Chapter 3

Distribution of insect seed predators on a native thistle.

INTRODUCTION

A substantial amount is known about factors structuring insect populations at local scales. Studies have shown that the occurrence and abundance of phytophagous insect species are affected by the timing of resource availability (Andrewartha and Birch 1954, Hunter 1992), resource size and concentration (Root 1973, Price 1991), resource quality (Coley 1987, Strong et al. 1985), architectural characteristics of resources and habitats (Denno and Roderick 1988, Zabel and Tscharntke 1998), and by the physical environment (Andrewartha and Birch 1954, Ritchie 2000). Despite our increasing knowledge of general controlling factors, we have limited ability to predict local occurrence or abundance patterns for individual taxa or guilds. Even for comparatively well-known groups, we know little about what structures populations across scales.

Thistle insects have been comparatively well-studied. Biological control research has produced large amounts of information about various aspects of prospective and actual biocontrol agents on Eurasian thistles (e.g.: Boldt and Jackman 1993, Goeden and Ricker 1985, Zwolfer 1988, Zwolfer and Arnold-Rinehart 1993). However, these studies have generally not examined the ecological factors shaping distribution and abundance of thistle herbivores, and the limited ecological work has focused chiefly on one scale (i.e. seedhead, plant or site). In addition, the vast majority of all thistle research has been directed primarily at Eurasian thistles and Eurasian herbivores; in comparison, North American thistle faunas are more poorly understood.

Much of the research in North America on thistles and their herbivores has been directed at the biological control of introduced Eurasian thistles by the introduction of

Eurasian herbivores. While a number of studies have examined the impact of herbivory on North American thistles (Louda et al. 1990, Louda and Potvin 1995, Palmisano and Fox 1997, Stanforth et al. 1997), these studies have generally focused on plant responses and have not investigated population ecology of thistle herbivores. With a few notable exceptions (e.g.: Headrick and Goeden 1990b, Louda et al. 1997, Louda etc 1998) most of the work focusing on the herbivores of North American thistles has consisted of host plant surveys (Goeden and Ricker 1986, Goeden and Ricker 1987, Pemberton et al 1985, Turner et al 1987a, Turner et al 1987b), life-history descriptions (Headrick and Goeden 1990a) and taxonomic and systematic treatments (Lange 1950). In particular, for North American thistles, there have been no studies examining the ecological factors structuring herbivore populations at multiple spatial scales.

A number of North American thistle species are rare, endangered, or species of conservation concern (e.g. in California alone: *C. andrewsii*, *Cirsium scopulorum*, *C. ciliolatum*, *C. fontinale*, *C. hydrophilum*, and *C. loncholepis*), and there is some evidence that herbivores may contribute to their rarity (J. Herr pers com). A number of herbivorous insects have been introduced for biological control of introduced Eurasian thistles, with additional insect species currently under investigation for potential introduction. In addition, at least one of these biocontrol agents attacks thistles native to North America, and may negatively impact both native thistles and their native herbivore communities (J. Herr pers com, Louda et al 1987, Louda et al 1998). Investigation of factors controlling occurrence and abundance of phytophagous insects on North American thistles provides important baseline information regarding the structure of thistle-herbivore systems. This information may also improve our ability to predict and understand the outcome of (intentionally or unintentionally) introduced organisms on native communities, and can help to improve the success rate and safety of future biological control introductions.

This paper addresses the following questions regarding the occurrence and abundance of insect herbivores on a California native thistle:

1) How do insect occurrence and abundance vary across spatial scales of investigation (i.e. among seedheads, among individual plants, or among sites)?

2) What factors shape variation in the occurrence and abundance of insects at each scale?

3) How do the answers to these questions vary among different insect species within a seed predator guild?

I examined these questions for 3 species of insect seed predators occurring within seedheads of *Cirsium brevistylum* Cronquist (Asteraceae), a thistle native to the Pacific coast of the United States. I quantified abundance of insects in seedheads collected from 19 distinct study sites, enabling analysis of patterns at three scales: among seedheads, among plants within sites, and among sites. At each scale, I collected data on seedhead, plant, and site characteristics in order to identify some of the factors potentially influencing variation in occurrence and abundance of insects at each level.

Study System

Field work was conducted at Jackson Demonstration State Forest (JDSF), near Fort Bragg, California. Study sites were located 6 to 12 kilometers 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 in the summer or drop below freezing in the winter. The forest is dominated by coast redwood (*Sequoia sempervirens*), and bulldozing associated with logging activities creates numerous soil disturbance patches ranging in size from 10 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.

Cirsium brevistylum is one of the first plants to occupy sites following disturbance. *C. brevistylum* is one of approximately 30 taxa of thistles native to California, and occurs in moist sites from southern California to the Canadian border. Like many thistles, these plants are strongly limited by competition with background vegetation, and populations are chiefly found on sites subject to frequent natural or anthropogenic soil disturbance (Gluesenkamp, Ch 1). *C. brevistylum* is a monocarpic perennial that grows for one to several years as a vegetative rosette and bolts and reproduces once before dying. 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, though plants are capable of bolting in their first year or of persisting for several years before reproduction.

Adult plants typically have one apical growth axis with numerous lateral branches. Flowers are borne in composite seedheads at the tips and axils of these branches. *C. brevistylum* inflorescences are composite seedheads in which hundreds of individual flowers (also called florets) are aggregated and enclosed within a collection of green bracts (phyllaries) to form a single seedhead (also referred to as inflorescence or capitulum), essentially identical to that of artichokes, a domesticated thistle. Ovules are borne at the base of florets atop a large mass of receptacular tissue.

At JDSF, *C. brevistylum* capitulum production begins in late April with the appearance of small buds at the apices of main and lateral branches. Capitula maturation begins with the apical bud, followed by lateral and then sub-lateral buds. As seedheads mature, the closed phyllaries of the developing seedhead reflex to expose florets to pollinators, then close again to protect developing ovules, and finally reflex again to open the capitulum and allow wind-dispersal of mature seeds. Thus, capitula pass through distinct developmental stages (developing bud, immature seedhead, seedhead anthesis, seed maturation, and senescence and dispersal), each stage separated by approximately two weeks.

Seedheads of *C. brevistylum* are a large, concentrated resource that can support several species of insect seed predators. These insects develop within seedheads and consume young florets, receptacular tissue, and developing ovules. While at least 6 species of insect seed predator occur at this location (Gluesenkamp, unpublished data), I examined occurrence and abundance of the three most common insect seed predators found at JDSF: one species of moth (*Platyptilia carduidactyla* Riley), one fly (*Paracantha gentilis* Hering), and one beetle (*Rhinocyllus conicus* Froelich). Together, these three species comprise over 99% of the herbivore individuals collected at JDSF.

The artichoke plume moth, *Platyptilia carduidactyla*, is the least specialized of the three insect species. Collections of this native pterophorid moth have been made from Canada to Costa Rica, and the species occurs throughout California with the exception of boreal zone (Lange, 1950). *P. carduidactyla* is one of 18 *Platyptilia* species found in California, and the only *Platyptilia* known to occur on *C. brevistylum* . In California, *P. carduidactyla* feeds on a variety of native and introduced thistles, including the cultivated globe artichoke *Cynara scolymus*, species in *Arctium*, *Carduus*, *Centaurea*, and *Silybum*, and at least 30 *Cirsium* taxa (Gluesenkamp per obs, Turner et al 1987a, Bragg 1971, Lange 1950). *C. brevistylum* is considered the moth's preferred host in coastal California (Lange 1950).

Eggs of *P. carduidactyla* are laid singly on the outside of seedheads, leaves, or other plant structures. After eggs hatch, larvae often feed externally on young leaves for the first two instars and then burrow within leaf stalks, stems, and seedheads for subsequent feeding and pupation. However, young larvae commonly feed internally, while old larvae often feed externally. Pupation can occur on any aboveground plant structures (Lange 1950). Thus, *P. carduidactyla* are not obligate seed predators and often damage meristems and other structures (Gluesenkamp Ch 1).

In contrast to *P. carduidactyla*, the other two insect species addressed in this paper are obligate seed predators. *Paracantha gentilis* is a tephritid fly native to the western United States and occurs as far south as Costa Rica. *P. gentilis* is one of 3 *Paracantha* species found in California, and the only *Paracantha* species collected from *C. brevistylum*. While the fly occurs on a number of *Cirsium* species (Headrick and Goeden 1990a), it has not been collected from other thistle genera, with the exception of a single individual collected from *Carduus pycnocephalus* (Goeden and Ricker 1986).

P. gentilis is univoltine, producing one generation per year. Oviposition occurs on immature seedheads, with several eggs per clutch (mean: 4 eggs / seedhead for *C. occidentale* var. *californicum* (Headrick and Goeden 1990a) placed among florets inside the seedhead. Larvae feed on florets in the first instar and on ovules and receptacular tissue in the second and third instars. Pupation occurs after the third instar, within a cavity excavated by feeding activities. Adults emerge during the summer and fall, and overwinter in unknown conditions before returning to host plants, establishing territories, and awaiting appearance of new seedheads the following spring.

Rhinocyllus conicus is a European weevil introduced to North America in the late 1960s as a biological control agent against several non-indigenous thistle species. While the principle target hosts of the insect are *Silybum marianum* and several species in the genus *Carduus*, the weevil also attacks a wide range of native *Cirsium* thistles, including *C. brevistylum* (Turner et al 1987b). The life history of *Rhinocyllus* is similar to that of *P. gentilis*. The weevil is univoltine and is an obligate seed predator. *Rhinocyllus* eggs are deposited on bracts on the outside of immature capitula, with from 1 to 9 eggs per clutch, and each clutch is covered with a cap of masticated plant material. Upon hatching, larvae burrow through bracts, feed on developing ovules and receptacular tissue, and form galls in the receptacle which ultimately become pupal chambers (Rees 1982). Adult weevils emerge after 3-6 weeks, overwinter beneath rocks and bark (Kok 1976), and congregate on bolting plants the following spring.

METHODS

Data collection

I collected *C. brevistylum* seedheads from plants at 19 separate sites across JDSF. Seedheads were dissected in the lab to determine the presence and abundance of each seed predator species. At each level of investigation (seedhead, plant, and site), I quantified the variables most likely to determine variation in insect occurrence and abundance; these included measures of resource size and density, resource phenology, architectural and spatial factors, plant and soil nutrient status, and site environmental characteristics.

Sites used in this study were discrete patches created by logging activities. These patches ranged in size from 50 to 100 m^2, and distance between nearest sites ranged from 100 to 1600 m. All patches contained similar vegetation, a mix of *H. lanatus*, *E. australis*, *Stachys* sp., *P. aquilinum* and other forbs. This study utilized a subset of unmanipulated sites presented in Gluesenkamp Ch 2. However, the present paper focuses on *C. brevistylum* and so excludes sites with only *Cirsium vulgare* present and excludes the few sites where sampling of *C. brevistylum* seedheads was not complete (minimum of 5 plants with minimum of 3 seedheads per plant). Site age was determined based on personal observation of disturbance events, and ranged from 1 to 5 years since disturbance.

In May 1998 I characterized vegetation density and site environment within 4 randomly-located 1 m^2 permanent quadrats at each site, as described in Gluesenkamp Ch 2. Background vegetation within each plot was quantified by visually estimating percent cover from above (Gluesenkamp Ch 1). At the same time, I measured availability of photosynthetically active radiation (PAR) by taking readings above the vegetation canopy (200 cm) using a handheld LI-COR PAR meter (LI-COR, Lincoln, Nebraska) in two randomly-chosen 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; while one-time measurements do not provide an integrated measurement of all the light incident in the course of a day, the index is sufficient for comparing among sites.

Soil moisture and available nitrogen pool sizes were determined from two 2.5 * 10 cm deep cores from each plot. In each of the 4 plots per site, cores were taken from two locations 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. Determinations of ammonium nitrogen (NH_4^+ -N) and nitrate nitrogen ($N0_3^-$ -N) were made colorometrically using a Lachat QC 8000 (Lachat Instruments, Milwaukee, Wisconsin), and Lachat values were converted to parts per million N in dry soil. While nitrogen pools were quantified at only a single time point

(May 1998), 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.

Independent of work in the four 1 m^2 permanent quadrats, I calculated population density of adult thistles at each site by measuring site area, counting the total number of adult *C. brevistylum* 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 plant characteristics and collection of seedheads. Phenological status at the period of peak physiology (June 1998) was determined for each marked plant by counting the number of capitula in each of five age classes: bud, immature capitulum, anthesis (= florets open and available to pollinators), ripening seedhead (= capitulum closed and florets senesced), and maturity (= capitulum open and seeds ripe for dispersal). For each plant, I then calculated the proportion of all capitula that had advanced to or past anthesis, in order to generate a single index of plant phenological stage.

At the same time, I collected leaf tissue for determination of tissue carbon and nitrogen content. I removed the most recently matured leaf from each marked plant (generally the most apical leaf). Each sample was placed in a separate paper envelope, dried at 60° C for 24 hours, and stored in a cool dry location until analysis. Leaf samples were ground using a Wiggle-Bug ® dental amalgamator (Crescent Dental Manufacturing, Chicago), 5 mg subsamples were rolled in tin capsules, and total percent carbon and percent nitrogen content determined using a Carlo-Erba combustive C-N-S autoanalyzer (Fisons Instruments, Beverly, MA).

Every 2 weeks, on each measured 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. I removed bagged seedheads after plant senescence at the end of the season, and stored these samples in a cool dry location until processing. While bags undoubtedly altered the microenvironment of seedheads, pilot tests using these same species detected no bagging effects on insect reproduction or survival (Gluesenkamp, unpublished data), and so significant biases due to seedhead bagging are unlikely.

Since a large number of seedheads were collected, I randomly selected a subsample such that at least 3 seedheads were dissected for each of 15 plants per site, or as many plants as were present at the site for sites with fewer than 15 *C. brevistylum* plants. Seedheads were dissected under a dissecting scope, and all insects or insect material removed, identified to operational taxa, and stored individually in 10 ml plastic vials. Final identification of the three insect species included in this study was made by comparison with samples from the Essig Museum, and was facilitated by the distinctive appearance of each species; while congeners of both *P. carduidactyla* and *P. gentilis* are present in California, these other species either do not attack *Cirsium* species (*Platyptilia* spp. and *Paracantha coulteri*) or are very rare on *Cirsium* and do not utilize seedheads (*Paracantha genalis*) (Pemberton et al 1987, Lange 1950).

For each seedhead, the date of bagging was noted; this bagging was done at the same phenological stage for each seedhead and so this date is an index of the timing of availability to insects. The location of each seedhead on the parent plant was noted: primary (1°) seedheads occurred on the apex of the plant, secondary (2°) seedheads on the tips of lateral branches, tertiary (3°) seedheads on the tips of branches emerging from lateral branches, and quaternary (4°) seedheads were borne on subsequent branches. Finally, I determined the size of each seedhead by measuring the diameter of the receptacle with calipers at the time of seedhead dissection.

Data analysis

Data analysis proceeded with two principal goals. The first goal was to determine the scale of investigation (i.e. seedhead, plant, site) with the highest variation in insect abundance. Second, I sought to understand, for each level, which of the factors I measured best explain variation in insect occurrence and abundance. Each of the three seed predator species was analyzed separately. Since there may be interactions among insect species, data for the three species were also pooled and the sum of all seed predators was analyzed concurrent with tests of individual species responses. I also looked for evidence of interactions between species by testing for correlations in occurrence and abundance of the three species.

All statistical tests were conducted using the JMP 3.1.7 statistical package (SAS Institute, 1996), unless otherwise specified. Numeric data were transformed prior to analysis in order to improve normality and homogeneity of variance. Counts (number of insects per seedhead) were transformed using log (X + 1), and proportions (percent of seedheads occupied / 100) were transformed using the arcsine square-root transformation. Julian day was used for seedhead maturation dates. Occurrence data (insects present vs.

absent) were not modified. All figures show untransformed data. For models that included both categorical and continuous data, I tested the significance of all interaction terms in order to satisfy the equal slopes assumption of ANCOVA; when significant, interaction terms were included in models. Estimates of variance given in text and figures are ± one standard error. R^2 presented for nominal models is the uncertainty coefficient U, calculated as ratio of negative log likelihood values. Due to high variability in the data, several tests produced patterns that appeared meaningful and consistent but were non-significant. To improve understanding of overall patterns, results with probability of Type I error of $P \leq 0.10$ are noted in all tables.

I used a nested ANOVA to partition variance components associated with the three levels of investigation in this study (among sites, among plants within site, and among seedheads within site). In order to estimate mean squares, I analyzed number of insects per seedhead using a nested ANOVA including site and plant nested within site (i.e. plant [site]), with plant [site] designated a random effect and plant [site] MS used to calculate *F* for site. I then utilized formulas presented in Sokal and Rohlf (1995) to determine variance components and the proportion of total variance attributable to seedhead, plant, and site levels.

For each level, I then explored the degree to which occurrence and abundance of insect seed predators was explained by measured characteristics versus blocking variables representing factors operating at higher levels. Thus, models analyzing variation among seedheads included the blocking factors site and plant nested within site, as well as seedhead characteristics that I measured; models analyzing variation among plants included the blocking factor site in addition to plant characteristics; models analyzing variation among sites included site characteristics. These analyses were performed for each of the four insect seed predator groups: *Platyptilia*, *Paracantha*, *Rhinocyllus*, and the sum of the three species. Since *Rhinocyllus* was not present at all 19 sites, seedhead-level and plant-level analyses of *Rhinocyllus* responses included only data from sites where the species was present; similarly, *Platyptilia* was absent from several sites and these sites were excluded from seedhead and plant-level analyses. *Paracantha* was present at all sites, so data from all 19 sites were included in analyses of *Paracantha* and of the sum of insects.

For seedhead-level investigation, two response variable were analyzed: (1) the presence or absence of insects and (2) number of insects present in the seedhead. Presence / absence data were analyzed using multivariate nominal logistic regression models including site and plant nested within site as blocking factors and the date of seedhead maturation, position of seedhead on plant, and seedhead diameter as measured predictors of insect occurrence. Significance of effects was evaluated using Wald chi-square. Number of insects per seedhead was analyzed using ANCOVA models including the same terms: site, plant [site] as blocking factors, with plant [site] designated a random effect; position of seedhead on plant as a categorical predictor variable; and date of seedhead maturation and seedhead diameter as continuous predictors.

To assess plant-level variability in herbivore occurrence and abundance, I calculated three response variables for each insect. For each plant, seedhead data were summarized to produce the following information: (1) presence or absence of insects, (2) proportion of seedheads with insects present, and (3) the mean number of insects per seedhead. Occurrence data were analyzed using multivariate nominal logistic models, including site as a random blocking factor, number of seedheads dissected as a covariate, and tissue percent carbon, percent nitrogen, plant height, plant phenological state at the June census, and number of meristems as measured predictors of insect occurrence. Significance of effects was evaluated using Wald chi-square. The proportion of seedheads with insects present was analyzed using ANCOVA models including the blocking term site, and tissue percent carbon, percent nitrogen, plant height, plant phenological state, and number of meristems as continuous predictor variables. Mean number of insects per seedhead was analyzed using identical ANCOVAs. Significant site × nitrogen interactions were detected for *Platyptilia*, and significant site × phenology interactions detected for *Rhinocyllus*, so these interaction terms were included in their respective models.

I summarized data for each site to calculate three response variables: (1) presence or absence of insects at each site, (2) proportion of seedheads with insects present, and (3) the mean number of insects per seedhead. Since *Paracantha* was present at all 19 sites, analyses of presence / absence data were only conducted for *Platyptilia* and *Rhinocyllus*. Data for all 19 sites were included in these tests. Limited degrees of freedom available for analyses at the site level prevented the inclusion of all 8 predictor variables in a single model. Therefore, each measured predictor variable was evaluated in a separate model; overall patterns resulting from these tests were the same as for models that included all 8 predictors.

Presence / absence of insects from each site was analyzed using individual nominal logistic models for site age, site area, soil nitrate, soil ammonium, soil moisture, light availability, vegetation cover class, and adult plant population size as measured predictors of insect occurrence. Number of seedheads dissected was initially included as a covariate in these models but was consistently non-significant in all cases and so was not used in the final models. The proportion of seedheads with insects present was analyzed using individual linear regressions for site age, area, soil nitrate, soil ammonium, soil moisture, light availability, and adult plant population size using 1-way ANOVA for vegetation cover class. Mean number of insects per seedhead was analyzed using identical models. Other research in this system has suggested that interactions differ between sites with dense cover by background vegetation versus sites with low cover (Gluesenkamp Ch 2), so percent cover was expressed as a categorical variable (greater than 80% cover Vs. less than 80% cover) to facilitate evaluation of interactions. Significant cover class × nitrate interactions were detected for *Paracantha* responses, and so the influence of vegetation cover class and of soil nitrate on *Paracantha* abundance were determined using nominal logistic regression and ANCOVA models that included cover class, soil nitrate, and the cover × nitrate interaction.

To test whether the occurrence and abundance of a given insect species was affected by occurrence or abundance of the other two species, I compared all possible combinations of occurrence and abundance of all three species at each of the three levels of investigation. To find relationships between abundance of different species, I calculated Pearson product-moment correlations between all possible combinations of proportion of seedheads attacked and number of insects per seedhead. I used *t*-tests to determine whether, for each species, the proportion of seedheads occupied (for plant and site levels) or the number of insects per seedhead (for seedhead, plant, and site levels) was influenced by the presence of the other two insect species. I used nominal logistic regression to determine whether, for a given species, occurrence was shaped by the abundance of the other two species. And, finally, I calculated Pearson chi-square for all combinations of occurrence at each level. For each test, Bonferroni's inequality was used to adjust α for multiple comparisons.

RESULTS

Of 457 *C. brevistylum* seedheads included in this study, pooled for all 19 sites, 275 (60%) seedheads showed evidence of insect attack. This included 44 *Platyptilia* individuals, 344 *Paracantha*, 77 *Rhinocyllus*, and 23 unidentified insects or insect parts. In addition, 20 seedheads contained parasitic wasps, including 12 individuals of *Pteromalus coloradensis* (which parasitizes *Paracantha*) and 20 individuals of unidentified hymenopteran parasitoids of *Platyptilia*). Of the three herbivore species included in this study, *Platyptilia* had the lowest population densities, with 0.12 insects per seedhead. The three species had distinctive patterns with respect to occurrence among seedheads, plants, and sites (Figure 1). While *Platyptilia* moths were present at the majority of sites (16 / 19), where the species did occur it only affected a small proportion of plants and even smaller proportion of seedheads. In contrast, *Rhinocyllus* occurred at only 6 sites, but rates of weevil occurrence at those 6 sites were greater than those observed for *Platyptilia*. *Paracantha* occurred at every site, and adults and larvae of these flies were found on nearly half of all plants and half of all seedheads collected.

These patterns of variation are also apparent when the variation in number per seedhead is partitioned (Figure 2). Since *Paracantha* is present at 100% and *Platyptilia* are present at 80% of sites, most of the variation in abundance of these species is among seedheads. *Rhinocyllus* is found at few sites, and so a much greater proportion of the total variance in number per seedhead is due to variation among sites.

Among seedheads

Much of the variation among seedheads and within plants was explained by seedhead characteristics, with the exception of *Platyptilia*. Occurrence and abundance of this species was not related to seedhead characteristics or to the blocking terms for site and plant ID (Table 1, Figures 2a,b,c). For *Paracantha*, insects were significantly less likely to occur in more distal seedheads or in late-maturing seedheads (Table 1). Their abundance responded similarly, with more insects in apical or early-maturing seedheads (Figure 3e, f), although this varied significantly among sites ($P = 0.02$) and among plants ($P = 0.10$). Occurrence and abundance also increased slightly with seedhead diameter in univariate models (occurrence $\chi^2 = 2.8$ $P = 0.09$; abundance $R^2 = 0.02$, $P = 0.009$; Figure 3d), but diameter proved non-significant in models including other seedhead characteristics.

For *Rhinocyllus*, both the likelihood of occurrence and the number of individuals per seedhead increased significantly with seedhead diameter (Figure 3g). Abundance also significantly differed among sites and plants (Table 1). *Rhinocyllus* patterns were not related to seedhead position or timing (Figure 3h,i). Analysis of all species pooled essentially reflected *Paracantha* results, with occurrence and abundance declining with seedhead position and date of maturation.

Among plants

Models explaining variation among plants differed substantially among the three insect species. For *Platyptilia* and *Paracantha*, probability of occurrence increased with sample size (number of seedheads dissected), but this covariate was not significant for *Rhinocyllus*. While the probability of encountering *Platyptilia* on a plant declined as a function of plant age, the model overall was only marginally significant (Table 2). The proportion of seedheads attacked was not explained by any of the variables, though the average number of *Platyptilia* per seedhead was positively related to plant tissue nitrogen. Similarly, the *Rhinocyllus* occurrence was not significantly explained by measured plant traits. Both the proportion of seedheads attacked by weevils and the average number per seedhead were unrelated to plant traits and varied only weakly as a function of site.

In contrast, the distribution of *Paracantha* among plants was related to several plant characteristics (Table 2). Likelihood of fly occurrence declined significantly with increasing plant nitrogen, and increased marginally with the number of meristems per plant. The proportion of seedheads attacked increased with increasing plant age and varied among sites. The average number of *Paracantha* per seedhead was unrelated to plant traits but varied as a function of site identity.

Patterns revealed by analysis of all species pooled were most similar to those of *Paracantha*; occurrence, proportion of seedheads attacked, and mean insect numbers all increased with increasing plant phenology, and the two measures of abundance varied significantly among sites. In addition, the proportion of seedheads attacked was marginally related to plant tissue carbon of plant tissue; this increase in insect abundance with plant carbon was also seen for *Paracantha* and *Rhinocyllus*, and is significant in the pooled data set probably due to increased sample size.

Among sites

Of the 8 measured variables included in analyses of site-level patterns, only 4 variables made any contribution to explaining variation; the 4 consistently non-significant variables (site age, soil moisture, light availability, and *C. brevistylum* population size) were therefore omitted from Table 3. Analysis of occurrence data also included the number of seedheads dissected as a covariate; this was non-significant and so was not included in the final analyses. Occurrence of *Platyptilia* was not explained by any of the models (Table 3). Likelihood of *Rhinocyllus* occurrence was positively related to soil ammonium.

Abundance of the three seed predator species was most consistently related to soil NO_3 (Table 3). The proportion of seedheads within a site attacked by *Platyptilia* and the mean number of *Platyptilia* per seedhead increased significantly with soil NO_3 (Figure 4a). For *Paracantha*, proportion attacked and number per seedhead increased with NO_3 in sites with greater than 80% cover by background vegetation but are unrelated to NO_3 in sites with sparse vegetation (Figure 4b). Overall, *Paracantha* were more abundant in densely-vegetated sites. At sites where *Rhinocyllus* was present, weevil abundance was not significantly related to soil NO_3, but rather increased with site area; this pattern was significant for number per seedhead and marginally significant for proportion of seedheads attacked (Table 3). Finally, abundance of all species in aggregate reflected factors shaping all three species; the mean number of all insects per seed head increased with soil NO_3 (Figure 4d), and the proportion of seedheads attacked by at least one species of seed predator was positively related to both concentration of soil NO_3 and the size of the thistle patch (Table 3).

Interactions among herbivore species

There was no evidence to support the hypothesis that patterns of occurrence and abundance are shaped by interactions among insect species. Full factorial comparisons of occurrence, proportion of seedheads attacked, and number of individuals per seedhead provided no evidence of interactions between any of the three insect species at any scale of investigation. All tests were highly non-significant even in the absence of Bonferroni adjustments (for all tests, $P > 0.30$).

DISCUSSION

Overall, a high proportion of variation in occurrence and abundance was explained by the characteristics that I measured, though explanatory ability differed among levels of investigation and among the three insect species. Variation among seedheads was more readily explained than variation at the other scales, and models at this level accounted for a large proportion of the variation, were highly significant, and the significance of explanatory terms was generally unambiguous (i.e. $P << 0.05$). The fit of models declined with increasing scales of investigation, with average R^2 of 0.66 at the seedhead level, 0.46 at the plant-level, and 0.36 at the seedhead level. Declining explanatory ability with scale may be linked to the greater degrees of freedom available for testing models at lower levels and to the lower amounts of variation at higher levels;

since most of the variation is among seedheads (Figure 2), models may tend to be more significant at this level. *Rhinocyllus* appears to be the exception that proves this rule, since variation among sites is larger for this species than for the others and site-level models of *Rhinocyllus* abundance have a correspondingly higher R^2. The good fit of seedhead-level models may also be due to the fact that relevant predictor variables at this level can be measured with accuracy, and that higher-level influences, such as plant and site characteristics, are included as blocking factors.

Species patterns

The occurrence of *Platyptilia* was not well explained by factors measured in this study, since models explained a small proportion of the variation and were generally not significant ($P > 0.10$). *Platyptilia* is a facultative seed predator in this system, and individuals of this species more frequently behave as folivores, consuming leaf tissue and undeveloped meristems. In addition, folivorous *Platyptilia* are very abundant on *C. vulgare*, a related thistle co-occurring with *C. brevistylum* in these same sites (Gluesenkamp Ch1, Ch 2). Thus, *Platyptilia* that act as seed predators in *C. brevistylum* seedheads are a small proportion of the total *Platyptilia* populations at these sites. While the abundance of the two feeding strategies are correlated (number of meristems destroyed Vs. mean number *Platyptilia* per seedhead, Pearson's $r = 0.3$, $P = 0.008$), a number of factors may determine the relative abundance of the two feeding strategies, including moth population density, genetic variation among moth populations, and plant and habitat characteristics. Exploration of these factors is beyond the scope of this paper, but it is clear that there are other sources of variation making it difficult to explain distribution of *Platyptilia* based on the factors included in this study alone.

The link between folivorous and seed predating *Platyptilia* is probably also responsible for the observed decline in occurrence of *Platyptilia* seed predation with increasing plant age. Plant age is determined as the proportion of all seedheads matured past anthesis. Plants with few folivorous *Platyptilia* are likely to have more immature seedheads and a lower value for plant phenology; plants with few folivorous *Platyptilia* are also less likely to contain *Platyptilia* within their seedheads. Thus, the negative relationship with plant age likely reflects the correlation between folivorous and seed-eating *Platyptilia*.

In sites where *Platyptilia* does occur, abundance appears to be chiefly related to nitrogen levels. This study shows that seed-predating *Platyptilia* are more prevalent and more abundant on plants with high tissue nitrogen ($P = 0.07$), and are more abundant at high soil NO_3 sites (percent of seedheads $P = 0.06$; number per seedhead $P = 0.1$). While only marginally significant, these results concur with other studies in this system (Gluesenkamp Ch 2) showing that fertilizer addition increases the number and proportion of *C. brevistylum* meristems destroyed by *Platyptilia*. They also agree with a number of other studies establishing a positive relationships between nutrient status and herbivore abundance (Feller 1995, Fraser 1998, and studies cited in Gluesenkamp Ch 2).

Analyses presented in this paper generally did a sound job of explaining variation in the distribution of *Paracantha*, particularly in the case of seedhead-level models. *Paracantha* density differed significantly as a function of seedhead position, with high fly densities in primary and secondary seedheads and declining density in more distal seedheads (Figure 3e). This pattern has been found in other systems. In studies of a related thistle-herbivore system (*Cirsium canescens* and the flies *Orellia occidentalis* and *Paracantha culta*), Louda found that fly abundance declined with increasing seedhead position (Louda and Potvin 1995), and comparable results have emerged from several studies of *Rhinocyllus* on other thistle species (Boldt and Jackman 1993, Boldt and De Loach 1984, Kok and Pierkowski 1984). However, the mechanisms behind this pattern are unclear. It appears that *Paracantha* may be preferentially selecting primary and secondary seedheads. This may be because plants allocate more resources to these seedheads or because these more apical seedheads are less likely to be aborted when resources are scarce. Alternatively, the fact that reproductive adults defend their territories from perches on these more apical seedheads may mean that primary and secondary seedheads may receive more attention from females.

Plant phenology contributed significantly to variation in *Paracantha* density, via both the date of seedhead maturation and whole-plant phenology. Flies were more common and more abundant in early-maturing seedheads than in seedheads maturing later in the season, and this is probably driven by the fact that *Paracantha* is an early attacker of closed young capitula (Headrick and Goeden 1990b), with reproductive adults prevalent when the first *C. brevistylum* become reproductive, with density of adults declining over time (Gluesenkamp, per obs). Timing of oviposition presumably reflects this window of activity.

Abundance of *Paracantha* also varied among sites and among plants within sites, as indicated by significant site and plant [site] blocking terms in the seedhead-level model. Plant-level variation in number per seedhead was due to differences in plant age and reflected the importance of seedhead maturation date; older plants were more likely to have seedheads blooming early in the season (when seedheads were scarce), and these early-blooming seedheads contained more *Paracantha* than did seedheads maturing later. The likelihood of *Paracantha* attacking a plant increased with the number of meristems and decreased with plant tissue nitrogen. The increase with meristem number probably indicates herbivore preference for larger plants, as observed for other thistle herbivores (Freese 1993). Mechanisms responsible for the negative relationship between fly occurrence and tissue nitrogen are unclear; while most other studies have found a positive relationship between tissue nitrogen and herbivore utilization (Feller 1995, Fraser 1998), flies could be less frequent on high nitrogen plants because of higher levels of qualitative defensive compounds (Coley 1987), greater abundance of natural enemies (Stiling 1997), or tissue nitrogen may simply reflect plant micro-environment, with high plant nitrogen a consequence of shadier microsites which are also less preferred by these insects (Louda and Rodman 1996).

Among-site variation in *Paracantha* abundance was strongly influenced by both soil NO_3 and by vegetation cover, with a positive relationship between fly abundance and NO_3 when cover by background vegetation was greater than 80% and a negative relationship when vegetation cover was less dense (Figure 4c). The most parsimonious explanation is that this pattern is driven by seedhead availability. Other research in this system has found that the number of seedheads produced declines with soil nitrogen in densely-vegetated sites and increases with nitrogen in sparsely-vegetated sites, the opposite of the pattern observed for *Paracantha*. Since density of *Paracantha* at these study sites is very high, with an average of 40% of seedheads attacked (Figure 1), it is reasonable to expect that seedheads may be more heavily utilized when few are available.

Distribution of *Rhinocyllus* was explained very well by seedhead and site characteristics, and the proportion of variation explained was greater for the weevil than for either of the other species. Occurrence and abundance increased with seedhead diameter but did not vary with seedhead position or date of maturation. These results are contrary to most other studies of this species, which have generally found that *Rhinocyllus* are more common in more apical seedhead positions (Boldt and Jackman 1993, Boldt and DeLoach 1984, Kok and Pierkowski 1984). A number of studies have also found that occurrence and abundance of *Rhinocyllus* decrease with increasing seedhead maturation date; in several cases, timing of weevil activity is so early that weevil reproduction is completed prior to the period of maximum seedhead production, resulting in herbivore-plant asynchrony that reduces effectiveness of this biocontrol agent (Goeden and Ricker 1985, Youssef and Evans 1994).

Differences between these results and those of the present study may be partly explained by the fact that none of the other studies included measurements of seedhead diameter. Since I found that seedhead diameter is strongly correlated with seedhead position (ANOVA $P < 0.0001$) and date of maturation (Pearson's $r = -0.68$ $P < 0.00001$), *Rhinocyllus* patterns in other studies may actually be driven by the same relationship with seedhead diameter found at JDSF. In addition, timing of *C. brevistylum* reproduction is earlier than that of many other thistle species (Gluesenkamp Ch 1), and so phenological asynchrony may be less important in this system. Finally, these patterns may be influenced by evolutionary history of the herbivores and their host plants, since studies of

Rhinocyllus on it native hosts found that seedhead position and timing were important, just as I found for *Paracantha* on it's native host (*C. brevistylum*). It is possible that herbivores respond differently when occupying plants with a shared evolutionary history than they do on novel hosts, perhaps reflecting evolution of the seedhead community (Headrick and Goeden 1990b, Zwolfer 1988), evolutionary responses to natural enemies (Zwolfer and Arnold-Rinehart 1993), or subtle plant characteristics. Future studies of these herbivores should include measurements of seedhead diameter as well as position and date so that these alternative hypotheses can be evaluated.

Abundance of *Rhinocyllus* was influenced by variation among plants and among sites, as indicated by significant site and plant[site] blocking terms. Differences among plants appear due to unmeasured factors and stochasticity, since none of the measured plant characteristics were significant. In contrast, variation among sites largely explained by a positive relationship between weevil abundance and site area and an increasing likelihood of weevil occurrence in sites with high soil NH_4. While it is important that models are able to explain variation among sites, since variation among sites is greater for *Rhinocyllus* than for either of the other two insect species, it is unclear how site area and soil NH_4 influence distribution of the weevil. Weevil response to soil NH_4 may be due to plant responses to soil nitrogen, although this seems unlikely since *Rhinocyllus* occurrence is not influenced by plant tissue nitrogen or soil NO_3. Rather, the marginal significance of soil NH_4 ($P = 0.07$) could be a spurious result, or may reflect correlations between soil NH_4 and the physical environment of sites. Physical environment may also drive significance of site area, if larger sites are less shaded by surrounding forests and therefore more likely to possess the hot, dry, sunny conditions preferred by *Rhinocyllus*

(Gluesenkamp pers obs, J. Herr, pers com). This theory is weakened by the fact that abundance of *Rhinocyllus* at JDSF did not vary with light availability and soil moisture; however, evaluation of this hypothesis requires measurements of air temperature, humidity, and light availability that are more precise and more thorough than measurements conducted for this study. An alternative hypothesis for the significance of site area is that weevils may be more likely to locate large clearings, and so larger sites may have higher colonization rates. Colonization of new locations is important in this system, since *C. brevistylum* populations are short-lived, and since *Rhinocyllus* was introduced to California only in the last three decades and may still be in the process of invasion.

Interactions among species

While there are more than 100 species of thistle in 2 genera native to North America, Eurasia is the ancestral home of the subtribe Cardueae. Diversity of thistle herbivores mirrors diversity in host plants, with far more species in the palearctic than the nearctic (Zwolfer 1984). Work on European thistles has provided substantial evidence that insect seed predator communities of palearctic thistles are far more complex than North American communities, and are structured by competition among herbivore species, with species partitioning seedhead use via differences in timing of attack and different feeding strategies (Zwolfer 1988). Introduction of palearctic thistle herbivores into North America for the control of non-indigenous thistles has the potential to significantly modify these naïve herbivore communities. There is already evidence that utilization of several native *Cirsium* species by the European weevil *Rhinocyllus* has negatively affected the abundance of two native flies, *Paracantha culta* and *Orellia occidentalis* (Louda et al 1997).

At JDSF, comparisons of occurrence and abundance of the three species support the hypothesis that species are distributed randomly with respect one another. The absence of significant interactions may be due to the low abundance of two of the species, *Platyptilia* and *Rhinocyllus*, are somewhat uncommon at these sites; competition for seedheads may be greater when herbivore densities are higher and a greater proportion of seedheads are utilized. Abundance of *Platyptilia* in seedheads at JDSF is comparable to that observed at other locations (Gluesenkamp pers obs, Turner et al 1987a) and preferential utilization of meristems and foliage may prevent this species from becoming abundant and interfering with more specialized seed predators. Low prevalence of *Rhinocyllus* may be due to the lack of suitable habitat, since the weevil is more abundant in inland sites (J. Herr pers com) and may be less suited to occupying redwood rainforest sites. Low weevil abundance may also be due to the absence of non-native thistles which serve as alternate hosts and increase weevil populations (Gluesenkamp pers obs, Louda et al 1987). Finally, it may be that invasion of these sites by *Rhinocyllus* is not yet complete and that *Rhinocyllus* prevalence will increase with time.

It is likely that increased *Rhinocyllus* prevalence would impact *Paracantha* more than *Platyptilia*, since *Paracantha* already occupies a large proportion of seedheads and since *Paracantha* and *Rhinocyllus* are both early-attacking aggregative seed predators with similar feeding strategies. Increased interactions between these two species could substantially alter patterns of distribution. Since evidence from Louda et al (1987) suggests that *Rhinocyllus* may competitively displace native flies, greater abundance of *Rhinocyllus* at JDSF would likely result in *Paracantha* being excluded from larger diameter seedheads. In contrast, if *Paracantha* were the superior competitor, greater *Paracantha* prevalence in early-maturing seedheads could result in a pattern of *Rhinocyllus* occupying later-maturing seedheads. Since there are strong correlations between seedhead maturation date, seedhead diameter, and seedhead position, the weaker competitor in either scenario would be forced to occupy small, late-maturing, distal seedheads that contain fewer insects per seedhead and are available chiefly when reproduction is decreasing.

Conclusions

The seedhead, plant, and site characteristics measured in this paper allowed evaluation of five hypotheses that are commonly proposed to influence the occurrence and abundance of phytophagous insects. Results showed some evidence for a relationship between herbivores and plant and site nitrogen levels, and for a relationship with timing of resource availability. However, there was little support for the hypotheses that occurrence and abundance is controlled by resource size, architectural characteristics, or environmental factors. Rather, each species displayed a distinctive pattern of response, with variation occurring at different scales and related to different factors. These results show that knowledge of the basic life history and behavioral traits of a focal species is essential to understanding factors shaping its distribution.

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Table 1. Multivariate models for testing contribution of seedhead characteristics to variation in insect presence and number of insects per seedhead. Presence / absence was tested using nominal logistic models. Number of insects per seedhead was tested using ANCOVA. Symbols indicate significance and slope of each terms within the whole model, $P > 0.10$ for terms lacking symbols.

Response Variable	Whole Model R^2	Whole Model P	Site	Plant [Site]	Diameter	Position	Date
Platyptilia carduidactyla							
Insects present / absent from seedhead	.60	.	.	.	.	.	.
Number of insects per seedhead	.50	.	.	.	.	.	.
Paracantha gentilis							
Insects present / absent from seedhead	.70	***	.	.	.	*** ↘	*** ↘
Number of insects per seedhead	.60	***	*	§	.	** ↘	*** ↘
Rhinocyllus conicus							
Insects present / absent from seedhead	.83	*	.	.	* ↙	.	.
Number of insects per seedhead	.77	***	***	*	* ↙	.	.
All insects combined							
Insects present / absent from seedhead	.68	***	.	.	.	* ↘	*** ↘
Number of insects per seedhead	.65	***	***	§	.	* ↘	*** ↘

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ ↙ = positive slope; ↘ = negative slope

TABLE 2. Multivariate models for testing the contribution of plant characteristics to variation among plants in insect presence, mean number of insects per seedhead, and percent of seedheads attacked by insects. Presence / absence was tested using nominal logistic models. Mean number of insects per seedhead and the proportion of seedheads attacked by insects were tested using ANCOVA. Number of seedheads dissected was included as covariate in nominal models but not in ANCOVA and was significant in all cases except occurrence of *Rhinocyllus*. Symbols indicate significance and slope of each terms within the whole model, $P > 0.10$ for terms with dots.

RESPONSE VARIABLE	Whole Model R^2	P	Site	Percent carbon	Percent nitrogen	Plant height	Plant phenology	Number meristems
Platyptilia carduidactyla								
Insects present / absent from plant	0.40	§	.	.	.	.	* ↘	.
Proportion of seedheads attacked	0.29		.	.	§ ↙	.	.	.
Mean number of insects per seedhead	0.28		.	.	.	.	.	.
Paracantha gentilis								
Insects present / absent from plant	0.58	***	.	.	* ↘	.	.	§ ↙
Proportion of seedheads attacked	0.35	§	§	.	.	.	.	.
Mean number of insects per seedhead	0.36	*	§	.	.	.	* ↙	.
Rhinocyllus conicus								
Insects present / absent from plant	0.57	**	.	.	.	.	.	.
Proportion of seedheads attacked	0.52		§	.	.	.	.	.
Mean number of insects per seedhead	0.57		§	.	.	.	.	.
All insects combined								
Insects present / absent from plant	0.58	**	.	.	.	.	* ↙	.
Proportion of seedheads attacked	0.48	***	***	.	.	.	§ ↙	.
Mean number of insects per seedhead	0.58	***	***	§ ↙	.	.	** ↙	.

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, ↙ = positive slope; ↘ = negative slope

TABLE 3. Tests of the relationship between site characteristics and variation among sites in insect presence, mean number of insects per seedhead, and percent of seedheads attacked by insects. Details of all models given in text. Site age, soil moisture, light availability, and plant density were non-significant for all responses and so were omitted from this table. Whole model fit is not given for *Platyptilia* occurrence, due to lack of significant model. Symbols indicate significance and slope of each factor, $P > 0.10$ for terms with dots.

RESPONSE VARIABLE	Whole Model	Site area	Soil nitrate	Soil ammonium	Vegetation cover class
Platyptilia carduidactyla					
Insects present / absent from site	. .	.	.	.	.
Proportion of seedheads attacked	0.25 §	.	§ ↙	.	.
Mean number of insects per seedhead	0.20 §	.	§ ↙	.	.
Paracantha gentilis					
Proportion of seedheads attacked	0.32 §	.	* ×	.	* ×
Mean number of insects per seedhead	0.30	.	§ ×	.	* ×
Rhinocyllus conicus					
Insects present / absent from site	0.25 *	.	.	§ ↙	.
Proportion of seedheads attacked	0.62 §	§ ↙	.	.	.
Mean number of insects per seedhead	0.67 *	* ↙	.	.	.
All insects combined					
Proportion of seedheads attacked	0.33 *	§ ↙	§ ↙	.	.
Mean number of insects per seedhead	0.29 *	.	* ↙	.	.

§ $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ ↙ = positive slope; ↘ = negative slope; × = interaction

FIGURE LEGENDS

FIGURE 1. Percent of seedheads, plants, and sites with insects present. For *Platyptilia* and *Rhinocyllus*, seedhead and site occupancy data are the mean values for sites with the respective insects present. Bars are mean ± standard error.

FIGURE 2. Partitioning of variance in number of insects per seedhead. For each species, bars represent proportion of total variance accounted for by each level.

FIGURE 3. Relationships between seedhead characteristics and number of insects per seedhead. (a, b, c) *Platyptilia carduidactyla*, (d, e, f) *Paracantha gentilis*, (g, h, i) *Rhinocyllus conicus*, (j, k, l) all insects pooled together. Figures are significant as determined by multivariate analyses described in text. Note: Y axis for *Platyptilia* is smaller than for other species. For seedhead position figures, different letters within a panel indicate significant differences as determined by Tukey HSD. Solid lines indicate relationship is significant in multivariate model, broken lines indicate term is not significant.

FIGURE 4. Relationships between soil nitrate and mean number of insects per seedhead. In (c) solid lines and filled boxes denote sites with greater than 80% cover by vegetation, thin lines and empty boxes sites with less than 80% cover. (a) *Platyptilia carduidactyla*, (b) *Paracantha gentilis*, (c) *Rhinocyllus conicus*, (d) all insects pooled together. Note: Y axes differ among species. Relationship for *Rhinocyllus* is non-significant, all others significant as given in text.

FIGURE 1

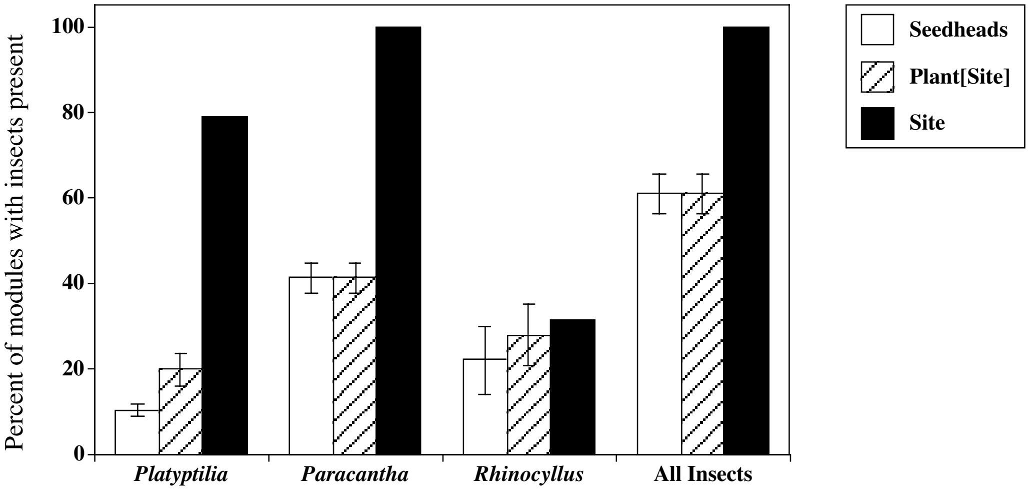

Percent of modules with insects present
0
20
40
60
80
100
Platyptilia
Paracantha
Rhinocyllus
All Insects
Seedheads
Plant[Site]
Site

FIGURE 2

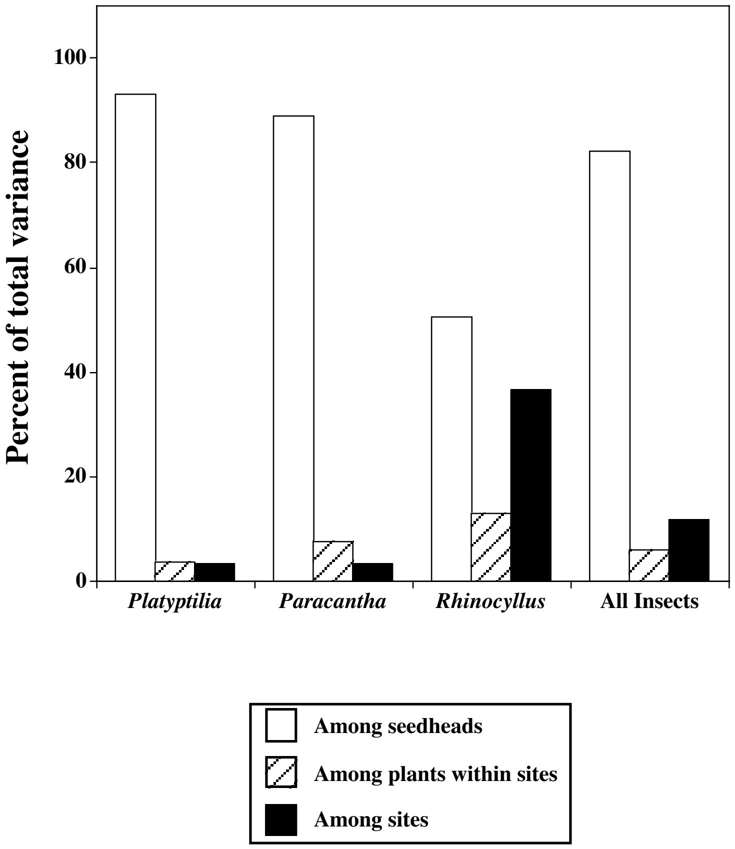

Percent of total variance
100
80
60
40
20
0
Platyptilia
Paracantha
Rhinocyllus
All Insects
Among seedheads
Among plants within sites
Among sites

FIGURE 3

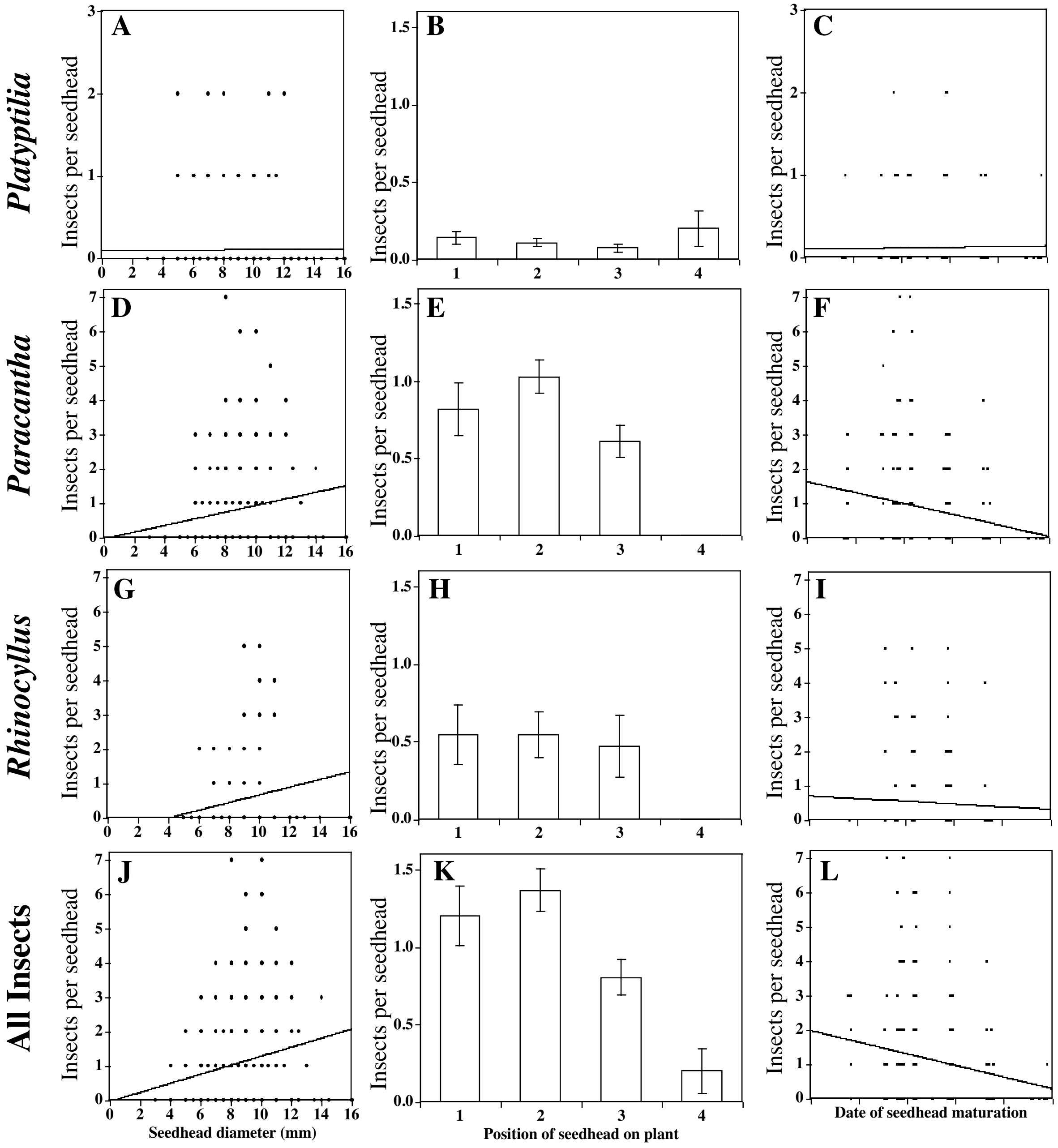
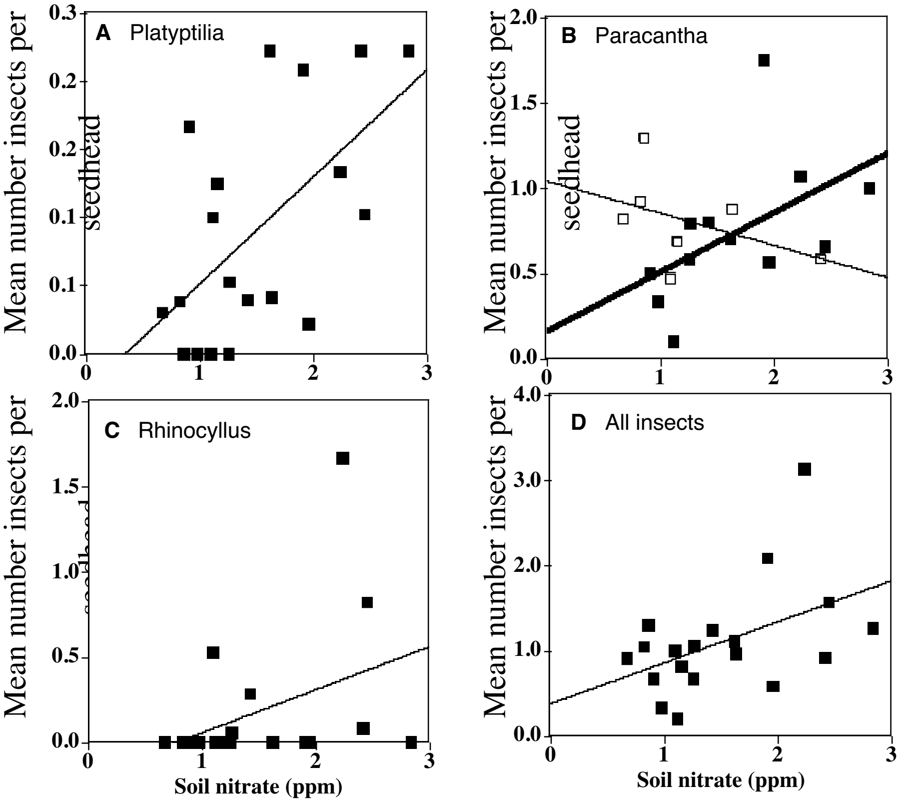

Platyptilia
Paracantha
Rhinocyllus
All Insects
A
B
C
D
E
F
G
H
I
J
K
L
Insects per seedhead
Seedhead diameter (mm)
Position of seedhead on plant
Date of seedhead maturation
0
2
4
6
8
10
12
14
16
1
2
3
4
0.0
0.5
1.0
1.5
5
6
7

FIGURE 4


A Platyptilia
B Paracantha
C Rhinocyllus
D All insects
Mean number insects per seedhead
Soil nitrate (ppm)
0.3
0.2
0.2
0.1
0.1
0.0
2.0
1.5
1.0
0.5
0.0
4.0
3.0
2.0
1.0
0.0
0
1
2
3