Central Plains states, and its range is contracting. *H. longipilum* is currently listed as a species of Special Concern in Tennessee, is Threatened in Kentucky, and is Presumed Extirpated in Ohio (USDA PLANTS Database, http://plants.usda.gov/cgi bin/topics.cgi). In the *Flora of Cedar Creek*

Natural History Area (Delaney 1989), *H. longipilum* is described as an "occasional" species, meaning that it is not commonly found in areas of the appropriate habitat type at the site.

It is unclear whether *H. aurantiacum* is in direct competition with *H. longipilum*, and what impact, if any, it is having on the native species. I addressed this question by performing a greenhouse competition experiment to determine whether each species was more limited by intraspecific or interspecific competition. If *H. longipilum* was more affected by interspecific competition from *H. aurantiacum* than from competition with individuals of its own species, that would indicate that the invader is having a negative impact on the native species. In a second experiment, I manipulated nitrogen levels to see whether enhanced nitrogen levels would change the outcome of competition.

METHODS

Experiment 1

Seeds of *H. aurantiacum* and *H. longipilum* were collected in summer 1998 in several old fields at Cedar Creek Natural History Area (Anoka and Isanti Counties, Minnesota). On February 8, 1999 at the University of Washington's Botany Greenhouse, ninety one-gallon pots were filled to the top with Sunshine Mix # 4, a peat-perlite potting soil, and seeds of *H. aurantiacum* and *H. longipilum* were added to the soil surface. Seeds were placed at fixed locations that were equidistant from each other and from the edge of the pot to ensure that spacing was uniform within all pots of a given planting density and there was no effect of plant position on growth.

The experiment followed a modified de Wit replacement design (de Wit 1960) in which both density and proportions of the two species planted were manipulated. Pots were planted with 2, 4, 8, or 12 plants, and all possible combinations of *H. aurantiacum* and *H. longipilum* were represented at each density level. For instance, the four-species density treatment included pots with the following species combinations: 4 *H. aurantiacum*, 0 *H. longipilum*; 3 *H.a.*, 1 *H.l.*; 2 *H.a.*, 2 *H.l.*; 1 *H.a.*, 3 *H.l.*; and 0 *H.a.*, 4 *H.l.* Each density-proportion combination was replicated three times, for a total of 90 pots.

When the seeds germinated, seedlings were thinned to a density of one seedling per planting location to control plant density within each pot. In locations where no seeds had germinated by February 24, replacement seedlings were transplanted into the pots from trays planted with extra seeds. Pots were watered daily with clear (unfertilized) water and once during the experiment with fertilized water (containing N, P, K, Ca, Mg, S, Cu, Zn, Mn, Fe, B, and Mo) to replenish nutrients in the pots. Pot positions were randomized once every 7-10 days to reduce effects of greenhouse microclimatic variation on plant growth.

All plants were harvested between April 14 and 21, 1999. At the time of harvest, the following measurements were recorded for each plant: length of the longest leaf, height of the flowering stalk, and number of flowers. Vegetative and reproductive biomass were separated, dried, and weighed for each plant. Because of the difficulty of accurately separating roots of multiple plants growing in one pot, all root tissue was discarded.

Experiment 2

A second experiment was conducted to examine the effects of increasing nitrogen availability on competition between *H. aurantiacum* and *H. longipilum.* Seeds were collected in summer 2000 from the same old fields where seed was collected for Experiment 1. *H. longipilum* seed was relatively scarce in 2000, so additional seed was collected from both species in summer 2001. On May 20, 2002, seeds were planted in the greenhouse following the methods described for Experiment 1.

Because of a lack of sufficient quantities of seed, the experimental design was modified to reduce planting densities. Pots for Experiment 2 were planted with 1, 2, 4, or 8 plants. All possible combinations of the two species were planted for all density levels, except the 8-plant pots. For pots with 8 plants, the species combinations were as follows: 8 *H.a.*, 0 *H.l.*; 6 *H.a.*, 2 *H.l.*; 4 *H.a.*, 4 *H.l.*; 2 *H.a.*, 6 *H.l.*; 0 *H.a.*, 8 *H.l.*

In addition to the density and species proportion treatments, half of the pots in Experiment 2 received added nitrogen, applied as ammonium nitrate solution. Field additions of nitrogen often enhance levels by 1 to 5 g N m^{-2} y^{-1}, a range equivalent to the current rates of atmospheric nitrogen deposition in North America (Tilman 1993, Wedin and Tilman 1996, Reich et al. 2001). Nitrogen was enhanced to a level approximately equivalent to 2.75 g N m^{-2} y^{-1} for this experiment so that nitrogen enhancement would fall within the range of current deposition rates. Pots receiving enhanced nitrogen were watered with 200 mL of NH_4NO_3 solution (~120 ppm) on

June 13 and July 3. Control pots were watered with 200 mL clear water at the same time.

Apart from the two nitrogen additions, watering and randomization schedules were identical to those used in Experiment 1. Plants were harvested between July 17 and July 19, 2002. Leaf length, number of leaves, and dry weight of aboveground biomass were measured for each plant. Because none of the plants had bolted or flowered by the time the plants were harvested, no data were collected on height, flower number, or reproductive biomass.

Analysis

When comparing the performance of different plant species in a competition experiment, the results can be difficult to interpret if one species is bigger than the other. This problem can be solved by calculating relative yield for each plant, in which the growth of each species in mixture is compared with its growth in monoculture (Fowler 1982, Meekins and McCarthy 1999). Relative yields allow comparison of a plant's performance in mixture relative to what would be expected if all its neighbors were conspecifics. Relative yield was calculated using the following equations from Fowler (1982). Given,

p = proportion of species i in mixture
q = proportion of species j in mixture

Y_i = mean yield of species i in a pure stand of species i
Y_{ij} = yield of species i in a mixture of species i and j

The relative yield per plant grown in mixture, is calculated as

$$RYP_{ij} = Y_{ij}/(pY_i) \text{ and}$$

$$RYP_{ji} = Y_{ji}/(qY_j)$$

Yield in a pure stand must be calculated separately for different density treatments and species. Relative yields were calculated for each species in each pot. A relative yield value greater than 1 indicates that intraspecific competition is greater than interspecific competition for that species. A relative yield less than 1 means that interspecific competition is stronger.

Aggressivity, a measure of how interspecific competition affects the biomass of each species, can be calculated from relative yield values using McGilchrist and Trenbath's formulas (McGilchrist and Trenbath 1971).

$$A_i = RY_{ij} - RY_{ji}$$

$$A_j = RY_{ji} - RY_{ij}$$

Within a pot, the species with the higher value of A is considered to be more aggressive and, therefore, the stronger competitor (Meekins and McCarthy 1999).

The design of a de Wit replacement series experiment is such that not all species proportions are possible for all density levels. For instance, a species proportion of 0.25 or 0.75 is not possible for a pot with a density level of 2, preventing the use of a standard ANOVA for data analysis. To analyze the results for this experiment, I used ANCOVA, in which the proportion of individuals that were conspecifics was included in the model as a covariate, with species identity, planting density, and nitrogen treatment (for Experiment 2 only) as main factors and relative yield as the response variable. Also, ANOVA was used to analyze data on height and reproductive biomass of *H. aurantiacum* across treatments for Experiment 1. *H. longipilum* plants did not bolt or flower during the experiment, and therefore these analyses were not run for the other species. All data were $\log_{10}$-transformed to improve normality and analyzed using SYSTAT 9.0.

RESULTS

Experiment 1

The relative yield values calculated from the vegetative biomass data, indicate that both species are more limited by intraspecific competition than by interspecific competition. All mean relative yield values for both species were greater than 1 (Table 1.1), sometimes substantially greater, indicating that interspecific competition is less important for growth in these species than is competition with conspecific neighbors. The same is true for calculations of mean relative leaf length for both species; they indicate that intraspecific competition has a greater negative effect on plant size (Table 1.1). Relative yield in *H. aurantiacum* increased markedly as density increased. *H. longipilum* showed a less consistent pattern, with relative yields increasing between densities of 2, 4, and 8, but declining again in the highest density pots. Relative leaf lengths seemed to be less affected by density for both species, but the patterns followed those seen for relative yields in both species.

Aggressivity values are another way to compare the interactions of two species growing in a pot. *H. longipilum*, the native species, had higher mean aggressivity values at the planting densities of 2, 4, and 8 species per pot (Table 1.2).

However, highest planting densities, *H. aurantiacum* had a higher mean aggressivity value. These values suggest that *H. longipilum* may actually be a stronger competitor when fewer individuals are present.

Relative yield and relative leaf length data can also be examined with respect to both density and proportion of conspecifics planted in the pot. Relative yield declined with increasing proportion of conspecifics for both species at all planting densities (Figs. 1.1 & 1. 2). *H. aurantiacum* showed a consistent rate of decline in relative yield at all density levels (Fig. 1.1). For *H. longipilum*, the decline in relative yield with increasing proportion of neighbors that were conspecifics was most pronounced at a density of eight individuals per pot. These declines in relative yield with increasing proportion of conspecifics again demonstrate that intraspecific competition is stronger than interspecific competition for both species. The pattern is the same for relative leaf lengths, with both species showing declines in leaf size relative to the monocultures as the proportion of neighbors that were conspecifics increased (Figs. 1.3 & 1.4). There were no differences in growth form of either species with changing density or proportion of conspecifics.

Species identity, density, and the proportion of conspecifics in the pot all had a significant effect on relative yield (Table 1.3). The effect of species identity was due to factors other than size differences between the two species, because absolute size differences are corrected through the calculation of relative yield. There was also a significant interaction between species and density (Table 1.3).

ANCOVA results for relative leaf length data, show that only species identity and proportion of conspecifics had a significant impact on relative leaf length (Table 1.4). Density did not have a significant effect on relative leaf length for these species.

None of the *H. longipilum* plants bolted during the course of the experiment, but many *H. aurantiacum* individuals did. The height of *H. aurantiacum* individuals decreased with increasing proportion of conspecifics, with the effect being the most distinct at higher planting densities (Fig. 1.5). Both density and proportion of conspecifics had a statistically significant impact on height (Table 1.5).

Biomass of reproductive tissues showed the same pattern; biomass declined with increasing proportion of conspecifics, and the effect was more pronounced as density increased (Fig. 1.6). Both density and proportion of conspecifics had a significant effect on reproductive biomass (Table 1.6).

Experiment 2

Relative yield values from the second experiment were all greater than 1 (Table 1.7), as they were for Experiment 1, again indicating that each species is more limited by its conspecifics than its congeners. The values are very similar for pots that received added nitrogen and pots that did not. Overall, relative yields were smaller than they were for Experiment 1. Relative yield, relative leaf length, and relative leaf number all appear to increase with density for *H. aurantiacum*, but for *H. longipilum*, all three measures were fairly similar at all density levels, with no indication of a consistent trend toward increasing or decreasing plant size with increasing density (Table 1.7).

The mean aggressivity values for Experiment 2 (Table 1.8) show a different pattern than that seen in Experiment 1. *H. aurantiacum* consistently had higher aggressivity values than *H. aurantiacum* did, suggesting that *H. aurantiacum* was a stronger competitor than *H. longipilum* in these pots.

Relative yield declined with increasing proportion of conspecifics for both species at all density levels (Figs. 1.7 & 1.8). Increasing proportion of conspecifics had a greater effect on *H. aurantiacum* (Fig. 1.7) than it did on *H. longipilum* (Fig. 1.8) as indicated by the steeper negative slope for relative yield of *H. aurantiacum* biomass. An analysis of covariance showed that both species identity and proportion of conspecifics had significant effects on relative yield, but there was no effect of density or nitrogen treatment on the relative yields of these species (Table 1.9). There was a significant interaction between species and density, as seen in Experiment 1, but there were no other significant 2- or 3-way interaction terms.

Relative leaf length (Figs. 1.9 & 1.10) and relative leaf number (Figs. 1.11 & 1.12) also declined with increasing proportion of conspecifics for both species. ANCOVAs for both relative leaf length (Table 1.10) and relative leaf number (Table 1.11) showed that species identity and proportion of conspecifics were again the only significant main effects. There was a significant interaction between species identity and density for both variables.

DISCUSSION

These experimental results indicate that neither *H. aurantiacum*, the invasive species, nor *H. longipilum*, the native species, appears to be more limited by its congeners than it is by members of its own species. In both experiments, the mean relative yield values calculated for each density level indicate that both species performed better when grown with congeners than they did when grown in monoculture (Tables 1.1 and 1.7).

The mean aggressivity values from Experiment 1 also indicate that neither species was consistently a stronger competitor (Table 1.2). *H. longipilum* had higher aggressivity values at the lower planting densities in Experiment 1, although in the most crowded pots (density = 12), *H. aurantiacum* plants were more aggressive. In contrast, in Experiment 2 the mean aggressivity values were higher for *H. aurantiacum* than for *H. longipilum* for all treatments (Table 1.8), suggesting that *H. aurantiacum* had a stronger negative effect on the growth of *H. longipilum* than *H. longipilum* had on *H. aurantiacum*. The aggressivity values from these experiments do not indicate that *H. aurantiacum* is the dominant competitor.

Both species are clearly more limited by intraspecific competition than they are by interspecific competition, as evidenced by their strong declines in relative size as the proportion of conspecifics increased. This decline is visible for all measures of plant size: relative yield (Figs. 1.1, 1.2, 1.7, & 1.8); relative leaf length (Figs. 1.3, 1.4, 1.9, & 1.10); and relative leaf number (Figs. 1.11 & 1.12).

It is worth noting, however, that although relative yields were used to control for absolute differences in size between species, in the field these species achieve similar sizes (see Chapter II). This suggests that the exotic species, *H. aurantiacum*, has a much faster growth rate than its native congener. *H. aurantiacum* also flowers and reproduces much more quickly, as evidenced by the fact that in Experiment 1, 35 % of *H. aurantiacum* individuals flowered and 91 % were reproducing vegetatively through the production of stolons. In Experiment 2, none of the plants flowered. This was surprising, as Experiment 2 was nine days longer in duration than Experiment 1. Different sections of the greenhouse were used for the two experiments, so there may have been some climatic differences that led to differences in flowering time for plants in the two experiments. Nevertheless, 95% of *H. aurantiacum* individuals in Experiment 2 produced stolons and were therefore reproducing.

Density had a significant effect on the growth of both species only in Experiment 1. In Experiment 2, there was a significant interaction between density and species, but no significant main effect of density, because only *H. aurantiacum* had reduced plant sizes as a result of increasing density. The effect of density on both species in Experiment 2 can be seen clearly by plotting biomass data from the monoculture pots (Fig. 1.13). There was no difference in size of *H. longipilum* individuals as density increased, but *H. aurantiacum* biomass declined steeply with increasing planting density. It is possible that the effect of density does not have a significant effect on growth until the pots reach some critical level of crowding. If so, it is possible that the significant effect of density on *H. longipilum* in Experiment 1 was driven by the highest density treatment, 12 plants per pot. It is interesting that density has a stronger effect on the growth of *H. aurantiacum* than on *H. longipilum*, because *H. aurantiacum* reproduces vegetatively by producing stolons, whereas *H. longipilum* does not. Because it is a clonal species, *H. aurantiacum* is usually found in dense, monotypic stands, and as a result it is more typical for *H. aurantiacum* to experience high densities of conspecific neighbors than for *H. longipilum* to be surrounded by many individuals of its own species.

Species identity also had a significant effect on growth in both experiments. These species differences are not due to species-specific differences in plant size, because all measures of growth were corrected for size. That is, plants grown in mixture were compared with members of their own species grown in monoculture for each planting density. Thus, the differences in growth resulting from species identity are attributable to species traits other than absolute size.

There was no effect of nitrogen treatment on plant growth or competition between the two species. It is possible that the there was little or no competition for nitrogen in these experiments, because the levels of nitrogen in the greenhouse potting soil (~0.60 %N, ~38 C:N) were much higher than those found in the field at Cedar Creek (~0.07 %N, ~ 10 C:N). The addition of nitrogen may have had little effect on altering competition, because nitrogen was already quite abundant. However, Cedar Creek soil is atypical of the region; in most of the tallgrass prairie region, where these two species co-occur, soils are much more rich in organic matter and have higher nitrogen concentrations. The fact that these species are not in strong competition under high nutrient conditions suggests that at areas outside of Cedar Creek, competition between these species should not limit their growth.

It also possible that nitrogen is not the limiting resource for these plants. Though nitrogen is usually considered to limit terrestrial plant growth (Tilman 1997), these species may be more limited by light, water, or another soil nutrient. In the field, *H. aurantiacum* grows most densely in wet areas, so future experiments should examine the potential for water to be an important factor in *H. aurantiacum* growth. A third possible explanation for the lack of a nitrogen treatment effect is that the experiment was too short to see an increase in growth in response to elevated nitrogen availability. Plants may need a longer amount of time to respond to increased nutrient availability with increased growth. However, this explanation seems unlikely, given the fact that *H. aurantiacum* individuals, expected to respond positively to nitrogen addition, achieved large sizes and were undergoing extensive vegetative reproduction by the end of the experiment.

Finally, root biomass was not measured in these experiments, because it is difficult to disentangle the delicate, fibrous roots of these plants without tearing them off the plant before it can be determined which plant produced each root. However, it is possible that a response to elevated nitrogen would have been manifested in increased root biomass, rather than increased vegetative growth. Witkowski (1991) found that *Acacia saligna*, an invader, consistently allocated more of its resources to producing root biomass than did a co-occurring native species. If *H. aurantiacum* or *H. longipilum* responds to increased nitrogen by augmenting root growth, I would not have been able to detect that effect with this experiment.

Greenhouse experiments are useful in that they provide a controlled environment in which one can isolate and test certain factors of interest, in this case competition between a native and exotic species under ambient conditions and with enhanced soil nitrogen. However, results from a competition experiment in a controlled environment are difficult to apply to the field where spatial and temporal heterogeneity can modify competitive outcomes. In general, however, heterogeneity often allows for coexistence while homogeneous conditions might favor one species over the other. These experiments should enhance the likelihood of detecting competition between the two species. The fact that no strong competitive effects between these species were found under ideal growing conditions provides compelling evidence that these species are truly more limited by competition from conspecifics than from congeners.

Competition is often predicted to be stronger between congeners than between two less closely related species, because congeners are often more similar in growth form and are therefore expected to have more similar resource requirements (Goldberg 1987). Despite the morphological similarities and close taxonomic relationship between *H. aurantiacum* and *H. longipilum*, strong interspecific competition was not found. This study has important implications for invasions ecology in its demonstration that successful invaders need not be superior competitors. These findings suggest that we should examine other traits of invaders and the communities they invade to achieve a better understanding of the causes of invasion success.

Table 1.1. Mean relative yields and mean relative leaf lengths by treatment, Experiment 1.

Density	Relative yield *H. aurantiacum*	Relative yield *H. longipilum*	Relative leaf length *H. aurantiacum*	Relative leaf length *H. longipilum*
2	2.510	4.772	2.027	1.539
4	4.211	6.119	2.468	1.594
8	6.042	9.305	3.115	1.616
12	7.033	4.309	3.288	1.388

Table 1.2: Mean aggressivity values, Experiment 1.

Density	Aggressivity of *H. aurantiacum*	Aggressivity of *H. longipilum*
2	-2.262	2.262
4	-1.908	1.908
8	-3.263	3.263
12	2.724	-2.724

Table 1.3: Analysis of covariance results for relative yield, experiment 1.

Source	df	F-ratio	P
Species	1	4.741	**0.031**
Density	3	4.615	**0.004**
Species x density	3	5.961	**0.001**
Proportion conspecifics (covariate)	1	118.418	**<0.001**
Error	123		

Table 1.4: Analysis of covariance results for relative leaf length, Experiment 1.

Source	df	F-ratio	P
Species	1	35.016	**<0.001**
Density	3	0.518	0.671
Species x density	3	1.205	0.311
Proportion conspecifics (covariate)	1	392.963	**<0.001**
Error	120		

Table 1.5: Analysis of variance results for *H. aurantiacum* height, Experiment 1.

Source	df	F-ratio	P
Density	3	26.502	**<0.001**
Proportion conspecifics	1	93.459	**<0.001**
Error	69		

Table 1.6: Analysis of variance results for *H. aurantiacum* reproductive biomass, Experiment 1.

Source	df	F-ratio	P
Density	3	28.688	**<0.001**
Proportion conspecifics	1	80.541	**<0.001**
Error	65		

Table 1.7. Mean relative yield, relative leaf lengths, and relative numbers of leaves by treatment, Experiment 2. *H. a.* = *H. aurantiacum* and *H. l.* = *H. longipilum*.

Density	Nitrogen treatment	Rel. yield *H.a.*	Rel. yield *H. l.*	Rel. leaf length *H. a.*	Rel. leaf length *H. l.*	Rel. # leaves *H. a.*	Rel. # leaves *H. l.*
2	+	2.185	1.866	2.023	2.061	2.087	1.897
	-	2.562	1.812	1.974	2.188	2.182	2.114
4	+	3.406	1.430	2.555	2.113	2.656	2.107
	-	3.424	1.499	2.500	2.309	2.473	2.317
8	+	3.435	1.152	2.639	1.997	2.698	2.070
	-	3.552	1.097	2.578	1.681	2.759	1.992

Table 1.8: Mean aggressivity values by treatment for Experiment 2.

Density	Nitrogen treatment	Aggressivity of *H. aurantiacum*	Aggressivity of *H. longipilum*
2	+	0.319	-0.319
	-	0.750	-0.750
4	+	1.976	-1.976
	-	1.925	-1.925
8	+	2.314	-2.314
	-	2.455	-2.455

Table 1.9: ANCOVA for relative yield, Experiment 2.

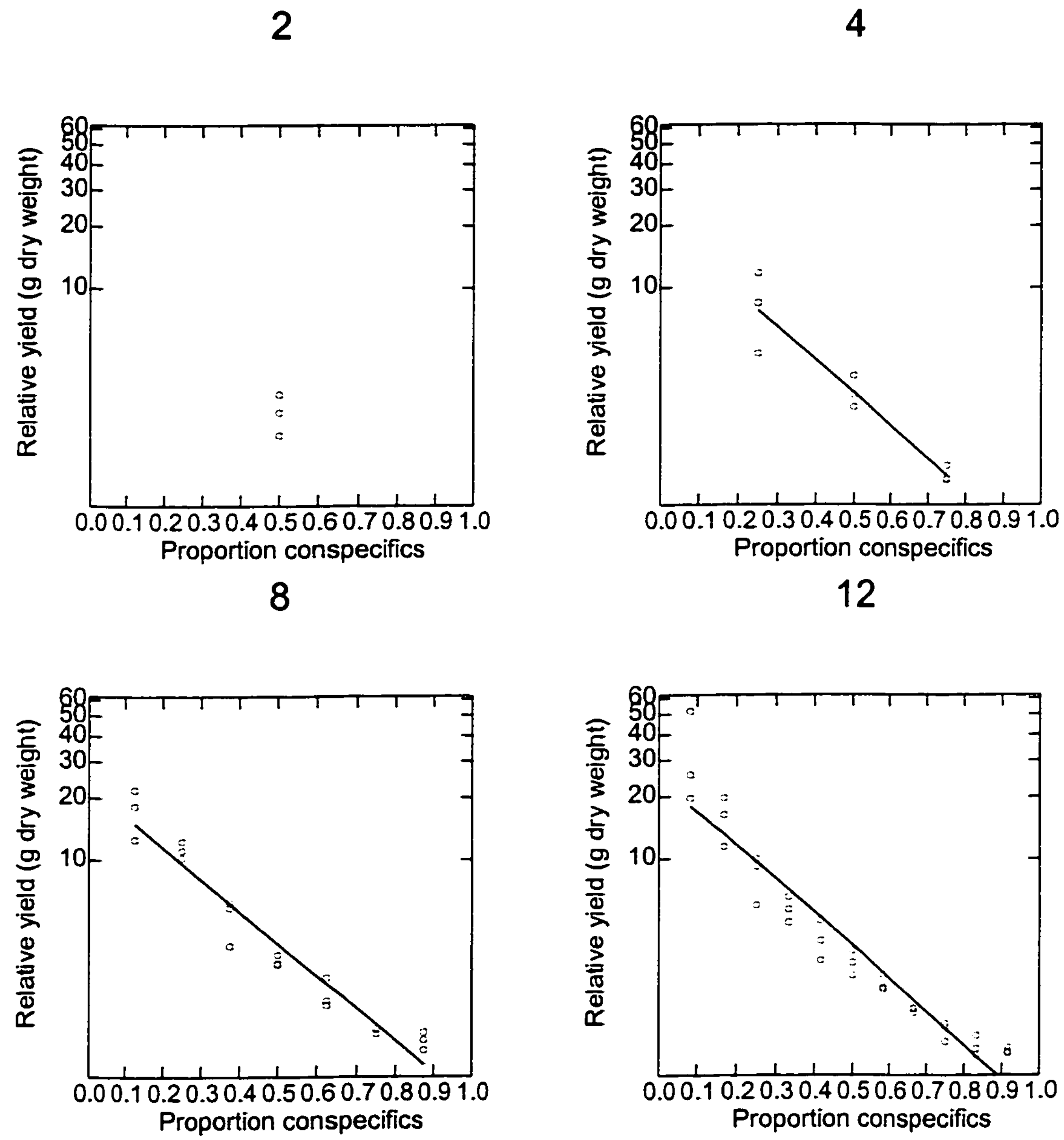
Source	df	F-ratio	P
Species	1	76.694	**<0.001**
Nitrogen treatment	1	0.025	0.874
Density	2	0.803	0.452
Species x N	1	0.276	0.601
Species x density	2	7.709	**0.001**
N x density	2	0.356	0.702
Species x N x density	2	0.006	0.995
Proportion conspecifics	1	102.798	**<0.001**
Error	71		

Table 1.10: ANCOVA for relative leaf length, Experiment 2.

Source	df	F-ratio	P
Species	1	15.881	**<0.001**
Nitrogen treatment	1	0.372	0.544
Density	2	2.714	0.073
Species x N	1	0.004	0.951
Species x density	2	9.898	**<0.001**
N x density	2	2.382	0.100
Species x N x density	2	1.971	0.147
Proportion conspecifics	1	649.318	**<0.001**
Error	71		

Table 1.11: ANCOVA for relative number of leaves, Experiment 2.

Source	df	F-ratio	P
Species	1	22.257	**<0.001**
Nitrogen treatment	1	0.919	0.341
Density	2	0.495	0.612
Species x N	1	0.650	0.423
Species x density	2	4.645	**0.013**
N x density	2	0.769	0.467
Species x N x density	2	0.424	0.656
Proportion conspecifics	1	783.149	**<0.001**
Error	71		



2

4

8

12

Figure 1.1. Relative yield of *H. aurantiacum* grown in mixture at different proportions of conspecifics and different densities, Experiment 1. Numbers at the top of each graph represent density treatment (2, 4, 8, or 12 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

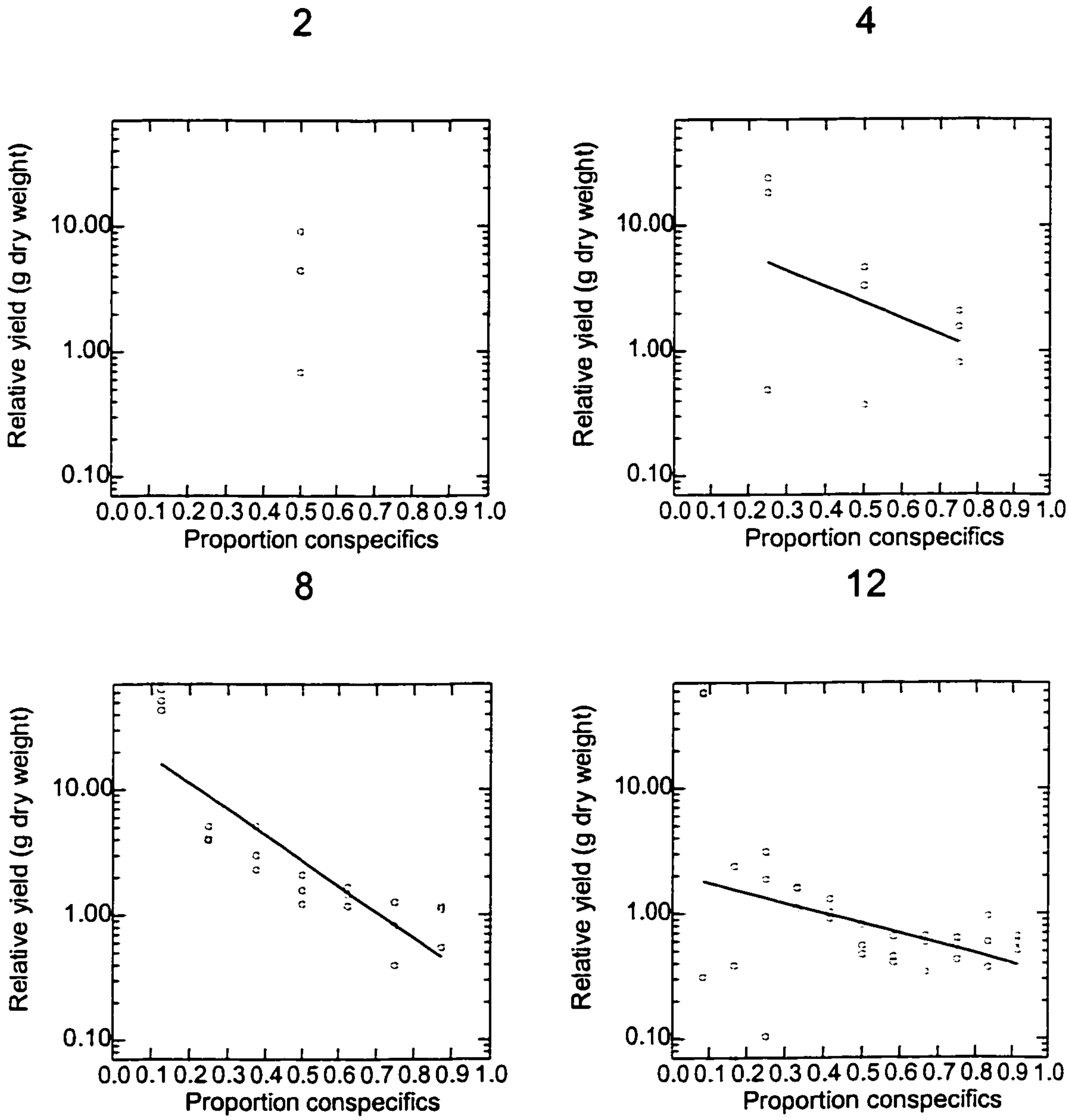


Figure 1.2. Relative yield of *H. longipilum* grown in mixture at different proportions of conspecifics and different densities, Experiment 1. Numbers at the top of each graph represent density treatment (2, 4, 8, or 12 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

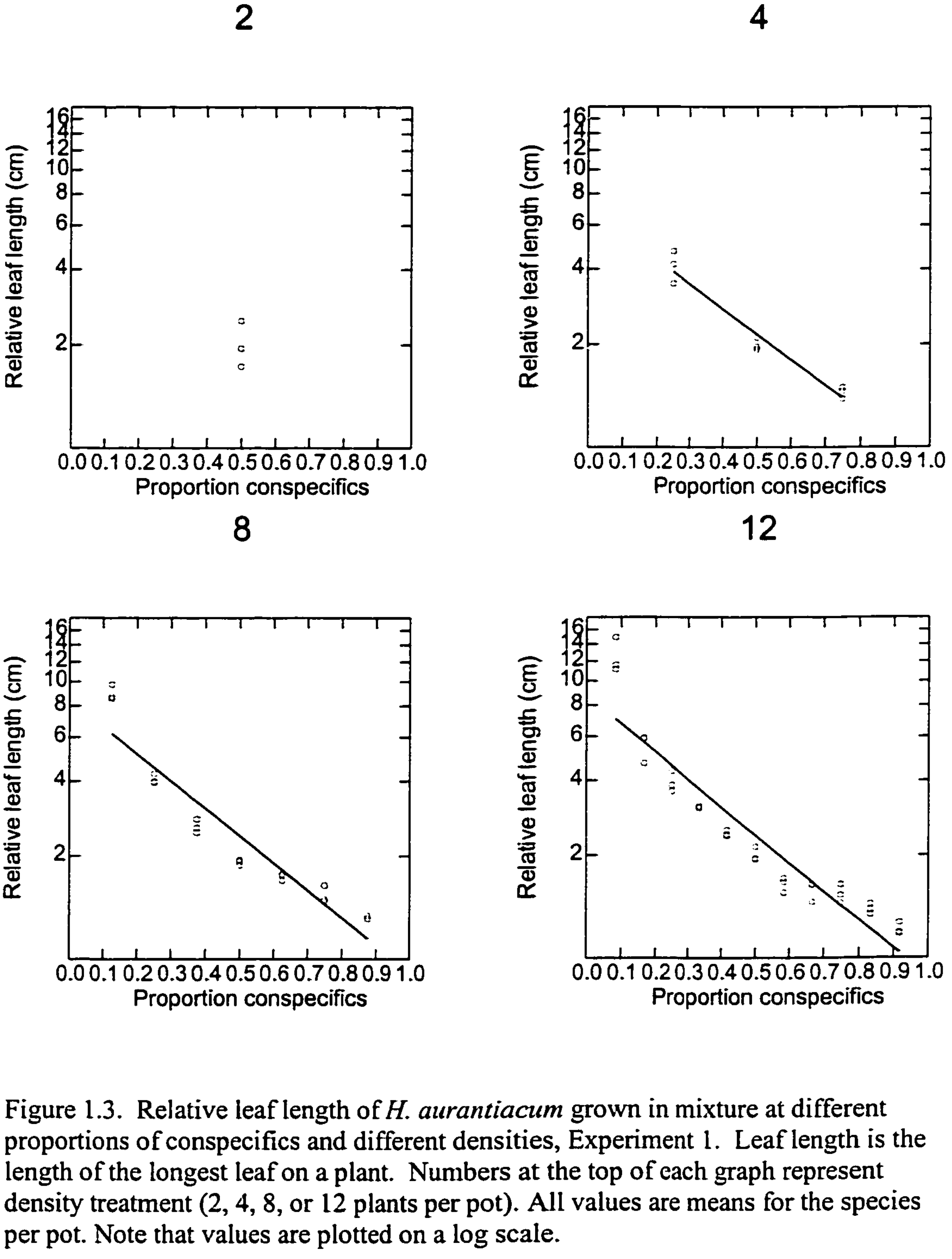


Figure 1.3. Relative leaf length of *H. aurantiacum* grown in mixture at different proportions of conspecifics and different densities, Experiment 1. Leaf length is the length of the longest leaf on a plant. Numbers at the top of each graph represent density treatment (2, 4, 8, or 12 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

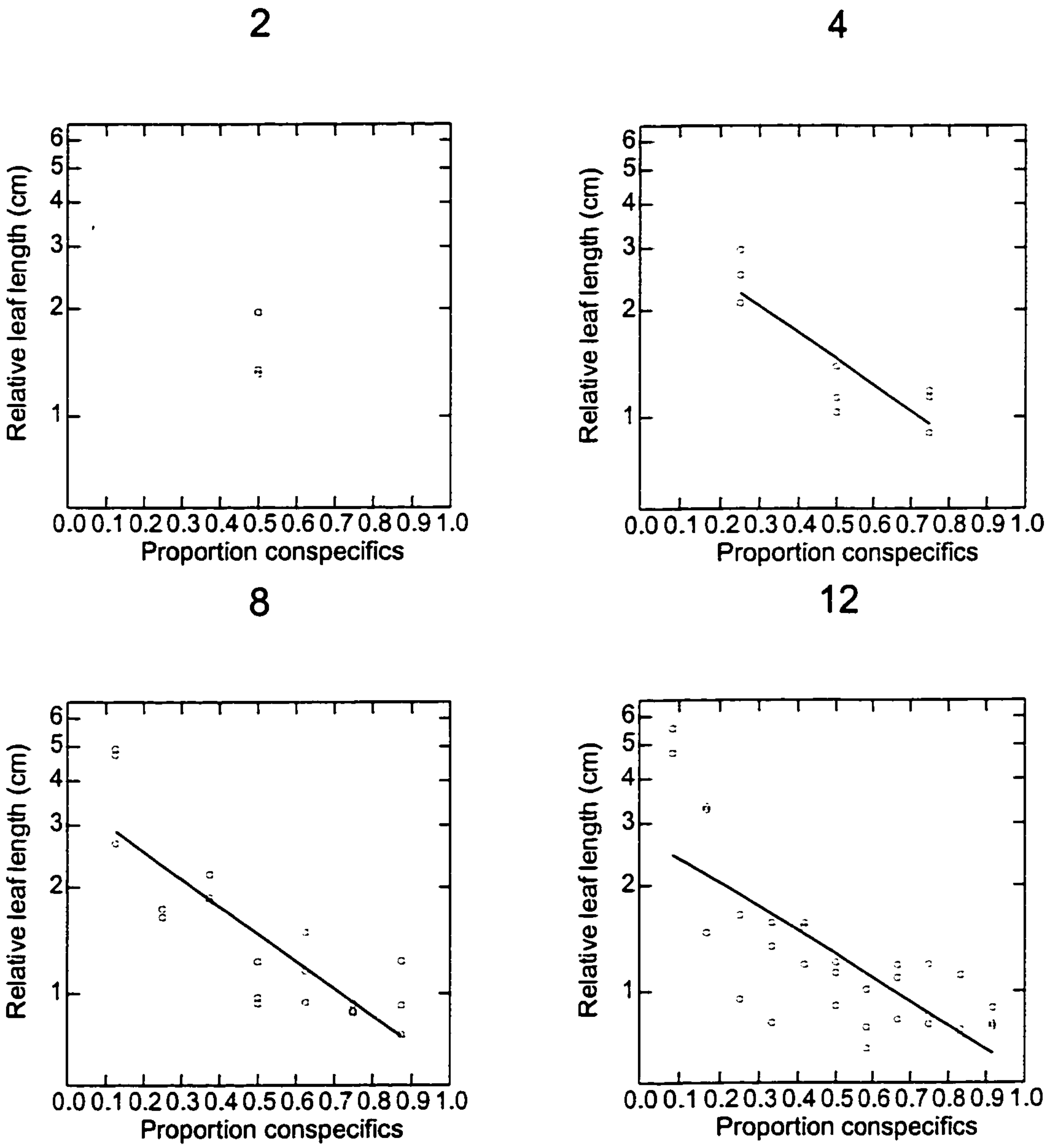


Figure 1.4. Relative leaf length of *H. longipilum* grown in mixture at different proportions of conspecifics and different densities, Experiment 1. Leaf length is the length of the longest leaf on a plant. Numbers at the top of each graph represent density treatment (2, 4, 8, or 12 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

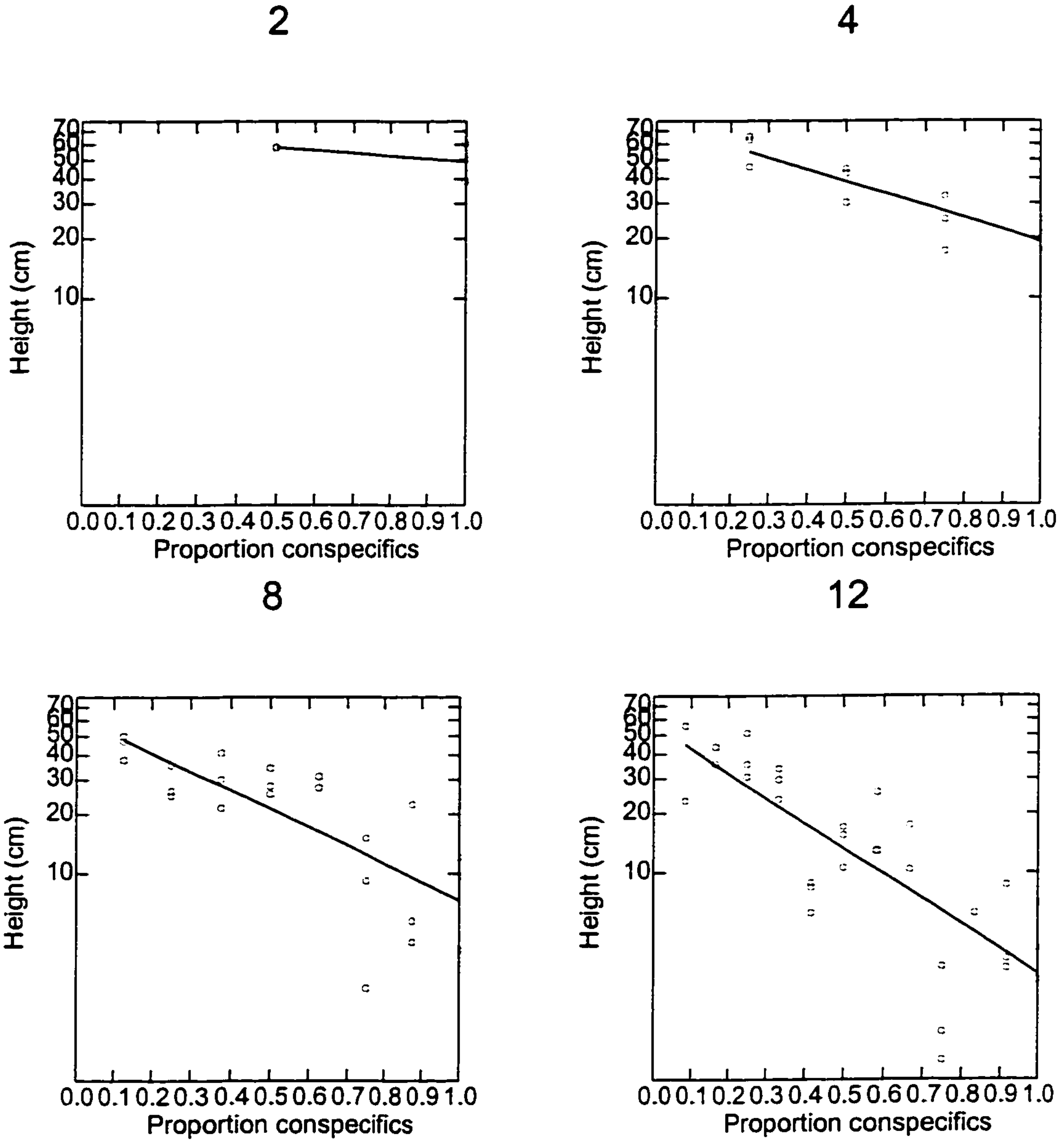


Figure 1.5. Mean height in cm of *H. aurantiacum* flowering stalks for plants grown in mixture at different proportions of conspecifics and different densities, Experiment 1. Numbers at the top of each graph represent density treatment (2, 4, 8, or 12 plants per pot). Note that values are plotted on a log scale.

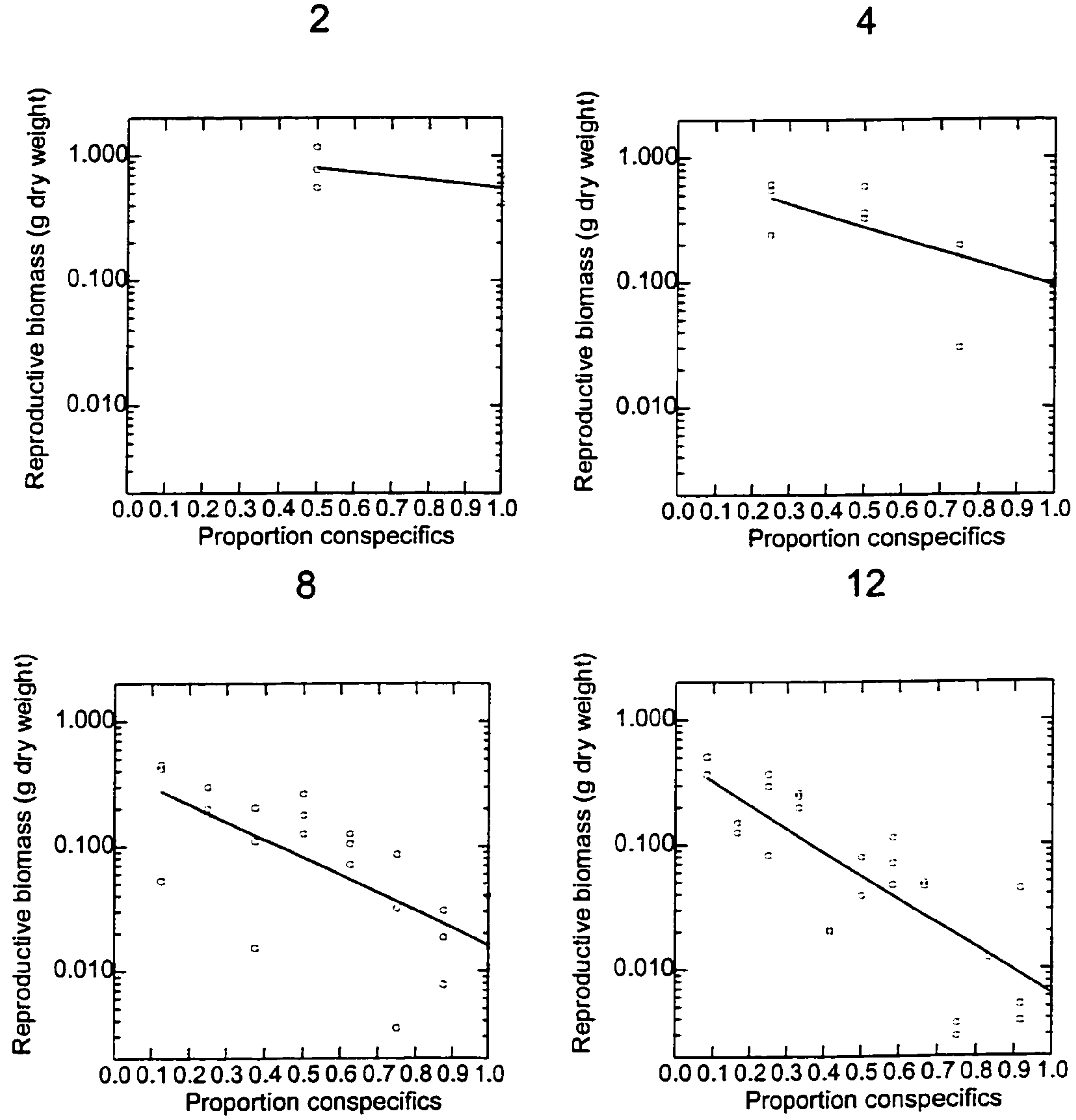


Figure 1.6. Reproductive biomass in g dry weight of *H. aurantiacum* plants grown in mixture at different proportions of conspecifics and different densities, Experiment 1. Numbers at the top of each graph represent density treatment (2, 4, 8, or 12 plants per pot). Note that values are plotted on a log scale.

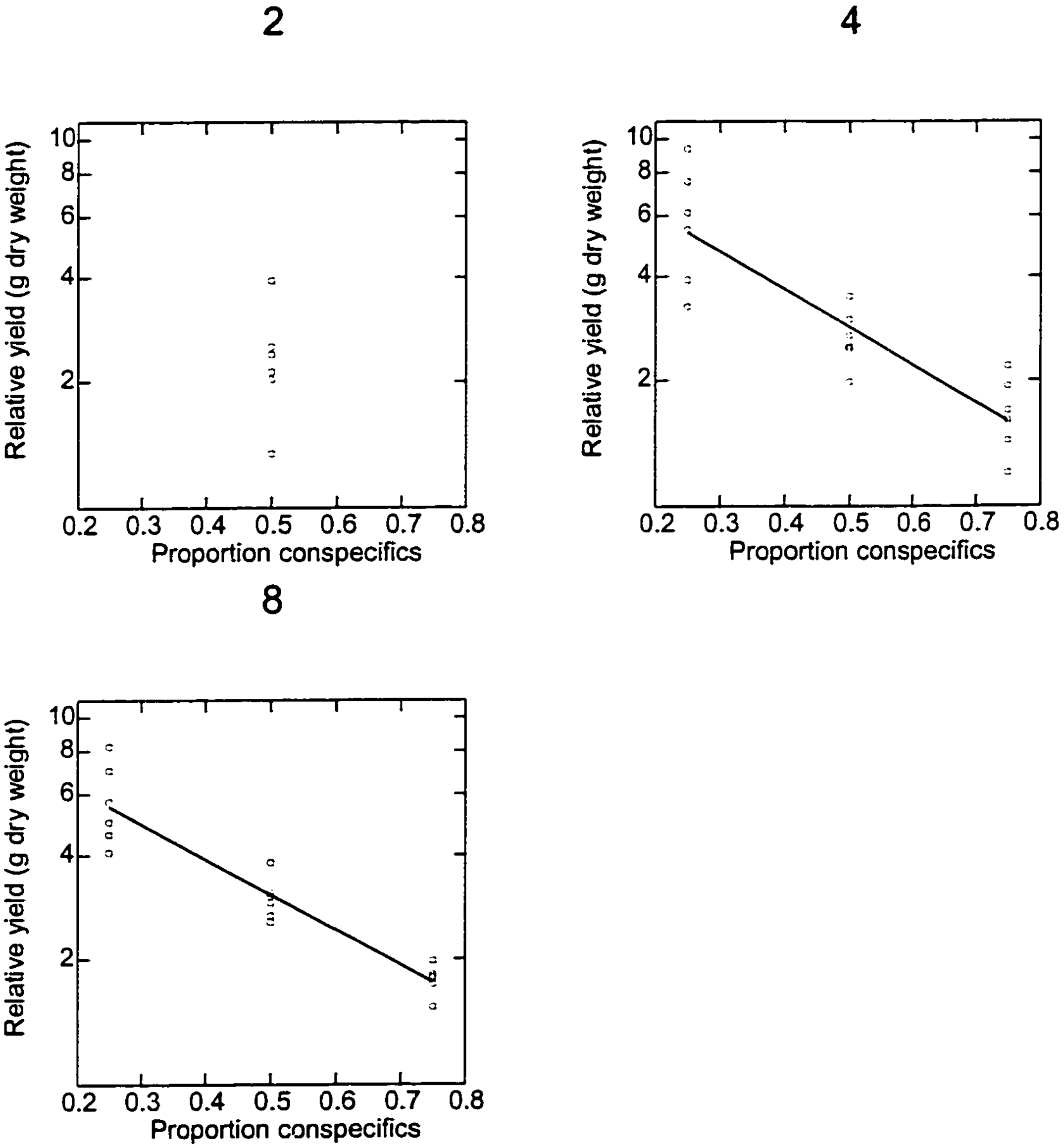


Figure 1.7. Relative yield of *H. aurantiacum* grown in mixture at different proportions of conspecifics and different densities, Experiment 2. Numbers at the top of each graph represent density treatment (2, 4, or 8 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

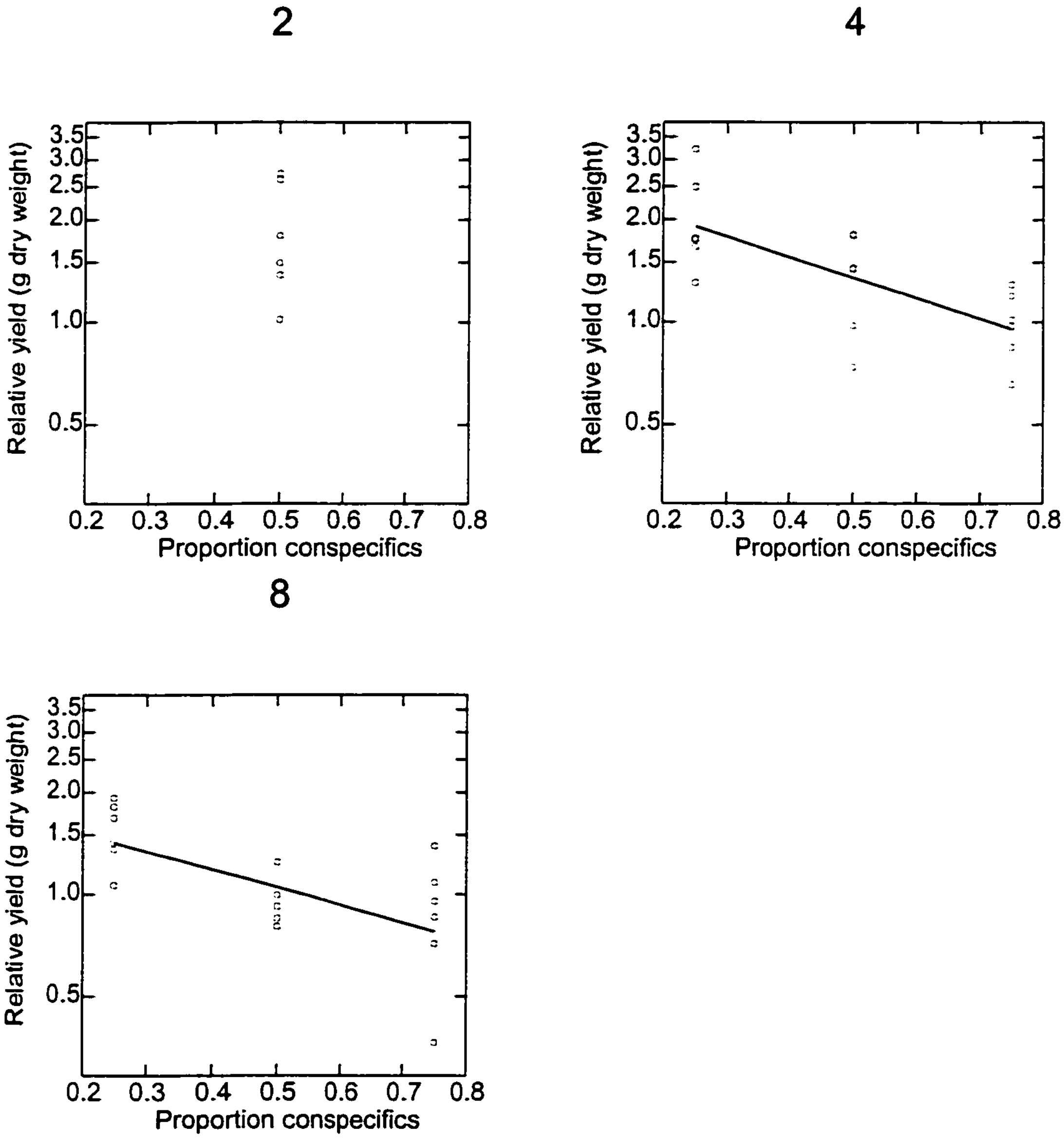


Figure 1.8. Relative yield of *H. longipilum* grown in mixture at different proportions of conspecifics and different densities, Experiment 2. Numbers at the top of each graph represent density treatment (2, 4, or 8 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

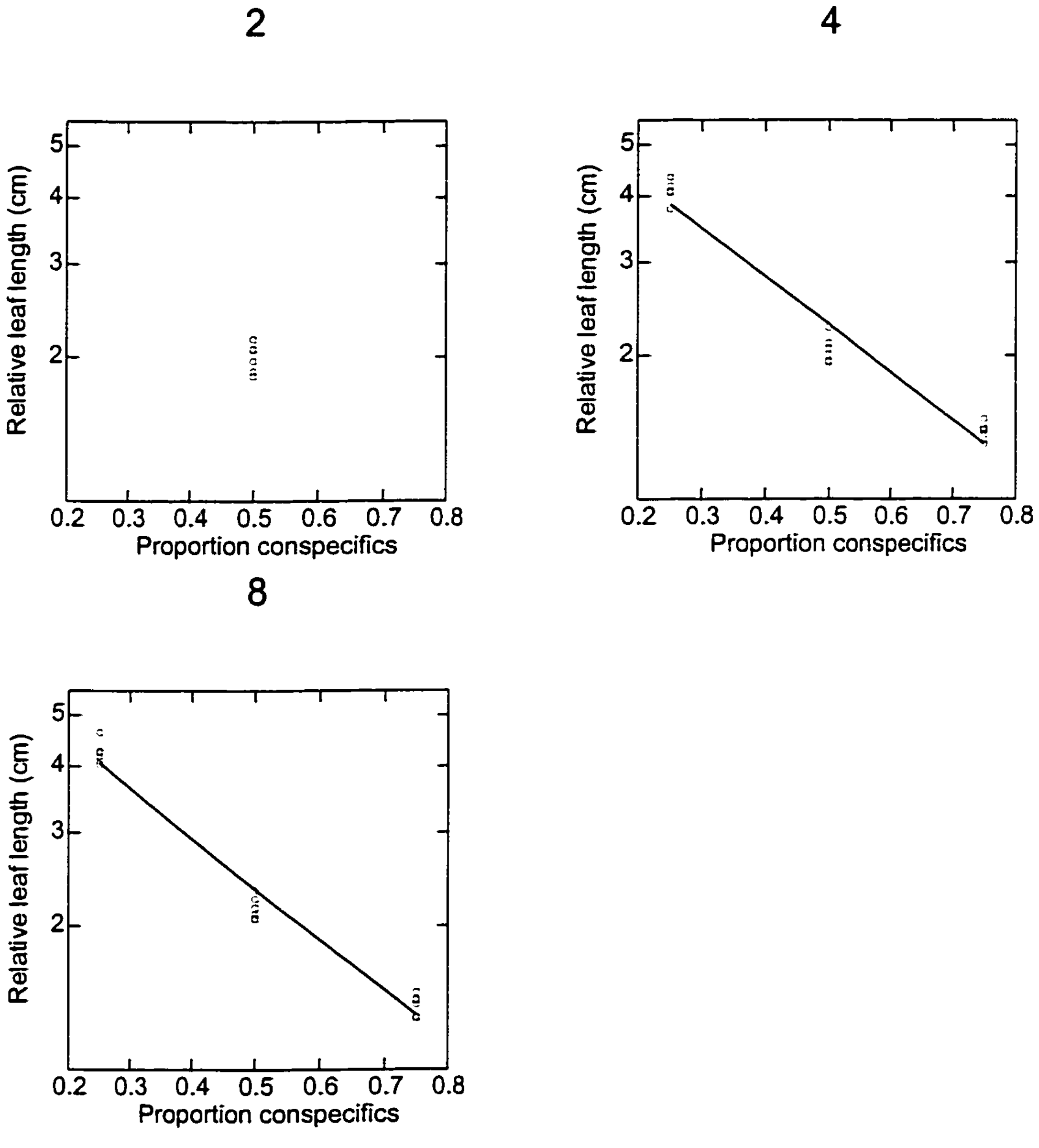


Figure 1.9. Relative leaf length of *H. aurantiacum* grown in mixture at different proportions of conspecifics and different densities, Experiment 2. Leaf length is the length of the longest leaf on a plant. Numbers at the top of each graph represent density treatment (2, 4, or 8 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

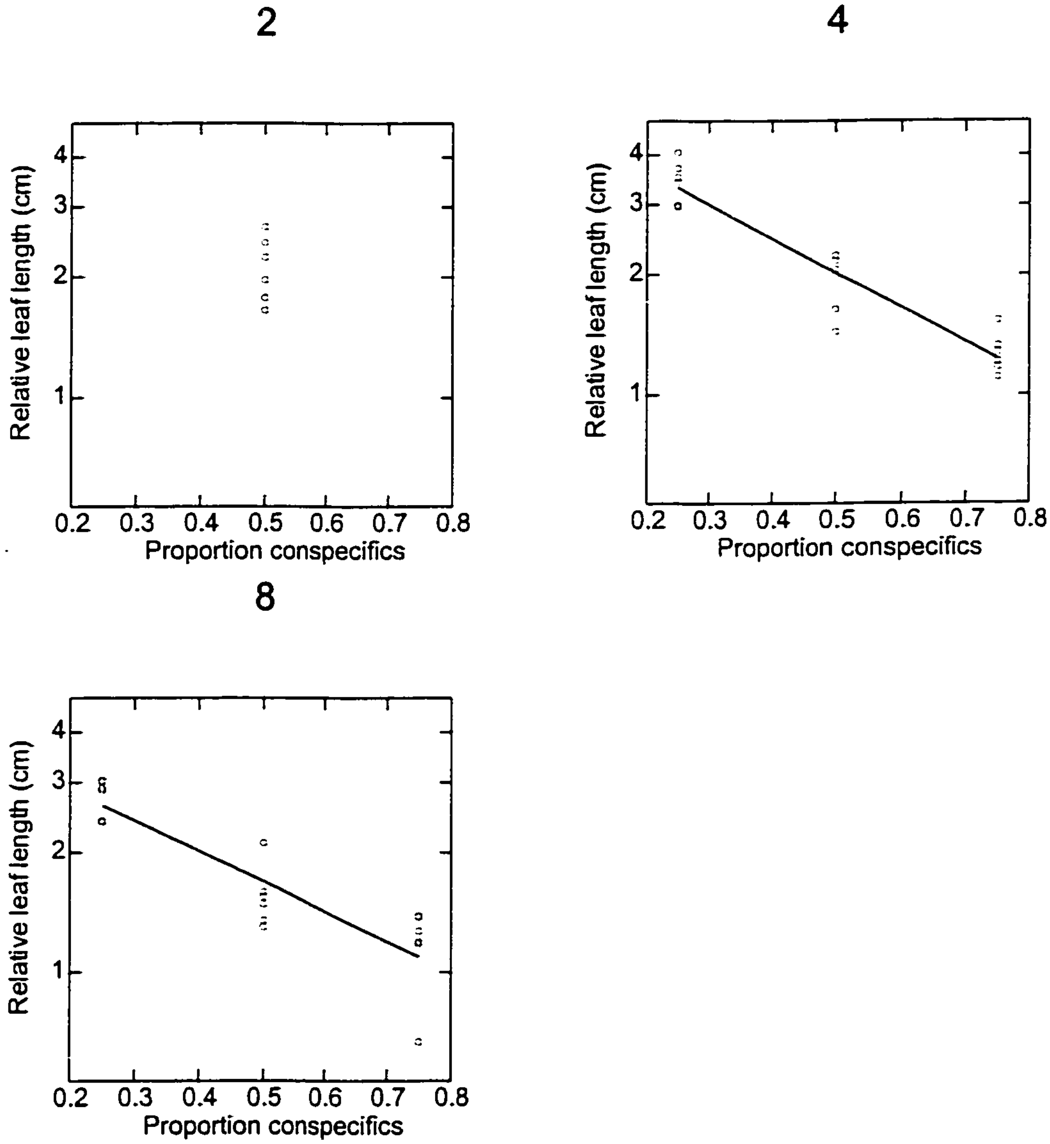


Figure 1.10. Relative leaf length of *H. longipilum* grown in mixture at different proportions of conspecifics and different densities, Experiment 2. Leaf length is the length of the longest leaf on a plant. Numbers at the top of each graph represent density treatment (2, 4, or 8 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

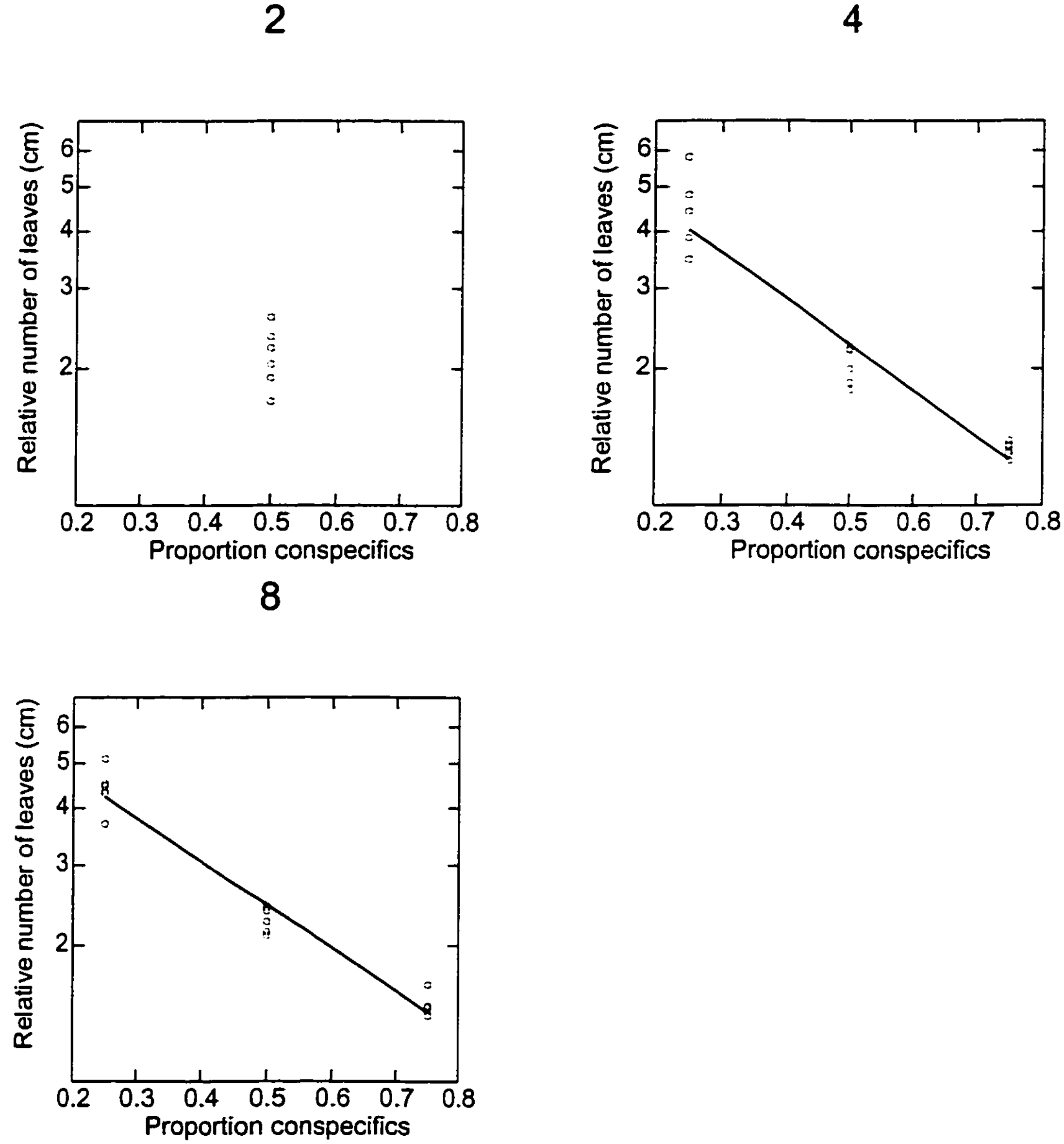


Figure 1.11. Relative number of leaves per plant for *H. aurantiacum* grown in mixture at different proportions of conspecifics and different densities, Experiment 2. Numbers at the top of each graph represent density treatment (2, 4, or 8 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

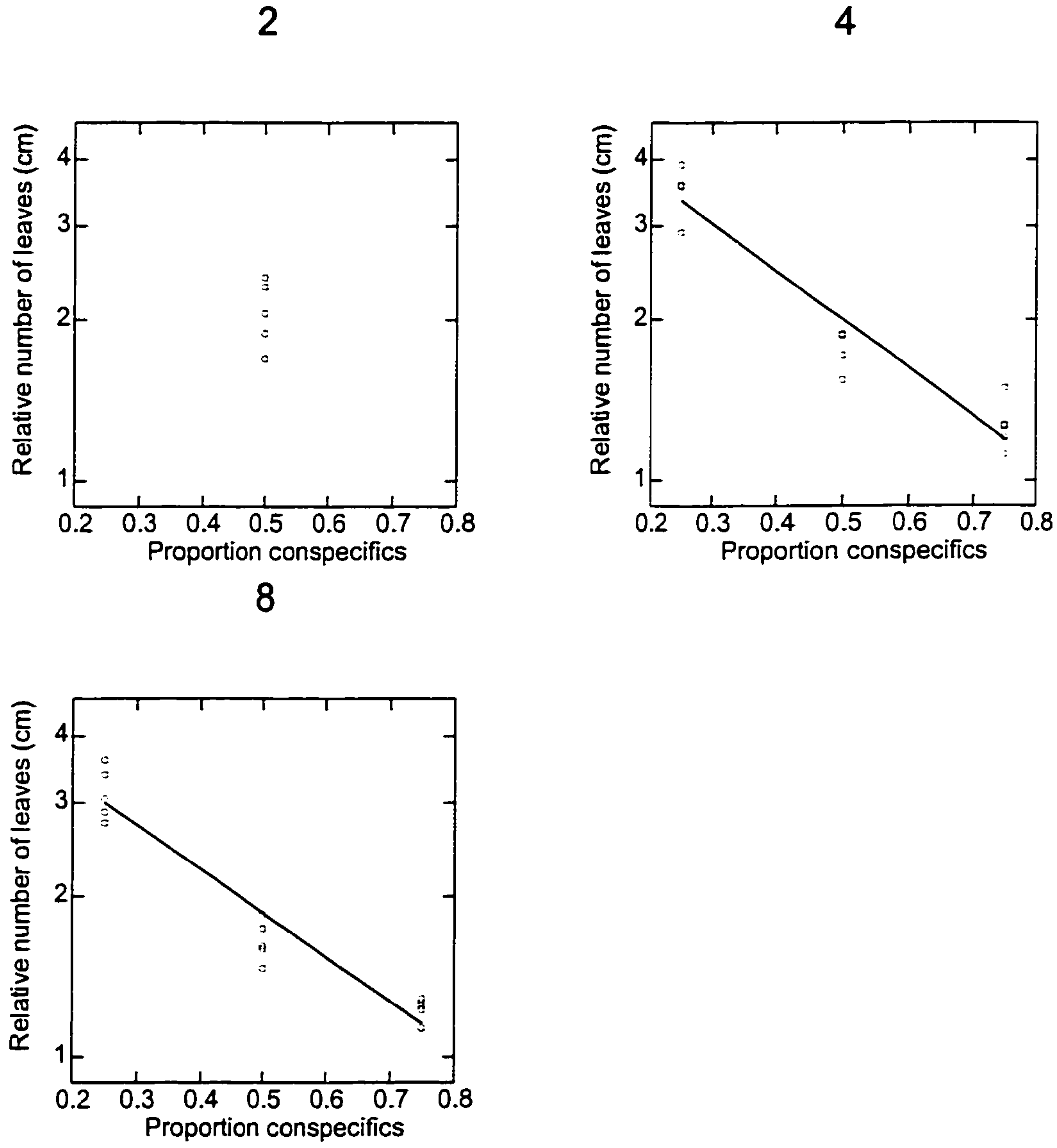


Figure 1.12. Relative number of leaves per plant for *H. longipilum* grown in mixture at different proportions of conspecifics and different densities, Experiment 2. Numbers at the top of each graph represent density treatment (2, 4, or 8 plants per pot). All values are means for the species per pot. Note that values are plotted on a log scale.

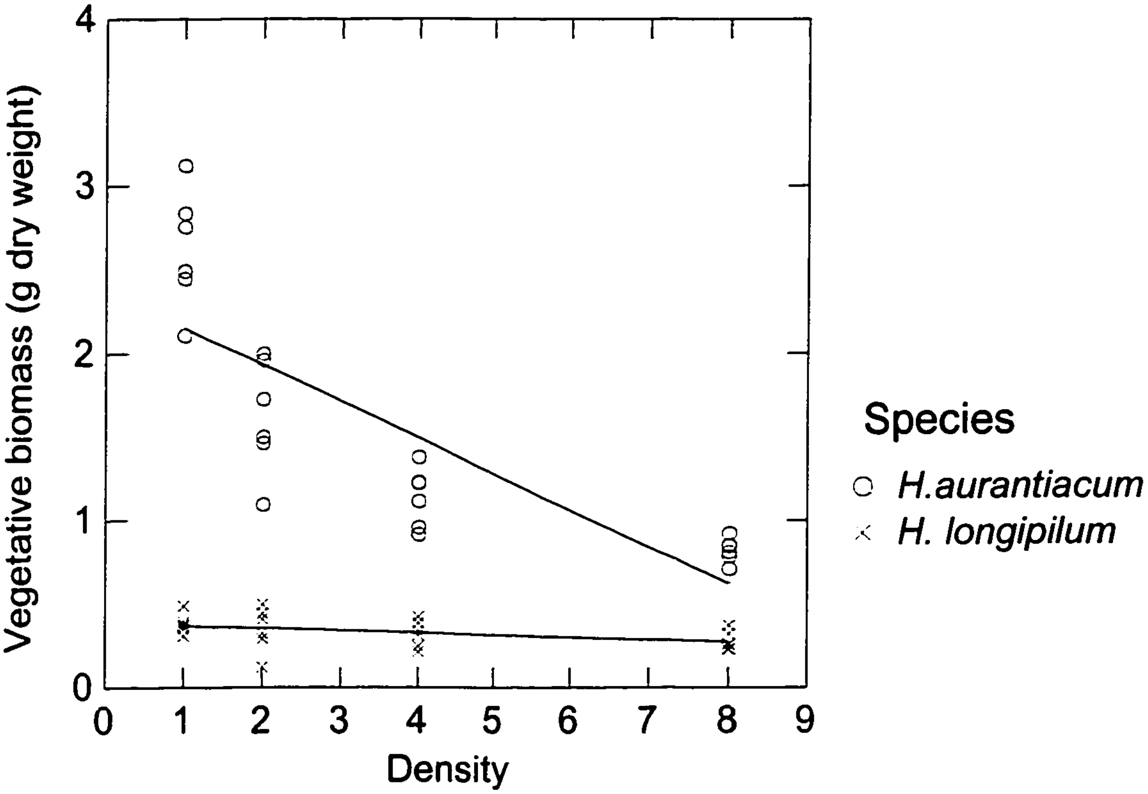


Figure 1.13. Vegetative biomass in g dry weight for plants grown in monoculture at different densities, Experiment 2. All values are means for the species per pot. *H. aurantiacum* is represented by (o) and *H. longipilum* is represented by (x).

CHAPTER II

REASONS FOR INVASION SUCCESS OF *HIERACIUM AURANTIACUM*: ENEMY ESCAPE OR UNIQUE MORPHOLOGY?

INTRODUCTION

The results of the greenhouse experiments reported in chapter one indicate that both *Hieracium aurantiacum*, an invasive species, and *Hieracium longipilum*, its co-occurring native species, are more limited by competition with members of their own species than they are by competition with congeners. Assuming that competition is likely to be most intense between closely-related congeners of similar growth form (Goldberg 1987), it appears that the invasion success of *H. aurantiacum* cannot be explained by superior competitive ability. In this chapter, I explore other reasons for the success of *H. aurantiacum*, using the congener comparison approach. First, I examine the potential role of enemy escape in favoring growth of the invader. Second, I present a detailed comparison of morphological traits of the two species to determine whether the invader has a unique characteristic that might explain its ability to invade areas already occupied by a native congener.

Enemy Escape

When a species arrives in a new region outside its original range, its interactions with resident enemies (predators, herbivores, parasites, or pathogens) may play an important role in its success in invasion (Maron and Vilà 2001). The exotic may be rapidly eliminated, because it has not evolved defense mechanisms to deal with native enemies. Alternatively, a species may be successful, either because it is not recognized as a food source by native enemies or it has some defense that prevents its consumption.

The idea that invasive species are successful because they have escaped the herbivores, pathogens, or predators of their native range was first introduced by Charles Darwin in his influential work *On the Origin of Species* (Darwin 1859). Charles Elton also discussed this concept in *The Ecology of Invasions by Plants and Animals*, the first comprehensive text on invasive species (Elton 1958). Today this idea, often referred to as the enemy escape hypothesis or the natural enemies hypothesis, is widely discussed in both the popular press and the scientific literature, yet there is equivocal evidence as to its validity.

The natural enemies hypothesis is the scientific basis for undertaking biological control (Maron and Vilà 2001), and much of the evidence supporting the natural enemies hypothesis comes from successful biological control efforts. For example, the introduction of the herbivorous cactus moth, *Cactoblastis cactorum*, was extremely successful in controlling cacti in the genus *Opuntia* that had invaded

Australia and sub-Saharan Africa (Zimmerman et al. 2000). This example and others (McEvoy et al. 1991, Kok 2001) in which an invasive species was controlled by introducing a natural enemy from its native range, lend support to the idea that enemy escape allows a species to become a successful invader.

For every example of a biological control effort that was successful, however, there are many more that were unsuccessful. In some cases, biological control agents become successfully established but fail to control the target invader (Callaway et al. 1999, Kriticos et al. 1999). Callaway *et al.* (1999) actually found that *Centaurea*, an aggressive invader, had a greater negative effect on the native grass *Festuca idahoensis* when attacked by a biocontrol agent, possibly because herbivory stimulated greater production of allelopathic chemicals by *Centaurea*.

There are many other examples of biological control efforts that have failed. In fact, a 1995 government report stated that 30 of the 51 documented efforts in the U.S. to control weeds with a biological agent had completely failed (OTA 1995). Of those that were successful, the extent of the weed control ranged from "complete" to "substantial" to "partial".

Failure of an introduced natural enemy to control an invasive species could occur for one of two reasons. First, it is possible that the biocontrol agent failed because the natural enemy that was introduced was not one that limited population growth in the invader's home range. Second, the introduced natural enemy may not control the invader under the novel conditions of the introduced range. Populations of the biocontrol agent may be reduced by climate or other abiotic factors or by predation from new enemies of its own. Alternatively, the biocontrol agent may feed on a non-target species in its new range, reducing the damage done to the target invader by the biocontrol agent. The success of a biocontrol effort is likely to depend on the community and ecosystem characteristics of its introduced range.

Therefore, it is difficult to determine from the anecdotal evidence of biological control whether the absence of natural enemies explains the invasion success of exotic species. A recent study of 474 invasive plant species (Mitchell and Power in press) showed that invasive plants tend to have fewer pathogens in their introduced ranges than they do in their native ranges. Furthermore, the invaders found to have fewer pathogens were also more aggressive invaders.

Experimental studies of the effects of enemy escape on invasion success are few. Congener comparison studies, in which closely related native and invasive species are compared, have been useful in approaching this problem; by comparing species that share most of their traits, it is possible to minimize differences in herbivory resulting from something other than species origin. In one such study, Schierenbeck *et al.* (1994) found that *Lonicera sempervirens* (coral honeysuckle), a shrub native to the southeast U.S., experienced less damage from herbivores than did its invasive congener, *Lonicera japonica* (Japanese honeysuckle). *L. japonica* also had a greater ability to regrow lost tissue after it was removed by herbivores. These data suggest that both partial enemy escape (less damage from herbivores than the native species) and greater tolerance of herbivory contribute to the invasion success of *L. japonica*. Greater compensatory growth following herbivory also appears to explain the invasion success of *Agropyron desertorum*, an exotic bunchgrass in the western U.S., in an area occupied by a native congener, *Agropyron spicatum* (Caldwell et al. 1981).

These studies (Mitchell and Power *in press*, Schierenbeck *et al.* 1994, Caldwell *et al.* 1981) provide some evidence that enemy escape may play a role in improving invasion success, but the quantity of evidence is small. In this chapter, I examine the role of enemy escape in the success of *Hieracium aurantiacum*, as well as community and ecosystem characteristics that may affect the interactions between *H. aurantiacum* and native enemies as a model study system to test the natural enemies hypothesis. Any changes in herbivore and pathogen abundance are likely to affect plant community composition and edaphic properties, which in turn are likely to have an impact on the performance of *H. aurantiacum* and *H. longipilum* (Fig. 2.1). In this study, I experimentally test the effects of enemy removal on both species, as well as the effects of the plant community and edaphic properties on *Hieracium* success.

Species Traits

Another possible explanation for the success of an invasive species is that some unique morphological or physiological trait allows it to occupy a vacant niche in its introduced range. Until recently, much of the work done to identify the traits of invasive species involved compiling anecdotal evidence from case studies of biological invasions. Baker (1965, 1974) used this approach in compiling a list of "ideal weed characteristics" specific to plant invaders. Lodge performed a similar study approximately 30 years later (Lodge 1993), expanding the list to include traits of invasive animals as well as plants.

In an effort to get more quantitative information about the characteristics of invasive species, congener comparison studies have also been used to identify physiological and morphological traits of a pair of native and invasive congeners (Eissenstat and Caldwell 1989, Kloeppel and Abrams 1995, Schweitzer and Larson 1999, Larson 2000, Van Clef and Stiles 2001). A comparison of 34 native and 30 invasive species in Hawaii indicated that invasive species had greater nutrient use efficiencies and faster growth rates than the native species (Baruch and Goldstein 1999). However, a similar study, which made comparisons between closely related invasive and native species rather than invaders and natives in general, found that there were few significant differences in resource use and growth based on species origin (Smith and Knapp 2001). Despite several decades of interest in the topic, there is still a significant dearth of information about what traits are associated with invasion success.

In the second part of this chapter, I will compare some key morphological traits of *H. aurantiacum* and its native congener, *H. longipilum* to determine whether it is likely that *H. aurantiacum* has some unique trait that might explain its invasion success.

METHODS

Study Site

All data were collected at Cedar Creek Natural History Area in Bethel, Minnesota. Cedar Creek is a 2200 ha Long-Term Ecological Research (LTER) site and protected scientific and natural area, owned by the University of Minnesota. Cedar Creek contains a mosaic of habitat types (Fig. 2.2), including oak forest, oak savanna, floating bogs, marshes, lakes, and old fields abandoned from agriculture between 1938 and 1986.

Study Species

Hieracium longipilum is a perennial forb native to Cedar Creek, and *Hieracium aurantiacum* is an invasive exotic species, first recorded at Cedar Creek in 1975. These species have similar growth forms and life histories. Both species are perennials that spend the majority of their lives in rosette form, sending up a flowering stalk with multiple, apomictic flower heads no more than once a year. Both species are also well defended with dense trichomes on the leaves and stems and have a milky, white latex. For a further description of the ecology of these two species see Chapter I. My field observations indicated that the major forms of damage to *H. aurantiacum* and *H. longipilum* were herbivory by spittle bugs (*Philaenus spumarius*) and white-tailed deer (*Odocoileus virginanus*) and disease caused by a rust fungus (*Puccinia dioicae*).

Observational Data Collection

Data on plant damage and plant performance were collected for naturally occurring populations of both *H. aurantiacum* and *H. longipilum* in several old fields from 1999-2001. In fields where one or both species of *Hieracium* occurred, sampling locations were selected by using randomly generated coordinates relative to a fixed point of origin. At each sampling location, a 1m x 1m quadrat was placed on the ground, and all species present within the quadrat were recorded. When one or more *Hieracium* individuals occurred within the quadrat the following measures of plant performance were recorded for each plant: length of longest leaf, number of leaves, height, number of flowers. The percentages of the plant lost to insect herbivory, deer herbivory, and fungal disease were also recorded.

In 2001, five plants of each species were collected for carbon and nitrogen analysis, to determine whether differences in plant damage between the species were related to tissue chemistry. Plants were divided into roots, leaves, flowering stalks, and flowers and then dried and weighed. Dried plants were ground with a coffee grinder, then further macerated with a mortar and pestle to homogenize the sample. Subsamples of each part from each plant were analyzed for carbon and nitrogen content using a Costech Elemental Combustion System 4010.

Experimental Design

In September 1998, preliminary data were collected on the effect of deer herbivory on reproductive success of *H. longipilum*. *H. longipilum* individuals growing inside or outside of existing deer exclosures were haphazardly selected, and both the number of flowers and the height of the flowering stalk were recorded. In each of two fields, 27 individual plants were sampled inside and 27 outside the exclosure, for a total of 108 plants.

In 1999, plots were established in two old fields, Fields 22 and 54 (Fig. 2.2), where both *H. aurantiacum* and *H. longipilum* were present. Plots were assigned treatments for species planted (*H. aurantiacum*, *H. longipilum*, or both species), exclosure type (insect + deer exclosure, deer exclosure, or no exclosure), and fungicide treatment (fungicide or no fungicide). Each treatment combination was replicated three times for a total of 54 $1 m^2$ plots in each field.

Seeds harvested from fields 22 and 54 in 1998 were planted in each plot in May 1999. Approximately 15 seeds were added to each plot. Germination rates were extremely low, and as a result, adult plants were transplanted from the surrounding fields into the plots in June 1999. Each plot received 2 individuals of each assigned *Hieracium* species. In June 2000 plots in which *Hieracium* individuals had not survived received new transplants.

Two additional sets of plots were constructed in 2001. These plots were located in Fields 63 and 70 (Fig. 2.2), where both *H. aurantiacum* and *H. longipilum* were also naturally occurring. The plots were added to increase the number of plots with deer exclosures and fungicide treatment in an effort to improve the ability to detect effects of those treatments. All the treatments were the same as those for the plots established in 1999, with the exception that there were no insect exclosure plots. Each treatment combination was replicated four times for a total of 48 plots in each field. All plants were transplanted into the plots from the surrounding fields.

Deer exclosures were constructed of 4.5-foot tall mesh fencing with one-inch openings, erected around the four sides of the plot with the top open to prevent shading. Mesh openings were large enough to allow insects to move freely in and out of the plot. Insect exclosures were constructed of window screening erected around the four sides of the plot with the tops open to prevent shading of the plants. Screening reduces insect abundance within plots by limiting lateral movement (Mark Ritchie, personal communication) but still allows insects to enter through the top of the cage. In order to further reduce insect abundances, plots were sprayed once every 2 weeks with esfenvalerate (Dupont™ Asana® XL), a natural pyrethrin insecticide derived from *Chrysanthemum* spp. (Asteraceae) (DuPont 2002). Esfenvalerate is classified by the EPA as a class II toxin (moderately toxic) and has been shown to have no non-target effects on Cedar Creek plants (Mitchell *in review*). All plots not receiving insecticide (i.e. plots with no insect exclosure treatment) were sprayed with an equal volume of water as a control. Insect exclosures also excluded deer by preventing them from entering the plots.

Foliar fungal pathogens were excluded by spraying plots with mancozeb (Penncozeb), an EPA class IV pesticide (practically nontoxic). Mancozeb is not active in the soil and should therefore have no effect on mycorrhizal fungi. Mitchell (Mitchell *in review*) found no non-target effects of mancozeb on Cedar Creek plants. In June 2002, our supply of mancozeb was depleted, and because the product had been discontinued we were unable to purchase more. As a result, the plots designated for fungal pathogen exclusion were sprayed with chlorothalonil (Ortho Daconil 2787; EPA toxicity class II) in July and August 2002. No information was available on effects of chlorothalonil on the plant community.

Insecticide and fungicide were applied to plots on a biweekly basis from June through August from 1999-2002 for fields 22 and 54 and 2001-2002 for fields 63 and 70. Deer cages were left in place year-round, but insect cages were put up in May and taken down in September each year to prevent snow damage to the screening. In 2002, the insect cages were not put up in order to increase the number of plots that were exposed to deer herbivory. Insecticide treatments in the insect exclosure plots were continued as normal.

Experimental Data Collection

In all plots, I recorded several measures of plant damage and plant performance. Plant damage was divided into three categories (insect, deer, and fungal pathogen) and the percent of the plant lost to each type of herbivore or pathogen was estimated through comparison of plants to cards representing fixed percentages of damage taken from James (1971). Measures of plant performance included length of the longest leaf, number of leaves, height of flowering stalk, and number of flowers. I also recorded the other species present in each plot. These data were all collected 2000-2002 in fields 22 and 54 and in 2002 for fields 63 and 70. In 2001, I also estimated the percent cover of all species present in each plot in Fields 22 and 54 to determine whether treatments had an effect on cover of other plant species. Percent cover was estimated by comparing plant cover to cards of fixed size (e.g. 1 cm^2, 5 cm^2, 10 cm^2). Total percent cover was required to total between 99 and 101%. Percentages of visible bare ground and leaf litter cover were also recorded. For the purpose of analyses, plant species were grouped into four functional groups based loosely on differences in resource use: legumes, non-leguminous forbs, graminoids, and mosses and lichens.

Data were collected on deer abundance in fields 22 and 54 to determine if deer were equally abundant both early and late in the season. If deer were not equally abundant during the flowering times of the invasive and native species (June and August, respectively), that would have implications for the likelihood of deer herbivory on the two species. Four to six Non-Typical Deer Finder Game Monitor infrared sensors were placed in each field from June 20-26 and August 14 –20, 2002. Sensors were attached to trees along the forest/field edge in areas with signs of visible deer activity (e.g. trails or fecal pellets). The sensors were set to take readings on deer presence up to 40 feet away every 5 seconds, 24 hours a day, for one week during each sampling period. Sensors were placed approximately two feet off the ground to prevent detection of smaller animals but to allow for detection of juvenile deer.

Soil measurements

I collected data on soil moisture, soil temperature, and soil carbon and nitrogen content to determine whether any of those variables had an effect on plant performance or plant damage. Soil moisture was measured with a Campbell Scientific Hydrosense water content sensor using time domain reflectometry (TDR) in 2000 and 2001. Soil temperature was measured with Taylor soil thermometers in 2000 and HOBO soil temperature data loggers in 2001. To measure soil carbon and nitrogen content, two 10 cm soil cores were removed from each plot and homogenized. Soil from each plot was passed through a sieve with 2mm openings to remove roots, rocks, and large leaf litter. Sieved soil was ground in a coffee grinder to further homogenize the sample. A 12-18 mg subsample of soil from each plot was analyzed for C and N content using a Costech Elemental Combustion System 4010. Soil samples were collected from fields 22 and 54 in 2000 and from all four fields in 2001.

Species Traits

Data on plant performance were also used to compare differences in morphology between the two species. In 2002, additional data were collected on leaf thickness and density of trichomes. Leaf thickness was measured using a micrometer.

To determine trichome density, one leaf from each plant was examined under a dissecting microscope, and the number of hairs in a 1-cm^2 area was recorded.

Statistical Analysis

Species differences in plant damage from observational surveys were analyzed using t-tests. Multi-variate analysis of variance (MANOVA) was used to analyze differences in carbon-to-nitrogen (C:N) ratios between *H. aurantiacum* and *H. longipilum*, using flower, leaf, root, and stem C:N ratios as response variables.

Preliminary data on the effects of deer herbivory on *H. longipilum* reproductive success were analyzed using two ANOVAs to compare the effects of both location (inside or outside of deer exclosure) and field identity on height and number of flowers. ANOVA was used to verify that the treatments were effective in reducing plant damage for both sets of plots.

Other experimental data were analyzed using MANOVA. In 2000 and 2001, the insect exclosures also excluded deer. However, in 2002 when the exclosures were removed and insects were removed only by the application of insecticide, those plots were susceptible to deer herbivory. This change in treatments during the experiment prevented me from using repeated measures ANOVA to analyze the data from all three years. Instead, I analyzed the data separately by year. For each year, I ran two MANOVAs; one examined the effect of treatments on plant size (length of longest leaf and number of leaves) and the other examined the effect of treatments on plant reproduction (height of flowering stalk and number of flowers). The data from the plots established in 2001 were analyzed separately, again using two MANOVAs to look for treatment effects on plant size and reproduction.

Two additional MANOVAs were used to look for treatment effects on edaphic properties and on plant community composition. Stepwise backward multiple regression was then used to determine if changes in edaphic properties or plant communities affected the size of *H. aurantiacum* and *H. longipilum* individuals.

RESULTS

Observational Data

H. aurantiacum and *H. longipilum* incurred different amounts of damage from herbivores and pathogens in unmanipulated censuses of naturally-occurring populations. *H. longipilum* experienced much greater damage from fungal pathogens (Fig. 2.3; $t = -21.44$, $df = 565$, $p < 0.001$) and deer herbivory ($t = -4.496$, $df = 567$, $p < 0.001$) than *H. aurantiacum* did. *H. aurantiacum* was damaged more by insect herbivores than *H. longipilum* was (Fig. 2.3; $t = 8.722$, $df = 562$, $p < 0.001$).

H. aurantiacum and *H. longipilum* had significantly different carbon to nitrogen ratios (Table 2.1). The canonical correlations from the MANOVA indicate that differences in root and flowering stalk C:N ratios contributed most strongly to the interspecific differences. *H. aurantiacum* had a much higher C:N ratio in its roots, whereas *H. longipilum* had significantly higher C:N in its flowering stalk than *H. aurantiacum* did (Fig. 2.4).

Experimental Data

Analysis of preliminary data showed that deer exclosure had a significant effect on the reproductive success of *H. longipilum*. Plants growing outside of the deer exclosures had significantly fewer flowers at the end of the growing season than plants protected from deer herbivory (inside the exclosures) (Table 2.2, Fig. 2.5A). Plants inside the exclosures were also taller than those outside the exclosures (Fig. 2.5B), but the difference in height was not statistically significant (Table 2.2).

For the experimental plots constructed in fields 22 and 54, I first tested to see if the insect, deer, and fungicide treatments were effective in reducing damage to *H. aurantiacum* and *H. longipilum*. Plants showed less damage from deer herbivory (df = 1, F = 5.710, p = 0.017) in plots with deer exclosures than in plots without exclosures. Damage from fungal disease was also significantly reduced by the application of fungicide (df = 1, F = 4.929, p = 0.027). However, there was not a significant decrease in damage from insect herbivory in plots from which insects were excluded (df = 1, F = 2.397, p = 0.123). Because the primary insect herbivore of *Hieracium* spp. at Cedar Creek is spittle bugs (*Lepyronia gibbosa*; Cercopidae: Homoptera), which are xylem feeders, the damage from spittle bugs is often inconspicuous, and therefore visual estimates of insect damage are likely to underestimate the total amount of plant tissue lost to spittle bugs (Carson and Root 2000). The correlation between original species treatment (*H. aurantiacum*, *H. longipilum*, or both species planted) and the species present at the end of the experiment was low for fields 22 and 54, because plants migrated into other plots or did not survive where they were planted. As a result, I did not test for species treatment (i.e. the presence of one or both species in a plot) in the analyses from those fields.

In 2000, plants of both species were larger in plots where insects and deer were excluded (Fig. 2.6). This difference was most likely due to insect, rather than deer, removal, because there was no difference in plant size for either species when only deer were excluded (Fig. 2.8, Table 2.3). The canonical correlations from the MANOVA of treatment effects on plant size indicate that the significant difference in plant size when insects were excluded is driven mostly by differences in leaf length (Table 2.3). *H. longipilum* had longer and a greater number of leaves when fungal pathogens were excluded (Fig. 2.10), but the cumulative effect of fungicide on plant size was not significant (Table 2.3). There were also significant species differences in plant size, as measured by length of the longest leaf and number of leaves (Table 2.3). Height and number of flower heads were unaffected by field, species, or treatment differences (Table 2.4, Figs. 2.7, 2.9, & 2.11).

In 2001, the results were identical to those in 2000, with both species identity and insect exclusion causing significant differences in plant size (Table 2.5, Fig. 2.6). As in 2000, deer had no effect on plant size (Fig. 2.8) and though plants in fungicide treated plots tended to be larger (Fig. 2.10), there was no significant effect of fungicide treatment on plant size (Table 2.5). Species identity was the only factor that caused significant differences in plant reproductive success (Table 2.6).

The results from 2002 indicate that both species identity and field contributed to differences in plant size (Table 2.7). Insect exclusion also caused a significant increase in plant size, for the third year (Table 2.7, Fig. 2.6). Deer exclusion had no influence on plant size (Fig. 2.8), but there was a significant improvement in reproductive success in plots where deer were excluded (Table 2.8). The canonical correlations indicate that this difference was driven primarily by height differences between plants in plots with and without deer herbivory. *H. longipilum* flowering stalks were taller in plots with no deer herbivory (Fig. 2.9). As in previous years, there was no significant difference in growth or reproductive success of either species when fungal pathogens were excluded (Tables 2.7 & 2.8, Figs. 2.10 & 2.11).

In 2002, measurements were also taken from the plots in fields 63 and 70, established in 2001. The deer exclosures in these fields were successful in reducing deer damage to *Hieracium* (df = 1, F = 7.223, p = 0.008), but there was no difference in disease damage, as measured by visual estimates, in plots sprayed with fungicide and those not sprayed (df = 1, F= 0.195, p = 0.659).

Field identity contributed to differences in plant size (Table 2.9), and there was also a significant two-way interaction between field and species identity. Plants of both species were significantly larger in plots occupied by both species of *Hieracium* than they were in plots where they grew alone (Table 2.9, Fig. 2.12). Both species also responded to deer exclosures by exhibiting significant decreases in plant size when deer were excluded (Table 2.9, Fig. 2.13). Fungicide treatment had no effect on plant size (Table 2.9, Fig. 2.14). None of the other interaction terms were significant (three-, four-, and five-way interactions not reported).

Deer were recorded at all sampling locations in both June and August. When there were multiple consecutive recordings of deer presence at a sampling location, it was impossible to determine whether those recordings indicated that a group of deer had passed by the sensor or that one individual had stopped in front of the sensor and was counted multiple times. Therefore, I have tabulated the data in four separate ways for the purpose of comparison: total number of recordings, total number of minutes in which deer were recorded, total number of hours in which deer were recorded, and total number of days on which deer were recorded. An ANOVA using month and field as factors and total number of recordings as the dependent variable indicated a marginally significant effect of month ($p = 0.066$) on the total number of deer recordings (Table 2.10). There were more deer counted in August than in June in both fields (Fig. 2.15). There was no significant difference in the number of deer counted between fields, nor was there a significant interaction between month and field. When the data were analyzed using number of minutes, hours, or days on which deer were recorded as the dependent variable, neither of the main effects was statistically significant and there was no significant interaction of field and month.

Soil and Plant Community Measurements

A MANOVA used to determine whether field identity and treatments affected the composition of the plant community revealed differences in percent cover of plant functional groups between fields (Table 2.11). The analysis also indicated that both the insect and deer treatments caused significant differences in plant community composition. The cover of graminoids was most strongly negatively influenced by deer exclosures. Insect exclosures caused an increase in both forbs and legumes (Table 2.11). Deer exclusion also caused an increase in moss and lichen cover, probably as a result of reduced trampling.

Stepwise backward multiple regression revealed that the percent cover of legumes, mosses and lichens, and leaf litter all had a significant negative effect on the size (measured by length of the longest leaf) of *H. aurantiacum* (Table 2.12). Changes in graminoid, forb, and bare ground cover did not significantly influence *H. aurantiacum* size. *H. longipilum*, on the other hand, increased in size with increasing cover of legumes, graminoids, and leaf litter (Table 2.13), but showed no response to changes in forb, moss and lichen, or bare ground cover.

The exclosure treatments did not have a significant impact on soil properties, but there were significant differences between fields in soil temperature, moisture, and C:N ratio, with soil moisture accounting for most of the difference between fields (Table 2.14). Insect treatment also appeared to have a marginally significant effect on soil properties, possibly driven primarily by the decrease in soil temperature in plots from which insects were excluded, though this cannot be confirmed.

Regressions of plant size on soil properties showed that soil moisture had a significant negative effect on *H. aurantiacum* size (Table 2.15). None of the soil characteristics measured had a significant impact on *H. longipilum* size, although mean soil temperature and August soil C:N ratio both showed marginal significance (p = 0.06 and p = 0.065, respectively).

Species Traits

Despite similarities in morphology and growth form between *H. aurantiacum* and *H. longipilum*, there are many significant differences in the morphology of these two species. *H. longipilum* has longer leaves, taller flowering stalks, more flower heads, thicker leaves, and more trichomes per unit leaf area than does *H. aurantiacum* (Table 2.17). *H. aurantiacum* has a different growth strategy, producing smaller but a greater quantity of leaves. In addition, it is capable of vegetative reproduction through the production of stolons; this characteristic may compensate for the significantly smaller number of flower heads (and therefore seeds) that each plant produces.

DISCUSSION

Observational Data

Surveys of damage to *H. aurantiacum* and *H. longipilum* from herbivores and pathogens lend support to the natural enemies hypothesis, by demonstrating that *H. aurantiacum*, the invasive species, is damaged much less frequently by deer herbivory than the native species. Furthermore, the invasive species appears to be less susceptible to infection by *Puccinia dioicae*, the pathogenic rust fungus that accounts for the greatest amount of damage to *H. longipilum* plants. It is particularly interesting that *H. aurantiacum* appears to be resistant to infection by *Puccinia*, because the fungal spores are wind-dispersed and infect a wide range of species in the family Asteraceae (Farr et al. 1989).

Although *H. aurantiacum* has escaped damage from a major fungal pathogen and shows less deer damage than the native species, the data indicate that *H. aurantiacum* experiences more insect herbivory than its native congener does. Furthermore, visual estimates of insect damage are likely to be underestimates of the effect of insects, because spittle bug damage is often inconspicuous (Carson and Root 2000). Therefore, although *H. aurantiacum* is exposed to fewer enemies than *H. longipilum*, it has not entirely escaped herbivory in its new range.

H. aurantiacum and *H. longipilum* have significant differences in their carbon and nitrogen concentrations, but these differences do not appear to explain the different rates of deer herbivory on these species. Deer graze primarily on nitrogen-rich forbs and legumes (Knops et al. 2000) so if they were selecting plants based on high nitrogen concentration, one would expect to see higher levels of nitrogen in *H. longipilum* than in *H. aurantiacum*. *H. longipilum* does have a much lower C:N ratio (and thus more nitrogen per unit carbon) in its roots than *H. aurantiacum* does, but it is unlikely that this would affect deer preference, as the deer are eating only the flowers and flowering stalks of the plants. *H. aurantiacum*, on the other hand, has more nitrogen-rich stems (lower C:N ratio), contrary to the expectation that deer would choose to eat the more nitrogen-rich plant. *H. longipilum* flowers have a slightly lower C:N ratio, but the difference does not appear to be very great between flower heads of the two species (Fig. 2.4). Differences in tissue nutrient concentrations do not appear to explain the preference of deer for *H. longipilum*.

There are several other possible explanations for the greater deer herbivory on *H. longipilum*. There may be some difference in plant secondary chemistry between the two species. *Hieracium* species are known to contain phenolic compounds (Almeida-Cortez et al. 1999), but it is unclear whether these compounds are toxic or unpalatable to deer. Differences in secondary chemistry were not explored in this study.

Another possible explanation for the differential deer herbivory between *Hieracium* species is difference in phenology. *H. aurantiacum* flowers from late May through August, with its peak period of flowering in early to mid June, whereas *H. longipilum* flowers from late July through August, with most individuals flowering in early August. It is possible that *H. aurantiacum* avoids deer herbivory by flowering primarily early in the growing season when deer have multiple alternative food sources, especially from adjacent farmlands. By August, the crops in nearby fields have been harvested, and there may be more deer in the grasslands. My data on deer activity did not indicate that there was a significant difference in deer numbers between June and August, but there was a visible increase in deer activity in August. This difference between months may have been significant if I had been able to record deer activity at a greater number of locations and over multiple years.

Finally, the difference in rates of deer herbivory between the two species may be explained simply by a difference in plant visibility. *H. longipilum* plants have taller flowering stalks (Table 2.17), which are much closer to eye level for deer than *H. aurantiacum* plants are. Deer may eat more *H. longipilum* because they are more likely to notice them.

Data from the experimental plots lend little support to the natural enemies hypothesis. Neither species responded to the fungicide treatment by increasing in size or reproductive output in any of the years of the experiment. It appears that although fungal damage is common on *H. longipilum*, it does not significantly affect its growth or reproductive success. Therefore, the fact that *H. aurantiacum* is able to avoid damage from *Puccinia* likely does not give it a significant advantage over *H. longipilum*. Both species responded to insect exclusion by increasing in size, indicating that insect herbivory does limit growth for *H. longipilum* and *H. aurantiacum*. These data support the observational surveys, which suggest that *H. aurantiacum* has not escaped insect herbivory in its new range.

In 2000 and 2001 there was no effect of deer exclusion on either plant species. However, in 2002 deer exclosures did affect both species of *Hieracium*. It is possible that this effect was only apparent in 2002, because the sample size of plants exposed to deer herbivory was increased by taking down the insect cages that prevented deer from accessing those plots. In 2002, deer exclusion had different effects on *H. aurantiacum* and *H. longipilum* in different fields. In fields 22 and 54, *H. longipilum* plants showed an increase in reproductive performance (height of flowering stalk and number of flower heads) in response to deer exclosures, while *H. aurantiacum* plants had decreased reproductive success in the absence of deer herbivory. The negative response of *H. aurantiacum* to deer exclusion is likely an indirect effect caused by an increase in other vegetation in the absence of deer herbivory. In fields 63 and 70, however, both *H. aurantiacum* and *H. longipilum* responded to deer exclosures by decreasing plant size. This result may be a response to an increase in another species that is particularly susceptible to deer herbivory but can overgrow *Hieracium* when herbivores are excluded. Because percent cover estimates were not taken for these plots, it is not possible to determine which species might be responsible for this observed effect. Another possible explanation for the larger size of plants growing in plots without deer exclosures is that there may be some compensatory growth of plants in response to deer herbivory (Caldwell *et al.* 1981; Schierenbeck *et al.* 1994). If that were the case, plants would respond by producing larger or more leaves to increase their photosynthetic capacity and replace lost tissue.

In fields 63 and 70, both species responded positively to the presence of their congeneric species. This result supports the findings of the greenhouse study on these species (see Chapter I), which indicated that both species grew larger when their neighbors were congeners than when their neighbors were conspecifics. In these experimental plots, however, *H. aurantiacum* and *H. longipilum* were planted at least a few inches from each other and were usually not in direct aboveground contact with each other; it is possible that the interaction between these two species is occurring belowground instead.

In addition to differing in their responses to herbivores and pathogens, *H. aurantiacum* and *H. longipilum* respond differently to soil conditions and the surrounding plant community. *H. longipilum* size is not significantly influenced by differences in soil characteristics, but *H. aurantiacum* size is affected by soil moisture. Furthermore, *H. aurantiacum* responds negatively to increases in the surrounding vegetation of all types, with the exception of other non-leguminous forbs which have no effect on its size. Conversely, *H. longipilum* size increases as cover of legumes, graminoids, and leaf litter increase. The mechanism for this increase in size is unclear, but it is possible that increases in these groups causes favorable changes in microclimate, mycorrhizal abundance, or soil nutrients that have a positive effect on *H. longipilum*. Nevertheless, these results indicate that certain soil and plant cover conditions are more favorable for *H. longipilum* than for *H. aurantiacum*. This suggests that there are certain areas of Cedar Creek in which *H. aurantiacum* is unlikely to ever replace *H. longipilum* populations. *H. aurantiacum* may not present as much of a conservation threat to *H. longipilum* as originally believed.

A more pressing conservation concern for *H. longipilum* is the extensive removal of its flowering stalks by deer. The problem is clearly illustrated by Figure 2.5, showing that plants exposed to deer herbivory have fewer flower heads at the end of the season, and have a tendency to have shorter flowering stalks. Deer herbivory significantly decreases the number of propagules being produced, and reduced plant height means that seeds will tend to have a shorter dispersal distance. Over many generations, this decrease in reproductive success could cause a significant decline in the size of *H. longipilum* populations. White-tailed deer populations are artificially high in much of eastern North America because of food subsidies provided by increased agricultural production and the removal of top predators, which historically controlled deer population sizes. The consequences of dramatically altering the food web in Minnesota grasslands is likely a more immediate threat to the conservation of *H. longipilum* than the introduction of *H. aurantiacum*.

Escape from natural enemies may play a role in the invasion success of *H. aurantiacum*, but it is possible that a unique morphological or physiological trait explains its spread. *H. aurantiacum* has several traits that are distinct from those of *H. longipilum*, which may allow it to exploit resources not used by *H. longipilum*. Most notably, *H. aurantiacum* is capable of reproducing vegetatively, which may make it a better disperser than *H. longipilum*. In many of the experimental plots constructed in fields 63 and 70, the original two plants transplanted into the plots in 2001 had multiplied to eight or ten individuals just one year later. However, it is likely that *H. longipilum* has greater dispersal of seeds, because it produces more seeds and has taller flowering stalks.

H. aurantiacum plants also showed a faster growth rate in the greenhouse experiment, achieving similar sizes to individuals in the field more quickly than *H. longipilum* individuals did. Growth rates were not measured for plants in the field, so it is unclear whether this faster growth rate was a product of the optimal growing conditions of the greenhouse or whether it is true of plants in the field as well.

H. aurantiacum plants also have a longer growing season and a more flexible flowering time, with plants flowering between May and August as opposed to the more constrained flowering time of *H. longipilum*. This plasticity may benefit *H. aurantiacum* by allowing it to respond opportunistically to optimal conditions for reproduction.

Nevertheless, *H. longipilum* plants are larger, are better defended from insect herbivory (greater density of trichomes), and have thicker leaves, which likely make them more resistant to dry conditions. It is difficult to determine which of these traits are most important for growth and reproductive success, but there is some evidence that these two species, despite their close taxonomic relationship, are fairly different in their important species characteristics and as a result may respond differently to biotic and abiotic factors.

In conclusion, while this study provides some support for the natural enemies hypothesis, it strongly supports a complex, multiple factor model for what regulates the relative success of an invasive species over a native species. *H. aurantiacum* has fewer enemies than its native congener does, but it has not completely escaped herbivory in its new range. Insect herbivory does limit the growth of *H. aurantiacum* as well as *H. longipilum*. There is no information in the scientific literature about what natural enemies *H. aurantiacum* may be exposed to in its native range, and therefore I am unable to make any comparisons between the amount of damage from herbivory in the invader's native and introduced ranges. *H. aurantiacum* also has several unique species traits that may improve its invasion success, even in areas already occupied by a closely related native species. The example of *H. aurantiacum* suggests that there may not be any easy answers to the question of what makes a species a successful invader. It is likely that invasion success is the result of a combination of unique species traits and favorable community conditions, such as reduced herbivory and disease and appropriate soil conditions and plant community composition, all of which have been shown to affect invader performance.

Table 2.1. Canonical correlations from multivariate analysis of variance for plant C:N ratios by species. P-value corresponds to Wilks' lambda F-statistics.

	Leaf	Flowering stalk	Flower head	Root	P
Canonical correlation	0.125	0.389	-0.010	-0.683	**0.034**

Table 2.2. ANOVA results for effect of deer exclosure on reproductive success of *H. longipilum* in fields A and B, 1998. Location refers to the position of the plant inside or outside a deer exclosure.

Response variable	Factor	Sums-of-squares	df	F-ratio	P
Height					
	Field	9282.236	1	30.266	**<0.001**
	Location	940.460	1	3.067	0.083
	Field*Location	94.043	1	0.307	0.581
	Error	31895.232	104		
Number of flowers					
	Field	2.772	1	40.639	**<0.001**
	Location	0.271	1	3.974	**0.049**
	Field *Location	0.169	1	2.473	0.119
	Error	7.095	104		

Table 2.3. Canonical correlations from MANOVA for plant growth, as measured by length of the longest leaf and total number of leaves, for fields 22 and 54 in 2000. P-values correspond to Wilks' lambda F-statistics.

Factor	Length of longest leaf (cm)	Number of leaves	Canonical correlation	P
Field	0.990	0.221	0.205	0.079
Species	-0.116	0.886	0.677	**<0.001**
Insect Treatment	0.978	0.155	0.347	**<0.001**
Deer Treatment	-0.485	0.644	0.100	0.551
Fungicide Treatment	0.813	0.834	0.166	0.191

Table 2.4. Canonical correlations from MANOVA for plant reproduction, as measured by height of the flowering stalk and total number of flower heads, for fields 22 and 54 in 2000. P-values correspond to Wilks' lambda F-statistics.

Factor	Height (cm)	Number of flower heads	Canonical correlation	P
Field	-0.361	0.762	0.454	0.177
Species	0.568	0.964	0.292	0.512
Insect Treatment	0.747	0.873	0.350	0.374
Deer Treatment	0.537	0.973	0.209	0.714
Fungicide Treatment	0.794	-0.313	0.162	0.820

Table 2.5. Canonical correlations from MANOVA for plant growth, as measured by length of the longest leaf and total number of leaves, for fields 22 and 54 in 2001. P-values correspond to Wilks' lambda F-statistics.

Factor	Length of longest leaf (cm)	Number of leaves	Canonical correlation	P
Field	0.609	0.990	0.217	0.065
Species	-0.159	0.781	0.361	**<0.001**
Insect Treatment	0.826	-0.082	0.378	**<0.001**
Deer Treatment	0.801	-0.125	0.149	0.283
Fungicide Treatment	0.297	0.977	0.170	0.192

Table 2.6. Canonical correlations from MANOVA for plant reproduction, as measured by height of the flowering stalk and total number of flower heads, for fields 22 and 54 in 2001. P-values correspond to Wilks' lambda F-statistics.

Factor	Height (cm)	Number of flower heads	Canonical correlation	P
Field	0.998	0.800	0.301	0.219
Species	0.943	0.494	0.469	**0.019**
Insect Treatment	-0.483	0.209	0.163	0.651
Deer Treatment	1.000	0.745	0.276	0.281
Fungicide Treatment	0.891	0.377	0.244	0.374

Table 2.7. Canonical correlations from MANOVA for plant growth, as measured by length of the longest leaf and total number of leaves, for fields 22 and 54 in 2002. P-values correspond to Wilks' lambda F-statistics.

Factor	Length of longest leaf (cm)	Number of leaves	Canonical correlation	P
Field	-0.301	0.804	0.348	**0.005**
Species	0.321	1.000	0.370	**0.002**
Insect Treatment	0.794	-0.317	0.270	**0.043**
Deer Treatment	0.863	-0.197	0.158	0.350
Fungicide Treatment	-0.188	0.868	0.076	0.787

Table 2.8. Canonical correlations from MANOVA for plant reproduction, as measured by height of the flowering stalk and total number of flower heads, for fields 22 and 54 in 2002. P-values correspond to Wilks' lambda F-statistics.

Factor	Height (cm)	Number of flower heads	Canonical correlation	P
Field	-0.120	0.280	0.202	0.410
Species	-0.472	-0.087	0.881	**<0.001**
Insect Treatment	0.564	0.843	0.170	0.534
Deer Treatment	-0.529	-0.152	0.364	**0.047**
Fungicide Treatment	0.810	0.975	0.073	0.892

Table 2.9. Canonical correlations from MANOVA for plant growth, as measured by length of the longest leaf and total number of leaves, in fields 63 and 70 in 2002. P-values correspond to Wilks' lambda F-statistics. Interactions between three or more factors are not reported, but none had p-values <0.05.

Factor	Leaf length (cm)	Number of leaves	Canonical correlation	P
Field	-0.235	0.924	0.407	**0.002**
Species	-0.189	0.941	0.220	0.191
Species Treatment	0.903	0.563	0.526	**<0.001**
Deer Treatment	0.658	0.846	0.462	**<0.001**
Fungicide Treatment	0.282	0.991	0.236	0.147
Field * Species	0.659	0.845	0.230	0.161
Field * Species Treatment	0.905	0.560	0.315	**0.030**
Field * Deer Treatment	0.961	-0.127	0.174	0.356
Field * Fungicide Treatment	-0.407	0.840	0.159	0.423
Species * Species Treatment	0.952	0.448	0.251	0.112
Species * Deer Treatment	0.493	0.935	0.264	0.089
Species * Fungicide Treatment	0.983	0.330	0.212	0.213
Species Trt. * Deer Trt.	-0.346	0.874	0.181	0.329
Species Trt. * Fungicide Trt.	-0.524	0.761	0.210	0.221
Deer Trt. * Fungicide Trt.	0.868	0.624	0.223	0.180

Table 2.10. ANOVA results for deer abundance by field and month. The response variable is the total number of recordings by the deer sensors.

Source	Sums-of-squares	df	F-ratio	P
Month	1.517	1	3.855	0.066
Field	0.008	1	0.021	0.885
Month * Field	0.001	1	0.002	0.966
Error	6.688	17		

Table 2.11. MANOVA results for treatment effects on percent cover of plant functional groups.

Factor	Forbs	Legumes	Graminoids	Moss/ Lichen	Leaf litter	Bare ground	Canonical correlation	P
Field	0.064	0.841	-0.573	0.232	-0.099	0.073	0.579	**<0.001**
Insect Treatment	0.606	0.518	-0.295	-0.099	-0.336	-0.273	0.522	**<0.001**
Deer Treatment	0.029	0.196	-0.576	0.536	0.053	0.221	0.479	**<0.001**
Fungicide Treatment	0.322	-0.816	-0.130	-0.364	0.388	0.064	0.234	0.267

Table 2.12. Results of stepwise backward multiple regression of percent cover on *H. aurantiacum* size, measured by length of the longest leaf. $R^2 = 0.334$, $p = 0.001$.

Effect	Standardized coefficient	F	P
Legumes	-0.425	10.514	**0.002**
Graminoids	-0.274	3.403	0.071
Mosses and lichens	-0.441	9.210	**0.004**
Litter	-0.472	9.681	**0.003**
Bare ground	-0.253	2.317	0.134

Table 2.13. Results of stepwise backward multiple regression of percent cover on *H. longipilum* size, measured by length of the longest leaf. $R^2 = 0.191$, $p = 0.004$.

Effect	Standardized coefficient	F	P
Legumes	0.433	10.982	**0.002**
Graminoids	0.286	5.537	**0.022**
Litter	0.338	7.498	**0.008**

Table 2.14. MANOVA results for treatment effects on edaphic properties.

Factor	Mean soil temperature	% soil moisture	July C:N ratio	August C:N ratio	Canonical correlation	P
Field	-0.088	0.771	-0.173	0.396	0.706	**<0.001**
Insect Treatment	-0.808	0.088	-0.173	0.264	0.301	**0.054**
Deer Treatment	-0.250	-0.677	0.703	0.293	0.171	0.575
Fungicide Treatment	0.833	0.265	0.328	0.257	0.183	0.502

Table 2.15. Results of stepwise backward multiple regression of edaphic properties on *H. aurantiacum* size, measured by length of the longest leaf. $R^2 = 0.153$, $p = 0.013$.

Effect	Standardized coefficient	t	P
% soil moisture	-0.282	-2.175	**0.034**
July soil C:N ratio	0.225	1.732	0.089

Table 2.16. Results of stepwise backward multiple regression of edaphic properties on *H. longipilum* size, measured by length of the longest leaf. $R^2 = 0.156$, $p = 0.012$.

Effect	Standardized coefficient	t	P
Mean soil temperature	-0.230	-1.916	0.060
% soil moisture	0.194	1.621	0.110
August soil C:N ratio	0.224	1.875	0.065

Table 2.17. Morphology data for *H. aurantiacum* and *H. longipilum*. Values for height and number of flower heads include only the individuals that produced flowering stalks. Means for all characters are significantly different between the two species with $p < 0.001$.

	Length of longest leaf (cm)	Number of leaves	Height of flowering stalk (cm)	Number of flower heads	Leaf thickness	Number of hairs (per $1 cm^2$)
H. aurantiacum						
Minimum	1.70	2	0.31	1	0.22	17
Maximum	16.70	28	66.55	33	0.37	43
Mean	7.32	7.55	9.83	7.67	0.28	27.31
H. longipilum						
Minimum	0.76	1	3.3	1	0.28	36
Maximum	60.87	25	112.48	49	0.40	85
Mean	9.67	6.01	43.32	10.17	0.34	54.07

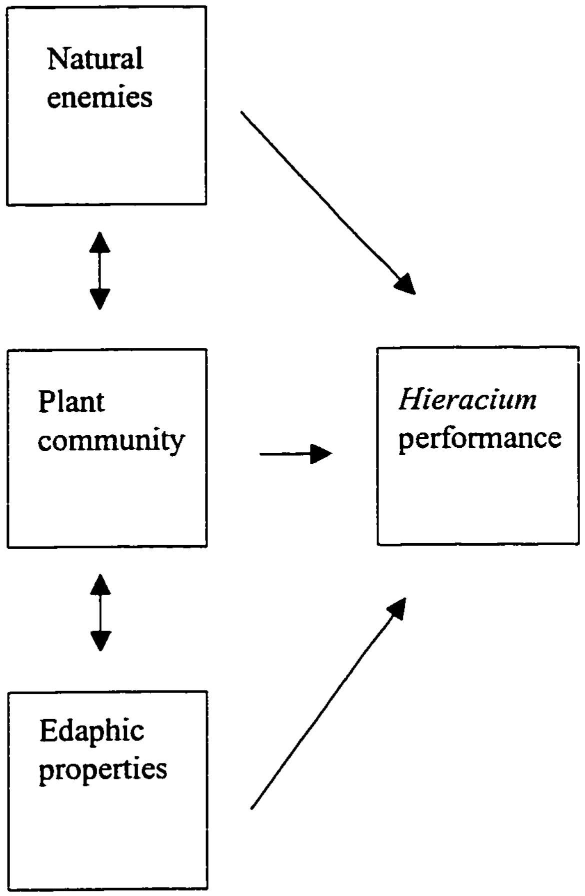


Figure 2.1: Diagram showing influence of community and ecosystem elements on the performance of native and introduced *Hieracium* spp. Natural enemies influence plant communities, which in turn affect edaphic properties. These factors may all potentially influence the performance of *Hieracium* spp. See text for further explanation.

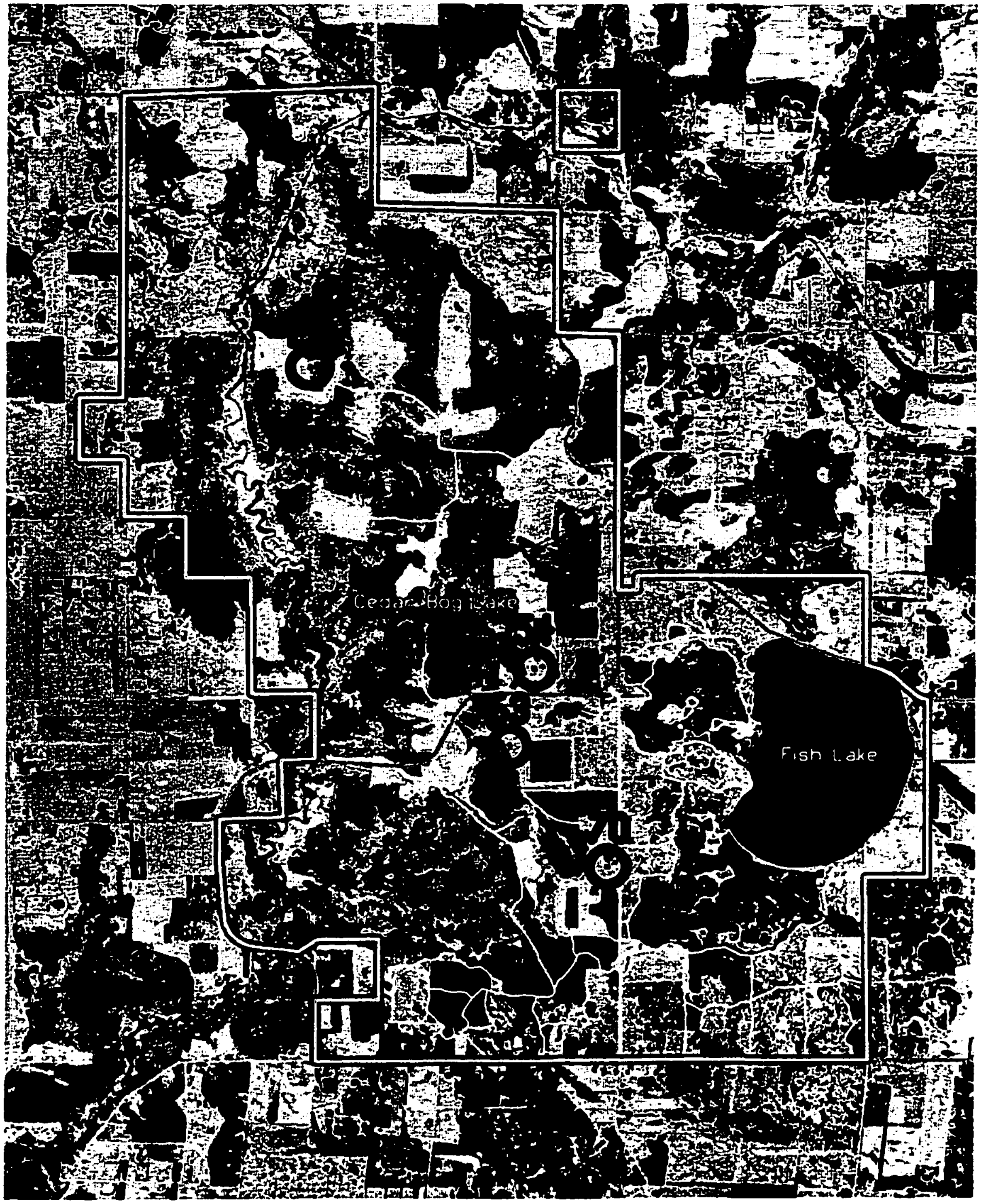


Figure 2.2: Map of Cedar Creek Natural History Area showing locations of experimental plots. Cedar Creek land is outlined by gray border. Experimental plots are located in circled fields, numbered 22, 54, 63, and 70.

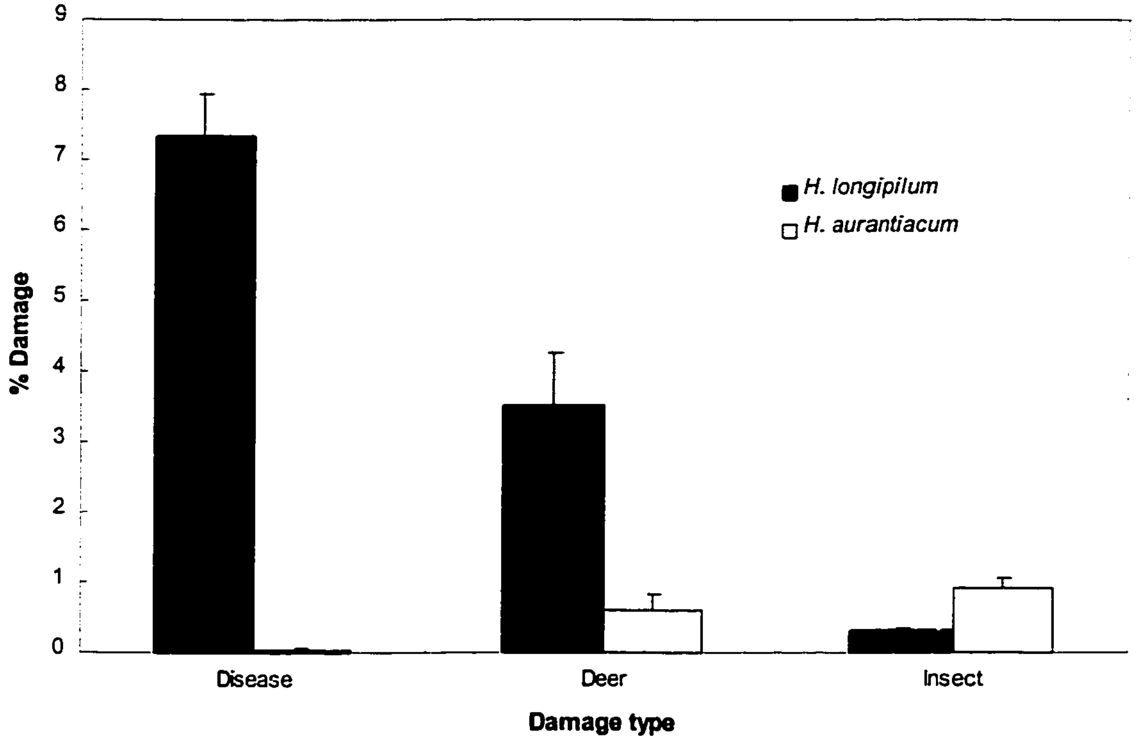


Figure 2.3: Estimates of herbivory and disease damage to *H. aurantiacum* and *H. longipilum*. Damage is divided into three types: disease caused by a pathogenic rust fungus, browsing by deer, and all insect damage. Bars represent mean damage for 1998-2001. Error bars represent one standard error.

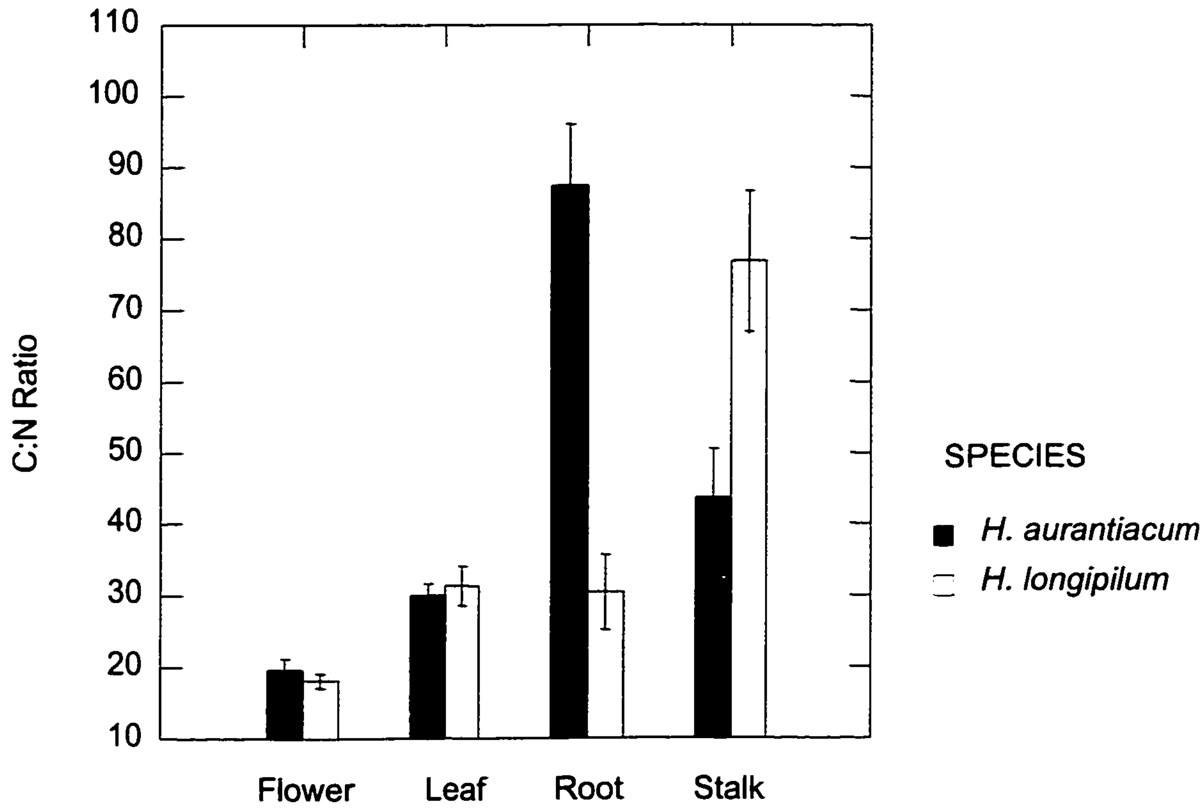


Figure 2.4: Carbon to nitrogen ratios of *H. aurantiacum* and *H. longipilum* flowers, leaves, roots, and flowering stalks. Higher C:N ratio indicates lower nitrogen concentration. Error bars represent one standard error.

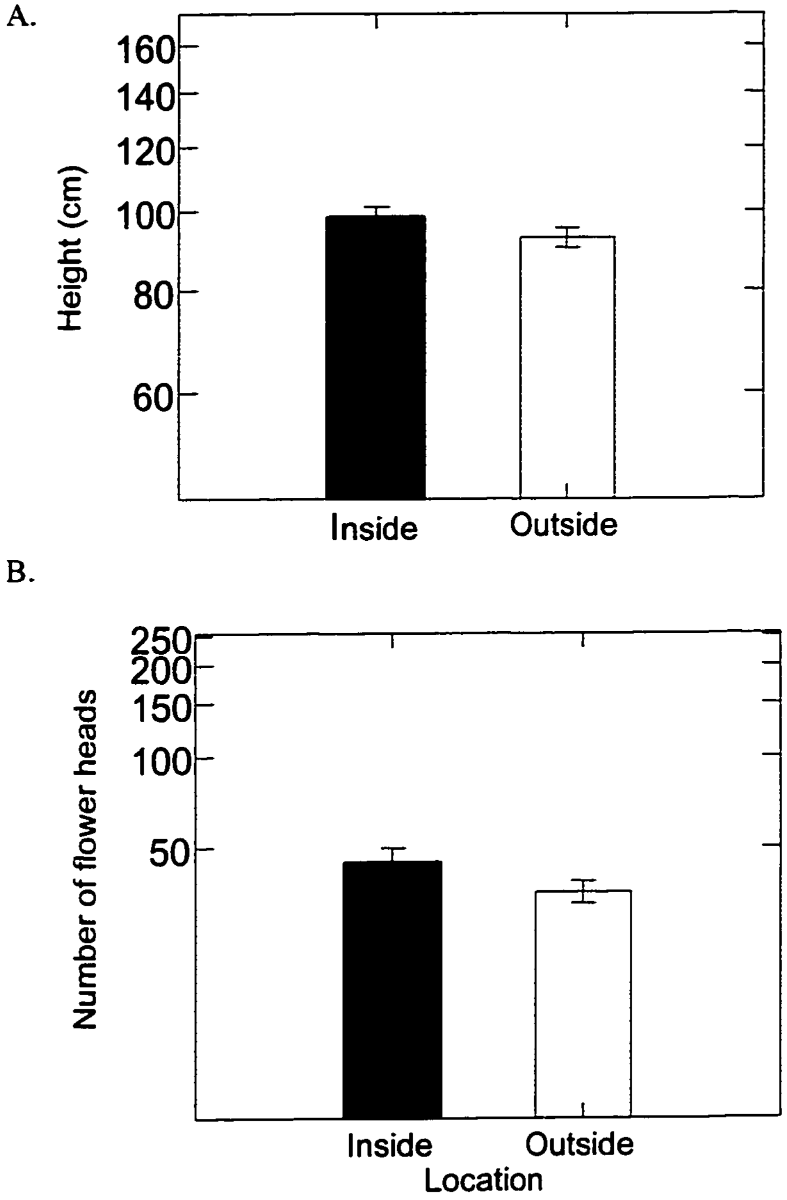


Figure 2.5: Height (A) and number of flowers (B) of *H. longipilum* growing inside and outside of large deer exclosures in two fields, A and B. Data were collected in September 1998 at the end of the field season. Error bars represent one standard error.

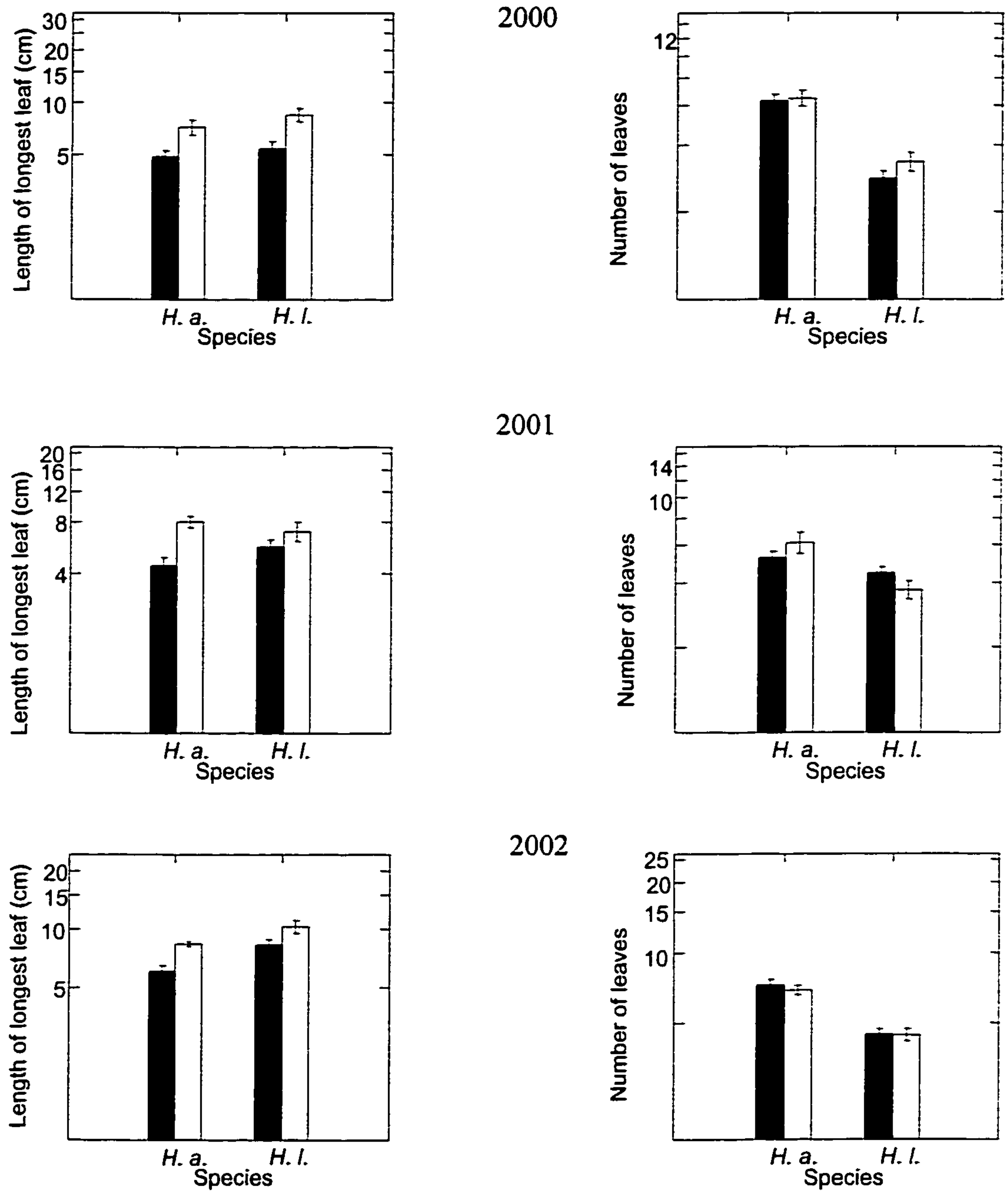


Figure 2.6: Effects of insect exclosure on plant size, measured by length of the longest leaf and number of leaves, in fields 22 and 54 for 2000-2002. *H. a.* = *H. aurantiacum*, *H. l.* = *H. longipilum*. Black bars show plots with insects. White bars show plots with insect exclosures. Error bars represent one standard error.

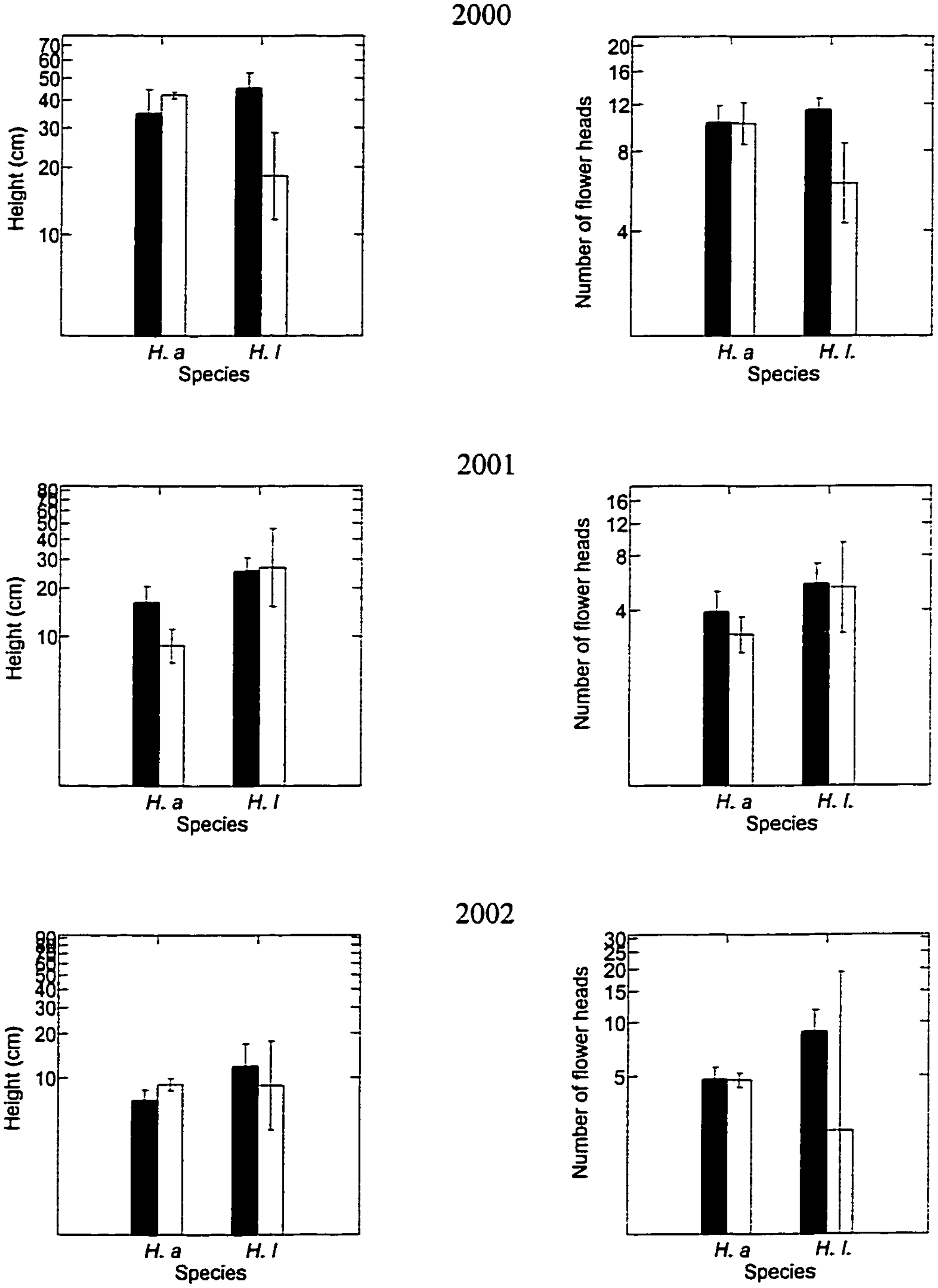
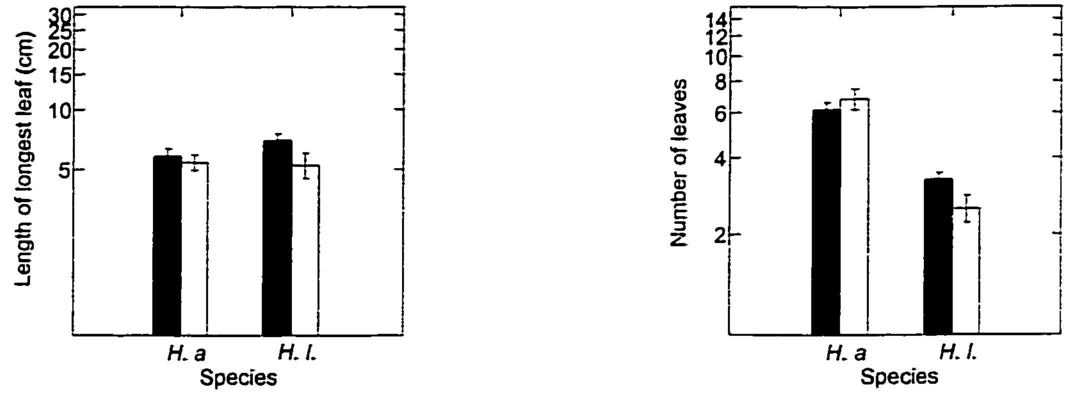
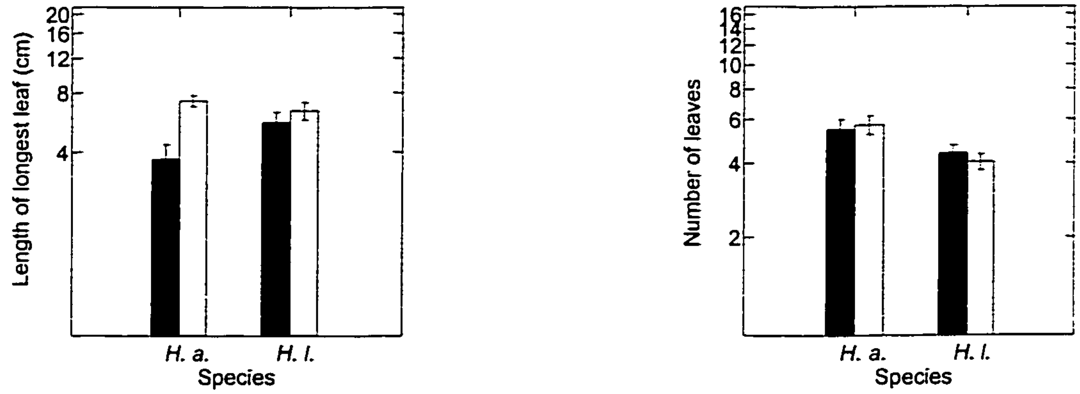


Figure 2.7: Effects of insect exclosure on plant reproductive success, measured by height of the flowering stalk and number of flower heads, in fields 22 and 54 for 2000-2002. *H. a.* = *H. aurantiacum*, *H. l.* = *H. longipilum*. Black bars show plots with insects. White bars show plots with insect exclosures. Error bars represent one standard error.

2000



2001



2002

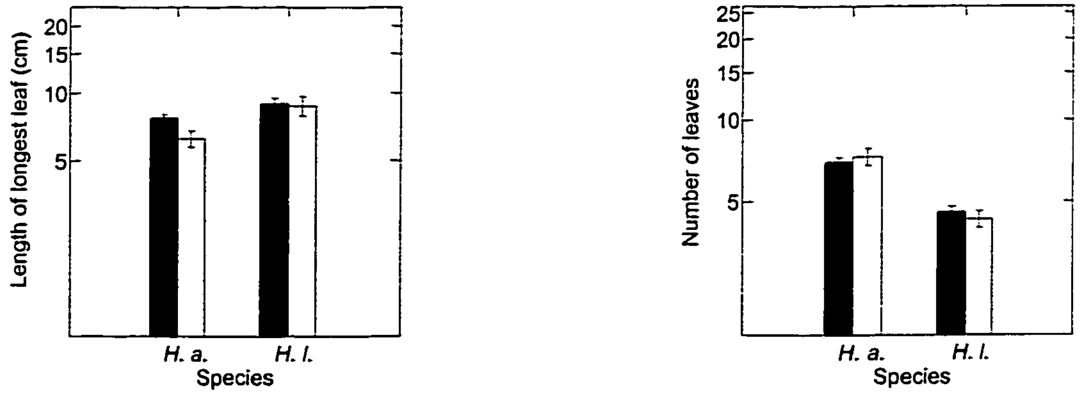


Figure 2.8: Effects of deer exclosure on plant size, measured by length of the longest leaf and number of leaves, in fields 22 and 54 for 2000-2002. *H. a.* = *H. aurantiacum*, *H. l.* = *H. longipilum*. Black bars show plots with deer. White bars show plots with deer exclosures. Error bars represent one standard error.

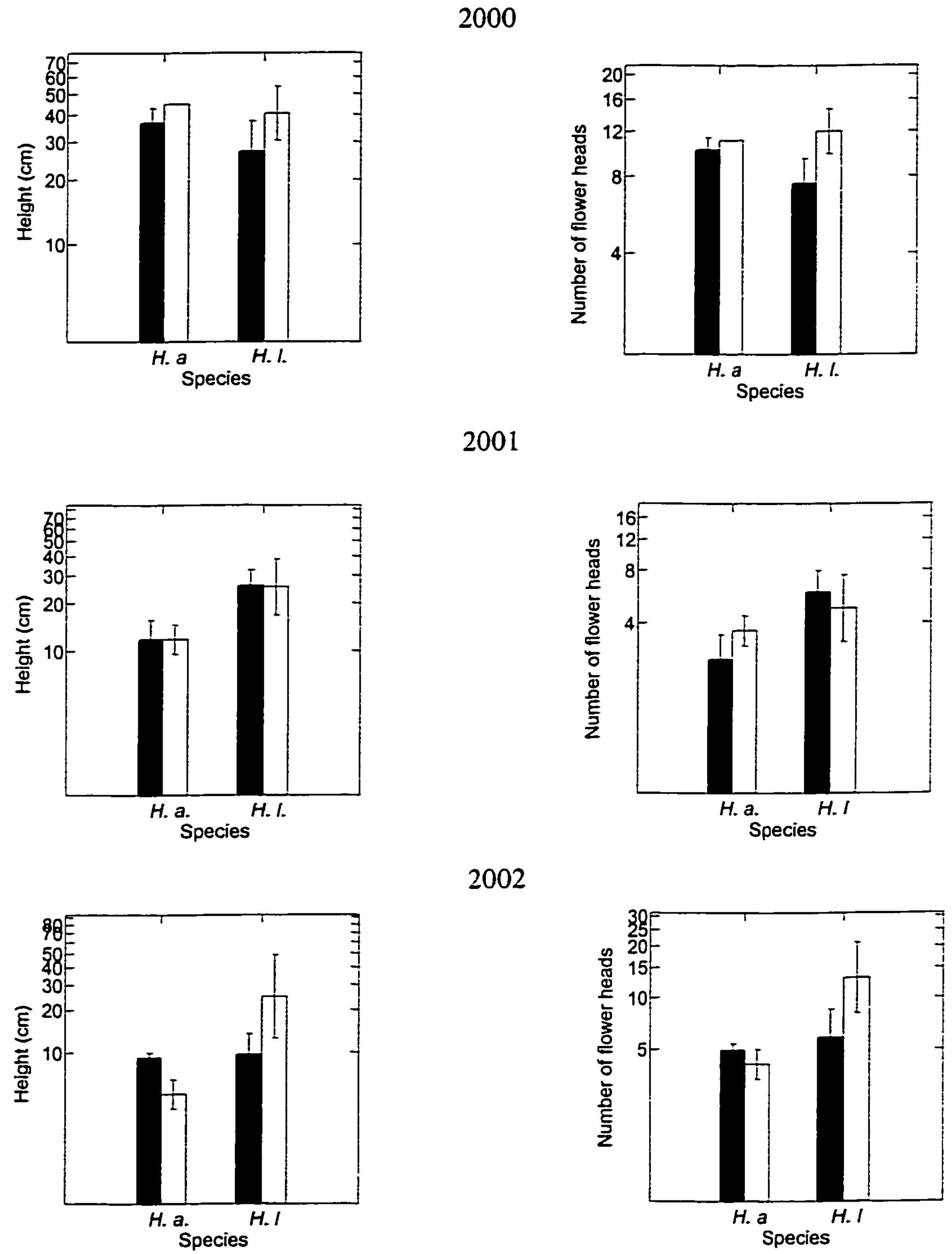


Figure 2.9: Effects of deer exclosure on plant reproductive success, measured by height of the flowering stalk and number of flower heads, in fields 22 and 45 for 2000-2002. *H. a.* = *H. aurantiacum*, *H. l.* = *H. longipilum*. Black bars show plots with deer. White bars show plots with deer exclosures. Error bars represent one standard error.

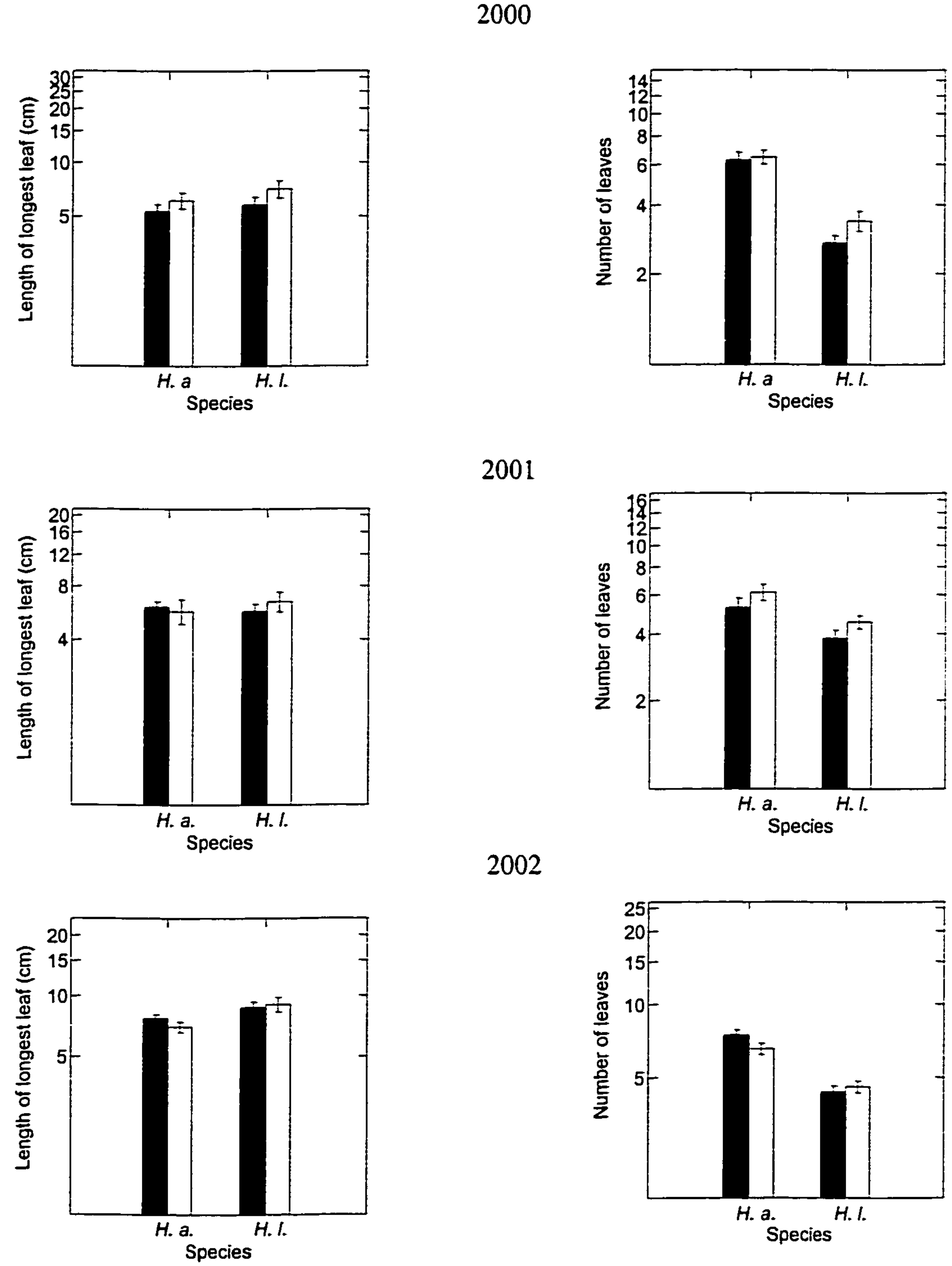
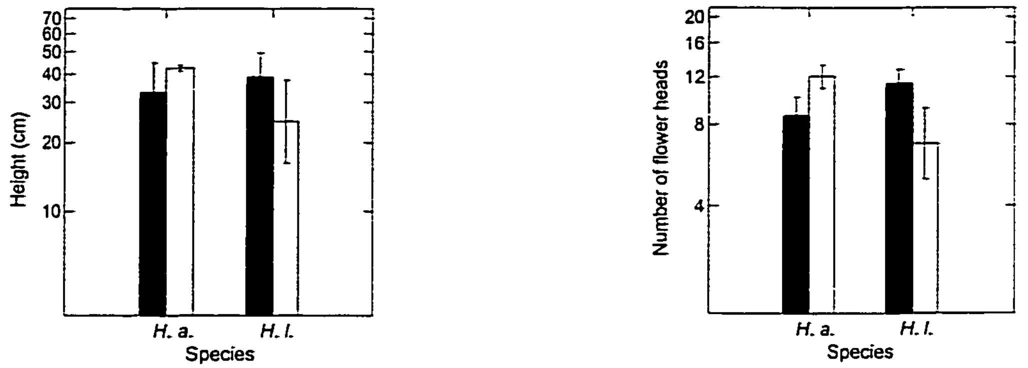
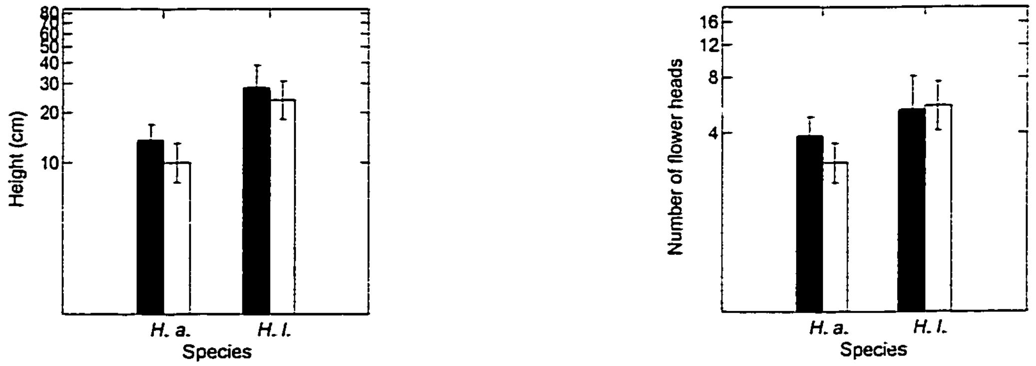


Figure 2.10: Effects of fungal pathogen exclosure on plant size, measured by length of the longest leaf and number of leaves, in fields 22 and 54 for 2000-2002. *H. a.* = *H. aurantiacum*, *H. l.* = *H. longipilum*. Black bars show plots with pathogens. White bars show plots with pathogen exclusion. Error bars represent one standard error.

2000



2001



2002

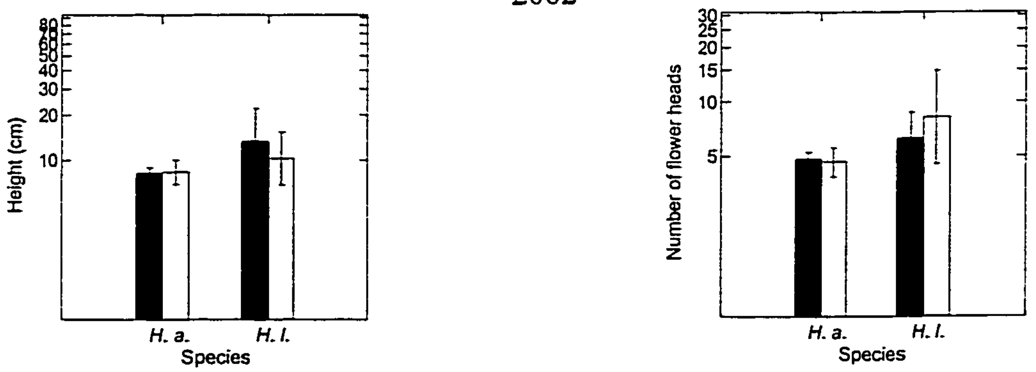


Figure 2.11: Effects of fungal pathogen exclosure on plant reproductive success, measured by height of the flowering stalk and number of flower heads, in fields 22 and 45 for 2000-2002. *H. a.* = *H. aurantiacum*, *H. l.* = *H. longipilum*. Black bars show plots with pathogens. White bars show plots with pathogen exclusion. Error bars represent one standard error.

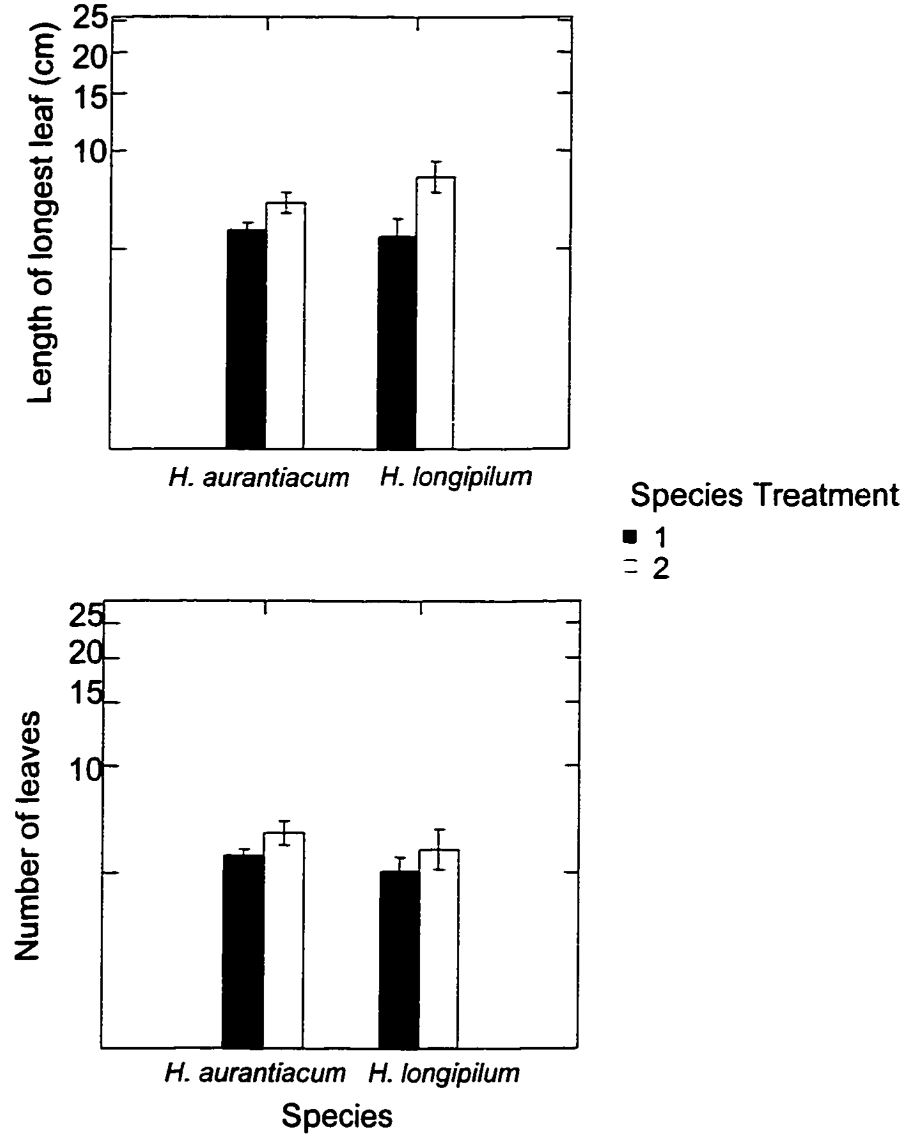


Figure 2.12: Effects of species treatment on plant size, measured by length of the longest leaf and number of leaves, in fields 63 and 70 for 2002. Species treatment = 1 indicates that the species was growing alone in a plot. Species treatment = 2 means that both species of *Hieracium* were planted in a plot. Error bars represent one standard error.

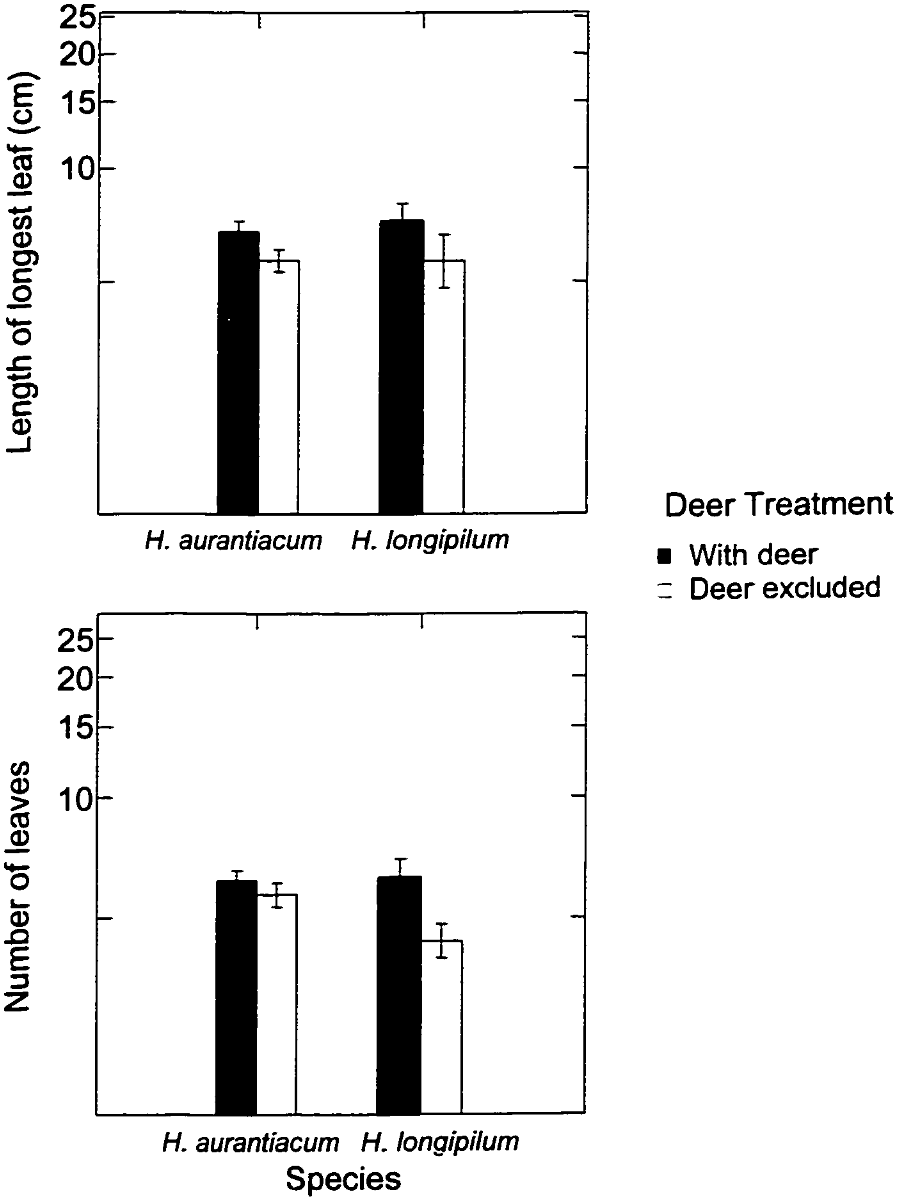


Figure 2.13: Effects of deer exclosure on plant size, measured by length of the longest leaf and number of leaves, in fields 63 and 70 for 2002. Error bars represent one standard error.

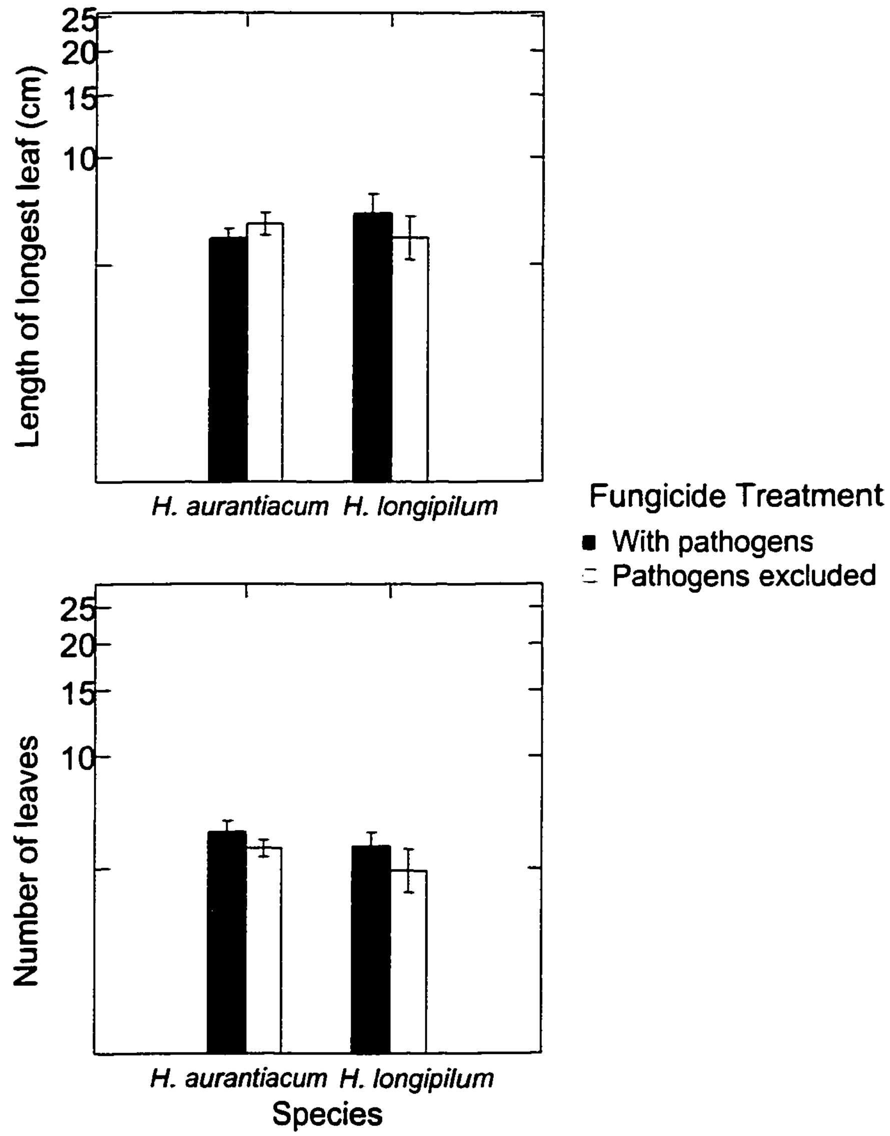


Figure 2.14: Effects of fungal pathogen exclosure on plant size, measured by length of the longest leaf and number of leaves, in fields 63 and 70 for 2002. Error bars represent one standard error.

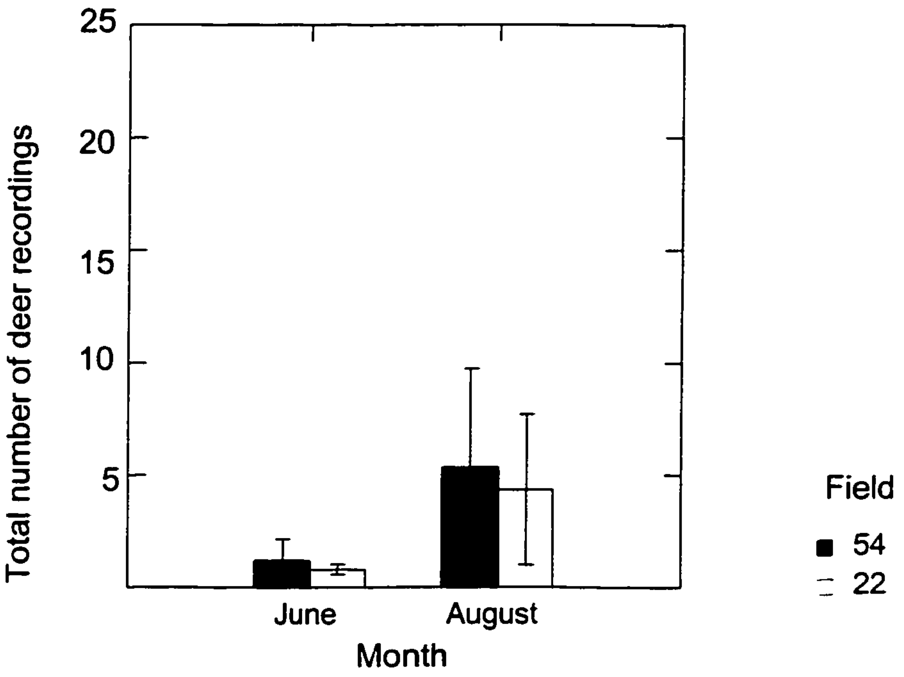


Figure 2.15: Total number of deer recordings in fields 22 and 54 in June and August, 2002. Error bars represent one standard error.

CHAPTER III

PLANT INVADER SUCCESS AND THE ROLE OF NEIGHBORHOOD BIODIVERSITY*

INTRODUCTION

The success of an exotic species invading a new ecosystem is determined by three factors: 1) propagule pressure; 2) abiotic influences, or ecosystem properties; and 3) biotic influences, including both the properties of the invader and the properties of the native species living in the invaded community (Hobbs 1989, Lonsdale 1999). While the initial establishment of a plant invader is a function of the frequency of arrival, the number arriving at each event, and site suitability, biotic interactions with the surrounding community have the potential to enhance or reduce the success of an invader after its arrival and establishment (Maron and Vilà 2001, Byers 2002, Prieur-Richard et al. 2002). While it seems plausible to expect biotic interactions to affect invasion success, evidence demonstrating this influence is relatively scarce.

Studies of the characteristics of invasible communities often focus on large-scale community characteristics. However, the most immediate and potentially strongest component of biotic influences over the success of an invasive plant is the structure and composition of its neighborhood, made up of individuals in its

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*This work was done in collaboration with Dr. Shahid Naeem (University of Washington).

immediate vicinity (Harper 1977, Silander and Pacala 1985, Naeem et al. 1999). Natural enemies, such as pathogens and herbivores (Schierenbeck et al. 1994), and important mutualists, such as mycorrhizal fungi (Callaway and Aschehoug 2000) and pollinators (Brown and Mitchell 2001) can act as biotic influences on invasion success at a small scale. An invader must also compete for space, nutrients, water, and light with its neighboring plants. Our focus is on plant neighborhood properties, which have been shown to influence performance of both resident plants (Mack and Harper 1977, Waller 1981, Silander and Pacala 1985, Goldberg 1987, Armstrong 1993, Cain et al. 1995, Lessin et al. 2001) and invaders (Gordon et al. 1989, Bush and Auken 1991, Knops et al. 1999, Naeem et al. 2000) (Dukes 2002, Kennedy et al. 2002).

One neighborhood property of particular interest is resident biodiversity and the role it plays in the regulation of invader success. Elton hypothesized that high levels of resident diversity should yield highly competitive communities that are relatively resistant to invasion, however the relationship between biodiversity and invasibility is still unclear (Cronk and Fuller 1995, Levine 2000). Contrary to Elton's conjecture, observational studies have shown that areas of high native species richness tend to have larger numbers of exotic species (Stohlgren et al. 1999, Levine 2000). Experimental studies, however, have provided evidence in support of Elton's hypothesis, by demonstrating that when native diversity is lost from within a community, that community becomes more susceptible to invasion (Knops et al.

1999; Naeem et al. 2000; Kennedy et al. 2002). For example, Naeem et al. (2000) demonstrated that the sizes of *Crepis tectorum* and *Digitaria ischaemum*, two annual invaders common to grasslands of the North American Midwest, are strongly regulated by the species richness of their plant neighborhoods, with larger plants occurring in more species-poor neighborhoods. Neighborhoods with more resident species tended to be more crowded and have fewer available resources. This mechanism appears to explain the strong inverse relationship between within-site variation in resident biodiversity and invader performance (Knops et al. 1999, Kennedy et al. 2002). These results also support Davis et al.'s (2000) theory of fluctuating resources, which suggests that an increase in the amount of unused resources (e.g. through loss of resident species) increases susceptibility to invasion.

Though recent work has given important insights into the role of resident plants on regulating post-establishment, within-site invader success under experimental conditions (Naeem et al. 2000; Knops et al. 1999; Levine 2000; Kennedy et al. 2002), the relationship between invaders and their small-scale plant neighborhoods in natural settings is less well understood. It is unclear how important neighborhood-level regulation of invader success is relative to the background of natural variability. To test the role of neighborhood properties on invader performance, we looked for statistical associations between the success of invaders and properties of their plant neighborhoods. The presence of associations would not support any particular mechanism but would elucidate the neighborhood-based correlates of invader success. Because we did not experimentally manipulate neighborhood properties, it is difficult to know if invaders are regulating neighborhood properties or if neighborhood properties are regulating invader success; however, if we were to find no associations this would indicate that there is no support for biotic influences in either direction.

In this study, we quantified plant neighborhood properties for 320 individual plants made up of 13 species commonly found in old-field or grassland habitats at Cedar Creek Natural History Area, Minnesota, USA to determine whether there are consistent characteristics of the neighborhoods of successful invaders. We explore basic patterns of associations between invader performance (size of plant) and statistical properties of the distribution and abundance of neighbors surrounding an invader. Our goal was to determine the relative importance of invader species identity, neighborhood properties (a biotic factor), and habitat location, which reflects the influence of extrinsic or site-specific factors on invader success.

MATERIALS AND METHODS

Field site and dates

We examined 8 sites at Cedar Creek Natural History Area, Bethel, Minnesota, USA between 1999-2001. All study sites were old fields, abandoned from cultivation between 1943 and 1965. Study fields were dominated by herbaceous, grassland plants, both native and introduced. Cedar Creek is located on the Anoka Sand Plain and is characterized by sandy, nutrient-poor soil.

Invasive species

We examined 13 species of herbaceous invasive plant species - listed in Table 3.1. The term invader is used here to refer both to aggressive species of exotic origin and native weedy species. Ten of the study species are exotic species introduced from Europe or Eurasia. The other three are native North American plants with weedy characteristics.

Quantification of plant neighborhoods

Plant neighborhoods were quantified by running one-meter transects through plant neighborhoods. Invader plant species were selected haphazardly from fields, and a meter stick was centered at the base of the focal plant. The compass orientation was selected by tossing the meter stick in the air and aligning it next to the focal plant along the angle at which the stick fell. A compass heading was taken to record the angle of the meter stick, treating 0° (or 360°) as north.

We recorded the size and species identity of each plant located within 1 inch of the near edge of the meter stick. Absolute distances from the focal invader plant were not recorded; instead we recorded distances in 10 cm increments in both directions along the meter stick (0-10 cm, 10-20 cm, etc.). The sizes of the focal invader plant and plants in its neighborhood were determined by visual estimation through comparison to cards of fixed area (e.g. 1 cm^2, 2 cm^2, 5 cm^2).

Neighborhood properties

We divided neighborhood characteristics into two groups, one set describing the size-distribution of plants in the neighborhood and the other set describing community composition properties of the neighborhood. Size-distribution properties included the mean, median, and sum of plant sizes, standard error of the mean (SE), variance (V), coefficient of variation (CV), kurtosis, and skewness. Community composition properties used were the number of plants or neighborhood density, species richness, and a modified Shannon index of diversity in which size was used as the measure of relative abundance.

Statistical analyses

Our questions concern both the general relationships between invader performance and neighborhood properties irrespective of invader species identity or field identity as well as properties specific for each species. We therefore divided analyses into two sets referred to as *broad-scale* and *fine-scale* investigations. Broad-scale analyses included the entire data set irrespective of invader species identity or field identity. Fine-scale analyses examined invader response by invader species identity and field identity. Because the fine-scale analysis is essentially a two-way analysis in which species identity and field identity represent factors, we used a subset of the data that included only neighborhoods of invader species that appeared in multiple plots for these analyses. We used parametric statistics in all analyses after log-transformation of variables that were not normally distributed.

Although we collected neighborhood data along a one-meter transect through the neighborhood of each focal invader, we wanted to determine the effective neighborhood size for a given plant, i.e. whether invader size is affected by plants growing up to 50 cm away or if only closer plants influence the focal invader. To examine the importance of neighborhood size, we calculated linear regressions of invader size against the sum of the area of plants within 10, 20, 30, 40, or 50 cm radii from the focal invader plant. These regressions were calculated for each species in each field when there were multiple occurrences of a species within a field. Multiple occurrences were found for all 13 invader species, but not all field sites contained all 13 species (Table 3.1). In total, we calculated 180 regressions for this analysis. Both area of plants within neighborhoods and size of invader were $\log_{10}$ transformed for this analysis.

Many of the variables associated with neighborhood properties were highly correlated (see Table 3.4). To avoid problems with colinearity in parametric analyses, we used principal component analyses (PCA) to derive multivariate indices of neighborhood properties based on PCA scores. Each component describes axes that are orthogonal to one another thus each index based on a different component is uncorrelated with other PCA-based indices. Separate PCAs were conducted with the broad-scale and fine-scale data sets. These indices were then employed in ANCOVAs and regressions to examine the effects of invader identity, field identity, and neighborhood characteristics on invader success (i.e. size) at both scales.

We also used discriminant function analysis (DFA) to determine how distinct invader plant neighborhoods were with respect to different invader species and how distinct neighborhoods were with respect to field sites.

To facilitate reading, we provide additional details of the parametric techniques specific to each analysis as they arise in the results section below. All analyses were performed using SYSTAT 8.0.

RESULTS

Broad-scale patterns

The invader species we selected were generally larger than plants in their neighborhood (Fig. 3.1). Thus, relative to resident species, the set of invasive plants we studied were successfully growing within their neighborhoods. Average invader size, neighborhood density, and neighborhood species richness varied by focal invader species (Table 3.1) and among fields (Table 3.2). Not all invader species were found in all fields; Table 3.3 shows sample sizes of neighborhood transects conducted for each species in each field.

We regressed invader size against the sum of neighbor sizes within neighborhoods of different radii (10, 20, 30, 40, or 50 cm) to examine the influence of neighborhood size on invader success. The results of these regressions showed that the influence of neighborhood size on the strength of the relationship between invader size and total neighbor area was small. Regression coefficients (slopes) for the influence of total plant area within a neighborhood of a given size on invader size ranged from –4.00 to 4.00 with a mean of 0.08 (SE = 0.06) and a mode close to 0 for all neighborhood sizes (Fig. 3.2a). The R^2s for these regressions (Fig. 3.2b) indicated very low predictive power ranging from a minimum of 0.001 to a maximum of 0.99 with a mean of 0.16 (SE = 0.20) and median of 0.001. Because the difference between neighborhoods of different sizes was small, we used the intermediate neighborhood size of 30 cm from the focal invader in the rest of our analyses.

Most of the neighborhood properties we measured were highly correlated (Table 3.4), so we combined several neighborhood characteristics (maximum neighbor size, range of neighbor sizes, mean neighbor size, standard error of the mean, coefficient of variation, median neighbor size, sum of neighbor sizes within 30 cm, neighborhood density, species richness, and Shannon index) using principal components analysis (PCA). We then used the first principal component (PC I) to examine field site and invader species effects on neighborhood patterns. PC I accounted for 54.5% of the variance in invader size (Table 3.5). Maximum invader size, range of invader size, mean invader size, and standard error of the mean loaded most strongly for PC I (Table 3.5). The second principal component (PCII), however, showed the largest loadings for the Shannon index, species richness, and neighborhood density, in that order, and accounted for 18.65% of the variance explained (Table 3.5). The largest loadings for PC II were negative values, unlike for PC I, in which the loadings of largest magnitude were the most positive (Table 3.5). Thus, PC I captured variance in plant neighborhood properties due largely to differences in neighbor plant sizes among invader neighborhoods, while PC II captured variance due to differences among invader neighborhoods in plant diversity. Henceforth, we use PC I as an index of neighborhood properties positively associated with variation in neighborhood plant sizes and PC II as an index negatively associated with neighborhood diversity.

We included PC I and PC II as covariates in an analysis of covariance (ANCOVA) to examine the effects of invader species identity, field identity, and neighborhood characteristics on invader size. The ANCOVA revealed significant main effects due to species identity but not field identity. PC I (neighborhood size) covaried significantly with invader size but there was no significant effect of PC II (neighborhood diversity) (Table 3.6). Therefore, invader size was significantly influenced by invader species identity and neighborhood properties associated with size, but not by field identity or neighborhood diversity. A regression of invader size against PC I showed a significant positive relationship between these two variables (df = 1, 318; $p < 0.005$), however the R^2 was very low (0.025) indicating extremely low predictive power for neighborhood size properties in determining invader size (Fig. 3.3).

Fine-scale patterns

To examine the relative effects of field versus species identity we conducted two, two-way ANCOVAs. In the first ANCOVA, the model included both species identity and field identity as main effects, with the PC I index of the neighborhood properties and the PC II index of neighborhood diversity as covariates, and log-transformed invader size as the response variable. The second analysis used the same main effects and covariates but substituted the proportional log-transformed invader size as the response variable. By using the proportion, all invader plant species had a maximum size of 1 and a minimum size of 0 with all intermediate sizes scaled linearly between 0 and 1. This transformation eliminated the main factor associated with species identity; namely the differences in sizes among invaders. Our data permitted analyses of only two sites (Biodiversity and Pots) and six invader species (*A. repens*, *B. incana*, *C. tectorum*, *P. oligosanthes*, *T. dubius*, and *V. villosa*).

Because these analyses are constrained to these 2 sites and 6 species, we recalculated PC I and PC II, using only these neighborhoods (Table 3.7). Although there is some difference in loadings and percent variation explained by principal components (compare Table 3.5 with Table 3.7), the primary difference is in the sign of the loadings for PC II. As in the broad-scale PCA conducted across all sites and all species, PC I for the fine-scale data set was most strongly associated with variation in neighborhood plant sizes, while PC II is most strongly associated with neighborhood diversity characteristics (species richness, Shannon index, and plant density), though in the opposite direction (Table 3.7).

The first ANCOVA, using actual invader size as the response variable, revealed that invader species identity and plant neighborhood diversity (PC II) had significant effects on invader size (Table 3.8). There was no significant interaction between invader species identity and field identity. These results indicate that invader species identity is the dominant variable that determines the size of an invader. This result is not surprising given the enormous range in sizes of the invader species we examined (Table 3.1).

The second ANCOVA used the scaled proportional invader size as a response variable, this removing the effects due to differences in size among invader species. In this analysis, invader species identity was no longer significant, but a significant interaction between species identity and field identity emerged (Table 3.9). This interaction occurs because the sizes of the invader species differ in an inconsistent way between the two sites used in this analysis (Fig. 3.4).

Most importantly, however, neighborhood diversity (PC II) remained a significant covariate (Table 3.9). Although this covariation is significant, a linear regression indicated that the significant positive linear association between PC II and invader success (df = 1, 120; $P < 0.01$) has very low predictive power ($R^2 = 0.05$) (Fig.3. 5). Neighborhood diversity appears to have a negative effect on invader size, but the effect is small.

The two old fields used in the fine-scale analyses are distinct when classified by PC I and PC II. Discriminant function analysis (DFA) was able to successfully classify fields accurately on average 83% of the time using only PC I and PC II (Table 3.10). In contrast, the six species varied considerably in their correct categorization using DFA. For example, *V. villosa* was classified correctly 79% of the time while *P. oligosanthes* was classified correctly only 23% of the time (Table 3.11). The 95% confidence ellipses illustrate these DFA results by showing that plant neighborhoods for Pots and Biodiversity were quite distinct (Fig. 3.6) while neighborhoods of invader species show overlap for some species and not for others (Fig. 3.7).

DISCUSSION

Our study suggests that invader performance, as indexed by above-ground invader size, is a function of two factors with their importance ranked in the following order (most important to least important); (1) invader species' identity (Tables 3.6 and 3.8), (2) properties of the plant neighborhood surrounding an invader (Tables 3.6, 3.8 and 3.9), and (3) site identity. We found no evidence that site identity had a direct effect on invader performance, but when invader size was controlled for, there was a significant interaction between invader species and field identity (Table 3.9). While neighborhood properties were significantly associated with invader success, these associations were weak and provided little predictive power.

This study, because it was purely observational in nature, did not test the mechanisms by which resident diversity may endow a community with resistance to invasion. Our measurements provide information about post-establishment invader success. Without manipulating neighborhood properties, we are unable to determine if neighborhoods with certain properties provide greater resistance to invasion, because resistance often involves pre-establishment invasion processes. In our study, invaders were larger than their neighbors (Fig. 3.1), which implies that the properties of the neighborhoods we are examining are those associated with successful invader establishment. Nevertheless, our study provides several insights into the issues surrounding Elton's conjecture that diverse assemblages of native species should provide biotic resistance to establishment of invasive species.

First, the properties of plant neighborhoods do appear to have some effect on invader performance. Invaders appear to be more successful in neighborhoods that are less crowded (Table 3.6; Fig. 3.3). These results support previous work by Naeem et al. (2000), who found that invaders were less successful in neighborhoods with greater crowding. Invaders also appear to be more successful in neighborhoods with lower diversity (Tables 3.8 and 3.9; Fig. 3.5). These results support previous experimental studies at the same site that have shown a negative relationship between diversity and invader success (Knops et al. 1999, Naeem et al. 2000, Kennedy et al. 2002) and contradict previous observational studies that have found positive relationships between native species richness and exotic species richness (Stohlgren et al. 1998, Levine 2000). Both relationships between invader size and neighborhood properties have very low predictive power, however, explaining only a small portion of the variance in invader size.

Second, our data indicate that plant invader neighborhoods are not random. Some invader species have similar neighborhood properties while others differ in their neighborhood properties (Fig. 3.7). *Vicia villosa* appears to grow in neighborhoods with the greatest diversity and largest neighbors. *V. villosa* is a legume, and as such, is likely able to grow in areas with higher diversity because it is less limited by nitrogen availability. It is also a vine that is capable of growing on top of other plants, so crowding may not limit *V. villosa* as much as it does other plants either. *Panicum oligosanthes*, on the other hand, appears to grow primarily in neighborhoods with smaller neighbors and lower levels of neighborhood diversity than the other invaders do. *P. oligosanthes* is the only C-4 species examined in this study, and its neighborhood properties may be related to its functional group classification. Because C-4 species are warm-season plants (i.e. they do the bulk of their growing in the hot mid-summer months), they may be more successful in areas where the cool-season, C-3 plants have not achieved large sizes before the peak growing season for *P. oligosanthes*. *Agropyron repens*, a C-3 grass, shows a fair amount of overlap in neighborhood properties with the remaining three invader species, all C-3, non-leguminous forbs, which tend to be found in neighborhoods with intermediate levels of diversity and neighbors of intermediate size.

Third, habitats have different neighborhood properties which means that invaders that are sensitive to their neighborhoods will vary in their success among habitats. Figure 6 shows that neighborhood properties were distinct for Biodiversity and Pots fields. Invader success is therefore likely to vary in different habitats, depending on how habitat characteristics affect resident plants at each location. Site identity was not found to directly affect invader performance in our analyses (Tables 3.6, 3.8, and 3.9), but when invader size was controlled for, a significant interaction between invader species and field identity did materialize. Differences in neighborhood properties by field do not appear to be related to time since abandonment from agriculture, because neighborhoods in Pots field are, in general, more diverse than neighborhoods in Biodiversity field, which was abandoned 6 years earlier than Pots field.

To explicitly test the effects of neighborhood properties, we would need to manipulate the properties of interest and examine their effects on invader success. This study complements previous experimental work done in the same system (Knops et al. 1999, Naeem et al. 2000, Kennedy et al. 2002), by describing the relationship between invader success and neighborhood properties in naturally-occurring invader plant neighborhoods. We are unable to identify the mechanism by which neighborhood properties affect invader performance, but the mechanistic basis for these patterns has been explored in the aforementioned experimental studies.

This study has important implications for restoration, conservation, and management. We have demonstrated that plant neighborhood properties can influence the success of invasive species. Plant neighborhoods with larger neighbors are less hospitable for invaders, so increasing crowding of resident plants may reduce the success of invaders. Neighborhood diversity has been shown to reduce the establishment of successful invaders (Knops et al. 1999, Naeem et al. 2000, Kennedy et al. 2002), and those results are corroborated here. Therefore, improving resident plant diversity is likely to reduce the success of invasive species and lessen their impact on native ecosystems.

We conclude that the strength of biotic influences operating at the level of the plant neighborhood differs among species, is sensitive to plant neighborhood properties, and can be relatively insensitive to differences among habitats within a region. Observational studies of the spatial composition and abundance of plants in a habitat can provide insights into the relationship between resident diversity and post-establishment invader success, but they are relatively weak as predictive tools and cannot identify mechanisms. Pluralistic approaches that employ both experimental and observational methods are likely to be the most informative.

Table 3.1. Summary statistics for invader neighborhoods by species.

Species	**Species origin**	**Functional group**	**N**	**Mean Size (SD)**	**Neigh. density**	**Neigh. S**
Agropyron repens (quackgrass)	exotic	C-3 grass	27	1.5 (1.2)	19.9	3.52
Berteroa incana (hoary allysum)	exotic	forb	39	8.4 (11.5)	19.5	4.36
Bromus inermis (smooth brome)	exotic	C-3 grass	23	3.1 (5.1)	16.8	3.70
Crepis tectorum (narrow leaf hawk's beard)	exotic	forb	25	9.6 (6.8)	24.0	4.72
Conyza canadensis (horseweed)	native	forb	36	18.5 (35.2)	21.5	3.75
Hieracium aurantiacum (orange hawkweed)	exotic	forb	9	43.3 (37.5)	23.8	5.67
Lychnis alba (white campion)	exotic	forb	2	60.5 (77.1)	40.5	2.50
Panicum oligosanthes (Scribner's panic grass)	native	C-4 grass	315	69.6 (68.4)	18.2	4.14
Physalis virginiana (Virginia groundcherry)	native	forb	26	19.8 (12.6)	26.4	3.46
Polygonum convolvulus (black bindweed)	exotic	forb	10	2.4 (1.2)	16.2	2.60
Tragopogon dubius (goat's beard)	exotic	forb	34	44.7 (52.7)	20.4	3.71
Verbascum thapsus (mullein)	exotic	forb	27	492.4 (707.2)	16.2	4.00
Vicia villosa (hairy vetch)	exotic	legume	27	31.1 (22.3)	22.3	5.26

Table 3.2. Summary statistics for invader neighborhoods by field.

Field Site	**Year abandoned from farming**	**N**	**Mean Invader Size (SD)**	**Mean Neighbor Size**	**Mean Neighborhood Density**	**Mean Neighborhood S**
550	1943	55	208.0 (548.3)	1.61	17.5	3.76
Biodiversity	1958	53	16.7 (23.6)	2.51	20.9	6.45
E	unknown	29	50.4 (96.7)	1.06	18.1	3.79
Pots	1964	133	24.2 (40.4)	1.26	24.2	3.41
57	1943	20	20.7 (66.2)	1.28	14.6	3.20
58	1950	11	32.9 (38.6)	1.54	14.6	2.91
54	1951	7	50.3 (40.1)	6.87	24.8	5.43
525	1951	12	196.1 (166.6)	1.98	10.9	4.08

Table 3.3. Frequency of invaders in fields. Note that invaders co-occur in several fields, but only the Pots and Biodiversity fields contained sufficient numbers across several invader species.

FOCAL INVADER SPECIES	**54**	**57**	**58**	**525**	**550**	**Biodiversity**	**E**	**Pots**	**Total**
Agropyron repens	0	0	0	0	10	4	5	8	**27**
Berteroa incana	0	2	3	0	0	10	5	19	**39**
Bromus inermis	0	9	2	0	5	0	4	3	**23**
Crepis tectorum	0	0	0	0	0	10	0	15	**25**
Conyza canadensis	0	0	0	0	5	0	5	26	**36**
Hieracium aurantiacum	7	0	0	0	0	2	0	0	**9**
Lychnis alba	0	0	0	0	0	0	0	2	**2**
Panicum oligosanthes	0	3	2	5	7	7	5	6	**35**
Physalis virginiana	0	0	0	0	0	0	0	26	**26**
Polygonum convoluvulus	0	5	0	0	0	0	0	5	**10**
Tragopogon dubius	0	1	4	0	0	9	0	20	**34**
Verbascum thapsus	0	0	0	7	15	0	5	0	**27**
Vicia villosa	0	0	0	0	13	11	0	3	**27**
Total	**7**	**20**	**11**	**12**	**55**	**53**	**29**	**133**	**320**

Table 3.4. Correlation matrix for neighborhood properties. Numbers shown are Pearson correlation coefficients. Significant correlations are denoted by the following symbols: ** indicates p<0.001; * indicates p<0.01; bold type indicates p<0.05.

	S	**H**	**N**	**Skew**	**Kurt**	**Max**	**Sum**	**Range**	**Min**	**Med**	**Mean**	**SE**	**SD**	**Var**
H	*0,69													
N	0,13	0,18												
Skew	**0,29	0,13	0,11											
Kurt	**0,26	0,13	0,16	**0,97										
Max	0,15	-0,21	-0,03	**0,33	**0,32									
Sum	**0,33	-0,12	0,10	**0,25	*0,23	**0,87								
Range	0,15	-0,21	-0,03	**0,33	**0,33	**1,00	**0,87							
Min	0,17	0,17	*-0,22	-0,04	-0,04	0,00	0,05	0,00						
Med	**0,32	0,06	-0,16	-0,09	-0,07	0,13	**0,35	0,13	**0,41					
Mean	**0,27	0,19	-0,14	0,21	0,18	**0,88	**0,94	**0,88	0,13	**0,43				
SE	0,14	**-0,24	-0,14	**0,28	**0,26	**0,97	**0,84	**0,97	0,04	0,20	**0,93			
SD	0,16	*-0,23	-0,08	**0,30	**0,28	**0,99	**0,88	**0,99	0,02	0,17	**0,92	**0,99		
Var	0,02	-0,19	-0,02	0,16	0,16	**0,92	**0,70	**0,92	-0,04	-0,01	**0,72	**0,88	**0,90	
CV	*0,24	-0,10	-0,03	**0,81	**0,78	**0,56	**0,48	**0,56	0,11	-0,07	**0,48	**0,55	**0,56	**0,34

Table 3.5. PCA for plant neighborhood properties using all invader species in all field sites. For this analysis, 320 invader neighborhoods were used.

		PC I	PC II	PC III
Component loadings	Log_{10} (maximum)	0.98	-0.17	0.10
	Log_{10} (range)	0.98	-0.16	0.11
	Log_{10} (standard error of the mean)	0.95	-0.29	-0.09
	Log_{10} (mean)	0.95	-0.10	-0.21
	Log_{10} (sum(3))	0.73	0.32	0.16
	Log_{10} (coefficient of variation)	0.73	-0.37	0.45
	Log_{10} (median)	0.52	0.39	-0.62
	Log_{10} (density)	-0.07	0.53	0.72
	S	0.60	0.62	0.01
	H	0.21	0.82	-0.05
% of Total Variance Explained		54.49	18.65	12.12

Table 3.6. Analysis of covariance using general linear models for the relationship between invader success and invader species identity, field identity, and neighborhood properties. Bold face indicates significance at listed *P* value.

Source	**Sum of Squares**	**df**	**Mean Square**	**F ratio**	**P**
Invader species identity	103.851	11	9.441	43.991	**<0.001**
Field identity	2.408	7	0.344	1.603	0.134
PC I	1.037	1	1.037	4.834	**<0.05**
(covariate, neighborhood size)					
PC II	0.033	1	0.033	0.155	0.69
(covariate, neighborhood diversity)					
Error	63.74	297	0.215		

Table 3.7. PCA for plant neighborhood properties using only 6 species in Biodiversity and Pots sites. There 122 invaders in this set.

		PC I	PC II	PC III
Component loadings	Log_{10} (maximum)	0.98	0.16	0.10
	Log_{10} (range)	0.98	0.16	0.11
	Log_{10} (standard error of the mean)	0.97	0.21	-0.11
	Log_{10} (mean)	0.95	0.11	-0.22
	Log_{10} (sum(3))	0.69	-0.18	0.34
	Log_{10} (coefficient of variation)	0.74	0.27	0.46
	Log_{10} (density)	-0.18	-0.25	0.87
	Log_{10} (median)	0.55	-0.33	-0.65
	S	0.58	-0.71	0.09
	H	0.17	-0.92	-0.02
% of Total Variance Explained		54.49	17.22	12.12

Table 3.8. Two-way ANCOVA results for invader performance (size) with respect to field site, invader species identity, and plant neighborhood properties as a covariate. Data used are for six species and two field sites as described in the text.

SOURCE	**SS**	**df**	**MS**	**F-ratio**	**P**
Invader species identity	20.761	5	4.152	26.528	**<0.001**
Field identity	0.11	1	0.11	0.703	0.404
Invader species x field identity	1.397	5	0.279	1.785	0.122
PC I (covariate, neighborhood size)	0.132	1	0.132	0.846	0.36
PC II (covariate, neighborhood diversity)	0.818	1	0.818	5.225	**<0.05**
Error	16.748	107	0.157		

Table 3.9. Two-way ANCOVA results for proportional invader size with respect to field site, invader species identity, the interaction between these two factors, and plant neighborhood properties as a covariate. Data used are for six species and two field sites as described in the text.

SOURCE	**SS**	**df**	**MS**	**F-ratio**	**P**
Invader species identity	0.46	5	0.09	1.97	0.09
Field identity	0.05	1	0.05	1.15	0.29
Invader species x field identity	0.65	5	0.13	2.76	**<0.05**
PC I (covariate, neighborhood size)	0.04	1	0.04	0.82	0.37
PC II (covariate, neighborhood diversity)	0.23	1	0.23	4.83	**<0.05**
Error	5.029	107	0.047		

Table 3.10. Results of discriminant function analysis for categorization of fields based on neighborhood properties. PC I represents size-based neighborhood characteristics and PC II represents neighborhood diversity characteristics.

Field	**N**	**Constant**	**PC I**	**PC II**	**% Correct**
Biodiversity	56	-1.302	1.058	-1.079	84
Pots	66	-1.007	-0.760	0.775	82

Table 3.11. Results of discriminant function analysis for categorization of invader species based on neighborhood properties. PC I represents characteristics of neighbor size and PC II represents neighborhood diversity characteristics.

Invader species	**N**	**Constant**	**PC I**	**PC II**	**% Correct**
Agropyron repens	27	-2.73	-0.59	-0.20	19
Berteroa incana	39	-2.58	0.13	0.16	3
Bromus inermis	23	-2.65	0.04	-0.43	26
Crepis tectorum	25	-2.66	0.41	0.24	8
Conyza canandensis	36	-2.67	-0.41	0.27	3
Hieracium aurantiacum	9	-4.08	1.90	0.24	67
Lychnis alba	2	-3.68	-1.58	0.37	100
Panicum oligosanthes	35	-2.59	-0.14	-0.17	0
Physalis virginiana	26	-2.70	-0.42	0.35	54
Polygonum convolvulus	10	-3.49	-0.91	-1.14	40
Tragopogon dubius	34	-2.57	-0.06	-0.11	0
Verbascum thapsus	27	-2.57	0.06	-0.11	0
Vicia villosa	27	-2.96	0.96	0.21	37

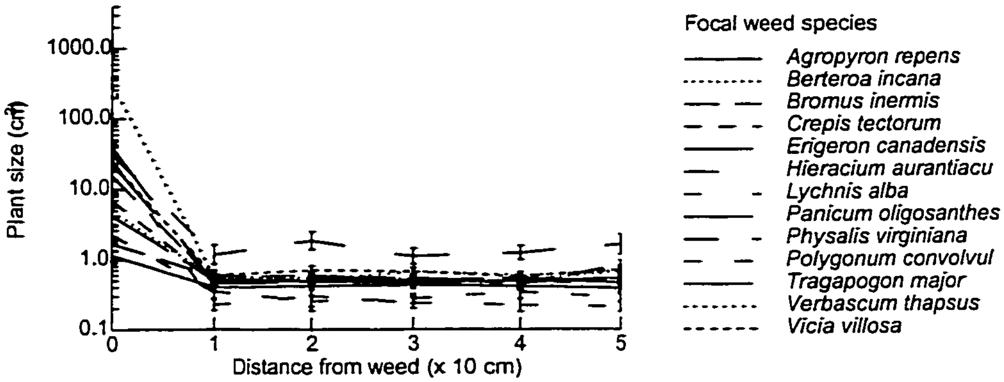

Figure 1. Sizes of focal plant and neighborhood plants. This figure shows the average size of the focal, invader species at the center of a 100 cm transect (distance = 0) and the average size of plants within every 10 cm increment away from the focal plant (distance = 10, 20, 30, 40 and 50 cm). Although it is difficult to distinguish individual focal species from one another, the figure illustrates clearly that the invaders selected for this study were, in general, larger than their neighboring plants. Error bars represent one SE.

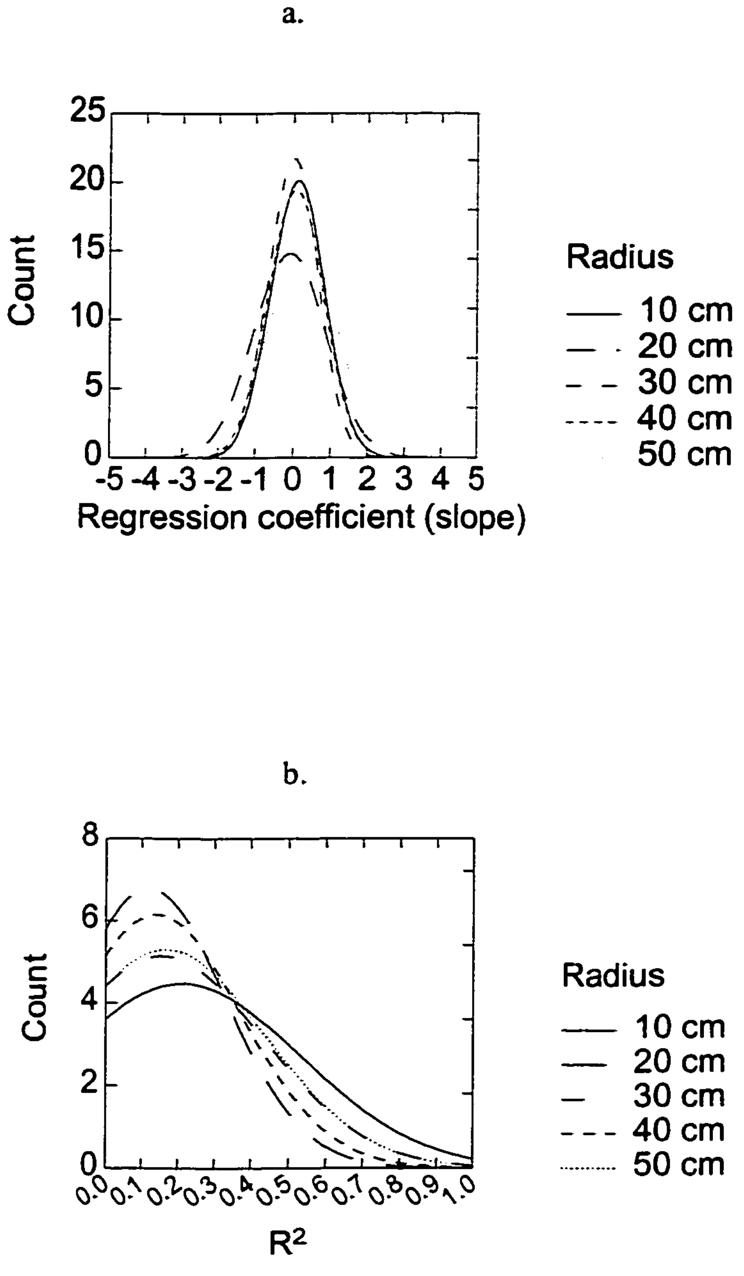

Figure 2. Normal curves fitted to frequency distribution of (a) regression coefficients and (b) R^2 values for the relationship between focal invader size and total area of plants within neighborhoods of 10, 20, 30, 40, or 50 cm radii from focal invader.

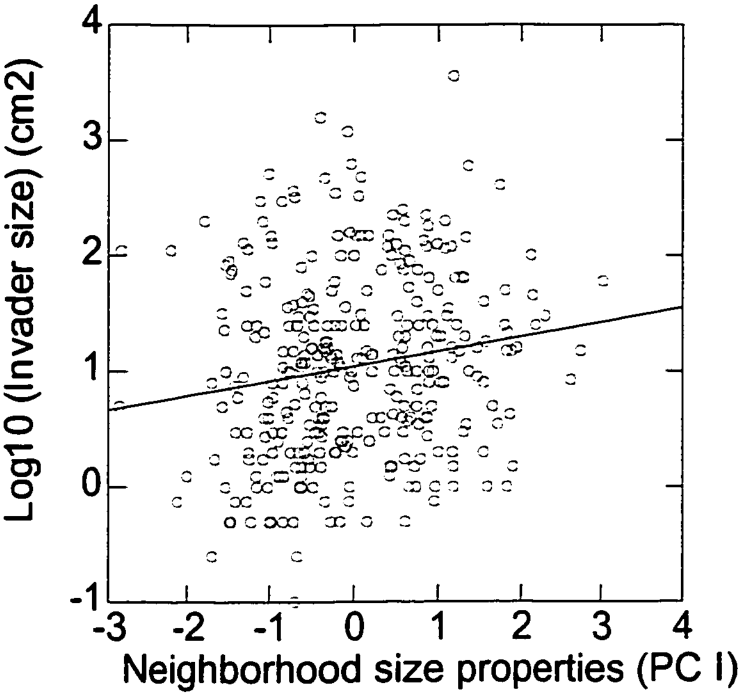

Figure 3. Regression of invader size on PC I for entire data set (broad-scale), where PC I represents neighborhood size properties. Invader size decreases with increasing size of neighbor plants ($p < 0.005$, $R^2 = 0.025$).

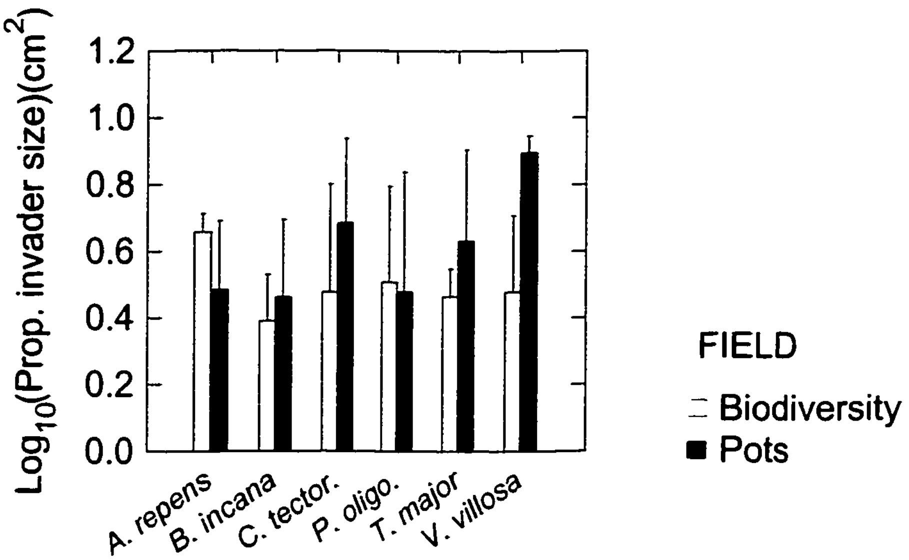

Figure 4. Proportional invader size by species and field. The proportional invader size varied in an inconsistent manner for different species in the two fields included in fine-scale analyses. Proportional invader sizes are log$_{10}$-transformed. Error bars represent one SE.

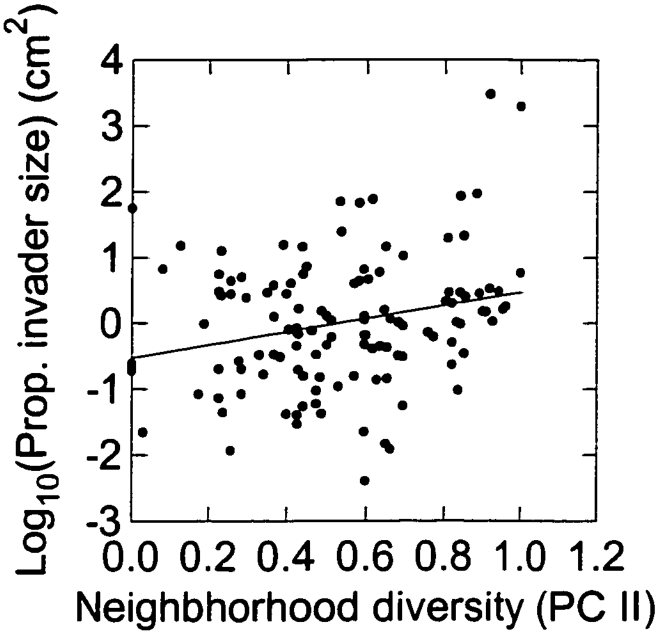

Figure 5. Regression of proportional invader size on PC II for reduced data set (fine-scale), where PC II is negatively associated with neighborhood diversity properties. Proportional invader size increases with increasing neighborhood diversity ($p < 0.01$, $R^2 = 0.05$).

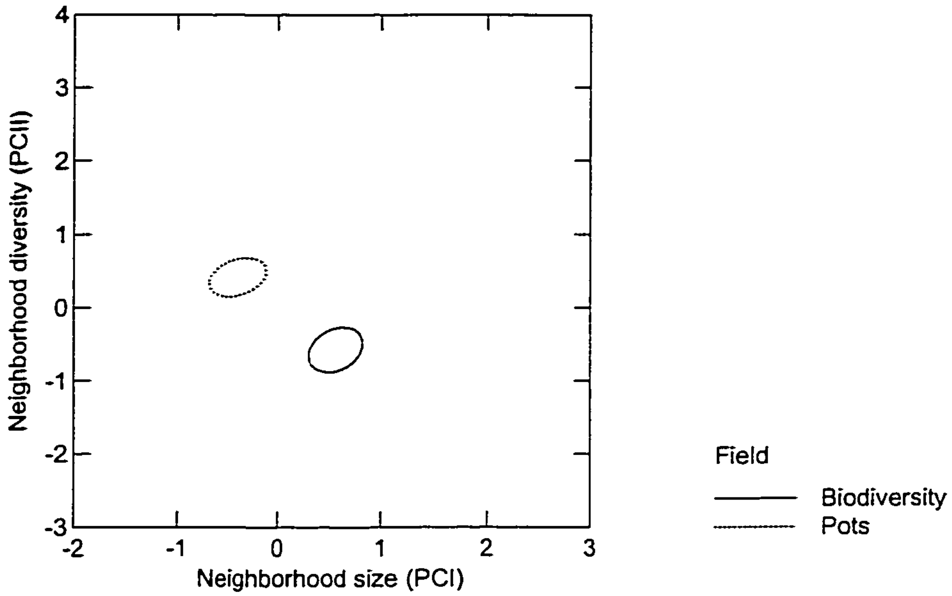

Figure 6. Categorization of Biodiversity and Pots fields based on neighborhood size (PC I) and diversity (PC II) properties from discriminant function analysis. The two fields have distinct neighborhood properties.

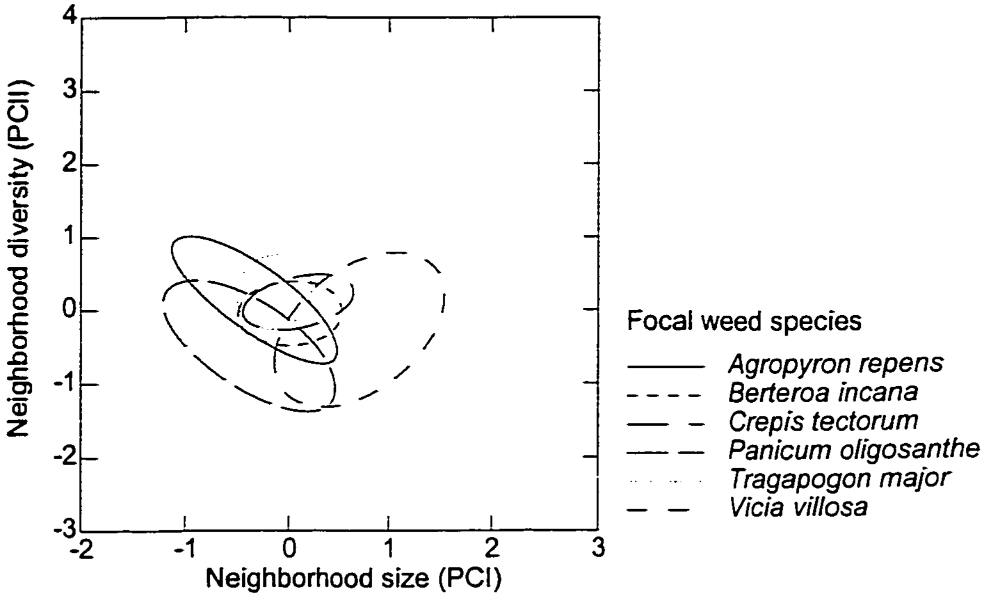

Figure 7. Categorization of six focal invader species based on neighborhood size (PC I) and diversity (PC II) properties from discriminant function analysis. Some species have relatively distinct plant neighborhoods, while others show significant overlap in their neighborhood characteristics.

CHAPTER IV

INVASION SUCCESS OF *CREPIS TECTORUM* AND *CONYZA CANADENSIS* IN EXPERIMENTAL GRASSLAND PLOTS: THE IMPACTS OF CO-OCCURRING CHANGES IN CO_2, N DEPOSITION, AND RESIDENT PLANT BIODIVERSITY*

INTRODUCTION

Increases in atmospheric CO_2 (IPCC 1994), increasing rates of N deposition (Vitousek et al. 1997, Wedin and Tilman 1996), and biodiversity loss due to a variety of factors (Global Biodiversity Assessment 1995, Wilcove et al. 1998) represent three, co-occurring aspects of global change. The accelerating spread of invasive plant species in virtually all terrestrial ecosystems (Mack et al. 2000) is likely to be affected by global change, but the interaction between global change and invasion is not well understood (Dukes and Mooney 1999).

Several studies have shown that invasion is affected by individual environmental or global change factors, but few have examined the impacts of co-occurring changes in CO_2, N, and resident plant diversity. Several invasive plant species have shown increased growth under experimentally elevated CO_2 conditions. CO_2 levels enhanced by free-air CO_2 enrichment (FACE) technology in a Mojave

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* This work was done in collaboration with Ndiya Ogba (Benedict College), Shahid Naeem (University of Washington), Johannes Knops (University of Nebraska), Peter Reich (University of Minnesota), and David Tilman (University of Minnesota).

Desert ecosystem caused increased vegetative growth and seed production of an invasive annual grass (*Bromus tectorum*) above the levels exhibited by native annual grasses (Huxman and Smith 2001). A study on *Prosopis glandulosa*, an invasive shrub in the southwestern U.S., showed that *Prosopis* produces greater root biomass and has increased water and nitrogen use efficiencies under elevated CO_2 conditions than under ambient conditions (Polley et al. 1994).

Nitrogen enrichment has also been shown to increase growth in invasive plant species. Maron and Jeffries (Maron and Jeffries 1999) found that invasive grasses in a coastal California grassland grew better in localized areas where nitrogen was added to the soil by decomposition of nitrogen-rich lupine litter. Experimental nitrogen enrichment of old field plots at Cedar Creek Natural History Area in Minnesota caused both a decrease in species richness and a switch from the dominant native C_4 grasses to invasive C_3 grass species (Tilman 1993).

The influence of species richness on invasion appears to be more complicated. Observational studies suggest that areas with greater species richness either have higher numbers of plant invaders or that there is no relationship between diversity and invasion resistance (Robinson et al. 1995, Planty-Tabacchi et al. 1996, Wiser et al. 1998, Stohlgren et al. 1999, Levine 2000). However, experimental studies (Levine 2000, Naeem et al. 2000, Knops et al. 1999, Kennedy et al. 2002) found a significant positive relationship between plant diversity and invasion resistance. Knops et al. (1999) demonstrated that invasion success of an introduced forb, *Crepis tectorum* L., and C_3 grass, *Digitaria ischaemum* (Schreb.) Schreb. ex Muhl., decreased with increasing species richness. Similarly, Naeem et al. (2000) and Kennedy et al. (2002) found that increased resident species richness caused decreased light and nitrogen availability and decreased biomass of *Cr. tectorum* as a result. Levine (2000) addressed this discrepancy between observational and experimental studies by using both methods to look at invasion resistance of tussock grassland plant assemblages. His results indicate that while certain environmental conditions promote both native and invasive species richness, at the neighborhood level, more diverse neighborhoods were less successfully invaded.

While providing valuable insights into the *independent* impacts of elevated CO_2, elevated N deposition, and declining biodiversity on plant invasions, manipulating all three factors simultaneously would also provide an opportunity to test for complex interactions among these factors. The Biodiversity, CO_2, and N (BioCON) experiment, consisting of 371 replicate experimental plots in a Minnesota grassland, follows a factorial design and was established expressly for examining such interactions. This design allows for partitioning the variance in response variables to the independent effects of varying resident plant species richness, atmospheric CO_2 levels, and N deposition rates as well as the interactions among them. We tested for the presence of such interactions on invasive species growth focusing on two common, ubiquitous weedy plants, *Crepis tectorum* L. and *Conyza canadensis* (L.) Cronq.

METHODS

Study Site

The BioCON (Biodiversity, CO2, and Nitrogen) Experiment is located at Cedar Creek Natural History Area, a Long-Term Ecological Research (LTER) Site in Bethel, Minnesota. Cedar Creek is characterized by sandy, nutrient-poor, glacial outwash soils and is located at the tallgrass prairie-oak savanna border. BioCON was established in a 10 ha old field, abandoned from agricultural production in 1964 and planted with brome grass (*Bromus inermis*) for erosion control.

BioCON Experimental Design

In the BioCON Experiment, species richness, CO_2, and N are manipulated in a factorial (4 x 2 x 2) design. Details of the BioCON experiment are described elsewhere (Reich et al. 2001). Briefly, six FACE rings (20 m diameter) were constructed in 1997 following Hendrey et al. (1997). The internal area of each ring was cleared of all vegetation, and the seed bank was killed using methyl bromide. Rings were subdivided into 2 x 2 m plots separated by a 0.45 m buffer made of cement blocks. A total of 359 plots were planted with a randomly assigned number (1, 4, 9, or 16) of grassland plant species from four different functional groups: C_4 grasses, C_3 grasses, legumes, and non-leguminous forbs (Table 4.1). Within a treatment level, species composition was also randomly assigned. All species used in the experimental treatments are either native or naturalized species at Cedar Creek. An additional 12 plots were not planted with any species and were maintained as bare ground plots. Species richness treatments were maintained by manual removal of all but the designated species for each plot.

CO_2 treatments were randomly assigned to the six rings. CO_2 was enhanced in three of the rings, using FACE equipment to increase CO_2 levels to a constant daytime level of 550 μmol mol^{-1}. The three remaining rings were exposed to ambient CO_2 (368 μmol mol^{-1}) but have the full FACE set up to control for any unexpected effects of the equipment on community and ecosystem processes.

Nitrogen treatments were also randomly assigned. Half of the plots were exposed to only ambient N, and the remainder received an additional 4 g m^{-2} yr^{-1}, added manually in granular form (NH_4-NO_3) three times a year (1998-2000). Current levels of N deposition in North America are between 0.5 and 2.5 g N m^{-2} $year^{-1}$ (Wedin and Tilman 1996).

Invasive Species

In early spring 2000, before the first weed removal of the season, we marked individuals of two common, non-resident (i.e. not planted in the experimental plots) annual forb species (*Crepis tectorum* and *Conyza canadensis*) in each plot. *Cr. tectorum* was introduced to North America from Eurasia, and *Co. canadensis* is a native weedy species, which was not planted in the experimental plots. Though *Co. canadensis* is not an alien species, it still serves as a test of how susceptible an assemblage is to invasion by a non-resident species. Both species are members of the family Asteraceae.

When available, three individuals of each species in each plot were marked for study. If fewer than three individuals of either species were growing in a plot, all individuals (one or two) of that species were marked. Marked individuals were protected from weeding by surrounding them with a 4" diameter PVC ring approximately 3" in height. These individuals were allowed to grow until their first flowers opened (late June to mid July for *Cr. tectorum*, mid July to early August for *Co. canadensis*). Upon flowering, plant height and the length of the longest leaf of each plant were measured. Plants were then removed from the ground, divided into aboveground and belowground biomass, dried, and weighed.

Statistical Analysis

Leaf length, plant height, root biomass, and aboveground biomass were all highly correlated for both *Cr. tectorum* and *Co. canadensis* (Tables 4.2 & 4.3). As a result, we selected total plant biomass as our measure of plant success for all other analyses to avoid problems associated with colinearity. We compared weed biomass in control (bare ground) and vegetated plots using a two-sample t-test. We examined the effects of CO_2, N, and species richness (1 or 4 species) on the total biomass of *Cr. tectorum* and *Co. canadensis* using analysis of variance (ANOVA). One data point considered to be an outlier (Studentized residual = 3.470) was removed from the model. Finally, we used stepwise backwards multiple regression to examine the effects of other plot variables (available nutrients, biomass of resident plant species) on total weed biomass. All analyses were performed using SYSTAT 8.0.

RESULTS

A total of 192 *Crepis tectorum* individuals and 236 *Co. canadensis* individuals were sampled, all from plots with 0, 1, or 4 species planted. Almost no individuals of *Cr. tectorum* or *Co. canadensis* were found in plots planted with either 9 or 16 species, and as a result, we could not examine the effects of the higher diversity treatments and their interactions with CO_2 and N on the success of the two study species. We also observed that no individuals of *Cr. tectorum* or *Co. canadensis* were found in plots that had been planted with *Achillea millefolium*, another non-leguminous forb in the family Asteraceae.

A comparison of weed biomass in bare ground and vegetated plots showed that both *Cr. tectorum* and *Co. canadensis* individuals achieved larger sizes when growing in plots without other vegetation. These differences in biomass were statistically significant for both species (*Cr. tectorum*: $t = 2.631$, $df = 22.8$, $p = 0.027$; *Co. canadensis*: $t = 4.847$, $df = 29.1$, $p < 0.001$).

The treatment effects differed for the two species. *Cr. tectorum* biomass decreased significantly under enhanced CO_2 conditions (Fig. 4.1, Table 4.2). Nitrogen addition and species richness treatments had no effect on total biomass of

Cr. tectorum. Conversely, *Co. canadensis* biomass increased when both CO_2 and N were added at all levels of species richness (Fig. 4.1), however, there was no statistically significant difference between treatments (Table 4.3). There were no significant interactions between treatments for either species (Tables 4.2 & 4.3).

Figure 4.2 shows the change in biomass for each species with each treatment, relative to ambient conditions. *Cr. tectorum* biomass consistently decreased with added CO_2 and N, with the greatest decrease in biomass (-76 %) occurring in the 4 species plots with both added CO_2 and N. *Co. canadensis* responded differently. When only CO_2 or N was added, *Co. canadensis* biomass increased in monocultures but decreased in 4 species plots. Under both enhanced CO_2 and N, *Co. canadensis* biomass increased dramatically (Fig. 4.2).

The differences in *Cr. tectorum* and *Co. canadensis* biomass in different plots can be partially explained by the biomass of certain resident plant species. We used a stepwise backward multiple regression model that included available ammonium, available nitrates and nitrites, total root biomass (0-20 cm depth), and aboveground biomass of all 16 resident plant species. For *Cr. tectorum*, the only significant factor in the model was biomass of *Lupinus perennis* ($p = 0.023$, $r^2 = 0.057$). Three resident species had significant effects on *Co. canadensis* biomass ($r^2 = 0.139$): *Anemone cylindrica* ($p = 0.016$); *Poa pratensis* ($p = 0.046$); and *Schizachyrium scoparium* ($p = 0.044$).

DISCUSSION

Our results indicate that the effects of increased CO_2 and N and decreased species richness on the success of *Cr. tectorum* and *Co. canadensis* may be less complicated than predicted (Dukes and Mooney 1999). We found no evidence of interactive effects of the treatments on the success of *Cr. tectorum* and *Co. canadensis* in our experimental plots. However, we did find some unexpected results. For instance, *Cr. tectorum* biomass decreased under elevated CO_2 conditions. This may be a result of increased biomass of *L. perennis*, which increased under elevated CO_2. *Cr. tectorum* lives in rosette form for most of the growing season and is therefore likely to be affected by changes in canopy cover of other plant species. *L. perennis* has broad leaves and grows early in the season (June to early July) at the same time as *Cr. tectorum*.

The two study species responded differently to the treatments. *Cr. tectorum* responded negatively to CO_2 enrichment, but was not affected by N and species richness treatments. These results confirm the results of Knops et al. (1999) who found that *Cr. tectorum* biomass decreased significantly only with a resident species richness of 6 or more species. Therefore, we expect that we would have seen a significant effect of species richness on *Cr. tectorum* biomass if we had been able to measure *Cr. tectorum* in the 9 and 16 species plots. The fact that *Cr. tectorum* and *Co. canadensis* both occurred rarely in the higher diversity plots provides some evidence that increasing species richness did, in fact, affect the invasion success of both species as found in previous studies (Naeem et al. 2000, Knops et al. 1999). This conclusion is further supported by the greatly increased size of plants in bare ground plots as opposed to plots planted with one or four resident plant species.

The differences in plant response may be attributable to several factors. First, *Co. canadensis* is a native species that has coevolved with the resident assemblage of species. It may be less susceptible to increases in biomass of neighboring species resulting from increased CO_2 and N than is the exotic species, *Cr. tectorum*. However, Prieur-Richard et al. (2000), examined the effects of species richness on *Co. canadensis* in a French grassland, where it is exotic, and found that reproductive biomass responded negatively to increasing richness, but there was no effect of species richness on vegetative biomass of *Co. canadensis*.

The growth form of the two species may also contribute to the observed differential responses of biomass to treatments for *Cr. tectorum* and *Co. canadensis*. *Cr. tectorum* spends much of its life in rosette form, bolting just before flowering, and then dying. The rosette stage of the plant is likely to be more susceptible to increases in resident species biomass, which would tend to decrease amounts of available light. *Co. canadensis*, on the other hand, does not grow in rosette form, and therefore can grow toward the canopy to access light. As a result, increased resident plant biomass resulting from increased CO_2 would not have the same effect on *Co. canadensis*.

Finally, phenology may also play a role in the effects of the treatments on the two species. *Cr. tectorum* grows and flowers early in the season; peak flowering time for *Cr. tectorum* at Cedar Creek is mid-June. As a result, *Cr. tectorum* is more likely to be affected by changes in C_3 grasses responding to increased CO_2 with increased growth, because C_3 grasses are cool-season plants, i.e. most of their growth occurs in May and June.

Several studies have raised the issue that effects often attributed to diversity might be explained by what is referred to as the sampling effect, the idea that the more species that are present, the more likely the chance that a species with key ecosystem function is a member of the community (Huston 1997, Doak et al. 1998, Wardle 2001). We examined the possibility that species identity, rather than species diversity might explain our results by using a multiple regression model that included the biomass of each resident species as factors in the model.

The results of the multiple regression for *Cr. tectorum* showed that total plant biomass was significantly positively affected by the amount of *L. perennis* in that plot. It should be noted, however, that the amount of variance explained by this factor was very low. *L.* perennis is a legume, which may have increased N availability for *Cr. tectorum*. For *Co. canadensis*, on the other hand, total plant biomass was partially explained by the biomass of three resident plant species: *A. cylindrica*, *P. pratensis*, and *S. scoparium*. All three species, members of different functional groups (Table 4.1) had negative impacts on *Co. canadensis* biomass. It is also worth noting that no individuals of either weed species were found in plots where

Achillea millefolium was a resident species. These results suggest two things. First, species identity of the resident plant species may explain some of the variance in weed performance in different plots. Some resident species, such as *A. millefolium*, may be especially successful in outcompeting colonizing species. Second, with the exception of *A. millefolium* (also a member of the Asteraceae), which seemed to deter both *Cr. tectorum* and *Co. canadensis*, different resident species affected the performance of different weeds.

We conclude that for at least some invasive species, predicting response to environmental variance or global change may be possible from single-factor studies. While *Cr. tectorum* and *Co. canadensis* are both annual composites (Asteraceae), they represent an important class of common, weedy species. Of particular importance in this study is the role resident diversity appears to play, which may be applicable to many invasive species. Factors such as resident species composition, relative phenologies of resident species, and the functional group of dominant competitors may all play important roles in determining the relative success of an invasive plant independent of CO_2 and N. Clearly, further study is necessary, as we cannot readily extrapolate to other invasives such as late-season grass invaders (e.g. *Digitaria ischaemum*). However, since invasive species are a leading cause of local extinction (Wilcove et al. 1998), this feedback, in which invasion leads to changes in diversity that permit further invasion, (Simberloff and Von Holle 1999) may represent an important component of community and ecosystem response to global change.

Table 4.1. Study species planted in BioCON experiment, listed by functional group.

Functional Group	Species
C_3 grasses	*Agropyron repens* *Elymus canadensis* *Koeleria cristata* *Poa pratensis*
C_4 grasses	*Andropogon gerardi* *Bouteloua gracilis* *Schizachyrium scoparium* *Sorghastrum nutans*
Legumes	*Amorpha canescens* *Lathyrus venosus* *Lespedeza capitata* *Lupinus perennis*
Non-leguminous forbs	*Achillea millefolium* *Anemone cylindrica* *Asclepias tuberosa* *Rudbeckia serotina*

Table 4.2. Analysis of variance results for *Cr. tectorum*, bare ground plots and outlier excluded.

Source	Sum-of Squares	df	Mean-Square	F-ratio	P
CO_2	8.891	1	8.891	7.037	**0.010**
N	3.009	1	3.009	2.382	0.127
Species richness	0.235	1	0.235	0.186	0.667
CO_2*N	0.235	1	0.235	0.186	0.667
CO_2*Species richness	1.324	1	1.324	1.048	0.309
N*Species richness	1.575	1	1.575	1.247	0.267
CO_2*N*Species richness	0.143	1	0.143	0.113	0.738
Error	104.866	83	1.263		

Table 4.3. Analysis of variance results for *Co. canadensis*, bare ground plots excluded.

Source	Sum-of Squares	df	Mean-Square	F-ratio	P
CO_2	2.560	1	2.560	1.023	0.314
N	6.715	1	6.715	2.685	0.105
Species richness	6.126	1	6.126	2.449	0.121
CO_2*N	3.279	1	3.279	1.311	0.255
CO_2*Species richness	0.234	1	0.234	0.094	0.760
N*Species richness	0.135	1	0.135	0.054	0.817
CO_2*N*Species richness	1.829	1	1.829	0.731	0.395
Error	245.130	98	2.501		

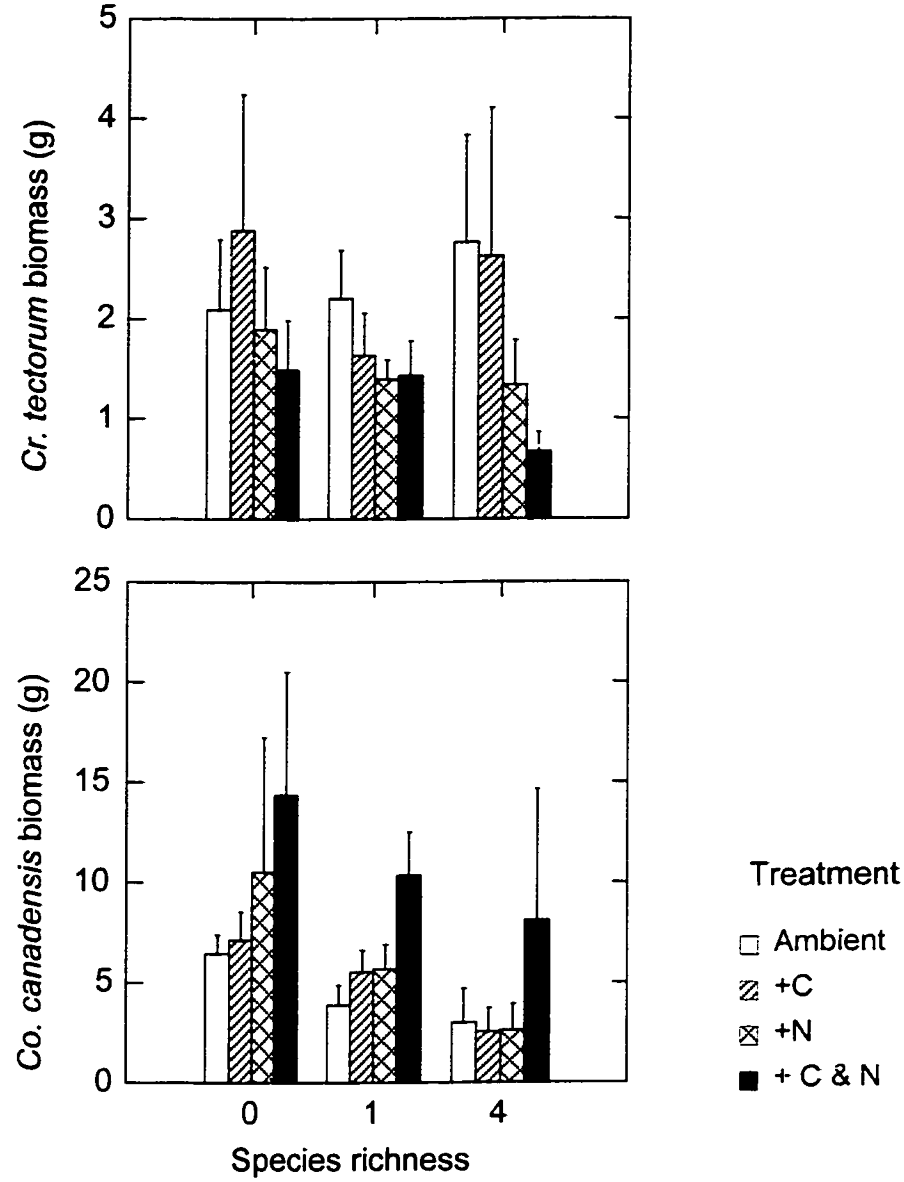

Figure 4.1: Effects of CO_2, N, and species richness treatments on average total biomass of (A) *Cr. tectorum* and (B) *Co. canadensis*. All values are log-transformed. Error bars represent standard error.

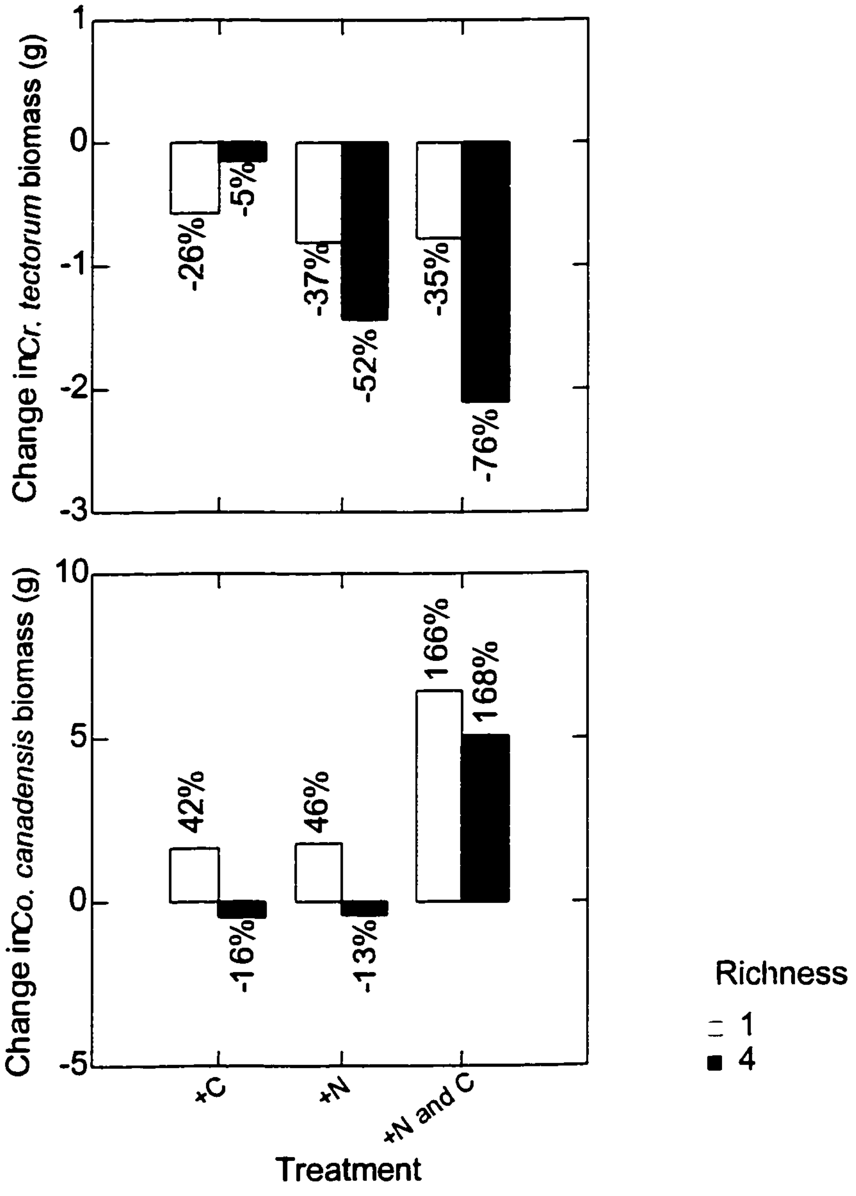

Figure 4.2: Difference between *Cr. tectorum* (A) and *Co. canadensis* (B) biomass between ambient CO_2 and N treatments and enhanced CO_2 and N treatments.

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