Chapter 2

Direct and indirect effects of soil fertility on the population biology of two thistles

INTRODUCTION

There is substantial evidence that the evolution of plant life histories and the structure of ecological communities are influenced by variation in habitat productivity. For example, plants native to low productivity ecosystems are likely to possess adaptations to low nutrient availability, including long-lived leaves and roots, low relative growth rates, high root:shoot ratios, and low root absorption capacity; plants from high productivity ecosystems are likely to have rapid turnover of tissues, high relative growth rates, low root:shoot ratios, and high root absorption capacities (Chapin 1980). In spite of a strong understanding of the characteristics of low and high productivity systems and of the plant traits common to these systems, much less is known about how habitat productivity affects the species interactions that shape plant populations.

Habitat productivity can affect plants via several interacting pathways. For a given target species, productivity is likely to have direct positive effects on survival, growth, and fecundity. However, conditions that enhance growth of the target species are likely to also benefit potential competitors, thereby influencing resource availability and the competitive environment experienced by the target species. Finally, habitat productivity can indirectly alter the impact of herbivores on a target plant, via changes in the abundance, apparency, or palatability of target plants.

A significant body of work has been produced by the effort to understand the effect of site productivity on competitive interactions. While some theories of plant competition predict that intensity of competition should remain constant across varying levels of habitat productivity (Tilman 1987, Tilman 1988), many studies have detected increasing competition intensity with increasing habitat productivity (Briones at al. 1998, Edwards et al. 2000, Van der Wal et al. 2000), and others have suggested that the relationship between productivity and competition intensity may vary with the response metric used (Grace 1993, Goldberg and Novoplansky 1997). Explorations of the relationship between productivity and herbivory have been similarly inconclusive, detecting both positive and negative relationships between herbivory and habitat productivity (Reader 1992, Bonser and Reader 1995, Feller 1995, Fraser 1998, Van der Wal et al. 2000).

While the experimental work and theoretical explorations of the last decade have produced advances in understanding the nature of these interactions, efforts to search for general patterns have been frustrated by several methodological deficiencies. First, many studies do not have well-quantified productivity gradients, and instead utilize variation in standing biomass of different habitats, which can vary independent of productivity. Too few studies have examined effects of habitat productivity on the entire life-cycle of the target plants, but rather have utilized transplanted seedlings or monitored germination and early growth of seedlings. Finally, effects of competition or herbivory on fecundity are often poorly quantified, especially in studies of herbivory, and biomass or survival is often monitored rather than reproductive output.

Only a handful of recent studies (Bonser and Reader 1995, Van der Wal et al. 2000) have attempted an integrative understanding of the sum effects of productivity on plant populations, investigating the direct positive effects of productivity on growth and survival of target plants, indirect negative effects mediated by growth of competitors, and indirect effects mediated by herbivores. In addition, there remains a need for studies that explicitly examine whether productivity significantly shapes plant populations under natural field conditions. Plant populations in the field often occur in a complex competitive environment, with functionally and structurally diverse herbivore groups, and a high degree of spatial and temporal heterogeneity in interaction occurrence and strength. These interactions may take place in the context of profound environmental variability, often differentially affecting distinct components of stage-structured target plant populations. Productivity may indeed have strong effects on the density of competing vegetation or the abundance of herbivores, but the indirect effects of productivity that are mediated by competitors or herbivores may be compensated for by direct positive effects, such as enhanced survival and growth of target plants, or may be lost altogether in the noise of multiple simultaneously-operating factors.

This paper examines how site productivity affects the population biology of two short-lived plant species, *Cirsium brevistylum* Cronquist (Asteraceae) and *C. vulgare* (Savi) Tenore, and characterizes the influence of productivity on all plant stages under both experimental and natural field conditions. A small number of other studies have included multiple species, generally with the goal of determining whether patterns of response are generalizable among dissimilar species. I chose, instead, to include two closely-related, well-understood (Gluesenkamp Ch.1), ecologically-similar species, in order to assess the degree to which patterns of plant response to habitat productivity are consistent among similar species; in a sense, this is a test of the repeatability of results. For each of the two target plant species I addressed the following questions:

1) How does the strength of competition with background vegetation vary with productivity?
2) How does the strength of herbivory vary with productivity?
(3) Does the relative importance of competition versus herbivory vary as a function of site productivity?
(4) Does the structure of plant populations vary across natural gradients in habitat productivity under field conditions, and are patterns of variation the same among target plant species with similar life histories?
5) What is the level of agreement between experimental results and natural patterns?

I evaluated these questions using both experimental and observational approaches. First, I manipulated habitat productivity, vegetation density, and herbivory in order to assess how the intensity of herbivory and competition change as a function of productivity and to explore whether the relative importance of the two factors differs between high and low productivity environments. Second, I characterized the density of vegetation and abundance of herbivores on unmanipulated thistle populations occurring in sites that naturally varied in soil fertility; these data were used to examine the degree to which indices of productivity, vegetation density, and herbivory are correlated with the population structure of the two target species and their distribution over the landscape.

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 12 km from the Pacific ocean and range in elevation from 100 to 180 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, and winter temperatures rarely drop below freezing. 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 bulldozing associated with logging activities creates discrete disturbance patches ranging in size from 20 to 400 m^2. Following logging these patches are colonized by perennial grasses and forbs including *Holcus lanatus*, *Erichtites australis*, and *Pteridium aquilinum*. Patches are successively dominated by longer-lived forbs, followed by shrubs, and ultimately by saplings of forest trees if undisturbed for more than a decade (Gluesenkamp pers obs).

Cirsium brevistylum and *C. vulgare* are among the first plants to occupy sites following disturbance. Though *C. brevistylum* is native to California and *C. vulgare* native to Europe, the two species are morphologically and ecologically similar, share the same general habitat requirements, and co-occur at sites within JDSF. Seeds are released in late summer, germinate with the winter rains, and grow as vegetative rosettes until reproduction. Rosettes typically bolt and flower in their second year, and, although plants are capable of bolting in their first year or of persisting for several years before reproduction, plants always die following reproduction. Both species are strongly limited by competition with background vegetation and by herbivory (Gluesenkamp, Ch 1). Common herbivores include folivorous lepidoptera (primarily *Platyptilia carduidactyla* and *Vanessa carduii)* which consume leaf tissue and young meristems, insect seed predators (*Paracantha gentilis* and *Rhinocyllus conicus*) that develop within seedheads and destroy immature ovules, and vertebrates such as birds, chipmunks (*Tamias* sp.), and deer which destroy seedheads of *C. vulgare* and browse young shoots of both species.

METHODS

Experimental manipulations

Experimental plots were established in October 1997 and the last data collected 2 years later, in October 1999. The experimental sites were dominated by the perennial forbs *H. lanatus*, *E. australis*, *Stachys* sp., and *P. aquilinum*. Each of the sites included in this experiment comprised a single thistle patch, ranging in size from 50 to 100 m^2. All patches had formed on sites that were initially disturbed in winter 1995, at which time bulldozers used in salvage logging scraped the surface down to mineral soil. Removal of topsoil resulted in a visible reduction in productivity, insuring that fertilization treatments would create a difference in productivity. In addition, bulldozing removed the seedbank of the two target species, making it easier to follow the fate of seeds which I added.

I selected 7 sites for manipulation, each site receiving a complete, unreplicated, block of treatments. Treatment plots were established in a split-plot design, with fertilization and clipping assigned to main plots in order to minimize edge effects involved with these treatments and to best make use of the limited space available (Figure 1). At each site, 4 plots of 2.2 * 2.6 m were demarcated and each plot randomly assigned one of 4 fertility by clipping treatments: Fertilized + Clipped (FC), Not Fertilized + Clipped (NC), Fertilized + Vegetation not clipped (FV), and Not Fertilized + Vegetation not clipped (NV). Within each of these 4 plots I established 6 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 boundary of the enclosing plot in order to minimize edge effects, and were separated from adjacent subplots by 40 cm. In this paper, the term “plot” refers to the larger, whole-plot manipulations, and the term “subplot” refers to these subplots nested within whole plots. Three of the 6 subplots in each plot were then randomly selected for each of 2 herbivory treatments: herbivores excluded versus not. Within each herbivory treatment, 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 control (= subplots left without seed addition in order to control for germination of seeds already present at the site).

Vegetation removal was initiated in October 1997. Vegetation in clipped plots was mechanically clipped at the soil surface and removed. Clipping treatment was maintained over the duration of the experiment by cutting the vegetation at 2 week intervals during the growing season (February through September) and once a month from October through January. Following clipping in 1997, fertilized plots received addition of ammonium phosphate and potassium chloride equivalent to 100 kg / Ha each of nitrogen, phosphorus, and potassium. The same amount of fertilizer was added again at the height of the growing season in May 1998. On both dates, the granular fertilizer was distributed evenly over plots by hand.

Vertebrates were excluded from reduced-herbivory subplots using cages constructed of 10 cm diameter × 50 cm tall cylinders of 1 cm^2 plastic bird netting, supported by cylinders of 4 × 10 cm mesh fence wire. Cages were anchored to caged subplots using 15 cm J-shaped lengths of wire driven into the ground. Insect herbivores were excluded from reduced-herbivory subplots using the insecticide Sevin ® (carbaryl) applied at the recommended concentration (7.5 mL / L active ingredient in water; Chemsico, St Louis, Missouri). Insecticide was applied every 2 weeks during the period of insect activity, March to October, by spraying target plants until all surfaces were wetted, an average of 25 mL per plant. Plants in herbivory control subplots received an equivalent volume of water also applied by spraying, in order to control for moisture added with insecticide application.

Seeds added to subplots were from a mix collected the previous year from > 30 individual plants across JDSF (as described in Gluesenkamp, Ch 1); the germination rate of these seeds in the lab was > 80% for both species. Seeds were added on October 11, 1997, and the experiment was monitored until October 1999, when the majority of plants had either died or reproduced. In addition to seeding subplots, I also transplanted rosettes of C. brevistylum and C. vulgare into plots. These transplants came from a single site and were all matched for size. Each of the four plots received 6 juvenile plants of each species, one species pair transplanted into each of the 6 40 cm buffers separating subplots. Plants in a species pair were situated equidistant from one another and from the subplot edges. These transplants were included in the experiment in order to insure that herbivore abundance and impact could be assessed should insufficient numbers of plants emerge from seed addition subplots. Transplants were not caged, but 3 pairs per plot were randomly assigned to receive insecticide application and 3 to receive water as described for subplots.

Finally, each of the 4 main treatment plots also received 3 transplanted seedlings of *Erichtites australis*, planted into the inner edge of the 50 cm buffer strips that lined plots. *E. australis* is a common plant at these sites and is a European native with few herbivores in this system. As such, it was considered an ideal plant for use as a phytometer (Goldberg and Barton 1992) to assess site productivity within each treatment independent of the target plants. All transplanted seedlings were the same size, 4.0 ± 0.5 cm tall, and all came from a single site.

Responses to experimental manipulations

To quantify the effect of clipping and fertilization treatments on environmental characteristics important to the two target species, I assessed environmental responses within each of the 4 main clipping × fertilization treatments. All measurements were made in May 1998, the period of peak physiology of the target plants and maximum density of background vegetation. I quantified soil moisture and nitrogen availability, air temperature and humidity, and light availability above and below the vegetation canopy. Soil moisture and nitrogen availability were determined from two 2.5 × 10 cm deep cores from each fertilization × clipping plot. In each of the 4 plots, cores were taken from two locations along the long axis and then each pair of cores was bulked before transport to the lab in iced coolers. Within 48 hours of sample collection, each bulked sample was hand sorted to remove rocks and plant material. A 100 mg subsample was dried at 100° C for 3 days for gravimetric determination of soil moisture. A 20 mg subsample was extracted by shaking with 100 mL 2 M KCL for 1 hour, filtered using Whatman #1 paper, and the supernatant stored at –20° C until analysis. Determination of ammonium-nitrogen (NH_4^+ -N) and nitrate-nitrogen ($N0_3^-$ -N) was made colorometrically using a Lachat QC 8000 (Lachat Instruments, Milwaukee, Wisconsin), and Lachat values were converted to parts per million N in dry soil.

I determined humidity and air temperature 4 cm above the soil surface using a Oakton WD-35612-00 thermohygrometer at two locations per plot. At the same time, I measured availability of photosynthetically active radiation (PAR) by taking paired readings above the vegetation canopy (200 cm) and 4 cm above the soil surface using a handheld LI-COR PAR meter (LI-COR, Lincoln, Nebraska) in two locations per plot. All measurements were made within 1 hour of solar noon over a single week in mid-June during which no cloud cover was present.

I quantified biomass and percent cover of background vegetation in the germination control subplots, since these subplots received the same manipulation as adjacent subplots but were not needed beyond the first census in February 1998 (see below). I visually estimated the percent cover by vegetation in each of the two control subplots per plot. Immediately following visual estimation of cover, vegetation in these subplots was clipped at ground level and removed to the lab, where samples were dried at

60° C for 3 days and weighed. Aboveground portions of all *E. australis* phytometer transplants surviving to this date were collected, dried at 60° C for 3 days, and then weighed to determine biomass as an index of productivity.

In late February, 1998, I censused germination in subplots, identified seedlings to species, and marked each seedling with a color-coded cocktail stick. Since seedlings were counted only once during this period, this count includes germination less early seedling mortality; however, plots were examined every two weeks and almost no dead germinants found prior to mid-March, so this count is a reasonable estimate of germination. Very few seedlings emerged in the absence of seed addition (0.39 ± 0.16 seedlings per subplot) so germination control plots were excluded from subsequent analyses. Seedling censuses were repeated in October 1998 and in October 1999, in order to determine survival rates during the periods 1997-1998, 1998-1999, and 1997-1999. During the October 1999 census, 10 surviving juveniles were randomly selected in each subplot for size measurements. For each plant, I counted the number of living leaves, an accurate non-destructive predictor of juvenile biomass (Gluesenkamp, unpublished data).

I assessed reproductive responses each 2 weeks throughout the summer in 1998 and 1999. All plants that bolted were labeled with identification numbers. For each plant, I counted the total number of meristems present at the time of peak seedhead production (end of June for *C. brevistylum*, mid-August for *C. vulgare*). At this same time I also counted the number of meristems and seedheads destroyed by insects prior to pollination and seed maturation. These were evident as undeveloped meristems, buds, or seedheads that had been hollowed out or filled with insect frass. At the end of the season I counted the number of seed heads that had matured to seed production.

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 plant, all of the seedheads that had been pollinated but had not yet matured 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 insect reproduction and survival, so significant biases due to seedhead bagging are unlikely. I removed bagged seedheads after plant senescence at the end of the season and then dissected the seedheads in the laboratory, counting the number of fertile seeds produced and identifying and counting all insect seed predators trapped within the bag.

Analysis of experimental data

Soil moisture and nitrogen availability, air temperature and humidity, light transmittance, and vegetation cover and biomass were each analyzed using individual 2-factor ANOVAs, blocked by site, evaluating the effects of clipping and fertilization. Multiple measurements within a plot were averaged and plot means used in analyses. Data for proportion of light reaching the soil surface (light at surface / light at 2 m) were arcsine square-root transformed prior to analysis to improve normality and homogeneity of variance. All other environmental responses met assumptions of ANOVA without transformation.

Mean biomass per plot of *E. australis* phytometers was analyzed using 2-factor ANOVA. Likelihood of phytometers surviving to the October 1999 harvest date was analyzed using a multivariate nominal logistic model evaluating the effects of site, clipping, fertilization, and the clipping × fertilization interaction.

Wherever possible, target plant responses were analyzed individually using multi-factor, split plot ANOVAs, blocked by site, with site designated a random factor and all other factors fixed. Seed addition subplots and transplanted seedlings received a full factorial combination of fertilization (2) × clipping (2) × herbivore exclusion (2) treatments, with treatments applied to two different experimental units. Fertilization and clipping treatments were applied to main plots, and so fertilization, clipping, and fertilization × clipping effects were tested using whole plot error (= site × fertilization × clipping MS) as the denominator; in cases where unclipped plots were excluded from analysis, site × fertilization MS were used instead. Since species treatments and herbivore exclusion treatments were applied to seed addition subplots (or seedling transplants) within main plots, these treatments and all interactions were tested using residual variance. Where interactions were significant, I employed *F* tests to detect significant differences among least-square means. The basic ANOVA model used is shown in Table 2; additional interactions were included in some cases as detailed in *Results*.

In order to improve normality and homogeneity of variance, all proportional data (germination rate, survival rates, bolting rates) were arcsine square-root transformed and non-proportional data (total number of plants bolting, number of leaves on surviving rosettes) were transformed using log (variable × 100 + 1) prior to analysis. Residuals were examined and were found to meet the assumptions of ANOVA. Bolting rates were calculated only for subplots with > 9 seedlings present, since rates could not be accurately calculated for subplots with too few seedlings present.

Statistical analyses of adult plant responses (meristem production, meristem damage, seedhead production, insect seed predator abundance, seeds per seedhead) were complicated by the low numbers of plants that reached adulthood. Since almost no plants bolted in vegetated plots, only plants occurring in clipped plots were included in analyses. In order to achieve reasonable sample sizes and balance the data matrix, I pooled across plant types (those that matured from seeds added to subplots and those that matured from seedlings transplanted to plots) and across years (plants maturing in 1998 and in 1999). For each response variable, I calculated a mean for all plants within each site × species × fertilization × herbivory treatment. These values were analyzed using a split plot design 3-factor ANOVA, blocked by site, testing the effect of species, fertilization, herbivore exclusion, and the treatment interactions. Proportional data were arcsine square-root transformed and non-proportional data were log (variable $\times$ 100 + 1) transformed prior to analysis.

The number of seeds produced by each subplot was calculated by summing the fecundity of all plants present in each seed addition subplot. Fecundity of each plant maturing in seed addition subplots was calculated as number seedheads matured * mean number seeds produced per seedhead. Since some seedheads matured in the 2 weeks between field visits, seed production data are unavailable for a small number of plants (less than 15%). Fecundity of these plants was estimated by multiplying the number of seedheads matured by the mean number of seeds per seedhead for all other plants within the same treatment. Data for seed production per subplot were log transformed to satisfy assumptions of ANOVA and were analyzed using the hierarchical ANOVA model used to analyze seed germination.

In addition to examining the absolute magnitude of treatment effects, I also calculated indices of relative competition intensity as follows:

$$\text{RCI} = \frac{(\text{ no vegetation response - vegetation present response })}{(\text{ greater of the two responses }).} \qquad (1)$$

This method follows the suggestions of Grace (1993), with one modification. Grace's method uses removal treatment in the numerator, which produces maximum RCI of +1 for positive effects of vegetation removal but maximum RCI of $-\infty$ in cases where there is a negative effect of vegetation removal on target plant performance. To compensate for this problem, I calculated RCI by dividing removal effect by whichever treatment results in the greatest positive target plant response, resulting in RCI which are symmetrical around zero and range from +1 to –1. For each species, I calculated RCI for two separate responses variables (the number of seedlings surviving and the number of seeds produced per subplot) at each productivity level (fertilized and unfertilized). Since caging artifacts complicated interpretation of RCI calculated using data from herbivore exclusion subplots, I used only data from subplots without herbivore manipulation. RCI for each response variable were analyzed using a 2-factor ANOVA.

All statistical tests were conducted using the JMP 3.1.7 statistical package (SAS Institute 1996). *F* statistics are only cited in text when $P < 0.05$. Untransformed data are presented in figures and tables. Estimates of variance given in text and figures are ± one standard error.

Characterization of natural patterns

In summer 1998, I characterized site environment, vegetation density, and thistle plant populations at naturally-occurring thistle patches throughout JDSF. Of the 33 sites included in this study, 13 sites were disturbed in 1997, 16 were disturbed in 1996, and the other 4 sites were older than 2 years (as described in Gluesenkamp, Ch 1). Standing biomass of sites chosen for study encompassed the range found at JDSF. 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.

In May 1998 I characterized vegetation density and site environment within 4 randomly-located 1 m^2 permanent quadrats at each site; this plot size was subjectively judged appropriate for the scale of variation at these sites. Background vegetation was quantified by visual assessment of percent cover from above, the best predictor of vegetation biomass for this system (Gluesenkamp Ch 1). From opposite ends of each plot I collected 2 cores of 2.5 cm diameter × 10 cm deep, bulked the 2 cores, and transported them to the lab in iced coolers. These samples were processed and analyzed to quantify available nitrogen pool sizes as described earlier in *Responses to experimental manipulations*. While nitrogen pools were quantified at only a single time point, samples were collected during peak physiology of the target plants, after background vegetation had largely finished growth and begun to senesce, and are therefore likely to be sufficient for comparison of an index of soil fertility as experienced by the thistles.

At each site, I calculated population density of adult thistles by measuring the size of each site, counting the total number of adult plants of each species present in this area at the end of the summer in 1998, and dividing the number of adult plants by the patch area. I labeled all plants and randomly selected 20 adult plants of each species per site (or all adults if fewer than 20 were present) for quantification of herbivore abundance and plant characteristics. On each plant, I counted the total number of meristems produced at peak seedhead production, the number of meristems and seedheads destroyed by insects, the number of seedheads matured by the end of the summer, and collected seedheads each 2 weeks for determination of seed production and insect abundance as described above. Fecundity of each plant was calculated as number seedheads matured × mean number seeds produced per seedhead.

I determined population density of thistle seedlings in the first week of March 1999 by censusing the 4 permanent plots per site. In each 1 m^2 plot, all seedlings were identified to species and marked with color-coded plastic cocktail sticks. Seedlings were classified by age class: seedlings belonged either to the 1998-1999 cohort, identified as recent germinants by the presence of cotyledons, or belonged to older cohorts, with no cotyledons and often in rosettes. Plots were recensused the first week of September, 1999, at which time I took special care to locate marked seedlings surviving from the March census.

Analysis of pattern data included three components. First, I assessed whether soil NO_3 and NH_4 were correlated with vegetation cover and light interception. Since it is likely that density of vegetation would be greater in older sites than in recently-disturbed sites, vegetation responses were examined using analysis of covariance (ANCOVA), including site age (1 year old versus greater than 1 year old) as a categorical predictor variable, soil NO_3 and soil NH_4 as continuous predictors, and the interactions of site age with both soil NO_3 and soil NH_4. Site was designated a random factor and all other variables as fixed factors. Next, I examined the degree to which variation in thistle population density is explained by vegetation cover and soil nitrogen pools. This was done using ANCOVA including vegetation cover class (less than 80% cover versus greater 80% cover by vegetation) as categorical predictor, soil NO_3, soil NH_4, and soil moisture as continuous predictors, and the interactions of site age with NO_3, NH4, and soil moisture. Cover class was included in these models because analysis of experimental results showed that relationship of soil fertility to response variables often differed substantially as a function of vegetation density. Finally, I tested whether performance of adult plants, including plant size (meristems initiated, seedheads matured, seeds produced per plant) and herbivore abundance (meristems destroyed, insect seed predator abundance) are explained by vegetation density and soil nitrogen pools. The model for these analyses included vegetation cover class as the categorical variable, soil NO_3 and soil NH_4 as continuous predictors, and the interactions of site age with both soil NO_3 and soil NH_4.

For each ANCOVA, I used *F*-max tests to test for equality of variances among groups, plotted each response variable against continuous predictors to ensure linearity, and examined residuals to verify that they were normally distributed. For each interaction term (categorical predictor × continuous predictor), I plotted each group separately in order to assess the nature of significant interactions.

RESULTS

Experimental manipulations

Plot environmental responses

Addition of NPK fertilizer to experimental plots increased soil nitrogen and enhanced productivity of sites (Table 1). Fertilizer addition increased NO_3 pools by 70% and NH_4 pools by 50% compared to levels in unfertilized plots. While percent cover by vegetation in unclipped plots increased 12% between fertilized and unfertilized plots, total aboveground biomass increased almost 2.5-fold. Biomass of *E. australis* phytometers was 7 times greater in fertilized plots than in control plots. *E. australis* survival was not significantly affected by fertilizer addition.

Removal of background vegetation resulted in warmer, drier, sunnier plot conditions (Table 1). Clipping decreased soil moisture to 10 cm depth by a third, decreased humidity 4 cm above the soil surface by almost the same amount, and increased surface temperature of plots by almost 2 C^o. While clipped plots received abundant sunlight, an average of 850 ± 130 μmol photons $* m^{-2} * s^{-1}$ at the soil surface, light interception by vegetation in unclipped plots was nearly complete; on average only 6% of full light made it to the soil surface. Vegetation also significantly affected the survival and growth of *E. australis* phytometers transplanted into plots; removal of vegetation almost doubled the number of transplants surviving 10 months, and increased their biomass more than 5-fold. Vegetation removal had no effect on soil nitrogen pool sizes, and no significant clipping × fertilization interactions were detected for any of the environmental factors examined, with one exception: percent light transmitted to the soil surface was further reduced in plots with fertilized vegetation (11% versus 1%, $F = 3.5$, $P = 0.007$). Significant site effects were detected for all responses with the exception of percent light transmitted, *E. australis* biomass and survival, and percent cover of vegetation ($F = 2.2$, $P = 0.09$).

Germination and survival in seed addition subplots

For both target species, the fate of seeds added to subplots was strongly influenced by clipping, fertilization, and herbivory treatments (Table 2). Germination rates of the two plant species differed, with seeds of *C. brevistylum* more likely to germinate than those of *C. vulgare* (Figure 2a,b). However, both species displayed the same general responses to the main treatments: addition of fertilizer decreased germination by 0.5 fold and removal of background vegetation increased germination by the same proportion. The negative effect of vegetation on germination was greater in fertilized than unfertilized plots, and this negative effect was stronger for *C. vulgare* than for *C. brevistylum*, leading to a marginally significant ($P = 0.07$) species × clipping × fertilization interaction term (Table 2).

Seedling survival was calculated for three intervals: the first year following germination (October 1997 – October 1998), the second year of the experiment (October 1998 – October 1999), and for the duration of the experiment (October 1997 – October 1999). These three intervals displayed identical patterns, and ANOVAs for the three sets of data were in complete agreement. For this reason, I present only data for the entire 2-year duration of the experiment. Survival of germinants over this period was very strongly influenced by background vegetation, and vegetation removal approximately tripled survival rates for both species (Figure 2c,d). The absolute effect of vegetation on seedling survival depended on level of fertilization; while survival of seedlings in clipped plots was enhanced by the addition of fertilizer, the negative effects of vegetation in unclipped plots increased with fertilization, driving survival rates down (Table 2). This same pattern is seen when the effect of vegetation is expressed as relative competition intensity (absolute effect normalized by response in the treatment with maximum survival; Figure 4a). For both thistle species, RCI in fertilized plots was consistently greater than unfertilized plots (Fertilization $F = 4.3$, $P = 0.06$); 5 of 8 fertilized comparisons showed complete displacement of thistle seedlings by vegetation (RCI = +1), while in 4 of 10 unfertilized comparisons vegetation removal had a negative effect on seedling survival.

Survival of *C. brevistylum* plants was typically one third that of *C. vulgare* (Figure 2c,d). However, the two species displayed the same overall responses to fertilization and clipping; patterns of survival differed only with respect to the effect of herbivore exclusion. Herbivore exclusion generally increased seedling survival, but for *C. vulgare*, this effect was weak or reversed with fertilizer addition. To further understand these patterns, I analyzed survival rates of each species individually, using the same ANOVA model but including full factorial interactions of the three main effects and excluding species effects. Results of these tests agreed with the significant species × fertilization × herbivory interaction present in the more complete model, and also showed that there is a significant positive effect of caging on survival of *C. brevistylum* (herbivory $F = 7.2$, $P < 0.01$; Figure 2c) and that this positive effect is greater for clipped than unclipped subplots (clipping × herbivory $F = 8.8$, $P < 0.01$). For *C. vulgare*, caging tended to have a positive effect on survival in unfertilized subplots and a negative effect in fertilized subplots; while this is only marginally significant in the single-species model (fertilization × herbivory $F = 2.9$, $P < 0.09$; Figure 2d), this pattern agrees with the significant species × fertilization × herbivory interaction shown in the two-species model (Table 2).

The size of seedlings surviving to the October 1999 census was also strongly determined by fertilization and vegetation removal. Overall, vegetation removal increased the average number of leaves per seedling by 50% (3.7 versus 2.4 leaves / plant, $F = 36.8$, $P < 0.0001$). The effect of fertilizer addition on seedling size depended on the presence of background vegetation (fertilization × clipping $F = 13.4$, $P < 0.001$); fertilization doubled seedling size in clipped subplots (5.5 versus 2.8 leaves / plant, Contrast $F = 19.4$, $P < 0.0001$) but had no effect when background vegetation was present (2.4 versus 2.4 leaves / plant). Seedling size did not differ between the two plant species.

Variation in reproductive output

Of 11,200 seeds added to subplots, only 186 reached reproductive maturity and bolted; 5% of vegetated subplots had adults present, while 52% of vegetation removal subplots contained adult plants. The number of bolting plants per subplot was most strongly determined by the presence of vegetation (Figure 2e,f), which reduced the probability of maturation; in 1999 4% of all juvenile plants in vegetated subplots matured versus 65% of the juveniles in clipped subplots. Over the course of the 2-year experiment, the average number of adult plants to mature in each subplot was increased 13 times by vegetation removal (Table 2, $F = 28.6$, $P < 0.01$).

Within vegetation removal plots, fertilization significantly increased the probability of seedling maturation (Wald $\chi^2 = 15.1$, $P < 0.0001$), by 2 times for *C. brevistylum* (Figure 2e) and 5 times for *C. vulgare* (Figure 2f). As a consequence, the number of adult plants in vegetation removal plots was significantly greater when plots were fertilized (clipping $\times$ fertilization $F = 5.6$, $P < 0.05$). Adult plants were virtually absent from vegetated plots, regardless of fertilization treatment.

Abundance of adult plants was also increased by herbivore exclusion treatments (Figure 2e,f). While herbivore exclusion had a positive effect on number of adults per subplot for both of the target species (Table 2), comparison of least-square means indicated that differences between caged and uncaged subplots were much stronger for *C. brevistylum* ($F = 12.8$, $P < 0.001$) than for *C. vulgare* ($F = 0.05$, $P = 0.08$). This is reflected in bolting probabilities; in 1999, *C. brevistylum* seedlings in caged subplots were twice as likely to mature as in uncaged subplots, while *C. vulgare* seedlings in caged subplots were 20% less likely to mature ($F = 7.2$, $P < 0.01$).

Among plants that reached reproductive maturity in vegetation removal plots, there was substantial variation in the number of meristems initiated and in their ultimate fate (Table 3). There were significant species differences in meristem production, with *C. brevistylum* on average producing twice as many meristems as *C. vulgare* (Figure 3a,b). For both species, fertilizer addition significantly increased the number of meristems present at peak seedhead production (Table 3), a 50% increase for *C. brevistylum* and a nearly 3-fold increase for *C. vulgare*.

While plants of *C. brevistylum* typically produced twice as many meristems as did plants of *C. vulgare*, they also suffered greater levels of meristem destruction by herbivores (Table 3). The absolute number of meristems destroyed by insects was 3 times greater for *C. brevistylum* than for *C. vulgare* (Figure 3c,d), and 17% of all *C. brevistylum* meristems were destroyed versus only 6% of all *C. vulgare* meristems. Fertilization consistently increased the number of meristems destroyed for both species, and herbivore exclusion reduced meristem destruction (Table 3). For *C. brevistylum*, fertilization doubled the number of meristems destroyed by insects (Figure 3c) and increased the proportion of all meristems destroyed from 12 to 21%. For *C. vulgare*, the number of meristems destroyed increased ten-fold with fertilizer application (Figure 3d), though the magnitude of this increase is influenced by the presence of a few large plants in fertilized plots and is smaller when expressed as a proportion of meristems destroyed: 3.5% when unfertilized versus 9.5% when fertilized. Finally, herbivore exclusion treatments reduced insect abundance, and the number of meristems destroyed was cut in half by the application of insecticide. Tests using proportion of meristems destroyed reveal the same patterns as do the absolute magnitude data, and lower levels of variation in proportional data make each of these terms highly significant (site $F = 4.7$, $P < 0.05$; species $F = 9.1$, $P < 0.01$; fertilization $F = 12.4$, $P < 0.01$; herbivory $F = 5.3$, $P < 0.05$).

There was a significant relationship between the proportion of meristems destroyed by insects and the proportion maturing to become seedheads (linear regression $R^2 = 0.33$, $P < 0.0001$), and the same treatments that increased insect abundance also reduced rates of meristem maturation. While *C. brevistylum* produced more meristems than *C. vulgare*, a lower proportion of *C. brevistylum* meristems became seedheads (52%

versus 74% respectively, species $F = 3.27.6$, $P < 0.05$). Fertilizer application significantly reduced the proportion of meristems maturing (fertilization $F = 5.4$, $P < 0.05$), with 82% of meristems becoming seedheads in unfertilized plots versus 52% of meristems maturing in fertilized plots.

The absolute number of seedheads produced depends both on number of meristems produced (Figure 3e,f) and on the proportion of meristems becoming mature seedheads. Initial analysis revealed a strong site effect in the number of seedheads matured per plant (Table 3), chiefly due to very poor seedhead production at two sites, both of which were noticeably shadier, cooler, and wetter than the other five sites. Plants at these two sites produced an average of only 1.2 seedheads, as compared with 5.3 seedheads per plant for the other 5 experimental sites. Analysis of seedhead production data following exclusion of these two sites showed that, for the remaining five sites, *C. brevistylum* produces significantly more seedheads than *C. vulgare* (species $F = 4.5$, $P < 0.05$) and herbivore exclusion results in a marginally significant increase in the number of seedheads matured (herbivory $F = 3.9$, $P < 0.06$).

Seed head dissections provided 2 measurements of seed head herbivore abundance: the proportion of seedheads with evidence of insect damage, and the number of insect seed predators per seedhead. These two measurements generally displayed the same pattern of response to treatments. Fertilizer application had no effect on either component of herbivore abundance (Table 3). While herbivore exclusion treatments reduced the proportion of seedheads damaged (23% damaged on sprayed plants versus 36% on unsprayed plants) and reduced the number of insects per seedhead (Figures 2 g,h), insecticide application had no effect on the number of seeds produced per seedhead

(Table 3). Finally, seedheads of *C. brevistylum* were more likely to have insect damage than were seedheads of *C. vulgare* (61% of *C. brevistylum* seedheads versus 13% of *C. vulgare* seedheads), and contained more insects on average (1.5 versus 0.05 insects per seedhead). The number of seeds produced per seedhead differed between the two thistle species (68 seeds per seedhead for *C. brevistylum* versus 157 seeds per seedhead for *C. vulgare*, $F = 14.0$, $P < 0.001$) but did not vary significantly as a function of fertilization or herbivore exclusion treatments.

Since the average number of intact seeds produced per seedhead is essentially constant within each species, fecundity per plant (= seeds per seedhead * seedheads per plant) simply reflects the number of seedheads produced per plant. While *C. brevistylum* produces more seedheads, *C. vulgare* makes larger seedheads, and so fecundity is the same for the two thistle species. Seeds produced per subplot, the sum fecundity of all plants bolting within each subplot, is a less redundant summary of treatment effects that combines both subplot demographic responses and the fecundity of individual plants. The number of seeds produced per subplot is most strongly affected by clipping treatments (Table 2), with an average of 15 seeds produced in each vegetated subplot versus nearly 759 seeds per clipped subplot (Figures 1g,h). Subplot seed production is also influenced by fertilization treatment, and fertilizer addition significantly increased seed production in clipped subplots but had no significant effect in vegetated subplots. These increases in the absolute intensity of competition with fertilization are due to increased seed production in clipped and fertilized plots, while very few reproductive plants emerge from vegetated plots in either fertilization regime; thus, relative competition intensity does not vary with fertilization treatment (Figure 4), with RCI of +1 for both species regardless of soil fertility.

Natural population patterns

Patch characteristics and thistle abundance

The 33 sites examined displayed considerable variation in soil mineral nitrogen pools. Available NO_3 ranged from 0.6 to 5.1 parts per million (mean = 1.5 ppm) and available NH_4 ranged from 0.7 to 16.1 ppm (mean = 4.7 ppm). Mineral nitrogen pools were unrelated to site age class (NO_3 $t = 0.13$, $P = 0.90$; NH_4 $t = 1.19$, $P = 0.24$; NO_3 + NH_4 $t = 1.03$, $P = 0.31$). Cover by background vegetation ranged from 20 to 100%. In general, sites disturbed one year prior to measurement had less vegetation than did older sites (76 ± 3 verses 96 ± 3% cover, site age class $F = 9.2$, $P < 0.01$). Vegetation cover and soil NO_3 pool size were positively related (NO_3 $F = 4.7$, $P < 0.05$), but only when age class was included in the model; a marginally significant age class × NO_3 interaction ($F = 3.0$, $P = 0.09$) shows that cover by vegetation increased with soil NO_3 pools in young sites but not in older sites (Figure 5a). Percent of light transmitted through vegetation to the soil surface (= {light at 4 cm / light at 200 cm} * 100) corresponds closely to patterns of percent cover by vegetation (Figure 5b): percent light transmitted is lower for old sites than young sites (age class $F = 12.1$, $P < 0.01$), and transmission decreases with increasing soil NO_3 in young sites but not in older sites (age class × NO_3 $F = 4.0$, $P < 0.05$). Percent cover by vegetation and percent light transmission were unrelated to soil NH_4 pool sizes.

50% of the plots censused in March 1999 contained thistle seedlings (56 of 117 plots). Of 33 sites censused, *C. brevistylum* was present at 19 sites and *C. vulgare* present at 18. On average, 25% of all seedlings censused were recent germinants, belonging to the 1998-1999 cohort. For both thistle species, the density of recently-germinated seedlings increased with soil NH_4 pool size (Figures 6a, 6b), and this relationship was stronger when vegetation cover was sparse than when vegetation was dense (Table 4). For the other 75% of seedlings, those that recruited prior to winter of 1998-1999, there were no significant patterns with respect to vegetation cover, soil nitrogen, or soil moisture (Table 4). Because a number of plots were lost to vandalism, survival data exists for only 12 sites. Consequently, it was impossible to analyze survival data using the complete model, and so analyses were performed using a model with only the main effects of vegetation cover class, NO_3, and NH_4 included. This limited analysis suggests a positive relationship between soil NH_4 and seedling survival (*C. vulgare* NH_4 $F = 19.2$, $P < 0.01$; *C. brevistylum* NH_4 $F = 4.0$, $P = 0.08$).

Population density of adult *C. brevistylum* was significantly related to background vegetation (Table 4), with greater density of adults in sparsely-vegetated than densely-vegetated sites (0.4 ± 0.2 versus 1.1 ± 0.3 adults / m^2). Density of *C. vulgare* adults was unrelated to percent cover by vegetation (Table 4). For both thistle species, adult plant density was unrelated to soil nitrogen pools (Table 4).

Landscape patterns of thistle reproduction

The number of meristems initiated by adult plants, the abundance of insect seed predators in mature seedheads, and the number of seeds produced varied as a function of vegetation density and soil nitrogen. While both thistle species showed the same relationships between environmental variables and plant responses, none of these relationships were statistically significant for *C. vulgare* (Table 5).

In sites with less than 80% cover by background vegetation, meristem production by *C. brevistylum* was positively related to soil NH_4 pools, while at sites with denser vegetation cover meristem production declined with NH_4 (Figure 6c). The absolute number of meristems destroyed by herbivores (Figure 6e) reflected the absolute number of meristems produced, with an average of 7% of *C. brevistylum* meristems destroyed across all sites. Both absolute and proportional rates of meristems destruction were highly variable, and so neither was statistically related to nitrogen availability (Table 5).

The relationship between soil NH_4 and production of mature seedheads by *C. brevistylum* also varied as a function of vegetation density (Figure 6g). Seedhead production increased with mineral nitrogen pools where vegetation was sparse and decreased with nitrogen pools where vegetation was dense (Table 5). Maturation rates were essentially constant across all conditions, with 71% of *C. brevistylum* meristems ultimately becoming mature seedheads.

For *C. brevistylum*, abundance of insect seed predators was greater in sites with high vegetation cover (Table 5). Abundance of insect seed predators generally increased with nitrate pool size, though this was only significant for number of insects per seedhead and not for proportion of seedheads attacked (Table 5). Proportion of seedheads attacked and number of insects per seedhead both increased with NH_4 pools in sites with dense vegetation, but were unrelated to NH_4 in sites with sparse vegetation (Figures 6m,o). Seed production per seedhead displays the opposite pattern (Figure 6i); seed production for *C. brevistylum* declines with NH_4 availability when vegetation is dense, but displays a positive relationship with NH_4 when vegetation is sparse (Table 5). Analysis of *C. vulgare* seed head data show no trends in seed predator abundance (Figures 6n,p) or in the number of seeds produced per seedhead (Figure 6j; Table 5).

Fecundity (seeds per plant) of *C. brevistylum* tended to be lower ($P = 0.08$) in sites with high vegetation cover than in low cover sites (1203 versus 3002 seeds per plant; Table 5). In addition, the relationship between soil NH_4 concentrations and *C. brevistylum* fecundity was contingent on vegetation density (Table 5); fecundity was unrelated to NH_4 at densely-vegetated sites but displayed a strong positive relationship at sites with less than 80% cover by vegetation (Figure 6k).

C. vulgare patterns of response were generally identical to those of *C. brevistylum*; in sites with less than 80% vegetation cover, soil NH_4 was positively correlated with the number of meristems produced, the number of meristems destroyed by herbivores, the number of seedheads matured, and the number of seeds produced per seedhead and per plant. In sites with greater than 80% cover by vegetation, these responses were either unrelated to soil NH_4 or declined with increasing NH_4 pool size. While patterns of response were the same for the two thistle species, differences between the two vegetation cover classes were less pronounced for *C. vulgare* than *C. brevistylum*, and so there are no statistically significant relationships between *C. vulgare* adult plant responses and the environmental variables examined in this study (Table 5).

Performance of *C. vulgare* adult plants was very similar to that of *C. brevistylum* plants in these naturally-occurring populations. Comparison of the two plant species using paired t-tests, with species paired by site, showed that *C. vulgare* adults initiated about the same number of meristems as did *C. brevistylum* plants (19.9 versus 21.8 meristems per plant; $t = 0.5$, $P = 0.063$) and produced the same number of mature seedheads (12.6 versus 12.1 seedheads per plant; $t = 0.3$, $P = 0.077$). Meristems of *C. vulgare* were twice as likely to be destroyed by insect herbivores than were meristems of *C. brevistylum* (3.8 versus 1.6 meristems per plant; $t = 4.8$, $P < 0.0001$), but *C. vulgare* seedheads were less likely to contain insect seed predators (29% versus 58% of mature seedheads; $t = 5.5$, $P < 0.0001$), contained fewer insects (0.1 versus 0.9 insects per seedhead; $t = 6.3$, $P < 0.0001$), and produced more seeds (187 versus 115 seeds per seedhead; $t = 5.4$, $P < 0.0001$), resulting in a marginally significant fecundity advantage (2810 versus 1720 seeds per plant; $t = 1.7$, $P = 0.10$).

DISCUSSION

The goal of this project was to examine how the intensity and relative importance of competition and of herbivory vary as a function of site productivity, and to learn whether the net effects of habitat productivity via competition, herbivory, and thistle growth lead to observable patterns in the dynamics and structure of thistle populations. I found significant variation in plant responses with respect to soil fertility, and these patterns of variation differed among the two species examined and between experimental and non-experimental approaches. In addition, the direction of species differences often depended on the approach employed. The lack of consensus in the literature, and interesting variation among results presented in this study alone, point to other considerations that must be included in any framework describing the relationship between habitat productivity and the population biology of plants.

Indices of productivity

Soil fertility measurements, specifically available NO_3 and NH_4 pool sizes, were used as indices of habitat productivity because available soil NO_3 and NH_4 pools were considered more reliable than other indices such as standing biomass of vegetation, which in a perennial-dominated system may not directly reflect production. Biomass of phytometers is unreliable when vegetation is present, since it reflects the sum effects of both productivity and competitive effects of vegetation. There are important limitations to the use of soil nitrogen pools as indices of productivity, chiefly due to the concern that pools are subject to depletion by vegetation, and the possibility that mineral nitrogen pools measured at a single time-point may not be representative of pool sizes throughout the growing season. I attempted to overcome the limitations of single-time point measurements by quantifying mineral nitrogen pools at peak physiology of the target plants. In addition, while plant uptake should result in smaller pools of available nitrogen where productivity of vegetation is greatest, my data reveal a strong positive correlation between mineral nitrogen and the percent cover by vegetation, light interception, and biomass of *E. australis* phytometers in clipped plots. These considerations suggest that these measurements of available nitrogen pools are a reasonable index of productivity for this system.

Intensity of competition

Results from both experimental manipulations and from unmanipulated thistle populations showed that background vegetation had strong negative effects on thistle performance, suppressing germination and survival of seeds added in the fertilization experiment, and reducing reproductive output in both experimental and naturally-occurring thistle populations. It is particularly interesting that reproductive maturation of plants was almost completely suppressed by background vegetation. The sensitivity of germination and establishment to interference by vegetation has received extensive discussion (Grubb 1977, Harper 1977, Gross and Werner 1982). Very strong suppression of reproduction has received less discussion but has been observed in numerous other systems (Campbell and Grime 1992, van der Wal et al. 2000) and may be a generally significant but under-appreciated effect of competition.

Absolute competition intensity (ACI), the difference between clipped and unclipped treatments, was greater under fertilized than unfertilized conditions. Likewise, in comparison of unmanipulated populations with comparable mineral nitrogen pools the absolute difference between sparsely-vegetated and densely-vegetated sites increased with soil fertility. These results are broadly consistent with the results of other studies; while a small proportion of studies have found the opposite relationship (Fowler 1990 and studies cited in Goldberg and Novoplansky 1997), the majority of studies investigating the relationship between habitat productivity and the intensity of competition have concluded that the absolute intensity of competition increases with productivity (Briones at al. 1998, Edwards et al. 2000, Van der Wal et al. 2000, and studies cited in Goldberg and Novoplansky 1997).

I calculated relative competition intensity (RCI) for two important variables in the fertilization experiment: seedling survival and seed production per subplot. RCI for these two responses showed different patterns of change with respect to productivity; for survival of seedlings, the relative intensity of competition was greater among fertilized than unfertilized plots, while seed production showed no change in RCI. While RCI could not be calculated for plant responses in the unmanipulated thistle populations, most of the response variables for these populations show a characteristic relationship with regard to soil NH_4, with a positive slope in sparsely-vegetated sites and a negative slope in densely-vegetated sites, that indicates increasing RCI with increasing soil fertility.

Thus, it appears that for this system the relative intensity of competition increases with productivity, with the important exception of seed production per subplot in the fertilization experiment. The increase in ACI observed for reproductive response variables was driven solely by positive responses to fertilization in clipped plots. Complete suppression of reproduction by competition in unclipped plots results in RCI = 1 regardless of responses in the absence of competition. While background vegetation certainly has a profound effect on population dynamics of these plants, the presence of adult plants in unmanipulated thistle populations shows that vegetation does not cause absolute suppression of thistle reproduction under natural conditions. Data from these unmanipulated populations (Table 5, Figure 6) show that, even in the presence of dense vegetation, there is variation in reproductive responses that correlates with soil nitrogen pools. It therefore seems likely that variation in the relative intensity of competitive effects on reproductive responses was not quantified by the fertilization experiment, due to very strong negative effects of vegetation and logistical limitations on the number of seeds added to plots, and that RCI for reproduction in vegetated plots may actually increase with productivity as does RCI for seedling survival.

A limited number of studies have assessed how RCI varies as a function of explicitly quantified indices of productivity, and careful analyses of the literature have failed to detect clear patterns in the relationship of relative competition intensity to habitat productivity (Goldberg and Barton 1992, Gurevitch et al. 1992, Goldberg and Novoplansky 1997). There are several possible explanations for this. First, there is the ubiquitous challenge of detecting a clear "signal" (the effect of productivity on RCI) in complicated systems subject to numerous other sources of "noise" (productivity effects on levels of herbivory, abiotic effects, variation in the composition, biomass, and structure of the competitive matrix, etc.). An increasing number of studies include consideration of these "noise" factors and it is likely that the "signal" will be more clearly resolved by this growing body of work.

Variation among the results of published studies may also be driven by differences among targets plants chosen for study and in the response variables examined. Based on their two-phase resource dynamics hypothesis, Goldberg and Novoplansky (1997) made two predictions: (1) that RCI is more likely to increase with productivity when target plants are limited primarily by water, less so when limited by nutrients, and (2) changes in RCI are more likely to be detected for plant survival than for response variables that are a function of plant growth rate and size. I did not test for water limitation and so can not address the first prediction. However, my data support their second prediction, since results of my fertilization experiment detected an increase in RCI with regard to seedling survival, but no change in RCI with regard to seed production per plot.

Finally, disagreement among studies regarding the relationship between RCI and productivity may be due to the fact that the sites or treatment levels included in most studies generally focus on the high productivity end of potential gradients; comparatively few studies successfully include very low productivity sites. The structure of the formula used to calculate RCI (Equation 1) is such that in most cases, RCI increases very rapidly at very low productivity but then asymptotes at modest levels and increases very slowly, if at all, at higher habitat productivity. Consequently, studies that do not include low levels of productivity are unlikely to detect a strong increase in RCI (e.g.. Campbell and Grime 1992, Turkington et al. 1993), while studies examining a greater range of productivity are more likely to detect increases in RCI (e.g. Bonser and Reader 1995, reanalysis of data in Edwards et al. 2000). In the present study, both the fertilization experiment and the natural populations studied included low levels of soil fertility, with an order of magnitude between low and high mineral nitrogen pools and comparable variation in plant size, and both studies displayed significant increases in RCI with soil fertility.

At very low productivity the sign of the interaction between target plants and background vegetation may change. In comparisons of seedling survival between clipped and unclipped plots, *C. brevistylum* and *C. vulgare* each showed positive effects of background vegetation on seedling survival about 50% of the time; this results in a negative RCI and is responsible for the large standard errors in Figure 4. These facilitatory effects were present only among unfertilized plots. This pattern agrees with the model of Bertness and Callaway (1994), in which they propose that positive interactions among plants will be more common in unfertile or stressful environments and negative interactions predominant in productive environments. The mechanisms by which background vegetation facilitates seedling survival in my system are probably the same as found for other thistles (Hamrick and Lee 1987, Weid and Galen 1998) and more generally for other systems (Myster and McCarthy 1989, Callaway and Walker 1997, Rebele 2000); moderate cover by vegetation and litter in low soil fertility plots shades seedlings and ameliorates hot, dry conditions that occur when vegetation is absent. These interactions may be especially important for plants which, like the thistles in this study, colonize disturbed habitats where vegetation is sparse and the physical environment is likely to be harsh.

Two decades ago, an extensive review of competition studies found that almost 10% of the plant species examined showed evidence of positive interactions (Connell 1983). Although our understanding and appreciation of facilitation has improved in these two decades (Callaway and Walker 1997), ecologists have failed to integrate positive interactions into the theories and methods used to investigate plant competition; this is demonstrated by the fact that the equation typically used to calculate RCI is incapable of handling positive vegetation effects. It is unlikely that the relationship between competition intensity and habitat productivity will be understood without theories that integrate both positive and negative interactions.

Patterns of herbivory

Herbivore exclusion treatments resulted in significant positive effects on seedling survival, seedling maturation, and abundance of insects on adult plants. Effects on seedling survival and maturation were most likely due to caging artifacts, rather than reduced herbivore abundance, since all of the major herbivores in this system attack adult plants, not seedlings, and no herbivory was observed on juvenile plants. It is more likely that cages increased humidity and moderated environmental conditions in the same way as did moderate vegetation cover, a hypothesis supported by significant interaction terms showing that positive caging effects were much stronger in clipped plots than vegetated plots, and stronger in unfertilized vegetated plots than in fertilized vegetated plots. Since space limitations did not permit inclusion of cage controls in the fertilization experiment, there is no way to exclude the influence of caging artifacts on seedling responses. While unintended cage effects on adult density prevent quantification of herbivore effects on total subplot seed production, the inability to assess herbivore effects on seedlings is unimportant, since seedlings were not attacked by herbivores. In addition, since adult plants emerged from cages and their herbivores were controlled by insecticide, not mechanical exclosures, cage artifacts did not affect assessment of herbivore impacts on meristems and seedheads of adult plants.

Quantification of herbivore impacts on plant fecundity in the fertilization experiment was, however, complicated by limited effectiveness of the insecticide used. Insecticide reduced the abundance of meristem herbivores and insect seed predators by approximately half as compared to water-sprayed plants, but insects were still present on insecticide-sprayed plants, especially adults of *C. brevistylum*. Nonetheless, patterns of herbivore abundance and plant damage I detected are still insightful.

Patterns of herbivore impact as a function of habitat productivity varied among the two guilds of herbivores examined and between experimental and observational data. In the fertilization experiment, herbivores that destroyed meristems were disproportionately abundant in fertilized compared to unfertilized plots, but abundance of insect seed predators did not vary between fertilization treatments. In unmanipulated thistle populations, meristem destruction was not significantly related to my indices of soil fertility, but abundance of insect seed predators on *C. brevistylum* varied significantly as a function of soil NO_3 and NH_4. Thus, while the intensity of herbivory in this system is related to levels of productivity under some conditions, the importance of productivity varies among herbivore guilds and among data sets.

Many of the published studies examining the relationship between herbivory and habitat productivity have found that the abundance and impact of herbivores increase with productivity (Onuf et al. 1977, Swank and Oechel 1991, Reader 1992, Bonser and Reader 1995, Feller 1995, Gange and Nice 1997). However, an equal number of studies have found other patterns (Landsberg 1995, Van de Koppel et al. 1996, Fraser 1998, Gough and Grace 1998, Uriarte and Schmitz 1998, Ritchie 2000, Van der Wal et al. 2000). Differences among studies are not easily explained by herbivore characteristics or by the responses examined; vertebrate and invertebrate herbivores are equally common in studies finding an increase versus a decrease, and pattern of change does not differ consistently among different metrics of herbivore abundance (numeric abundance of herbivores, proportion of plant modules damaged, absolute tissue loss, proportional loss) or plant response (biomass, survival, fecundity). It seems likely that patterns of herbivory with respect to productivity are obscured by variability arising from other factors.

In this study, site effects were an important source of variation in herbivory. Other research in this system (Gluesenkamp Ch. 3) has shown that variation among sites in herbivore occurrence and abundance is chiefly explained by soil nitrogen, with the density of background vegetation and site size (in m^2) also important; however, only about 30% of the variation among sites was explained by these factors. The large unexplained variance may be due to unmeasured variation in physical environment, insect colonization dynamics, or patch history and stochasticity. Such variability could easily obscure a weak relationship between herbivory and productivity.

Patterns of herbivory may also have been shaped by interactions between the two target species. In both experimental and observational data sets, levels of meristem destruction differed between the two plants, with the direction of these differences depending on the data set; in the fertilization experiment, destruction of meristems was greater for *C. brevistylum* than for *C. vulgare*, while in unmanipulated thistle patches *C. vulgare* meristem destruction exceeded that of *C. brevistylum*. Experimental and unmanipulated thistle patches were interspersed geographically and had the same environmental conditions and vegetation. The main difference between experimental and unmanipulated thistle patches is that each experimental patch contained both species of thistle, while several unmanipulated sites contained populations *C. vulgare* in the absence of *C. brevistylum*. It seems that differences in herbivore abundance between experimental and pattern studies might be best explained by differences in herbivore host choice. It appears that these insects, which are all native species, prefer the California native *C. brevistylum* over the Eurasian *C. vulgare*. While foliar herbivores attack *C. vulgare* in the absence of *C. brevistylum*, meristem destruction of *C. vulgare* is reduced where *C. brevistylum* is present. Consequently, average levels of herbivory on *C. vulgare* are greater in the pattern data set, where *C. vulgare* is more likely to occur without *C. brevistylum*, than in the experimental data set, where *C. brevistylum* is present at all sites.

This herbivore preference hypothesis was supported by further analysis of pattern data. Linear regression showed that both the number and the proportion of *C. vulgare* meristems destroyed declined with increasing *C. brevistylum* population size (for proportion destroyed versus number of *C. brevistylum* adults, $R^2 = 0.26$, $P = 0.008$), but were unrelated to *C. vulgare* population size ($R^2 = 0.002$, $P = 0.82$). Similar patterns were found in the abundance of insect seed predators and may be due to the same phenomenon. Though seed predators were consistently more abundant on *C. brevistylum* than *C. vulgare*, abundance of herbivores on *C. brevistylum* was greater in the experimental sites than in the unmanipulated patches, while the reverse was true for *C. vulgare*, and linear regression showed a (marginal) negative correlation between density of *C. brevistylum* adults and the proportion of *C. vulgare* seedheads damaged ($R^2 = 0.12$, $P = 0.09$). Herbivore movement may even have been responsible for the pattern of increasing meristem destruction with fertilization that was observed in the experiment; if herbivores preferred fertilized host plants over those in unfertilized plots, movement between host plants could elevate herbivore abundance in fertilized treatments and reduce abundance in unfertilized treatments. In this case, the proximity of high-quality and low quality hosts due to fertilizer addition may have biased in favor of finding an increase in herbivory with increasing productivity, and the true relationship between herbivore abundance and soil fertility may be the absence of correlation that was found in data from unmanipulated sites.

Relative importance of competition and herbivory

The impact of competition on individuals and populations of the two target species in this study far exceeds the impact of herbivores, and this difference increases with increasing productivity. Only two studies have examined the influence of habitat productivity on the relative importance of competition and herbivory in a terrestrial system. Bonser and Reader (1995) found that the intensity of competition and of herbivory both increased with increasing habitat productivity, with competition relatively more important at low productivity sites and herbivory more important at high productivity sites. Van der Wal et al. (Van der Wal et al. 2000) found that, though the intensity of competition increased and herbivory declined with productivity, effects of herbivory were more important than competition at all productivity levels. In addition to the two studies that varied habitat productivity, a number of studies have compared the importance of competition and herbivory under more general conditions. The majority of studies found that plants were very strongly limited by herbivores, and interference with vegetation was relatively less important than herbivory (Myster and McCarthy 1989, Swank and Oechel 1991, Reader 1992, Van der Wal et al. 2000).

Differences between my study and these others may be due to the life history of the study plants. Both of my target species were relatively poor competitors that generally occupy disturbed sites with low vegetation cover. Consequently, they performed poorly in the presence of dense vegetation. In contrast, many of the studies in the literature focus on later successional species, including trees colonizing old fields (Myster and McCarthy 1989), salt marsh plants (Van der Wal et al. 2000, Ellison 1987), and grasses and forbs in meadows (Bonser and Reader 1995, Reader 1992). The few studies that include species with life histories similar to those of *C. brevistylum* and *C. vulgare* generally have found that competition was more important than herbivory in shaping plant populations (McEvoy et al. 1993, Willis et al. 1998, Edwards et al. 2000).

Overall, the importance of herbivory to *C. brevistylum* and *C. vulgare* was far lower than that found in other studies (Myster and McCarthy 1989, Swank and Oechel 1991, Reader 1992, Bonser and Reader 1995, Van der Wal et al. 2000), including studies of other *Cirsium* species (Louda et al. 1990, Louda and Potvin 1995, Palmisano and Fox 1997, Stanforth et al. 1997). The greater importance of herbivory in many of these studies may be due to differences in the identity and characteristics of the herbivores involved. Most studies finding very strong effects of herbivory involved herbivores which kill or consume a large proportion of the host plant, including vertebrates (Van der Wal et al. 2000, Bonser and Reader 1995, Myster and McCarthy 1989, Swank and Oechel) and less commonly invertebrates (slugs: Reader 1992; cladode-mining lepidoptera: Burger and Louda 1994). Studies comparing the importance of herbivory and competition generally find herbivory less important when the herbivores act more as parasites on the host plant, consuming a small proportion of tissue or plant modules (Willis et al. 1998, Mutikainen and Walls 1995, McEvoy et al. 1993, Ellison 1987).

Since thistles at JDSF support very similar herbivores as thistles in other studies, differences in intensity of herbivory between my study and others are probably not related to herbivore traits (though rabbit herbivory contributed to high levels of damage found by Palmisano and Fox 199?). Rather, many of these other studies focused on thistle species that occur in highly erosive substrates where plants are able to maintain semi-permanent populations (sand blowouts: Louda et al. 1990, Louda and Potvin 1995; sand dunes: Palmisano and Fox 1997). Density of vegetation on these substrates is relatively low, leading to low importance of competition, and these more persistent thistle populations may enable development of larger herbivore populations. In addition, the sandy soils characteristic of these other studies are relatively unproductive, and the thistle plants are much smaller. Hence, low levels of damage may cause significant losses, and small size and low resource availability may make these plants less able to compensate for losses to herbivores (Maschinski and Whitham 1989, Rosenthal and Kotanen 1995, Bergelson et al. 1996, Sadras 1996).

Consequences of productivity for individuals and populations

The central goal of this study was to assess the individual and net strength of three pathways by which habitat productivity affects plant populations: the direct effect of soil fertility on plant growth and survival, the indirect effect of soil fertility mediated by growth of competing plants, and the indirect effect of soil fertility mediated by changes in the intensity of herbivory. Experimental and observational data show that, for both thistle species, there is a clear hierarchy of importance to these pathways: weak indirect negative effects of productivity mediated by herbivores are less important than positive direct effects on growth of *C. brevistylum* and *C. vulgare*. In turn, negative indirect effects of productivity mediated by background vegetation are much more important than either of the other pathways; thistle responses to productivity are entirely contingent on the density of background vegetation.

The species involved in this study are closely related to numerous pernicious pest plants, as well as several rare or endangered species (Turner et al. 1987), and results of this study may have important management implications. Since habitat productivity can have either negative or positive effects on target populations, depending on the presence of background vegetation, simultaneous manipulation of background vegetation and of productivity together is the most useful tool for management of *C. brevistylum*, *C. vulgare*, and similar species. For management of pest plant populations, application of fertilizer in the presence of background vegetation should result in reduced abundance of the target species, though at the risk of increasing the abundance of other weedy species present in the vegetation. To enhance populations of rare plants, simultaneous fertilizer application and vegetation removal (via soil disturbance, selective grazing, or mowing) should have strong positive effects.

These predictions are supported by two other studies. In a study of *C. arvense* occurring in grasslands (Edwards et al. 2000), fertilizer addition strongly enhanced thistle populations when rabbits and other grazers removed background vegetation, but strongly reduced thistle populations when plots were caged to exclude grazers. Invertebrate herbivores of *C. arvense* had no effect on thistle performance. Similarly, McEvoy et al. (1993) found that *Senecio jacobaea*, a fugitive pest plant with life history very similar to that of *C. brevistylum* and *C. vulgare*, was controlled well by competition with background vegetation, and that insect herbivores were most important for limiting *S. jacobaea* on unvegetated soil disturbances.

Prospects for generality

The chief methodological obstacle to understanding relationships between habitat productivity competition, and herbivory, is the failure of most researchers to quantify and present meaningful indices of productivity. The vast majority of studies do not evaluate habitat productivity numerically, but rather compare habitats that are thought to vary in productivity but that can vary in a number of other characteristics (e.g. ridge versus hollows, chalk grasslands versus pastures, early- versus late-successional seres); this may be especially problematic for studies of herbivory, since insect herbivores can be very sensitive to site effects. Very few studies quantify several indices of productivity in a manner that allows these numeric values to be compared with those of other studies by researchers seeking general patterns.

One method for overcoming the limitations of natural productivity gradients is to manipulate productivity. However, there is evidence that experimental productivity gradients differ from natural gradients in significant and poorly understood ways; reviews have found that experimental studies are more likely to find increases in intensity of competition with increasing productivity than are natural gradients (Goldberg and Novoplansky 1997), and this study has shown that movement of herbivores among host plants is capable of inflating differences in herbivore abundance. Manipulative experiments are limited in other ways. Many studies examine just a portion of the life-cycle, or use transplanted target plants, both of which may lead to different conclusions from studies that follow plants from seed addition to seed production. In addition, populations involved in experiments are often much smaller than natural populations and therefore risk missing rare events, such as thistle seedling maturation in the presence of vegetation at JDSF. Probably the best method of overcoming the problems inherent in both observational and experimental studies is to conduct both types simultaneously, as was done in this study.

Perhaps the most problematic limitations to understanding patterns of population structure with regard to habitat productivity involve construction of the frameworks ecologists use to interpret results. For example, many studies examining the relationship between productivity and competition have interpreted their results in the context of whether they support the Ruderal-Competitor-Stress model of Grime (Grime 1973, Grime 1977) or Tilman's resource-ratio model (Tilman 1987, Tilman 1988). The conventional view is that Grime predicts that the competition will increase with productivity and that Tilman predicts competition will stay the same. Important efforts toward resolving this debate have included the suggestion that Grime's theory is best tested using absolute competitive intensity and Tilman's using relative competitive intensity (Grace 1993, Grace 1995); according to this framework, since ACI often increases while RCI for the same data remains constant, the two theories are actually compatible. However, a few authors (Weldon and Slauson 1986, Goldberg and Novoplansky 1997) have pointed out that the two theories actually focus on very different questions: Tilman's model addresses how the intensity of competition will change along a short time and spatial scale; Grime's model makes few statements about intensity of competition, but addresses the overall importance of competition relative to other factors (such as environmental stress) and consequences for the evolution of plant species and regional vegetation. Continued focus on this debate almost certainly retards the exploration of other frameworks for understanding how competition and productivity interact to structure plant species and communities in ecological and evolutionary time.

Different patterns of response may also be expected for different plant life histories, since increasing productivity may have a different effect on plants native to high productivity systems versus those native to low productivity systems. For example, if low productivity systems select for plants that are good competitors for belowground resources while high productivity systems select for strong light competitors (Tilman 1988), then fertilizer addition that results in increased competition for light may have a more negative effect on plants from a low-productivity system than on plants already adapted to high-productivity conditions. Similarly, anti-herbivore defenses of plants native to low productivity habitats are generally based on tissue quality, while defenses of plants in high productivity habitats more often involve nitrogen-based defenses or increased growth (Coley et al. 1985); experimentally increased productivity that results in increased plant nutrient status may increase palatability and herbivore pressure on low-productivity plants, while high-productivity plants may be better capable of directing increased resource availability toward maintaining high levels of herbivore defense. Theoretical and empirical studies of plant limitation as a function of habitat productivity should consider the potential for plant life history strategy to explain discrepancies between results of otherwise similar studies.

The variety of methods and approaches used for studying productivity effects on herbivory and competition has resulted in equally inconsistent patterns of response. There is a need for more studies that better characterize indices of productivity, monitor a meaningful array of response variables, and explore the performance of a diverse array of plant life history types. It is very likely that, with even a limited number of such studies, ecologists will begin to see the emergence of useful synthetic frameworks describing relationships between habitat productivity and limitation by herbivory and competition.

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TABLE 1. Treatment effects on plot environmental characteristics and growth and survival of *E. australis* phytometers. Differences between treatment levels as determined by two-way ANOVA are indicated to the right of each pair. *E. australis* survival was analyzed using a nominal logistic model as described in *Analyses*. Site effect was significant for all responses except percent light transmitted and *Erichtites* responses. Fertilization × clipping interaction was significant only for percent light transmitted (F = 3.5, *P*=.07), so only tests of main effects are shown.

Factor	Fertilized	Unfertilized		Clipped	Unclipped	
Soil nitrate (ppm)	1.2 ± 0.2	0.7 ± 0.1	**	1.0 ± 0.2	0.9 ± 0.2	
Soil ammonium (ppm)	2.4 ± 0.4	1.6 ± 0.2	**	1.9 ± 0.3	2.1 ± 0.3	
Soil percent moisture	8.3 ± 0.8	9 ± 0.9		7.3 ± 0.8	9.9 ± 0.8	***
Percent humidity	44.4 ± 4.8	45.4 ± 4.9		38.3 ± 4.4	51.6 ± 4.6	***
Air temperature C^{o}	29.7 ± 1.5	30.2 ± 1.5		30.8 ± 1.4	29.1 ± 1.6	**
Percent light transmitted	1.1 ± 0.2	11.2 ± 4.7	*	96.2 ± 6.0	6.0 ± 2.7	***
Vegetation percent cover	102.5 ± 2.5	91.4 ± 5.5	**	0.0 ± 0.0	97.0 ± 3.3	*
Vegetation biomass (g / m^2)	112.6 ± 10	48.4 ± 8.5	***	91.2 ± 15.9	80.5 ± 10.9	*
Erichtites biomass (g / plant)	9.4 ± 3.7	1.3 ± 0.8	*	8.2 ± 3.3	1.4 ± 0.5	*
Erichtites percent survival	1.6 ± 0.3	1.9 ± 0.3		2.2 ± 0.2	1.3 ± 0.3	*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2. ANOVA results for analysis of seed germination, seedling survival, number of adult plants, and seed production per subplot. Treatment effects were analyzed using split-plot ANOVAs as described in text. All models are significant at $P < 0.05$. F statistics and significance of predictor terms are shown.

	Germination		Survival 97-99		Sum Bolting		Seeds / Subplot	
Factor	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Site	8.6	**	4.8	*	1.2		2.8	
Species	8.5	**	27.7	***	1.2		1.9	
Fertilization	30.1	***	0.4		4.3	.08	7.8	*
Clipping	31.6	***	27.2	**	28.6	**	28.1	***
Herbivory	0.8		1.1		5.6	*	2.6	
Species × Fertilization	0.8		0.01		1.3		0.5	
Species × Clipping	0.2		2.3		2.4		1.9	
Species × Herbivory	0.01		1.6		7.2	**	0.9	
Fertilization × Clipping	1.1		13.7	**	5.6	*	7.7	*
Fertilization × Herbivory	1.1		0.7		0.4		0.2	
Species × Fert. × Clipping	3.4	.07	1.5		0.03		0.2	
Species × Fert. × Herbivory	0.3		4.0	*	0.004		0.005	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3. ANOVA results for meristem production, meristem fate, and seedhead responses of adult plants. Treatment effects were analyzed using split-plot ANOVAs as described in text. All models are significant at $P <$ 0.05, except model for seeds per seedhead. F statistics and significance are shown.

Factor	Meristems produced		Meristems destroyed		Seedheads matured		% Seedheads with insects		Insects per seedhead		Seeds per seedhead	
	F	P	F	P	F	P	F	P	F	P	F	P
Site	2.7		3.0		4.3	**	2.6		1.5		0.3	
Species	8.8	**	3.4	.08	0.2	‡	29.4	***	56.8	***	14.0	***
Fertilization	12.0	**	13.0	**	0.1		1.0		0.5		1.4	
Herbivory	1.0		3.5	.07	2.7	‡	6.0	*	5.0	*	0.03	
Species × Fertilization	0.7		0.02		1.3		0.2		0.1		1.6	
Species × Herbivory	0.7		1.6		0.3		0.3		2.4		0.03	
Fertilization × Herbivory	0.1		0.6		1.9		0.3		0.4		0.4	
Species × Fert. × Herbivory	0.8		0.5				0.5		0.1		0.05	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, ‡ significant after exclusion of anomalous sites.

TABLE 4. ANCOVA results for thistle abundance as a function of vegetation cover class and soil nitrogen. *F* statistics and significance are shown.

Factor	Germinants		Older seedlings		Adults	
	F	*P*	*F*	*P*	*F*	*P*
C. brevistylum						
NO_3	0.01		0.03		1.8	
NH_4	12.05	*	0.005		2.9	
Vegetation cover class	2.3		1.5		4.2	*
Cover × NO_3	0.04		0.002		1.7	
Cover × NH_4	5.8	*	0.6		0.3	
C. vulgare						
NO_3	0.01		0.2		0.03	
NH_4	5.3	*	0.2		0.002	
Vegetation cover class	2.1		0.04		0.1	
Cover × NO_3	0.03		0.1		0.03	
Cover × NH_4	5.9	*	0.003		0.3	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 5. Results of ANCOVAs testing for effect of site age class and soil N on meristem production, meristem fate, and seedhead responses. Models for *C. brevistylum* meristem production, seedhead maturation, and seeds per plant are significant at $P < 0.05$; other responses are not significantly explained by this model.

Factor	# Meristems produced		# Meristems destroyed		# Seedheads matured		% Seedheads with insects		# Insects per seedhead		Seeds per seedhead		Seeds per plant	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
C. brevistylum														
NO_3	0.3		1.6		0.3		2.9		5.4	*	0.5		0.2	
NH_4	0.1		0.3		3.5	§	1.1		0.1		0.2		12.8	**
Vegetation cover class	0.04		0.02		0.3		3.8	§	5.0	*	0.5		3.6	§
Veg cover × NO_3	0.8		0.01		0.4		1.2		1.9		0.2		0.5	
Veg cover × NH_4	6.1	*	1.0		8.6	**	5.3	*	5.2	*	3.5	§	24.0	***
C. vulgare														
NO_3	0.3		0.3		0.0001		1.3		2.7		0.4		0.01	
NH_4	0.3		0.04		0.9		0.01		0.6		1.2		0.5	
Vegetation cover class	1.7		0.01		0.6		0.1		0.0004		0.4		0.4	
Veg cover × NO_3	1.9		0.9		1.2		0.3		0.7		0.7		1.0	
Veg cover × NH_4	2.7		0.5		1.9		1.0		1.9		1.0		1.6	

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

FIGURE CAPTIONS

FIGURE 1. Design of fertilization, vegetation, herbivory manipulation. Vegetation removal treatments are represented by gray shading. Seed addition subplots received either herbivore exclusion treatments (crosshatched circles) or were left unmanipulated (open circles). This block was repeated once at each of 7 field sites (see *Experimental Manipulations*).

FIGURE 2. Demographic responses of seed addition subplots. Crosshatching indicates caged subplots, which received herbivore exclusion treatment as described in text. Figures on the left are for *C. brevistylum*, figures on the right are for *C. vulgare*. Means and standard errors are shown. Significance of comparisons is given in Table 2. (a) germination rates of *C. brevistylum,* (b) germination rates of *C. vulgare,* (c) survival rates of *C. brevistylum*, (d) survival rates of *C. vulgare*, (e) number of *C. brevistylum* bolting, (f) number of *C. vulgare* bolting, (g) *C. brevistylum* seed production per subplot, (h) *C. vulgare* seed production per subplot.

FIGURE 3. Meristem production, meristem fate, and seedhead responses of adult thistle plants. All data are for plots with background vegetation removed. Crosshatching indicates caged subplots, which received herbivore exclusion treatment as described in text. Figures on the left are for *C. brevistylum*, figures on the right are for *C. vulgare*. Means ± one standard error are shown. Significance of comparisons is given in Table 3. (a) meristem production by *C. brevistylum,* (b) meristem production by *C. vulgare,* (c)

meristem destruction for *C. brevistylum*, (d) meristem destruction for *C. vulgare*, (e) seedheads produced by *C. brevistylum*, (f) seedheads produced by *C. vulgare*, (g) insects per *C. brevistylum* seedhead, (h) insects per *C. vulgare* seedhead.

FIGURE 4. Relative competition intensity (RCI) in fertilized versus unfertilized plots. (a) RCI for number of seedlings surviving in subplots in October 1999. (b) RCI for the total number of seeds produced per subplot. All data are for plots ambient levels of herbivory. Means and standard errors are shown; absence of SEs for seed production (Figure 4b) is due to uniformity of responses.

FIGURE 5. Effects of site age and soil nitrate pools on (a) percent cover by vegetation and (b) percent of light transmitted through vegetation to the soil surface.

FIGURE 6. Relationships between soil ammonium pools and plant reproductive variables for sites with high vegetation cover (solid symbols and thick lines) and low vegetation cover (empty symbols and thin lines). (a) number of meristems produced by *C. brevistylum,* (b) number of meristems produced by *C. vulgare,* (c) number of *C. brevistylum* meristems destroyed, (d) number of *C. vulgare* meristems destroyed, (e) number of seedheads produced by *C. brevistylum*, (f) number of seedheads produced by *C. vulgare*, (g) *C. brevistylum* seed production per seedhead, (h) *C. vulgare* seed production per seedhead, (i) *C. brevistylum* seed production per plant, (j) *C. vulgare* seed production per plant, (k) density of *C. brevistylum* germinants in permanent census plots, (l) density of *C. vulgare* germinants in permanent census plots, (m) proportion of *C.*

brevistylum seedheads attacked by insects, (b) proportion of *C. vulgare* seedheads attacked by insects (a) number of insects per *C. brevistylum* seedhead, (b) number of insects per *C. vulgare* seedhead. Figures on the left are for *C. brevistylum*, figures on the right are for *C. vulgare*. Significance of relationships is given in Table 4 and Table 5.

FIGURE 1

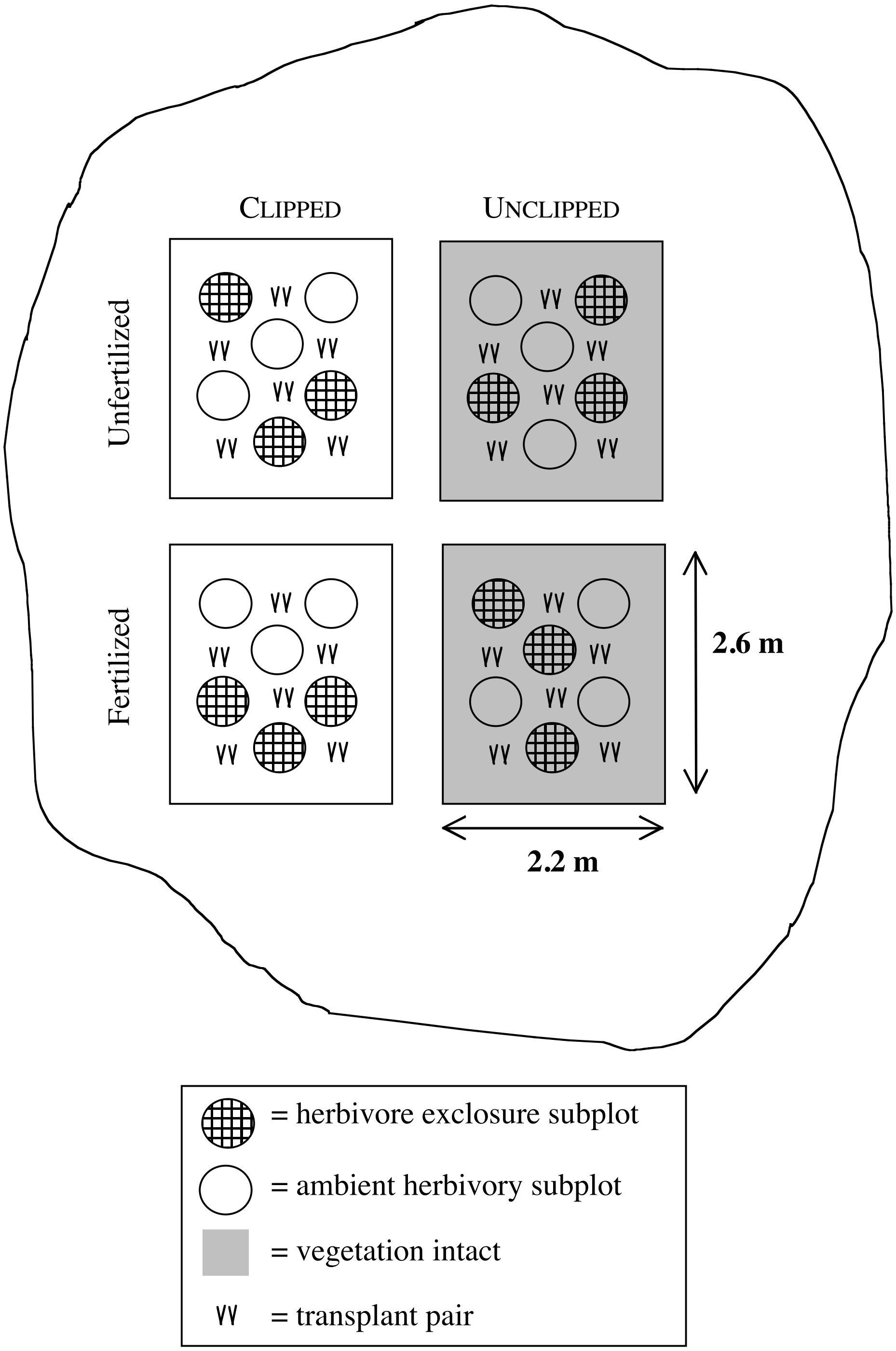

CLIPPED
UNCLIPPED
Unfertilized
Fertilized
2.6 m
2.2 m
⊞ = herbivore exclosure subplot
○ = ambient herbivory subplot
■ = vegetation intact
VV = transplant pair

FIGURE 2

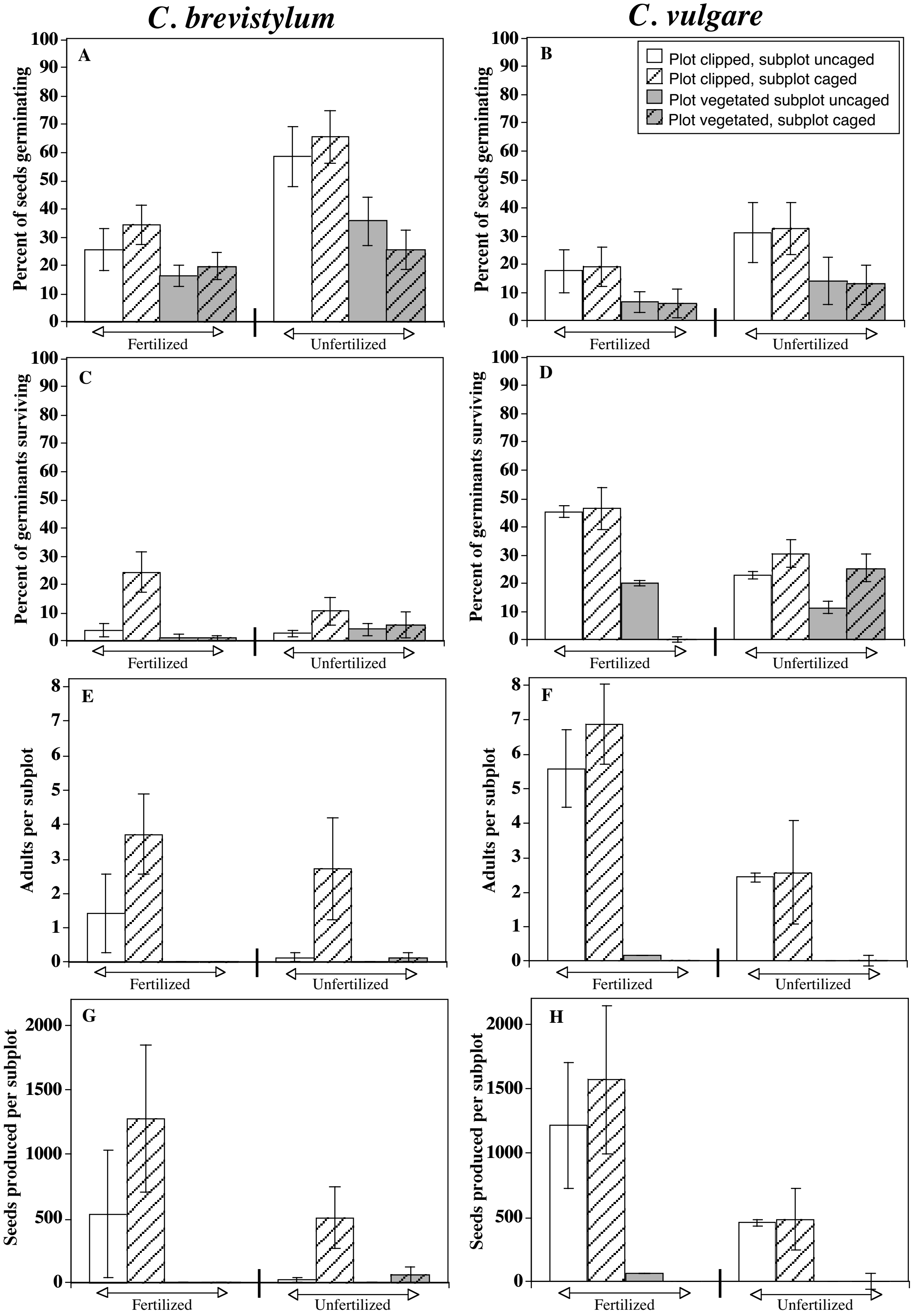
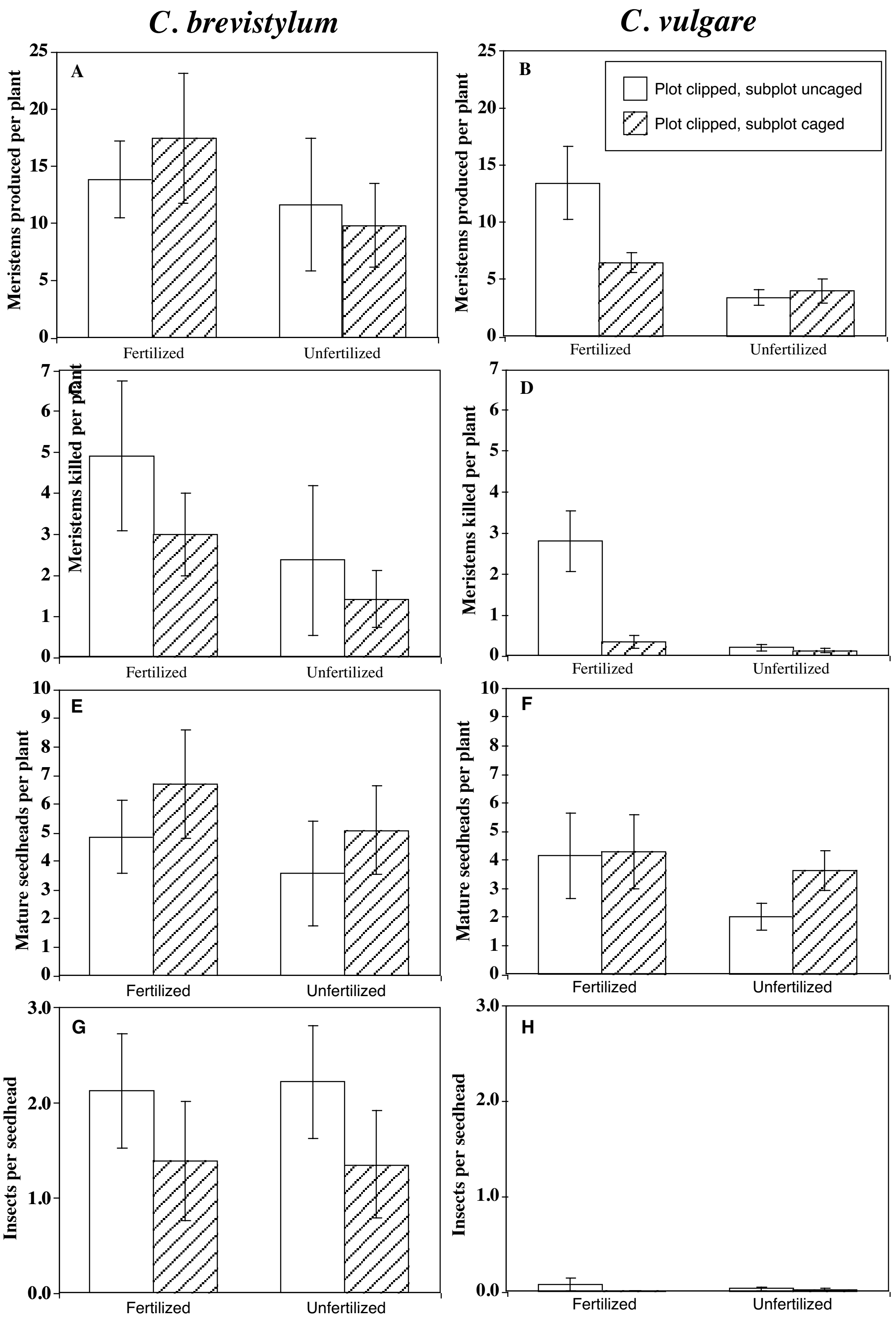

C. brevistylum
C. vulgare
A
B
C
D
E
F
G
H
Percent of seeds germinating
Percent of germinants surviving
Adults per subplot
Seeds produced per subplot
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
8
500
1000
1500
2000
Fertilized
Unfertilized
Plot clipped, subplot uncaged
Plot clipped, subplot caged
Plot vegetated subplot uncaged
Plot vegetated, subplot caged

FIGURE 3



C. brevistylum
C. vulgare
A
B
C
D
E
F
G
H
Plot clipped, subplot uncaged
Plot clipped, subplot caged
Meristems produced per plant
Meristems killed per plant
Mature seedheads per plant
Insects per seedhead
0
5
10
15
20
25
0
1
2
3
4
5
6
7
0
1
2
3
4
5
6
7
8
9
10
0.0
1.0
2.0
3.0
Fertilized
Unfertilized

FIGURE 4

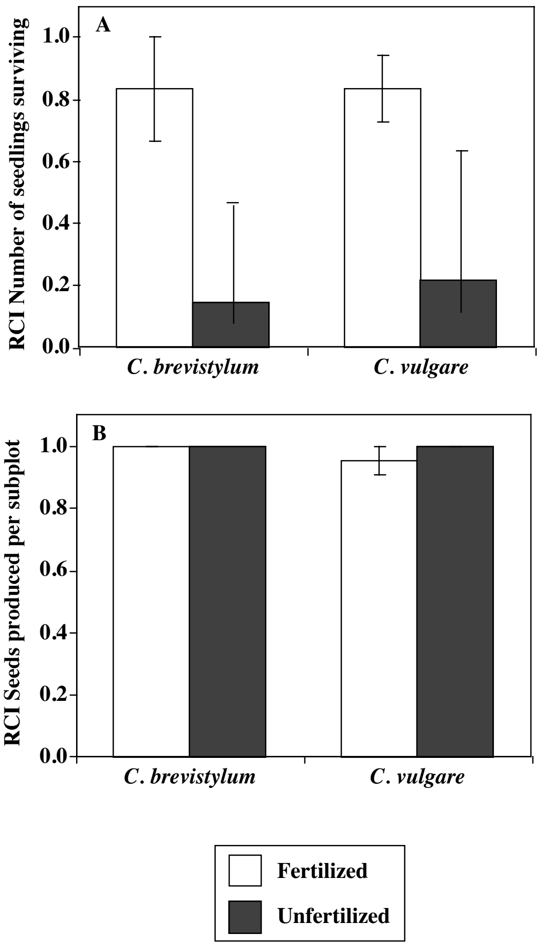

A
RCI Number of seedlings surviving
1.0
0.8
0.6
0.4
0.2
0.0
C. brevistylum
C. vulgare
B
RCI Seeds produced per subplot
1.0
0.8
0.6
0.4
0.2
0.0
C. brevistylum
C. vulgare
Fertilized
Unfertilized

FIGURE 5

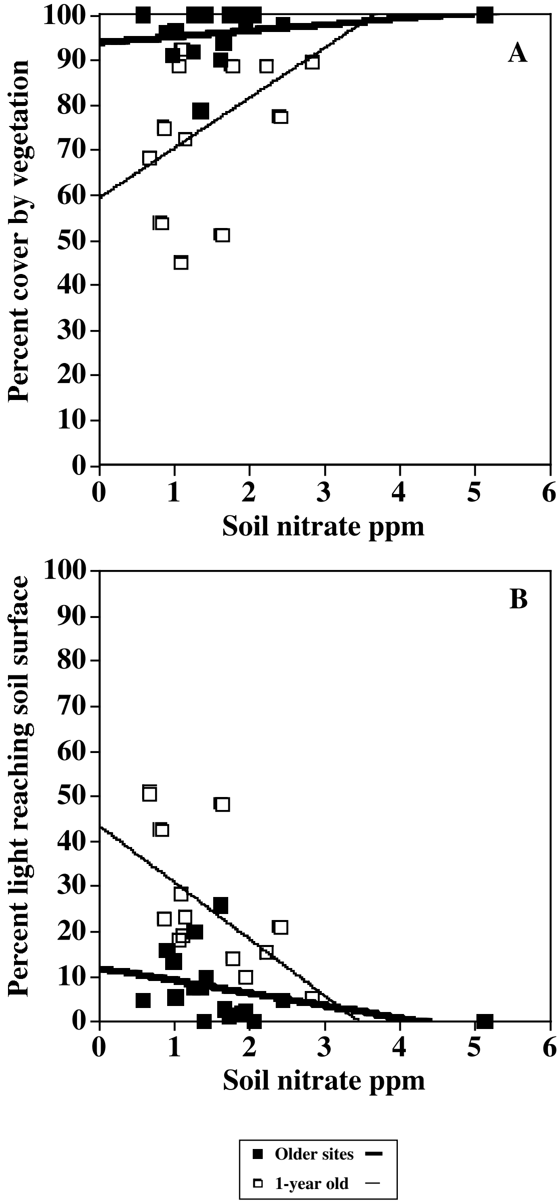

A
Percent cover by vegetation
100
90
80
70
60
50
40
30
20
10
0
0
1
2
3
4
5
6
Soil nitrate ppm
B
Percent light reaching soil surface
100
90
80
70
60
50
40
30
20
10
0
0
1
2
3
4
5
6
Soil nitrate ppm
■ Older sites
□ 1-year old

FIGURE 6

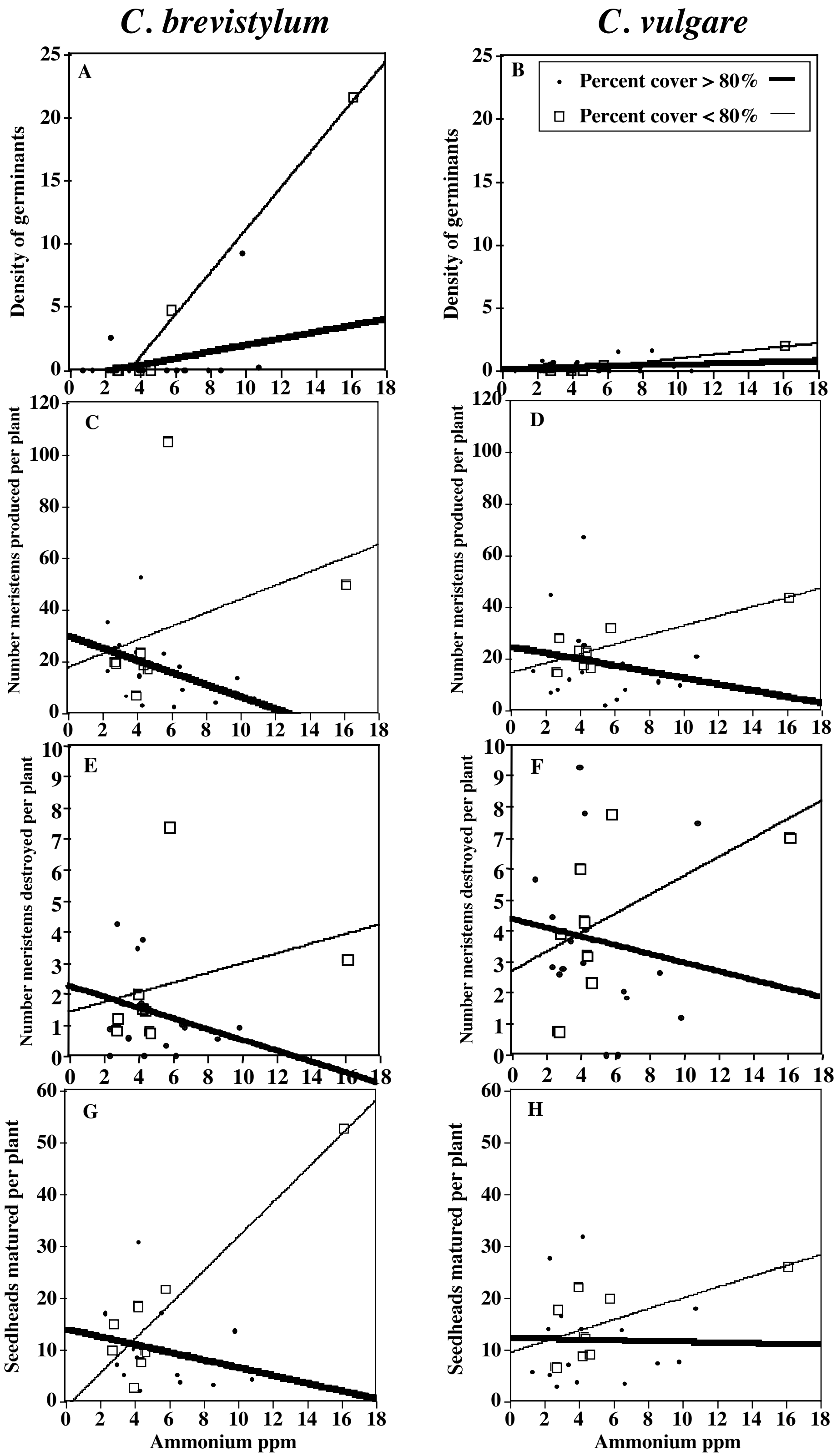

C. brevistylum
C. vulgare
A
B
• Percent cover > 80%
□ Percent cover < 80%
Density of germinants
0
5
10
15
20
25
0 2 4 6 8 10 12 14 16 18
C
D
Number meristems produced per plant
0
20
40
60
80
100
120
E
F
Number meristems destroyed per plant
0 1 2 3 4 5 6 7 8 9 10
G
H
Seedheads matured per plant
0
10
20
30
40
50
60
Ammonium ppm

FIGURE 6: EXTENDED