Chapter 1

Factors controlling the relative abundance of two thistle species

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INTRODUCTION

North America is home to a diversity of thistles, with more than 140 species native to the continent and several dozen species introduced from Eurasia in the last 200 years. Millions of dollars are spent annually on eradication and control of more than 20 non-indigenous thistle species that have successfully established and spread (Windle 1993). In contrast, native thistles in North America are typically much less abundant; populations are small and uncommon, and several taxa are rare and endangered (Turner et al. 1987; Louda et al. 1990).

In spite of the dramatic differences in abundance of these two groups, and in spite of the prevalence and importance of alien thistles, we still have a very limited understanding of the factors responsible for the success of introduced thistles. While invasive alien thistles possess many of the "ideal weed" traits outlined by Baker (1974), including short generation times, high seed output, and effective dispersal, the same traits are also found in non-invasive native thistle species. Comparison of congeneric invasive and non-invasive thistle species is promising technique for identifying the characteristics of successful invaders (Mack 1996). This approach effectively controls against traits common to the species under investigation, such as dispersal syndrome and generation time for thistles, and enables identification of traits that are likely to determine differences in performance of invaders and non-invaders.

I examined factors affecting the relative abundance of two congeneric thistles, the abundant alien *Cirsium vulgare* (Savi) Tenore and the native *C. brevistylum* Cronquist, in northern California. While both species can be characterized as "fugitives" (sensu

Harper 1977) and depend on soil disturbance to establish populations, the alien thistle is found at a greater proportion of sites. Preliminary observations suggest that the alien species is more likely to be present at older sites than is the native, and so greater regional abundance of the alien may be due to an ability to persist at sites from which the native has been excluded.

There are several potential explanations for the greater persistence of *C. vulgare*. Both species are strongly limited by interference by background vegetation (Gluesenkamp Ch 2), and so it may be that persistence of the alien thistle is due to differences in competitive ability of the two thistle species. This hypothesis is supported by studies showing that *C. vulgare* is capable of competitively suppressing native plants such as *Pinus ponderosa* (Randall and Rejmanek 1993). Alternatively, differences in susceptibility to herbivory may be important. A number of studies have shown that native thistles are limited by insect herbivores (Louda et al. 1990; Louda and Potvin 1995; Palmisano and Fox 1997; Stanforth et al. 1997), while introduced thistles have largely escaped the insects with which they evolved (Goeden and Ricker 1986; 1987). Reduced *C. brevistylum* fecundity due to differential herbivore impact could limit local abundance, population persistence, and colonization of new sites by the native. Finally, patterns of population decline over time could be due to seed and seedbank characteristics. If seed germination rates are lower in old sites than in young sites, and if this difference in rates is greater for *C. brevistylum* than for *C. vulgare*, then seeds produced by *C. vulgare* adults are more likely to contribute to the subsequent generation of adult plants and seeds of *C. brevistylum* more likely to contribute to the soil seedbank.

I quantified patterns of abundance of *C. brevistylum* and *C. vulgare* at naturally-occurring thistle populations that varied in time since disturbance. I then used pattern data and experimental manipulations to evaluate the degree to which patterns of abundance were explained by differences in competitive ability, insect herbivory, or seed and seedbank characteristics of the two plant species.

STUDY SYSTEM

This research was conducted within the boundaries of Jackson Demonstration State Forest (hereafter JDSF) in Mendocino county, California. Sites were located between 6 km and 15 km from the Pacific ocean and range in elevation from 100 to 240 meters. Mean annual precipitation at JDSF for the period 1962 to 1997 was 1190 mm (range: 305-2007 mm), with 90% of precipitation arriving as rainfall between the months of October and April (Henry 1998). The climate is Mediterranean, with a strong coastal influence; summer air temperatures are modified by coastal fog and rarely exceed 30° C in summer or drop below freezing in winter. Due to this coastal influence, the forest is dominated by coast redwood (*Sequoia sempervirens*), with Douglas fir (*Pseudotsuga menzesii*) and tanbark oak (*Lithocarpus densiflora*) present at drier sites. The forest is managed for timber extraction, and discrete disturbance patches are created in the process of bulldozing trails and staging areas for logging activities. Following logging these patches are colonized by perennial grasses and forbs such as *Holcus lanatus*, *Erichtites australis*, and *Pteridium aquilinum*. Patches are successively dominated by longer-lived forbs, followed by shrubs, and ultimately saplings of forest trees begin to dominate if sites remain undisturbed for more than a decade. For the purpose of this study, disturbance and logging / bulldozing events are considered synonymous.

C. brevistylum and *C. vulgare* are among the first plants to occupy sites following disturbance. *C. brevistylum* is one of 34 *Cirsium* taxa native to California, and populations of the plant have been documented at coastal sites ranging from the Mexican border into British Columbia, Canada (Hickman 1996). *C. vulgare* is native to Northern Europe and has successfully established on every continent except Antarctica (Forcella and Randall 1994). It was first introduced to the western United States in the late 1800s, probably as a contaminant in crop seeds, and now occurs in all 50 states.

While they have different biogeographic origins, the two species are morphologically and ecologically similar. They share the same habitat requirements and co-occur at sites within JDSF. Both species produce relatively large seeds (2.5 ± 0.1 mg for *C. brevistylum*, 3.2 ± 0.2 mg for *C. vulgare*) which bear a parachute-like pappus structure that enables wind dispersal. Seeds germinate with the winter rains and grow as vegetative rosettes until reproduction. Juvenile rosettes of the two species are comparable in size, with a mean diameter of 12 cm and a maximum of nearly 100 cm. Rosettes typically bolt and flower in their second year, May–July for *C. brevistylum* and June–August for *C. vulgare*, but are capable of bolting in their first year or in later years depending on conditions (Forcella and Randall 1994; Gluesenkamp Ch 2). Adult plants typically have one apical growth axis with numerous lateral branches, and flowers are borne in composite seedheads at the tips and axils of these branches.

Both species are self-compatible (Gluesenkamp, unpublished data), and flowers are also pollinated by a diverse assemblage of insects that includes *Papilio* sp., *Bombus* spp., *Apis melifera*, and several unidentified species of hymenoptera and diptera. *C. brevistylum* and *C. vulgare* also support two guilds of insect herbivores. Folivores include larvae of the lepidoptera *Platyptilia carduidactyla* (Lepidoptera: Pteriphoridae) and *Vanessa cardui* (Lepidoptera: Nymphalidae), which develop on rosettes and adults of both species and consume leaf tissue and young meristems. In addition, several species of insect seed predators develop within seedheads and destroy immature ovules. By far the most abundant of these insect seed predators is the native fly *Paracantha gentilis* (Diptera: Tephritidae). Potential vertebrate herbivores and seed predators at JDSF include mule deer (*Odocoileus hemionus columbianus*), chipmunks (*Tamias* sp.), voles, (*Microtus* sp.), and a variety of small birds.

METHODS

Patterns of thistle abundance and vegetation density

I surveyed belt transects within JDSF to quantify the relative abundance of the two thistle species. In September 1999 I established 6 transects with random azimuths in locations typical of the forest as a whole. Each transect consisted of a 4 m continuous strip within which all adult thistle plants were identified to species and counted. Total length of the 6 transects was 9.8 km, with a total of 39,000 m^2 of habitat censused.

Over three years (1996, 1997, and 1998) I monitored a total of 37 discrete disturbance patches (sites). Site ages were determined by personal observation of disturbance events. Criteria for selection of a patch for study were that the site was no more than 100 m from the nearest trail and contained at least 10 adult plants of either thistle species. Initially (1996) I established 3 sites at patches disturbed 1, 2, 3 years previously. In order to include a broader range of site ages, in 1997 I initiated study at an additional 16 sites that had been disturbed the previous year, and 5 sites that ranged in age since disturbance from 2 to 4 years. In 1998 I added 13 additional 1 year-old sites.

For each thistle species I quantified population density within each site by counting the total number of adult plants at the end of the summer in 1996, 1997, 1998, and 1999 and then dividing number of adult plants by the patch area. Differences in population density between the two species and among patch age classes were tested using a separate 2-factor ANOVA for each year. Unless otherwise specified, all statistical tests described herein were conducted using the JMP 3.1.7 statistical package (SAS Institute 1996).

In May of 1998, I characterized the density of background vegetation at each site by censusing vegetation in 4 randomly-located 1 m^2 quadrats (plots). I measured percent cover from above, maximum height, and mean height of vegetation in each plot. At this time I also censused vegetation at a fifth plot at 13 sites, and vegetation in these plots was then clipped to ground level, dried at 60° C until constant mass, and weighed to determine biomass. Linear regression showed that percent cover is the best predictor of biomass [log(Biomass) = 2.60 + 0.035 * Percent Cover, $R^2 = 0.36$, $n = 13$, $P < .05$], and so only percent cover is presented in this paper.

In each plot I also measured effect of vegetation on light availability by taking readings above and below the vegetation canopy (200 cm and 4 cm above ground-level) using a handheld LI-COR PAR meter (LI-COR, Lincoln, Nebraska). Light readings were made within 1 hour of solar noon over a single week in mid-June during which no cloud cover was present. Each plot was measured once. Finally, I visually estimated the percent of the soil surface in each plot that was covered by litter and the percent covered by bare soil.

Vegetation cover data were arcsine square-root transformed to improve homogeneity of variance prior to analysis. Single-factor ANOVA was used to test for differences in cover by vegetation among patches of different ages. Simple linear regression was used to establish correlations between cover data and light transmission and population density of the two thistle species.

Vegetation removal experiment

To the hypothesis that decline of *C. brevistylum* with increasing site age is due to interference from background vegetation, I grew plants of the two thistle species in plots with and without background vegetation present. In October 1997 I established pairs of 2.2 m $\times$ 2.6 m plots at 2 year-old sites throughout the forest (n = 7 sites). One plot was cleared by clipping vegetation at the soil surface and then maintained free of vegetation by clipping every 2 weeks. Vegetation in the other plot was left intact and allowed to develop ‘naturally’. Within each plot I established 3 subplots of 40 cm diameter, delineated by a ring of shadecloth extending 1 cm above- and 1 cm below-ground to facilitate relocation of subplots and prevent erosional loss of seeds. Subplots were located 50 cm from the edge of the enclosing plot in order to minimize edge effects and were separated from adjacent subplots by 40 cm. Each of the 3 subplots was randomly assigned a seed addition treatment: addition of either 100 seeds of *C. vulgare*, 100 seeds of *C. brevistylum*, or no seeds added as a control for germination of seeds already present at the site. Seeds used were a mix of seedheads from > 30 individual plants collected the previous year (as described below).

Plot preparation was completed before the first rains in 1997 and the experiment was monitored until October 1999, when the majority of plants had either died or reproduced. Plots were not censused until 3 months after seed addition, and so the first count includes germination less early seedling mortality. However, plots were examined at 2-week intervals prior to the first census and almost no dead germinants were found, and so the first census is considered a reasonable estimate of germination. I censused subplots at 3 month intervals, identified new seedlings to species, and marked each seedling with a color-coded plastic cocktail stick. When rosettes bolted and set seed I tagged each plant with a unique ID and counted the total number of seedheads matured.

Since many more germinants emerged in 1997-98 than in 1998-99 (95% Vs 5% of total germination), I assessed treatment effects on the first cohort only. Seedling emergence from control plots in 1997-98 was very small (0.79 ± 0.31 seedlings per subplot), indicating that seeds naturally present prior to seed addition did not influence determination of germination rates. Proportion of added seeds germinating in each subplot was calculated as (number germinants / 100 seeds). Plants that either reproduced or were alive in October 1999 were considered survivors, and proportional survival was defined as (number surviving / number germinants 1997-98).

Proportion of seeds germinating and proportion of germinants surviving were arcsine square-root transformed prior to analysis to improve normality and homogeneity of variance and were analyzed using separate two-way ANOVAs, blocked by site, evaluating effects of species, vegetation removal, and the species $\times$ vegetation interaction. Since the experiment was a split-plot design, F statistics for site and clipping terms were calculated using whole-plot error (= site $\times$ clipping MS) as the denominator, while significance of species and of the species $\times$ clipping interaction were tested using residual error.

Patterns of herbivory and plant fecundity

To quantify plant fecundity and natural patterns of herbivory I labeled with identification numbers all thistles at each of the 37 sites and, at each site, randomly selected between 20 and 30 plants per species for further study. For each of these plants I counted the number of seed heads that had matured to age of seed production by the end of the season. These seedheads were identified visually as the largest size class of seedhead, and had outspread phyllaries. I also counted the number of meristems and seedheads that were destroyed prior to pollination and seed maturation. These were evident as small, undeveloped meristems, buds, or seedheads that had been hollowed out and filled with insect frass.

I determined seed production and the abundance of insect seed predators within seedheads by collecting mature seedheads from these plants. Every 2 weeks, on each marked plant, I randomly selected 2 seedheads that had been pollinated but had not yet matured. These seedheads were enclosed in 8 cm * 10 cm cloth bags tied shut to prevent the escape of seeds and insect seed predators. While bags undoubtedly altered the microenvironment of seedheads, pilot tests using these same species detected no bagging effects on seed production or on insect survival, so significant biases due to seedhead bagging are unlikely. I removed bagged seedheads after plants senesced at the end of the season and then dissected seedheads in the laboratory, counting the number of fertile seeds produced and identifying and counting all insect seed predators trapped within the bag. Fertile seeds from these seed heads were stored in a dry room at 65° C and added to experimental plots the following season (see *Vegetation Removal Experiment*).

I calculated fecundity of each plant as (number seedheads matured * mean number seeds produced per seedhead). Within each year I used separate paired *t*-tests, with plant species paired by site, to test for differences between species in the proportion of seedheads damaged by insects, number of seedheads and meristems destroyed, number of seedheads matured, number of seeds produced per seedhead, and whole-plant fecundity.

Insect exclusion

I excluded insect herbivores with insecticide in order to test the hypothesis that differences in abundance of the two thistles are due to greater impact of herbivores on native versus alien plants. In May 1998, when plants of both species were beginning to mature, I selected 12 plants per species at each of 13 sites, haphazardly chosen to reflect the range of sizes at each site. These sites all were disturbed in 1997 and most sites contained populations of both *C. brevistylum* and *C. vulgare*. Plants of the same species were paired by size and randomly assigned one of two treatments: (1) the insecticide Sevin® (carbaryl) applied at the recommended concentration (7.5 mL / L active ingredient in water; Chemsico, St Louis, Missouri), or; (2) an equivalent volume of water also applied by spraying, in order to control for moisture added with insecticide application. Summer fog at these sites provides water well in excess of the volume of water applied here, and so I did not include a treatment to control for effects of spraying plants with water. Insecticide and water were applied to the appropriate plants every 2 weeks by spraying leaf surfaces, meristems, and immature seedheads until surfaces were wetted and runoff occurred, an average of 25 mL per plant. For each of the plants I counted the number of meristems and seedheads destroyed by herbivores, the number of seed heads produced, and I bagged maturing seedheads every 2 weeks for determination of seed production and insect abundance. I calculated fecundity as described above.

At each site, fecundity of the 6 plants in each treatment was averaged to calculate a mean fecundity for that site, and two-way ANOVA, blocked by site with no replication within blocks, used to evaluate effects of species, spraying treatment, and the species $\times$ spraying interaction on plant fecundity. Since some sites had only one thistle species present, the experimental design was unbalanced; the 5 sites lacking one species were used only to calculate spraying effects within species.

To improve the chance of detecting spraying effect and the species $\times$ spraying interaction, I calculated the difference in seed production between the insecticide-sprayed and water-sprayed plant in each pair, normalized by the fecundity of the water-sprayed plant [= (Sevin - Water) / Water], and calculated a mean difference for each species at each site. I used one-tailed *t*-test to test the hypothesis that this mean difference was positive, indicating that insecticide increased fecundity, and compared response of the two plant species using paired *t*-test for the 8 sites containing both species.

Seed dormancy and soil seed bank

Though thistle seeds possess adaptations for wind dispersal, the number of seeds dispersing more than 5 meters is very small (Matlack 1987; van Leeuwen 1987; Klinkhamer et al. 1988), and so differences in seed dispersal of *C. brevistylum and C. vulgare* are probably not important in determining patterns of abundance and patch occupancy. However, a disturbance return interval on the order of 5-10 years (Gluesenkamp, unpublished data) means that dispersal through time via the soil seed bank is likely to be an important means of colonizing new disturbance sites.

Size of the soil seed bank was determined at each of 37 thistle patches, ranging in size from 20 m^2 to 300 m^2. In October 1998 I randomly selected 3 points per site and collected 2 soil cores 20 cm north and 20 cm south of each point. Soil cores were 10 cm diameter and divided into two depths, 0-5 cm and 5-10 cm. At each point the two cores from the same depth were combined, for a total of 3 samples for each of 2 depths per site. Each combined sample was taken to the lab and distributed over the surface of a 25 cm diameter tray to which sand had been added to improve drainage. Trays were maintained in a greenhouse duplicating field conditions (daylength = 10 hours, night temperature = 40° C, day temperature = 55° C) for 2 months. They were watered daily, and the soil was mixed after 4 weeks to expose all seeds present in the cores. I counted the total number of seedlings of each species germinating over the duration of the experiment and averaged seedling counts for each site to calculate the mean seed density of each species at each site. These site means were expressed as seeds per surface area cored, and were analyzed using two-way ANOVA, blocked by site, evaluating effect of core depth, species, and the species $\times$ depth interaction.

I quantified survival of seeds in the soil seed bank by burying bags of seeds at JDSF. Bags were sewn out of 0.5 mm polyester mosquito netting and filled with 25 seeds of a given species. In January 1996 I buried bags at 4 sites chosen as representative of disturbed patches within the forest. At each site, 4 bags were buried at each of 4 haphazardly-chosen locations, 1 bag of each species at 5 cm depth and a second pair of bags at 10 cm depth. During the course of the experiment, bags at 2 sites were disturbed by bulldozers. I exhumed the remaining bags in October 1999, after 45 months of burial; this burial duration reflects the disturbance return interval in this system. Seed bags were transported to the lab where seeds were removed from bags and germinated in a growth chamber as described above. Seeds that failed to germinate were tested for viability with 0.1% tetrazolium stain after lightly nicking the seed coat with a razor blade and soaking seeds overnight in a 400 mg/L gibberellic acid at 4° C (Ellis et al. 1985). Cause of mortality was not determined. Low survival made statistical analysis of seedbag data unnecessary.

Since survival of buried seeds in the field was very low (see *Results*), I quantified survival and dormancy of seeds under ideal conditions by germinating seeds of the two species that had been stored in the lab for varying lengths of time. These seeds were collected from plants at JDSF over several years and stored in a dry room at 68° C until use in this experiment. Seeds were collected in 1996, 1997, 1998, and 1999 and thus ranged in age from 1 to 4 years. For each species × age combination I placed 20 seeds on Whatman #1 filter paper in a 50 mm petri dish, with 5 replicate dishes per species × age combination for a total of 20 petri dishes per species. Dishes were placed in a growth chamber set to duplicate January field conditions (daylength = 10 hours, night temperature = 40° C, day temperature = 50° C) and were watered with distilled water each week to keep seeds moist. All germinants were counted and removed each week. At the end of 4 weeks, seeds failing to germinate were tested for viability using tetrazolium treatment. Germination and viability data were analyzed using separate two-way ANOVAs evaluating effects of species, seed age, and the species × seed age interaction.

RESULTS

Patterns of thistle abundance and vegetation density

Belt transect surveys confirmed that the alien *C. vulgare* is significantly more abundant on a landscape scale than is the native species *C. brevistylum* (Pearson's χ^2 = 42.9, $P < 0.001$), with a total of 713 *C. vulgare* and 486 *C. brevistylum* individuals observed along 9.8 km of transects. In addition, census of adult plants in 37 sites revealed that the two species have very different patterns of abundance with respect to site age (Fig. 1; data shown is for 1998, patterns are the same for the other 2 years). Population density of *C. brevistylum* is greatest in the first year following disturbance and declines significantly in subsequent years. In contrast, population density of *C. vulgare* does not vary significantly with respect to time since disturbance. With the exception of first-year sites (*C. brevistylum* > *C. vulgare* , paired *t*-test, $t = 2.2$, $P < 0.04$), populations of *C. vulgare* tend to be larger than populations of *C. brevistylum* within the same site (paired *t*-test, $t = -3.0$, $P < 0.01$). *C. brevistylum* is also less likely to occur at patches older than 1 year, and so *C. vulgare* is present at a greater proportion of sites than is *C. brevistylum* (Pearson's χ^2 =3.6, P = 0.05).

Percent cover of background vegetation varied with patch age (F = 7.0, P < 0.001), with significantly less cover in first-year sites than in sites disturbed in earlier years (76% versus 96% cover). Population density of *C. brevistylum* was also significantly negatively correlated with percent cover by other vegetation in these 37 sites (Table 1). Similarly, abundance of *C. brevistylum* at each site is negatively correlated with the percent of plot area covered by litter, and is positively correlated with light availability and with the amount of bare soil in the plots. Population density of *C. vulgare* by contrast is not correlated with percent cover by vegetation or any of the other indices of background vegetation.

Effect of vegetation on germination and survival

The fate of seeds added to subplots was strongly influenced by the presence of background vegetation (Figs 2a,b). Removal of vegetation doubled the proportion of seeds germinating (CLIPPING F = 8.1, P < 0.0005; Fig. 2a). While interference by background vegetation had the same effect on germination rates of both thistle species (CLIPPING × SPECIES F = 0.3, P = 0.25), seeds of the native thistle had higher germination overall, averaging twice the germination rate of *C. vulgare* seeds under the same conditions (SPECIES F = 10.6, P < 0.0005; Fig 2a).

Seedling survival rates differed significantly between the two plant species but not among clipping treatments (SPECIES F = 14.5, P = 0.003; CLIPPING F = 1.3, P = 0.3). Overall, *C. vulgare* had higher survival than did *C. brevistylum*, with both a greater proportion of germinants surviving to 18 months and a greater number of individuals left in experimental subplots at the end of the experiment, 24 months after seed addition (Fig. 2b). Background vegetation had no significant effect on survival of germinants, and the two species did not differ in their response to vegetation removal (CLIPPING × SPECIES $F = 1.8$, $P = 0.2$). Size of plants surviving at the end of the experiment did not differ among species ($F = 0.2$, $P = 0.6$) but seedlings had significantly more leaves in clipped than in unclipped plots ($F = 6.6$, $P = 0.02$)

Vegetation removal did, however, affect one component of survival. While the number of plants reproducing in the course of the experiment was very low, all of the plants that reached reproductive maturity occurred in clipped subplots (Fig. 2b). Only plants of *C. vulgare* reached reproductive maturity, and no plants growing in the presence of vegetation matured.

Patterns of herbivory and plant fecundity

The most damaging herbivores observed on thistles at JDSF were larvae of the moth *Platyptilia carduidactyla* which destroyed meristems and immature seedheads; small rodents that removed mature seedheads prior to seed dispersal; and insect seed predators that consumed seeds within seedheads (Table 2). *P. carduidactyla* attacked both plant species, destroying an average of 18% of meristems. Damage by the moth was comparable among the two plant species in 1997, though in 1998 moth damage was significantly greater on *C. vulgare* than on *C. brevistylum* ($t = 9.1$, $P < 0.0001$).

Vertebrate herbivory was rare in most years, in agreement with results from another study at these sites (Gluesenkamp Ch. 2). In 1998, deer browsed 3 juvenile *C.*

brevistylum, and I observed limited predispersal seed predation by birds at 2 out of 37 sites. In 1998, however, chipmunks (*Tamias* sp.) destroyed 70% of *C. vulgare* seedheads immediately prior to seed dispersal (Table 2). This occurred in 1 of 3 years, and though the native *C. brevistylum* occurred in the same sites and was also in fruit, it was unaffected by these herbivores.

The most abundant herbivores in seedhead dissections were the native fly *Paracantha gentilis* (68% of individual insects found), followed by 3 species of lepidoptera (together, 16%), and the introduced weevil *Rhinocyllus conicus* (14%). These predispersal insect seed predators were consistently abundant on the native *C. brevistylum*, and were present in more than a third of seedheads that reached maturity (Table 2). In contrast, insect seed predators were present in less than 5% of seedheads of *C. vulgare*.

There were significant differences in fecundity between the two plant species (Table 2). *C. brevistylum* and *C. vulgare* produced essentially the same number of seedheads in each year except in 1998, when *C. vulgare* produced fewer seedheads than the native thistle due to chipmunk predation ($t = 7.4$, $P < 0.0001$). In all years, *C. vulgare* seedheads were significantly larger than those of the native, each producing from 45% to 270% more seeds (Table 2). Consequently, whole-plant fecundity of *C. vulgare*, the total number of seeds produced per plant, averaged more than twice that of the native *C. brevistylum* in all years except 1998.

Insect exclusion

Insecticide application increased the number of seeds produced per seedhead, from 115 ± 14 to 157 ± 18 seeds per seedhead for the native thistle and 202 ± 24 to 274 ± 31 for the alien (SPRAYING $F = 11.2$, $P = 0.003$). The number of seedheads matured per plant, however, did not differ between insecticide-sprayed and water-sprayed plants (19.0 ± 4.3 versus 19.4 ± 3.8 for *C. brevistylum*; 3.6 ± 0.6 versus 4.1 ± 0.4 for *C. vulgare*; SPRAYING $F = 0.4$, $P = 0.55$). As a result, insecticide application resulted in a net increase in whole-plant fecundity, calculated as number of seedheads * seeds / seedhead for each plant. These data were highly dependent on plant size, and so the insecticide effect on fecundity was only detected when comparing plants that had been paired by size at the beginning of the experiment. The mean difference in fecundity between the insecticide-sprayed and water-sprayed plant in each pair is greater than zero for both species but significantly greater only for the native plant; insecticide sprayed *C. brevistylum* made 173% more seeds than water-sprayed *C. brevistylum* plants ($t = 3.1$, $P < 0.005$) whereas insecticide increased fecundity of *C. vulgare* plants by only 20% ($t = 1.6$, $P = 0.07$). Comparing these mean difference values between plant species using paired *t*-test found no SPECIES × SPRAYING interaction in fecundity ($t = -0.002$, $P = 0.99$).

While the experiment detected a negative effect of insects on fecundity, the greatest differences in fecundity were between the two species (Fig. 3). Seedheads of the alien *C. vulgare* contained twice as many seeds as those of the native, averaging 238 seeds per seedhead as compared to 118 for *C. brevistylum*. However, whole-plant fecundity of the native *C. brevistylum* averaged twice that of *C. vulgare* in this experiment, due to unusually high rates of seedhead destruction by small mammals in this year (Table 2). In order to estimate patterns in fecundity of the two plant species expected in a "normal" year, in the absence of seed predation by chipmunks, I also calculated fecundity by including the seedheads removed by small mammals (last 2 columns in Figure 3); these data show that, in the absence of chipmunk predation, fecundity of *C. vulgare* is approximately 4 times greater than *C. brevistylum*.

Soil seed bank and seed dormancy

Thistle seeds were present in 44% of all soil cores, and 80% of sites had at least some seed bank. Seeds of the native *C. brevistylum* were found more often than seeds of *C. vulgare* (48% vs. 31% of cores, Pearson's $\chi^2 = 3.3$ $P = 0.07$), and occurred at densities averaging three times that of seeds of the alien plant (SPECIES $F = 10.5$, $P < 0.005$; Fig. 4). While the density of seeds was significantly greater near the surface (0-5 cm) than deeper (5-10 cm) in the soil profile (DEPTH $F = 16.6$, $P < 0.0001$), this attenuation of seed density did not differ between the two species (SPECIES $\times$ DEPTH $F = 2.4$, $P = 0.12$).

Survival rates of buried seeds was very low for both species. Of 225 seeds of each species that were recovered after burial for 45 months (9 bags with *C. brevistylum* and 9 bags with *C. vulgare*), only a lone *C. vulgare* germinant emerged, from a bag buried at 5 cm depth. All other seeds were dead upon examination, with seedcoat partly decayed and no embryo present.

By contrast, germination of seeds in the growth chamber was high even after 4 years of storage (Fig. 5). Mean germination rate was 81 ± 0.02% and there was no significant difference between species (SPECIES $F = 0.03$, $P = 0.87$), among seed ages (YEAR $F = 0.22$, $P = 0.88$), or in species-specific responses to seed age (SPECIES $\times$ YEAR $F = 0.48$, $P = 0.70$). There were, however, species differences in the fate of the 19% of seeds that failed to germinate during the growth chamber experiment. While tetrazolium staining showed that all of the remaining *C. brevistylum* seeds were dead, 32% of ungerminated *C. vulgare* seeds remained viable (SPECIES $F = 3.6$, $P = 0.07$). Viability of these seeds did not vary with seed age (YEAR $F = 1.0$, $P = 0.41$; SPECIES $\times$ YEAR $F = 1.0$, $P = 0.41$).

Discussion

For most monocarpic perennial plants, recruitment is linked to the availability of competition-free microsites suitable for germination, growth, and survival to reproduction (Gross and Werner 1982; de Jong et al. 1987; Klinkhamer and de Jong 1988; van der Meijden et al. 1992). These plants are disturbance colonists, often referred to as "fugitive species" (Harper 1977), and their reliance on soil disturbance to create recruitment sites makes populations both seed- and microsite-limited (Turnbull et al. 2000). Several studies have verified that population size of thistles is limited both by seed availability (Klinkhamer and de Jong 1988; Louda et al. 1990; Louda and Potvin 1995; van Leeuwen 1987) and by interference with vegetation (Louda et al. 1990; and citations in Forcella and Randall 1994). Data presented in this paper demonstrate that these same factors influence population densities of both *C. brevistylum* and *C. vulgare*; germination and establishment are enhanced by seed addition and by removal of background vegetation, juvenile plants growing with background vegetation present are smaller than those growing without it, and plants recruiting in the presence of background vegetation are less likely to reach achieve reproductive maturity.

While interference, herbivory, and seed dynamics all contribute to population regulation of thistles in this system, these factors vary in their ability to explain differences in abundance of *C. brevistylum* and *C. vulgare*. Data from long transects show that, on the scale of the whole forest, there are more individuals of the alien *C. vulgare* at JDSF than of the native *C. brevistylum*. These transects provide a coarse view, however, and do not resolve more specific components of abundance, such as population density and patterns of patch occupancy. Monitoring changes in population density at 37 sites reveals interesting variation among species in patterns of abundance with respect to time since disturbance. Population size of *C. brevistylum* is large following a patch-initiating disturbance, but populations decline and fail to persist as patches undergo succession. In contrast, initial populations of *C. vulgare* are smaller than those of the native, but populations persist for longer. Though the native plant is capable of greater maximum population density, a small proportion of thistle patches are disturbed in a given year, and so the ability of the alien thistle to persist in older patches makes it the most commonly encountered species. In order to understand differences in abundance of the two species on a large scale we need to explain both the initial abundance of *C. brevistylum* and the ability of *C. vulgare* to persist during patch succession.

Initial population size and the soil seed bank

Since patches are separated by dense forest and few seeds are likely to disperse to adjacent patches by wind (Matlack 1987; van Leeuwen 1987; Gluesenkamp, pers obs), seeds already present in the soil are the primary means by which newly-disturbed patches are "colonized." This origin is reflected in population densities in the generation following disturbance. Relative abundance of *C. brevistylum* and *C. vulgare* adults aboveground after disturbance (Fig 1) is nearly identical to the relative abundance of the two taxa in the seed bank (Fig 4). Two important questions emerge from comparison of adults densities, fecundity, and seed bank densities. First, differences between *C. brevistylum* and *C. vulgare* in the number of adults matured per seed bank seed (0.0025 ± 0.001 versus 0.0044 ± 0.002, $P = 0.08$, paired t-test) indicate that differences in germination, establishment, and survival help determine adult population densities (discussed in *Population persistence*). Secondly, though average fecundity of *C. vulgare* plants is greater than that of the native (Table 2), *C. brevistylum* has a larger seed bank, as measured by germination from cores. This suggests important differences between the input-output balance of the two seed banks.

Seed bank size is a function of the balance between inputs via seed rain, determined by intrinsic fecundity of each plant species less the effect of natural enemies, versus outputs via mortality and germination. The natural enemies hypothesis predicts that herbivory will differentially affect seed production of the native plant, since plants occurring in their native range will host specialist herbivores that have a large effect on fecundity, while the herbivore fauna of alien plants will chiefly include less effective generalist herbivores (Strong et al. 1985). However, my data show that the native *C.*

brevistylum has lower fecundity even in the absence of herbivores, and that patterns of herbivory on the two plant species did not support predictions of the hypothesis. Exclusion of both guilds of insect herbivores led to only minor increases in seed production, increases that did not differ between *C. brevistylum* and *C. vulgare*. In contrast, the chipmunk assault on *C. vulgare* led to a dramatic failure in seed production in 1998, since these herbivores consumed essentially all seeds present in each of the many seedheads they removed. Chipmunks showed a complete preference for *C. vulgare,* probably because seedheads of the native plant often contained insect seed predators and large amounts of distasteful frass (Gluesenkamp, pers obs). While the duration of this study was too short to characterize the frequency of these events, pre-dispersal seed predation by mammals could be an important explanation for the smaller seed bank of *C. vulgare*.

Differences in seed bank size are also determined by species differences in rates of loss from the seed bank, due to destruction of seeds by post-dispersal predators and pathogens, age-related loss of viability, or variation in seed dormancy and germination dynamics. Other studies have found that post-dispersal seed predation reduces seed densities of several species of *Cirsium* (van Leeuwen 1987; Louda et al. 1990), including *C. vulgare* (Klinkhamer et al. 1988). However, other work at JDSF (Gluesenkamp Ch 2) found that germination rates of *C. brevistylum* and *C. vulgare* seeds did not differ between caged and uncaged plots, suggesting that post-dispersal seed predation by vertebrates does not affect seed bank dynamics at these sites. These cages did not exclude insects, but predation by ants or other insects was also not observed. Under circumstances where vertebrate seed predation does occur, the larger, more light-colored seeds of *C. vulgare* would probably be more susceptible to discovery by these visually-oriented predators (Fenner 1985).

Pathogens and seed senescence have been shown to be important pathways of seed bank depletion, and were significant in this study: seeds that I buried for 45 months had extremely low survival rates, with only 1 of 225 seeds surviving burial for 3 germination seasons. While there is no evidence that seedbank loss rates differ between *C. brevistylum* and *C. vulgare*, levels of seed dormancy do differ between the two species, and may influence differences in apparent seed bank size and in plant density. I found that, though both species had very high germination rates when maintained in moist petri dishes, dormancy was shown by a small proportion of *C. vulgare* seeds but not by *C. brevistylum* (Fig 5). In addition, results of the clipping experiment show that *C. brevistylum* had consistently higher germination rates in the field (Fig. 2a). Since soil cores were not sieved to quantify viable but dormant seeds, counting the number of germinants emerging may have overestimated the difference between *C. brevistylum* and *C. vulgare* seed densities. Systematic undercounting of *C. vulgare* seeds in soil cores may help explain the seemingly small *C. vulgare* seed bank, if *C. vulgare* indeed has stronger dormancy.

Population persistence

While there is strong support linking recruitment limitation to the population density of monocarpic perennial plants, few studies have examined the factors contributing to population persistence (but see de Jong and Klinkhamer 1988). Since thistle seeds germinating in the presence of vegetation are unlikely to survive to maturity, population size in later successional-seres is linked to survival of the cohort that recruits following the patch-initiating disturbance. This is especially true in sites like JDSF, where soil disturbance by small mammals is rare (Gluesenkamp pers obs), vegetation is robust (mean 420 ± 168 g / m^2), and small-scale disturbances capable of maintaining populations are rare (Rice 1987; Klinkhamer and de Jong 1988). Under these conditions, most of the thistles to mature over the lifetime of a single patch, the period between catastrophic disturbances, recruit as a single cohort. Population density in each year is determined by survival, and duration of population persistence is determined by the lifespan of juvenile rosettes.

Differences in population persistence of *C. brevistylum* and *C. vulgare* at these sites are chiefly due to higher survival rates of the alien thistle. While a large soil disturbance results in large numbers of *C. brevistylum* plants initially, these plants are short-lived. In contrast, results of the vegetation removal experiment show that plants of *C. vulgare* have greater survival under all conditions examined in this study, often by an order of magnitude. These survival rates are reflected in the abundance of rosettes occurring in 1 m^2 plots, 4 plots per site, at 33 unmanipulated sites at JDSF (Gluesenkamp, unpublished data). I found that *C. brevistylum* was more abundant than *C. vulgare* in sites disturbed 1 year prior to measurements, but that the two species were equally abundant in 3-year old sites, and sites older than 3 years contained chiefly *C. vulgare* rosettes. This pattern is due to differential survival of the alien thistle, not due to continued recruitment.

Surviving juveniles comprise a rosette bank, analogous to a seed bank, that is capable of maintaining thistle populations even in the absence of adult plants. Seedlings typically form rosettes in their first year (Forcella and Randall 1994). Since juvenile thistles have low mortality rates once they have established rosettes (de Jong and Klinkhamer 1988), and maturation is triggered by plant size more than by age (Klinkhamer et al. 1987), populations are maintained by a few plants maturing each year. In addition, plants in the rosette bank are able to take advantage of small disturbances, such as minor soil disturbances (Silvertown and Smith 1989) or death of a nearby plant (McEvoy 1984), that liberate sufficient resources to enable maturation of a pre-reproductive plant but are not large enough to support growth from seed to adult. The larger, more persistent *C. vulgare* rosette bank results in higher density of adult plants for a greater number of years than does the short-lived, transient rosette bank of the native thistle.

Low mortality rates of *C. vulgare* are probably due to traits that enhance establishment of seedlings and contribute to growth of juvenile rosettes. Differences in establishment are likely linked to differences in seed characteristics of the two taxa. Dormancy in seeds reduces germination under conditions unsuitable for establishment (Fenner 1985), and greater dormancy of *C. vulgare* seeds (Fig 2a, Fig 5) may make *C. vulgare* less likely to germinate in microsites where seedlings are unable to grow and survive. Establishment success is also influenced by seed size (Gross and Werner 1982), since larger seedlings are more tolerant of interference and are buffered against environmental stress. The additional resources contained in *C. vulgare* seeds, which are 30% heavier than *C. brevistylum*, may enable more rapid growth, greater root elongation, and improved survival during the high mortality phase that follows germination.

High survival rates of *C. vulgare* may also be driven by greater allocation to roots. *C. vulgare* rosettes grown in a greenhouse in the absence of competitors (Teh and Gluesenkamp, in prep) allocated more biomass to roots than did plants of *C. brevistylum* (*C. vulgare* = 29.5 ± 7.2 g; *C. brevistylum* = 3.7 ± 0.8 g; $t = -3.9$ $P = 0.0002$), resulting in a significantly greater root:shoot ratio (R:S = 4.66 ± 0.8 versus 0.5 ± 0.1; $t = -5.2$ $P < 0.0001$). Similar trends occur in the field, where roots of *C. vulgare* are typically twice as long as those of *C. brevistylum* (Gluesenkamp, pers obs). Longer roots give *C. vulgare* access to more soil resources, potentially improving survival, growth, and likelihood of reproduction. Utilizing more of the soil profile reduces overlap with roots of neighboring vegetation, decreasing the impact of belowground competition. Longer roots also enable *C. vulgare* to tap deeper soil moisture, which may reduce over-summer rosette mortality and extend the period of positive growth in this seasonally dry system. Much of the belowground biomass of *C. brevistylum* and *C. vulgare* is in fleshy taproots. The resources stored in these taproots enable plants to survive unproductive periods, to grow rapidly and take advantage of openings in the vegetation, and ultimately are allocated to rapid growth of reproductive stems.

While some of these traits, such as root:shoot ratios, reflect differences in allocation strategies of the two species, more vigorous growth of *C. vulgare* makes it less constrained by allocation tradeoffs. For instance, plants typically trade off between seed size and seed number (Baker 1972); *C. vulgare* produces both more seeds and larger seeds than *C. brevistylum*. Seed size is negative correlated with both root:shoot ratio and relative growth rate (Westoby et al. 1992), but *C. vulgare* has larger seeds, higher R:S, and a higher RGR (Teh and Gluesenkamp, in prep) than the native thistle. It seems that greater survival of *C. vulgare* is ultimately due to it's ability to grow larger, faster, and thereby allocate from a larger pool of resources.

Managing thistle abundance

Since population density of *C. vulgare* is largely determined by survival of the first cohort of recruits, conditions that improve growth, survival, and maturation of the rosette bank will lead to *C. vulgare* increasing. *C. vulgare* is a common weed of overgrazed pastures (Harris and Wilkinson 1984), and several studies have found that abundance of *C. vulgare* increases in the presence of grazing (Forcella and Wood 1986; Silvertown and Smith 1989; others cited in Forcella and Randall 1994). While grazers also consume thistle seedlings and damage rosettes, the benefit accrued to rosettes from removal of competitor biomass and the creation of small resource-rich disturbances results in a net increase in survival, reproduction, population density and persistence. Abundance of the alien thistle is also limited by low seed bank densities, and a larger *C. vulgare* seed bank would result in larger initial population size and larger populations in subsequent years. There is a circular association between seed bank density and plant density that confuses cause and effect: are seed densities of *C. vulgare* lower because there are fewer adults, or are there fewer adults because the seed bank is smaller? It is possible that the alien thistle is still in the process of invading these sites, and that both above- and belowground *C. vulgare* populations will increase in density over time. This seems unlikely, however. This species has been present at JDSF for several decades (W. Decker, pers. com), and the high rate of soil disturbance, coupled with fact that *C.*

vulgare is present at almost every site examined, argues that densities found the forest today are at a dynamic equilibrium.

Rather, a likely explanation for lower *C. vulgare* seed densities is that very effective predation of seedheads by small mammals constitutes biotic resistance to further expansion at these sites. If this is the case, then attempts to control abundance of *C. vulgare* by introducing biological control agents such as insect seed predators could have unanticipated effects. Introduction of *Urophora stylata*, a tephritid fly which destroys ovules and seeds, to Canadian populations of *C. vulgare* resulted in significant decreases in seed production within just 4 years (Harris and Wilkinson 1984). However, it is conceivable that introduction of such natural enemies at JDSF could actually increase seed production of the alien thistle, if these insects make seed heads less palatable to the vertebrate herbivores that currently limit fecundity of *C. vulgare* at these sites. Thus, introduced biological controls could reduce abundance of *C. vulgare* in habitats where vertebrate seed predation is unimportant, while enhancing abundance in habitats with vertebrates present. While chiefly speculative, it seems reasonable that variable effects that can change patterns of habitat occupancy should be examined and carefully considered when assessing potential impact of introducing biological control agents.

While natural enemies reduce seed production of *C. brevistylum*, this plant still maintains a large seed bank. Abundance of *C. brevistylum* at these sites is most sensitive to the frequency of soil disturbance; management decisions that alter the disturbance return interval could have a profound effect on abundance of the native thistle. Shortening the interval between disturbance events would decrease mortality in the seed bank, leading to greater seedling densities. Greater seedling density could translate into more adults in the first generation, more rosettes surviving to maintain populations in subsequent years, and the resulting increase in seed rain could feed back to the soil seed bank.

Though the benefits of increased disturbance frequency may ultimately be limited by negative feedbacks such as increased herbivore or pathogen populations, there is some evidence that *C. brevistylum* has already benefited from anthropogenic modification of the natural disturbance regime. Of more than 160 populations observed between 1995 and 1999, only 5 occurred in the absence of human disturbance (Gluesenkamp, pers obs). These populations, 3 on steep creek banks subject to natural erosion and 2 in sites disturbed by elk, probably represent the ancestral habitat of this species: sites naturally subject to a high disturbance frequency. Trail-building, ditch clearing, fuel management, and logging have created numerous new disturbance which have almost certainly increased the number of populations, the size of populations, and the rate of population persistence.

These results show that small differences among very similar species can lead to important differences in patterns of abundance and nature of response to management actions. This is important, since several thistle species are listed as rare or endangered (Turner et al. 1987), and many others are the focus of weed control efforts. Despite numerous studies examining the ecology of thistles, we still have an incomplete understanding of the differences between invasive alien species and their native relatives, and have no general theory of thistle biology. Management decisions are therefore often based on limited knowledge of the biology of related species; under current practice, either *C. brevistylum* or *C. vulgare* could reasonably be used as a model for the management of rare or of noxious thistles. The data presented in this study, which show how two very similar plants achieve very different patterns of abundance, emphasize the importance of understanding the unique biology of individual species.

Conclusions

Differences in plant population density and in rates of population persistence are best explained by differences in size of *C. brevistylum* and *C. vulgare* soil seed banks and by differences in the survival of seedlings that germinate when the seed bank is exposed by soil disturbance. Population densities of adult plants in the first generation following disturbance reflect the relative abundance of seeds in the soil seed bank, while persistence of *C. vulgare* populations is due chiefly to high survival of this thistle under a range of conditions. This emphasis on different bet-hedging tactics, greater reliance on seed bank versus rosette bank, creates the potential for large shifts in relative abundance of the two species with small changes in herbivore density or disturbance regime.

Comparing congeneric taxa was essential to the conclusion that abundance of *C. vulgare* is due to relatively small, easily-overlooked, quantitative differences, rather than the presence of qualitatively different traits. Conclusions of this study would also have been very different if fewer hypotheses had been examined, since pattern data or more limited experiments might have reasonably determined that differences in competitive ability (Table 1) or herbivory (Table 2) shape relative abundance. Instead, simultaneous evaluation of several factors led to the conclusion that success of the alien *C. vulgare* was related more to vigorous growth, resulting in high root and seed mass allocation, rather than the three hypotheses enumerated at the beginning of the study.

It has been noted before that successful invaders are often more vigorous than non-invaders (Blossey and Notzold 1995 and references therein). Plant vigor has not received much discussion in the context of thistle invasions, chiefly due to the presence of other, more conspicuous, weed traits; this study suggests that a vigor hypothesis should be considered in other invasion studies. Reasonable questions include determining whether vigorous growth is more important for certain groups of invaders (ruderals versus wildland weeds, fugitive herbs versus long-lived woody species); whether vigorous growth is more important at particular stages of invasion (e.g. invasion versus population maintenance); and whether vigorous invaders are simply the few plants at the tail of the growth-rate distribution, are evolutionary anomalies such as polyploids (Baker 1974; Weber 1997), or are produced by processes such as selection for vigorous growth following release from natural enemies (Blossey and Notzold 1995). Answers to these questions may have important consequences for understanding, predicting, and managing biological invasions, the most widespread and enduring anthropogenic insults to the natural world.

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TABLE 1. Relationship between patch characteristics and population density of adult thistles. R^2 and P are the result of linear regressions including 30 sites.

	C. brevistylum			*C. vulgare*		
FACTOR	slope	R^2	P	slope	R^2	P
Percent cover by vegetation	-0.0255	0.17	**	0.0004	0.00	NS
Percent light transmitted	3.0290	0.19	***	0.4457	0.02	NS
Percent cover by litter	-0.0110	0.13	**	0.0013	0.01	NS
Percent cover by soil	0.0100	0.10	*	0.0000	0.00	NS

* $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$

Table 2: Prevalence of herbivore attack and components of fecundity for plants of the two species in three years. Mean response was calculated for all plants of each species at each site. Values in table are mean and standard error of these site means. Species were compared using paired *t*-tests with species paired by site. *** indicates $P < .0001$, dots indicate no difference between species. *Platyptilia* prevalence was not noted for 1996. Mature seedheads left at end of season escaped attack by *Platyptilia* and chipmunks but may contain insect seed predators.

Factor	Year	*C. brevistylum*	*C. vulgare*	*P*
Number of meristems destroyed by *Platyptilia*	1997	3.62 ± 0.31	2.67 ± 0.83	.
	1998	1.13 ± 0.20	3.53 ± 0.18	***
Number of seedheads removed by mammals	1996	0.0 ± 0.0	0.0 ± 0.0	.
	1997	0.0 ± 0.0	0.0 ± 0.0	.
	1998	0.0 ± 0.0	7.6 ± 0.6	***
Number of seedheads present at end of season	1996	9.5 ± 1.0	9.3 ± 1.0	.
	1997	13.1 ± 1.0	13.5 ± 3.3	.
	1998	10.0 ± 0.0	2.7 ± 0.7	***
Proportion seedheads attacked by insect seed predators	1996	0.63 ± 0.06	0.001 ± 0.001	***
	1997	0.35 ± 0.02	0.020 ± 0.010	***
	1998	0.38 ± 0.03	0.002 ± 0.002	***
Number of seeds per seedhead	1996	62.5 ± 9.98	231.7 ± 13.10	***
	1997	124.6 ± 4.76	274.3 ± 5.86	***
	1998	131.2 ± 5.45	190.9 ± 5.89	***
Number of seeds produced per plant	1996	598	2173	***
	1997	1636	3719	***
	1998	1316	518	***

FIGURE 1. Population density of adult *C. brevistylum* and *C. vulgare* in patches differing in time since disturbance. Mean and standard errors are shown. Filled bars represent density of adult *C. brevistylum*, empty bars represent density of adult *C. vulgare*.

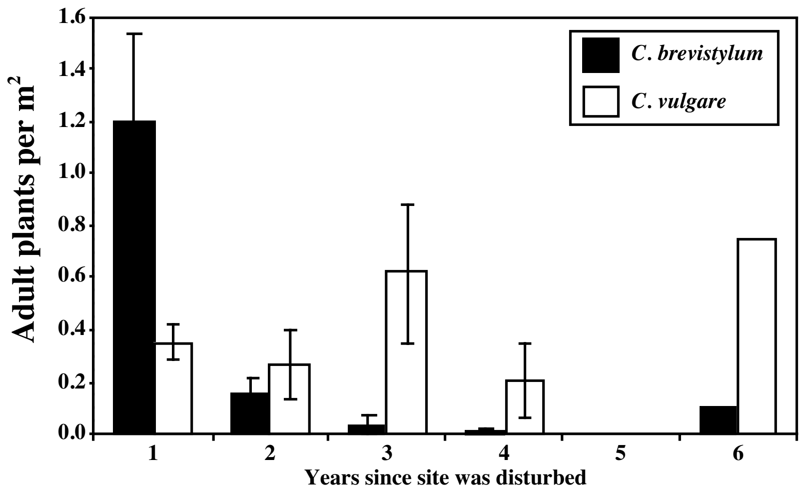
FIGURE 2. Germination rates and survival of germinants in seed addition experiment. (A) Germination rates of seeds added to subplots. (B) Proportion of germinants surviving from March, 1998 to October, 1999. Filled bars represent plots from which vegetation was removed, empty bars represent plots with vegetation present. For *C. vulgare* in (B), the proportion of survivors that became reproductive is indicated by cross-hatched column. All values are mean and standard error per treatment, n = 7 subplots. Values in parentheses indicate the mean number of plants per subplot.

FIGURE 3. Estimated whole-plant fecundity for plants in insect exclusion experiment. Filled bars represent plants receiving Sevin application, empty bars represent plants receiving water application. Values are mean and standard error of mean site values. Fecundity was calculated by multiplying number of seedheads by number of seeds per seedhead; fecundity for "*C. vulgare* net production" includes effects of chipmunk predation; "*C. vulgare* gross production" was calculated including seedheads that were actually removed by animals.

FIGURE 4. Soil seed bank of *C. brevistylum* and *C. vulgare* at 37 sites throughout the study area. Density of seeds at 2 depths is expressed as number of seeds per area cored, mean and standard error.

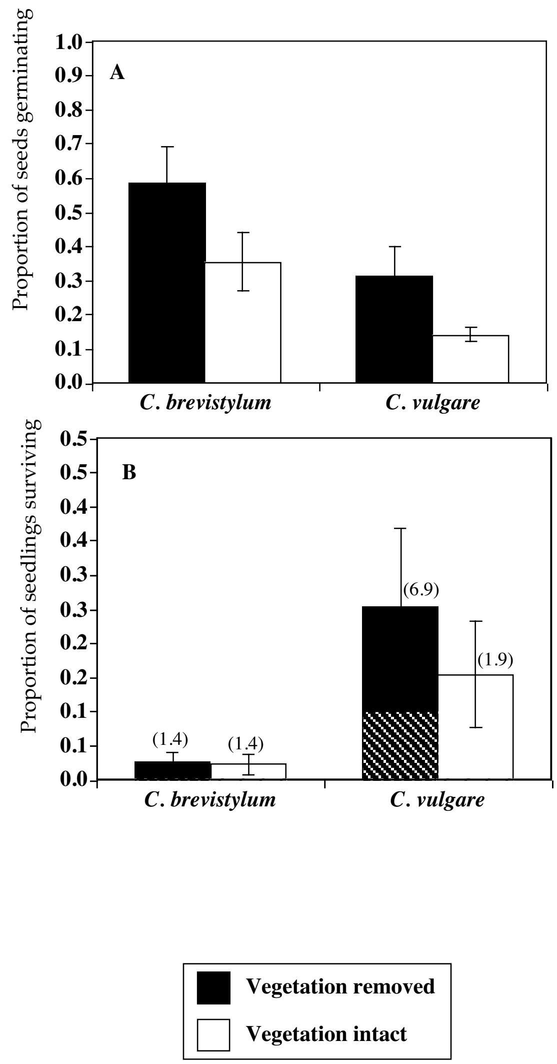
FIGURE 5. Performance of seeds of *C. brevistylum* and *C. vulgare* after storage in the lab for 1-4 years. Values are mean proportion of seeds in each category.

FIGURE 1



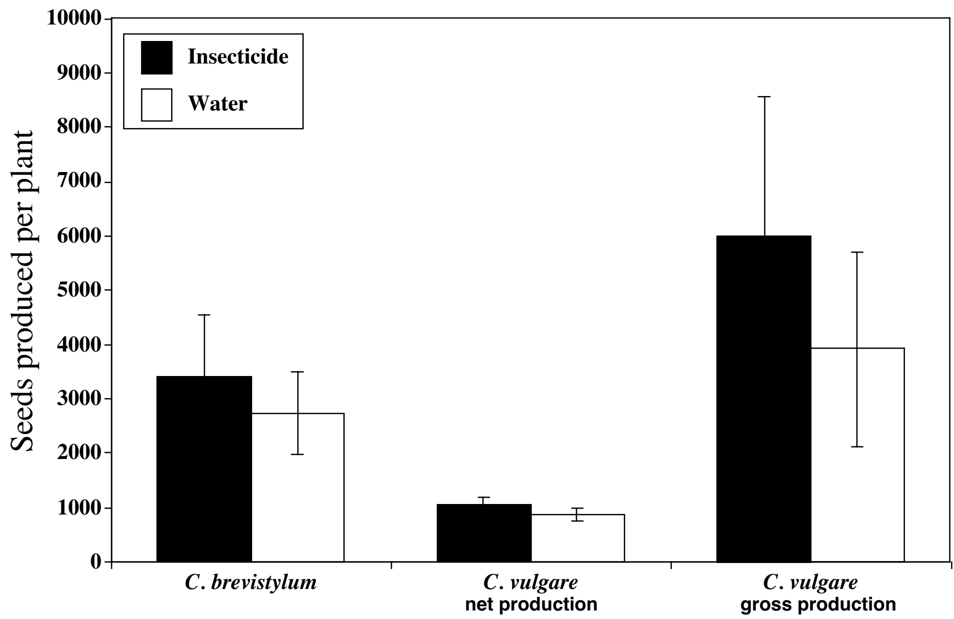
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Adult plants per m2
C. brevistylum
C. vulgare
1
2
3
4
5
6
Years since site was disturbed

FIGURE 2



Proportion of seeds germinating
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
A
C. brevistylum
C. vulgare
Proportion of seedlings surviving
0.5
0.5
0.4
0.4
0.3
0.3
0.2
0.2
0.1
0.1
0.0
B
(1.4)
(1.4)
(6.9)
(1.9)
C. brevistylum
C. vulgare
Vegetation removed
Vegetation intact

FIGURE 3



Insecticide
Water
Seeds produced per plant
10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
C. brevistylum
C. vulgare
net production
C. vulgare
gross production

FIGURE 4

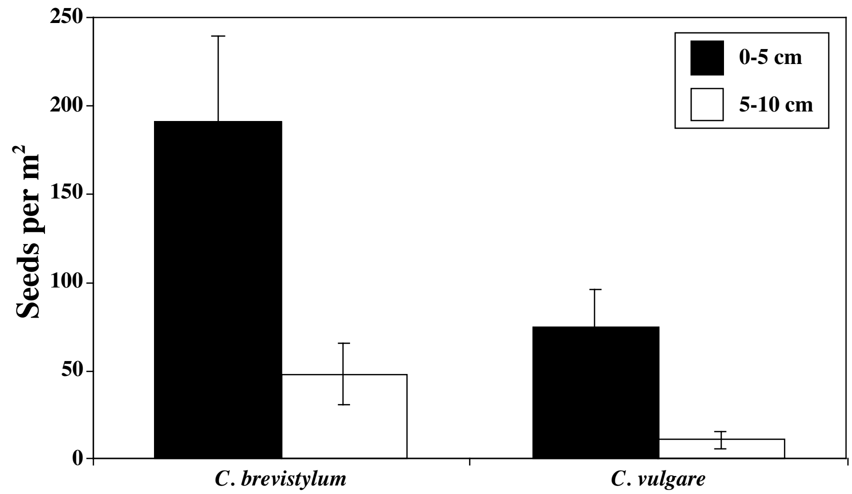
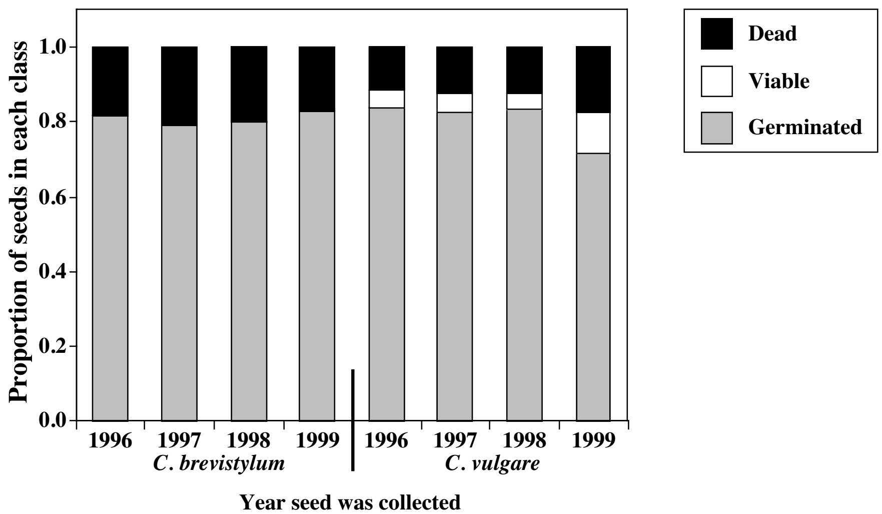

250
200
150
100
50
0
Seeds per m2
0-5 cm
5-10 cm
C. brevistylum
C. vulgare

FIGURE 5



Dead
Viable
Germinated
Proportion of seeds in each class
1.0
0.8
0.6
0.4
0.2
0.0
1996
1997
1998
1999
1996
1997
1998
1999
C. brevistylum
C. vulgare
Year seed was collected