Impacts of Insect Herbivores on Plant Populations

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Annu. Rev. Entomol. 2017. 62:207–30

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-010715-023826

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Keywords

insect-plant interactions, defoliators, seed predators, biological control, rare plants, enemy release, climate warming

Abstract

Apparent feeding damage by insects on plants is often slight. Thus, the influences of insect herbivores on plant populations are likely minor. The role of insects on host-plant populations can be elucidated via several methods: stage-structured life tables of plant populations manipulated by herbivore exclusion and seed-addition experiments, tests of the enemy release hypothesis, studies of the effects of accidentally and intentionally introduced insect herbivores, and observations of the impacts of insect species that show outbreak population dynamics. These approaches demonstrate that some, but not all, insect herbivores influence plant population densities. At times, insect-feeding damage kills plants, but more often, it reduces plant size, growth, and seed production. Plant populations for which seed germination is site limited will not respond at the population level to reduced seed production. Insect herbivores can influence rare plant species and need to be considered in conservation programs. Alterations due to climate change in the distributions of insect herbivores indicate the possibility of new influences on host plants. Long-term studies are required to show if density-related insect behavior stabilizes plant populations or if environmental variation drives most temporal fluctuations in plant densities. Finally, insects can influence plant populations and communities through changing the diversity of nonhost species, modifying nutrient fluxes, and rejuvenating over mature forests.

INTRODUCTION

Whether or under what circumstances insect herbivores limit or regulate densities of host plants remains an open question. The classic paper of Hairston et al. (47) argued that observations of herbivores severely depleting green plants are exceptional and that plants suffer little from the vagaries of catastrophic weather. Therefore, they posited that resources, not herbivores, must limit plant populations. Furthermore, predators and parasites must control insect herbivores and reduce their impacts. This paper has been cited more than 2,800 times in the 57 years since its publication and continues to be cited at a high level. Their corresponding "world is green hypothesis" remains a hot topic in ecology.

The simplest trophic cascades among parasites and predators, and insect herbivores, as well as plants and resources is just one of the possible scenarios. For example, introduced insects, outbreaking insects, and different abiotic conditions can shift the interactions and, thus, the effects of insect herbivores on host food plants (**Figure 1**). Interactions of insect herbivores and host-plant populations are also context dependent (87).

Many characteristics of insects such as population density, type of feeding damage, and distribution among host plants and of their food plants such as size, nutrient quality, and defenses can influence plant-insect interactions. A vast literature describes plant defenses as protection against insect herbivores and the conditions under which they may vary. According to the resource availability hypothesis, slow-growing plants should make higher investments in defense (24); according to the plant apparency hypothesis, plant defenses should be related to their apparency to herbivores (40). Here we ask, if given these variable qualities of host plants, can insect herbivores determine the densities of their food plants?

In general, the amount of insect-feeding damage is low. For example, Anstett et al. (4) found less than 3% damage to leaves, although more than 40% of fruits were damaged in the herbaceous herb *Oenothera biennis*. Schlinkert et al. (133) reported damage levels of 1% for leaves, 5% for fruits, and 30% for flowers in 21 annual Brassicaceae species. In a review of insect-feeding damage for woody plants globally, Kozlov et al. (72) reported an average loss of 7.6% of leaf area to insect herbivores. The highest levels of loss were in temperate regions. For pastoral communities, Coupe & Cahill (26) found in a meta-analysis that experimental removal of insects increased plant productivity by 15–23%. Thus, although obvious damage from insect herbivores appears to be slight, it can impact plants in a meaningful way.

How can the impact of insect herbivores on host-plant populations be evaluated? We begin by considering three different ways: (*a*) detailed population studies of host plants using life-table analyses, (*b*) evaluation of herbivore attack on high-density invasive plants compared with native plants or on plants in their native and exotic ranges [the enemy release hypothesis (**Figure 1*b***)], and (*c*) studies of the impacts of insect herbivores either accidentally or intentionally introduced to non-native areas. Insect populations vary from a vast number of rare species to fewer species that are common or undergo periodic outbreaks (162). The impacts of insect herbivores on invasive plants and those at high densities are likely to differ from that of species at low densities or of rare and endangered species (2). It is important to know if insect herbivores are a threat to rare plant species, particularly in situations where restoration and conservation are the aims of management. Given the changing climate, current interactions between insects and plants as well as distributions of both plants and insects may also change (87).

Finally, we consider whether insect herbivores reduce the average densities of their host plants or regulate their host plants in a density-dependent, stabilizing manner (151). The latter requires long-term quantification of both insect and plant densities. Important considerations include whether compensation by plants overcomes the effects of insect damage and whether insects

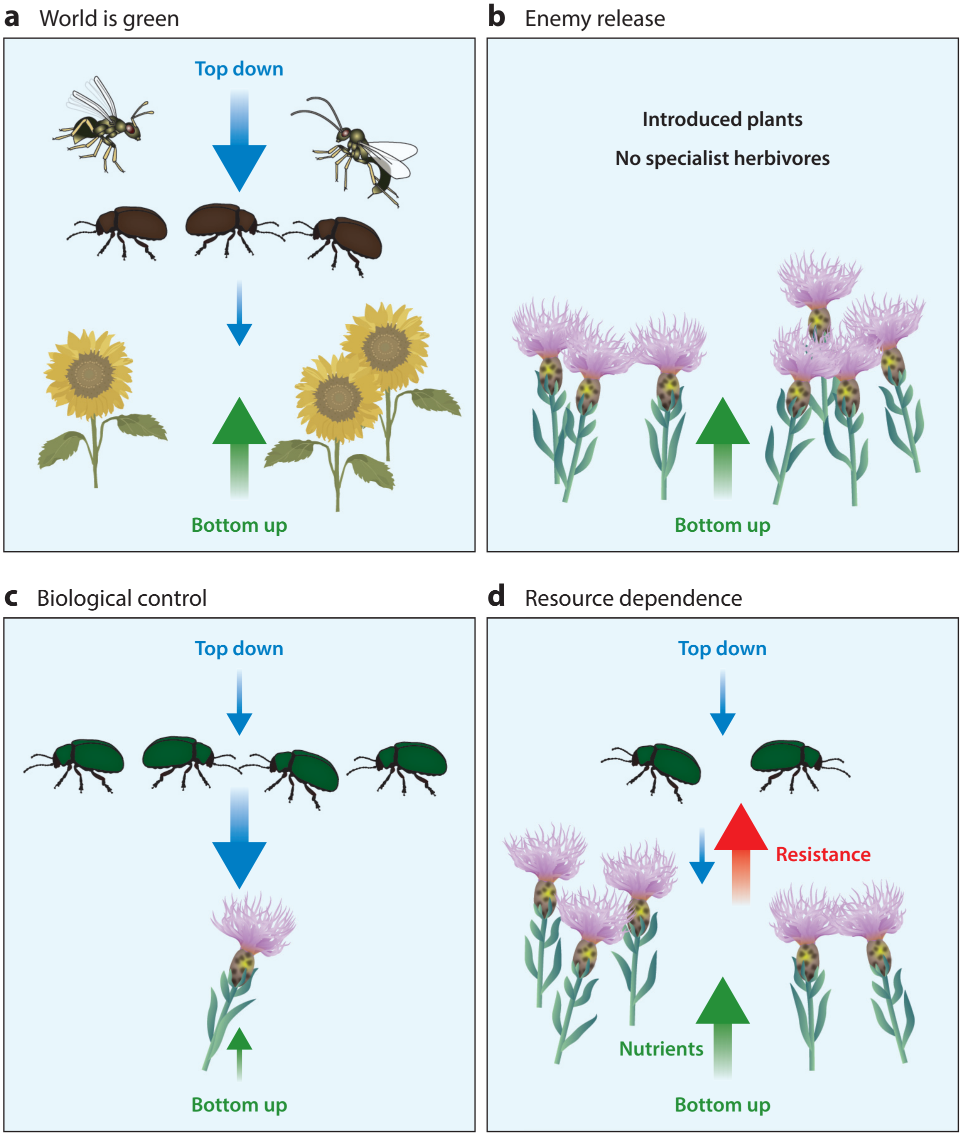

Figure 1

(*a*) The world is green hypothesis predicts that insect herbivores have little impact on the population densities of their host plants because predators and parasites keep them at low density. (*b*) According to the enemy release hypothesis, introduced plants that lack natural enemies will reach high densities. (*c*) Successful biological control results when introduced agents reach high densities and host plants cannot compensate for that feeding damage. (*d*) According to the resource dependence hypothesis, plants in high nutrient conditions resist damage by biological control agents. The width of arrows indicates the strength of the interaction.

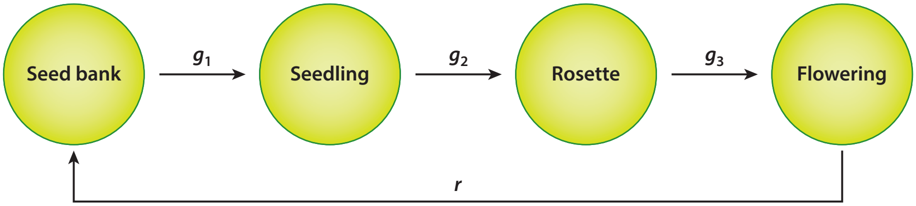

Figure 2

Life cycle for a simple stage-structured plant population. Circles indicate life stages, *g* is the probability of individuals of one stage moving to the next stage, and *r* is the contribution of flowering plants to the seed bank.

respond to host-plant density. We conclude that the impacts of insects on host plants is context dependent but can strongly influence plant populations in both limiting and regulating ways.

LIFE-TABLE ANALYSES

Population studies require long-term and detailed work accompanied by manipulation experiments to tease out the interactions between insect herbivores and host-plant population dynamics. An alternative approach is to use life-table studies detailing the transitions of plant life stages over time (see the sidebar titled Matrix Projection Models, as well as **Figure 2**). These can be used to estimate the asymptotic λ measuring the rate of population growth at a stable age structure. Matrix models that incorporate annual damage of insect herbivores on plant life stages have been widely used in the past 20 years in studies of plant demography (19, 96, 130). An important challenge in developing these life-table models is the need to incorporate density dependence of compensatory responses of plants to insect herbivore damage (48, 88, 106)

More recently, integral projection models based on the continuous functions of size, survival, and reproduction have been developed and are being increasingly used (37, 122). These studies estimate λ; however, unless plant populations are increasing (invading) or declining (going extinct), the average value of λ over time is 1. Crone et al. (28) reviewed approximately 350 plant population modeling studies and suggested that researchers' failure to include density dependence may be due to the assumption that environmental variation is a more important driver of plant dynamics than are density-related interactions. They call for more cautious interpretations of model results and highlight the need for long-term studies.

The complexity of using and interpreting models increases because various biotic (herbivores, pollinators, competitors) and abiotic (nutrients, weather, disturbance) factors that potentially

MATRIX PROJECTION MODELS

Plant population growth can be represented by $N_{t+1} = A(N_t)$, where A is a square matrix representing the annual transitions between life or size stages of plants [seeds, seedlings, juvenile plants, flowering plants (see **Figure 2**)]. The growth rate λ is the dominant eigenvalue of A (19). In addition, the sensitivity of particular transitions and the proportional sensitivity of λ to proportional changes in a matrix transition element, elasticity, can be determined to indicate which stages are most important to the population growth rate. An alternative measurement of λ is the ratio of the estimated population numbers measured in 1 year to that measured the next; $\lambda = \log_e N_{t+1}/\log_e N_t$. This also can be used to quantify the impact of insect herbivores.

influence plant population dynamics vary temporally. Thus, estimated values of λ and whether populations are at their stable age distribution, which is necessary for this type of analysis, will vary from year to year and place to place. Maron et al. (87) highlighted the importance of context in determining the interactions of plants with pollinators and predators. They proposed that researchers perform experiments over gradients of abiotic factors to evaluate and predict how interactions among plants and herbivores respond to changing conditions. Long-term studies that provide insights into population dynamics and trends are rare.

A field study by Miller et al. (98) used integral projection models based on a gradient in conditions and experiments to evaluate the impact of insect herbivores on host-plant populations. In this study, the density of the tree cholla cactus *Opuntia imbricata* increased with elevation, whereas herbivory by a suite of native insects decreased. The predicted plant population of growth rates at low and mid-elevations was higher and >1 when insects were excluded. However, λ did not differ with or without insect herbivores at the high-elevation site. A possible explanation of this finding is that the ant species that guards this cactus from insect herbivores at high elevation, *Liometopum apiculatum*, may be more effective than the species that guards plants at low elevation, *Crematogaster opuntiae*. Thus, herbivores should be more common and have a greater impact on λ of the *O. imbricata* population at lower elevations where plant densities are lower. At higher elevation sites with higher plant densities, intraspecific competition could have had a greater impact on λ than do insect herbivores. Without including density-dependent plant responses in models, the impact of insect herbivores may not be clearly expressed. Thus, the impact of insect herbivores was site dependent.

Another evaluation of the impact of insect herbivores (160) considered an invasive plant species in its native and introduced ranges. To compare the influences of insect herbivores and disturbance on population growth of hounds tongue, *Cynoglossum officianale*, Williams et al. (160) carried out small-scale experiments in native (Germany) and introduced (Montana, United States) habitats. To interpret the results of these perturbations, they collected demographic data on the plants and developed integral projection models. Insect effects were incorporated as reduced seed production following insect attack from the most common root and leaf-feeding species. The density of *C. officianale* was 3.5 times higher in the introduced range than in the native range. As might be predicted, λ was higher in the native range where plant density was lower than in the introduced range, yet in both situations, it was less than 1. The model results indicate insect herbivores have little effect, but disturbance strongly influences population growth rates.

Further analyzing these data, Maron et al. (89) used demographic modeling to project what could happen over 10 generations. Thus, they quantified the extent to which insect herbivores in the native and introduced ranges may modify the transient and asymptotic estimates of population growth as well as future population dynamics. Their analysis predicted that, despite only small differences in λ in the native range, hounds tongue populations would increase in the absence of insect herbivores. With herbivores, populations would decline slowly. Plant populations in the introduced range were projected to become extinct. However, the invasive weed in Montana has not followed this pattern, although populations have declined after the root-boring weevil *Mogulones cruciger* was introduced in British Columbia, Canada (31). Thus, insect herbivores can influence the density of hounds tongue populations.

Another study by Rose et al. (129) used an integral projection model as well as seed additions and herbivore removals for the native species tall thistle *Cirsium altissimum* in areas of high and low productivity in the Nebraska prairie. Experiments indicated that this species was seed limited and that insect herbivores reduced the plant population growth rate. Results were not influenced by the productivity of the ecosystem. No relationship between λ and plant density was apparent, which suggests that density-related compensation did not occur. Eight other studies including the one by Miller et al. (98) discussed above are listed in this study as showing population limitation by insect herbivores.

Finally, to determine why an introduced Eurasian plant, *Cirsium vulgare*, failed to become invasive in the tall grass prairie of eastern Nebraska, but was invasive in several adjacent states, Eckberg et al. (38) used seed additions, herbivore removals, and life-table analysis. At three of four sites, insecticide treatment significantly increased seedling survival and plant population growth rate λ. For all sites, attack by primarily native insect herbivores reduced λ below 1, thus indicating that natural herbivory is sufficient to prevent *C. vulgare* from becoming invasive in this prairie.

These examples using life-table analysis show that experimental removal of insects can modify λ for plant populations in some, but not all, situations. The experimental addition of seeds is a way to determine if plants are seed or site limited, which may be an important determinant of the influence insects have on plant population densities. More consideration of how insect damage interacts with plant density and the potential compensatory survival of plants following herbivore attack may help explain some of the variation in the results. Of the studies reviewed here, only Eckberg et al. (38) estimated the sampling variance in the calculation of λ (119). Given the possible variation in the estimates of transitions among plant life stages, these analyses should add estimates of variance to calculated λ.

ENEMY RELEASE HYPOTHESIS

Plants introduced to new habitats without their normal complement of insect herbivores often reach high densities and are categorized as invasive species. One possible explanation for the high population densities of invasive plant species is the enemy release hypothesis (63, 90) (**Figure 1**): Exotic plants can become invasive when they are released from their specialized insect herbivores. Comparisons of the levels of insect attack on invasive and noninvasive plants have yielded contradictory results. Hinz & Schwarzlaender (53) reviewed studies of 39 plant species in exotic and native ranges and found that in a majority of cases populations of invading species were more dense and had higher reproductive output in exotic ranges where insect attack was less frequent. They also found more specialist than generalist insect herbivores occurred in new habitats.

In 2006, Liu & Stiling (74) reviewed the evidence for the enemy release hypothesis and found few studies that had measured the actual impact of insects on plant populations. They did find that the number of insect species attacking plants was greater in native versus introduced habitats. Furthermore, in comparisons of introduced and native plant congeners, the native plants suffered greater insect attack. However, they reported only two studies that removed herbivores: Both showed improved plant growth following removal of herbivores in the native but not in the introduced range (132), and one did so only in understory conditions and not open environments (36).

Stricker & Stiling (144) compared the impacts of insects on three *Eugenia* congeners in Florida: a native species, an introduced and invasive species, and an introduced and noninvasive species. In contrast to the enemy release hypothesis, the invasive species suffered more damage from herbivores, yet it was still successful at invading. Schutzenhofer et al. (135) found a similar result in a comparison of a native and invasive plant species. The growth rate of the invasive species was considerably higher than that of the native species, but insect herbivory explained little of the difference.

A meta-analysis (21) that included 109 studies comparing the relative-damage effect sizes showed that introduced exotic plants do not always experience enemy release. Furthermore, enemy release might not always result in better plant performance. In the most recent review of studies testing the enemy release hypothesis, Heger et al. (51) reported that enemy release was supported by fewer insect herbivores and reduced damage on invasive plants in 54% of the 106 plant studies. When evaluated on the basis of impact on plant performance, less than 20% of the 48 studies supported the hypothesis. The strongest support for the hypothesis, approximately 80% of the studies, came from 26 comparisons of plants in their native and introduced habitats; insect attack was higher in native habitats. In a review of the response of native insects to introduced plants, Bezemer et al. (13) concluded that, although insect abundance on invasive plants is generally lower than on native plants in the same habitat, levels of attack are the same.

In summary, the enemy release hypothesis is supported in approximately half the situations in which it has been tested. However, most of these studies are based on the abundance and attack levels of insect herbivores and do not measure the densities of the host plant. Weak support for this hypothesis suggests the impact of insect herbivores on plant population densities might generally be low. We next consider testing the reciprocal hypothesis: Do introduced insect herbivores reduce densities of invasive plants in exotic habitats?

IMPACTS OF EXOTIC INSECTS ON HOST-PLANT POPULATIONS

Accidental Introductions of Insect Herbivores

Among the most obvious impacts of insects on host plants are those following the accidental introductions of foreign insect herbivores to new environments. Many of the most serious agricultural pests are introduced species, and invasive insects can have massive effects on populations of native trees, resulting in dramatic changes to forest communities (65). Recent examples in North America are the balsam woolly adelgid, *Adelges piceae*, and the hemlock woolly adelgid, *A. tsugae*, which kill and reduce recruitment of Fraser fir, *Abies fraseri*, as well as Eastern and Carolina hemlock, *Tsuga canadensis* and *T. caroliniana*. The emerald ash borer, *Agrilus planipennis*, a phloem-feeding beetle native to Asia, has killed millions of ash trees in the United States and Canada and changed the structure of forest communities (118). The spruce aphid, *Elatobium abietinum*, also threatens Engelmann spruce, *Picea engelmannii* (41, 84). Introduced populations of the European gypsy moth, *Lymantria dispar*, underwent severe outbreaks in northeastern North America during the 1980s and 1990s that killed trees in some areas and altered species composition of forests in defoliated sites (39). The cyclic dynamics of this species, however, meant that damage to trees occurred only during outbreak phases, and densities of gypsy moth have generally declined in northeastern United States in the past 20 years (107, 108). Thus, this species has not continued to have severe impacts on its host trees, various species of oaks.

Other examples of exotic insects killing trees in other areas of the world include the scale insect *Orthezia insignis* Browne that seriously damaged and killed the endemic gumwood *Commidendrum robustum* on St. Helena Island prior to successful biological control of the insect (43). Another scale, *Iceria purchasi* Maskell, severely affected populations of endangered plants in the Galapagos Islands (126). These examples all involve serious impacts of exotic insects on tree species and clearly show that insect herbivores, particularly sucking insects, released from their natural enemies are capable of killing trees, reducing host densities, and modifying the natural biodiversity of the forests.

Biological Control of Weeds with Introduced Insects

Although a lack of insect herbivores alone does not always explain plant invasions, the impacts of specialist insects in biological control programs provide alternative evidence of their role in determining host-plant population densities. Estimates of successful biological control of weed programs vary: 83% (42) and 24% (145) in New Zealand, 80% in Mauritius, 51% in Australia, and 50% in Hawaii (29). Complete and dramatic success that requires no other control occurred in approximately one-third of biological control programs reviewed by McFadyen (94). In South Africa, 36% of 44 target weeds have been substantially controlled, whereas 11% showed no control (101).

Clewley et al. (23) reviewed 61 studies of biological control programs that involved 28 target weeds and 49 biological control agents. On average, biological control agents significantly reduced plant size (28%), plant mass (37%), flower and seed production (35% and 42%, respectively), and, importantly, the target-plant density (56%). However, density was measured in only a few of the studies. These estimates might be biased, as cases in which no effect was observed are less likely to be published.

Another survey of 80 weed species involving 232 biological agents (mostly insect herbivores) showed an average proportional reduction in weed density of 0.44 (117). The greatest reduction was for aquatic weeds, asexual plants, and plants that were not major weeds in their native ranges. Interestingly, if a plant is suppressed by insect herbivores at home, it is more likely to respond to natural enemies abroad. This suggests that some plant species are more susceptible to herbivore attack than are others or that some types of insects are more effective than are others.

These summarized results show that introducing insect herbivores to areas invaded by their host plants can reduce host-plant densities; insect herbivores can have measurable impacts particularly when released from their own natural enemies. An example in **Figure 3** shows population dynamics of the diffuse knapweed, *Centaurea diffusa*, before and after the establishment of a biological control agent, *Larinus minutus.* Plant densities and population growth rates vary greatly both before and after successful control.

Cage experiments are necessary to test the impact of biological control agents, and these were used (109) to determine the impact of the flower weevil on diffuse knapweed, both alone and in conjunction with the root-feeding beetle *Sphenoptera jugoslavica*. *Larinus minutus* weevils feed on leaves and stems as adults, larvae develop in seed heads, and feeding damage can kill plants. The root-feeding beetle reduces the development and size of plants and seed production (120). Treatments included caged and uncaged plants as well as cages with both beetle species together and alone. In cages with and without *S. jugoslavica*, the flower weevils *L. minutus* caused higher levels of damage to plants, and plant densities were lower the next year.

In another successful biological control program, the tansy ragwort (*Senecio jacobaea*) system in Oregon, McEvoy et al. (93) manipulated the presence and absence of two control agents, the cinnabar moth, *Tyria jacobaeae*, and the tansy ragwort flea beetle, *Longitarsus jacobaeae*, as well as plant competition (control, clipped, and other vegetation removed). The cinnabar moth had little impact on tansy ragwort abundance, but the flea beetles, in association with plant competition, caused ragwort to disappear. As adults, the flea beetles feed on leaves. As larvae, they tunnel into petioles, stems, and roots of young plants; they can also kill the plants and thus reduce plant densities.

Whereas experiments are important for evaluating biological control programs, models can be used to tease apart the environmental and biotic influences of control programs. Maines et al. (85) developed a matrix model with 6 years of field data to evaluate spotted knapweed densities under four scenarios: (*a*) conspecific plant density dependence, (*b*) the effects of biological controls, (*c*) the influence of precipitation, and (*d*) combined biological control–precipitation interactions. Model results predicted that $\lambda < 1$ would occur only when biological control agents were present.

The use of insect specialist herbivores continues to play a role in reducing the impact and invasiveness of exotic plant species (136, 154). Similar to tests of the enemy release hypothesis, the success of biological control is variable (24–80% success in different areas), though what makes the difference is not clear. Testing the impact of insect herbivores in the native habitat before

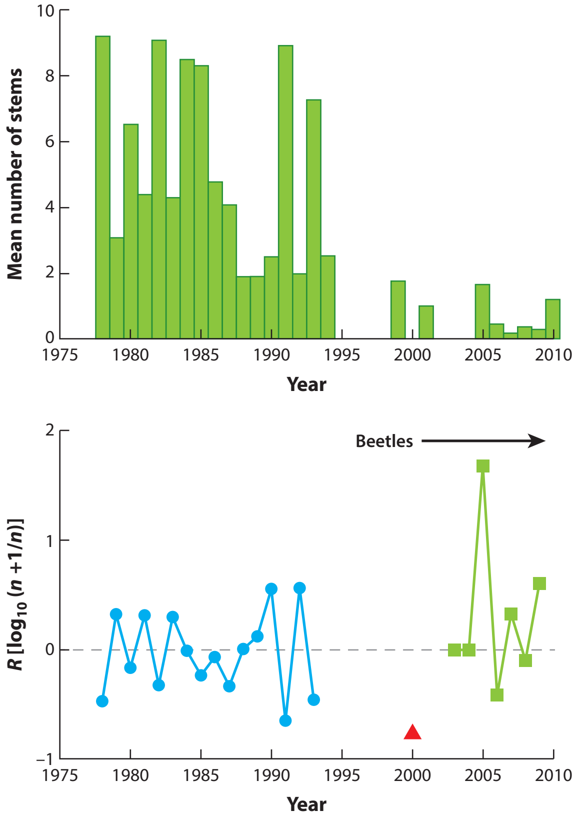

Figure 3

Density and population growth rates of diffuse knapweed at White Lake, British Columbia. Rates are shown before (*blue circles*) and after (*green squares*) biological control. Red triangle indicates the growth rate mid-decline. Figure based on Reference 109 and continued monitoring.

introducing them (160) might help predict which insect herbivores are most effective at reducing host-plant density.

How Many and What Kind of Species Are Required for Biological Control?

Biological control of weeds programs can be used to consider how many types of insect herbivores may be necessary to influence significantly host-plant densities as well as what types of insects are most successful. For biological control of weeds, Denoth et al. (33) showed that a single species of insect herbivore was usually sufficient to reduce host-plant density. Later, Myers (105) added 10 more examples of successful control with a single agent. These findings and the variable success of biological control programs suggest that only some types of insect herbivores reduce the densities of host-plant populations.

Many invasive plants produce large numbers of seeds and have multiple seed herbivores in their native habitats. For example, in some areas of its native range, the spotted knapweed, *Centaurea maculosa*, has 10 species of seed-feeding insects (102). Seed-head herbivores are relatively easy to find and collect when potential biological control agents are sought; thus, they are often introduced. In addition to the insects attacking flowers and seeds directly, other types of insect herbivores such as defoliators and root-feeding insects often affect plants by reducing seed production—for example, the cinnabar moth on tansy ragwort and the root weevil on diffuse knapweed mentioned above.

Whether a reduction in seeds associated with insect herbivory will influence host-plant density depends on three factors: the number of seeds, number of safe sites for seedling recruitment, and self-thinning that follows seedling establishment (150). Crawley (27) suggested that safe microsite limitation is more common than seed limitation; thus, seed predators should have little influence on many host-plant populations. Turnbull et al. (152) reviewed 27 seed-addition studies and found that approximately half the 90 plant species investigated were seed limited and thus should respond to seed predation. However, Clark et al. (22) cautioned that researchers performing seed-addition experiments must consider whether plants actually become established as reproducing adults.

Diffuse knapweed, *C. diffusa*, is a good example of a plant that is apparently not seed limited. For this invasive rangeland weed in western North America, high levels of seed predation failed to reduce its populations. Myers & Risley (110) created a population model to explore this phenomenon. It incorporated a function for density-related seedling mortality based on field observations and showed that *C. diffusa* populations were resistant to reduced seed availability. Garren & Strauss (44) used manipulative experiments to investigate the impact of seed predators on another weed, the yellow star thistle, *Centaurea solstitialis*. Self-thinning resulted in similar numbers of seedlings in plots with and without three introduced species of seed predators. Plots with low densities of yellow star thistle had high reproductive values and compensated for the loss of seeds.

The impact of seed predators can be site dependent, as Shea et al. (137) showed for the introduced weed *Carduus nutans*, nodding or musk thistle. In North America, the seed-head weevil *Rhinocyllus conicus* has been associated with the decline of thistle populations, but this has not been the case in New Zealand. In Australia, declines in nodding thistle have been associated with the root-crown weevil *Trichosirocalus horridus*. The root-crown weevil has also been used as a control agent in North America (70). Shea et al. (137) have developed life-history models to determine the importance of plant growth, survival and reproduction, seed dynamics, and germination rates to population growth in nodding thistle in Australia and New Zealand. These models show that even for introduced insects, λ for thistle populations is above 1 in New Zealand. By contrast, in Australia, λ is <1 if the seed reduction associated with *R. conicus* is included. The growth rate falls to 0.5 in the presence of the root-crown weevil. Using simulation models, Jongejans et al. (62) showed that florivores reduced the growth rate of *C. nutans* in its native range in France by 166%. In fact, growth rates were less than 1 in each of the three native populations studied; thus, it is surprising that these populations persist, unless there was an error in calculating the growth rates.

In a review of 10 studies, Kolb et al. (71) evaluated the effects of predispersal seed predation by using estimated changes in density-independent λ or changes in recruitment and subsequent adult density. In all cases, seed predators reduced recruitment and population growth, but the magnitude of the reductions varied among populations and over time. If the environment influences seed predators and plants in opposite ways, then the impact of predation can be ameliorated (157). Some seed predators can influence the population density of their host plants, but the effects are context dependent.

In contrast to those introduced herbivores whose feeding damage only reduces seed production, some species kill their host plants at high densities. This is demonstrated by the biological control of purple loosestrife, *Lythrum salicaria*, a European plant introduced into North America. Two species of small, folivore beetles, *Galerucella calmariensis* and *Galerucella pusilla*, have been widely introduced as biological control agents and have reduced weed densities in some but not all areas (14, 34, 45). Severe defoliation by these beetles can kill plants or reduce their size. To explain variation in the levels of *Galerucella* attack, Hovick & Carson (55) proposed the fertility-dependent hypothesis (also known as the resource dependence hypothesis), which states that invasive weeds can be controlled by top-down effects only if bottom-up effects are weak (**Figure 1*d***) and plants lack resistance to insect attack. This hypothesis predicts that insects are more likely to control target weeds in low-nutrient areas. The authors tested this hypothesis with observations on purple loosestrife at 46 sites in New York, Ohio, and Pennsylvania. At low-nutrient sites, the number of beetles per stem increased and stem density decreased with the time since beetle introduction. The trends were the opposite for high-nutrient sites. However, Hovick & Carson (55) noted that if plant quality is too low in nutrient-poor sites, beetles may not have sufficiently high reproductive rates, which could prevent successful control.

As discussed above, insects that defoliate seedlings and rosette plants can further reduce seed production if defoliation reduces plant size (106). The impact of defoliation is determined by the responses of plants and whether they can compensate for the damage through improved survival or refoliation. Plant density can be reduced by defoliating insects that kill plants after the growth stages during which compensation through improved survival of remaining plants occurs.

Nontarget Impacts of Introduced Biological Control Agents on Native Plants

Suckling & Sforza (146) reviewed the impacts of biological control agents on nontarget plant species and found their occurrences were very rare, $<-1\%$. Most examples are associated with two insect species introduced to control nodding thistle that have moved on to rare, native thistles. *Larinus planus*, a seed-eating weevil introduced and distributed in the United States and Canada to control noxious thistle species, has been detected on Pitcher's thistle, *Cirsium pitcheri*. Pitcher's thistle is federally designated as threatened in the United States and endangered in Canada. Using demographic data collected over 16 (Michigan) and 23 (Indiana) years for two natural, uninvaded populations of Pitcher's thistle, Havens et al. (49) reported that weevil seed predation reduced the reproductive rate of the thistle populations by 10–12%. This decrease reduced the projected time to extinction from 24 years to 13 years in the Michigan population and from 8 years to 5 years in the Indiana population. The impact of the exotic weevil is particularly concerning because Pitcher's thistle hovers near extinction throughout its range.

As described above, *R. conicus*, a flower-head weevil, was introduced into North America to control exotic thistles, especially musk or nodding thistle, *C. nutans*. It has become naturalized on the native Ownbey's thistle, *Cirsium ownbeyi*, a rare species found in parts of Colorado, Utah, and Wyoming. DePrenger-Levin et al. (35) reported that over 8 years the level of weevil damage to flower heads and developing seeds was consistent and independent of plant density. Despite weevil damage, the plant population remained stable over the course of the study ($\lambda = 1.03$), although there were large levels of inter-year variation. This suggests that Ownbey's thistle might still be prone to local extinction owing to weevil attacks.

To date, *R. conicus* has not been reported in the natural habitat of Pitcher's thistle. However, Louda and colleagues (78, 80, 81, 128) suggest, on the basis of extensive host-specificity tests and retrospective analyses, that Pitcher's thistle is well within the physiological host range of *R. conicus*. Thus, the weevil likely represents a significant threat to this rare thistle. Under the conservative assumption that oviposition by *R. conicus* on *C. pitcheri* occurs at the same rate as on the related *Cirsium canescens*, a simple demographic model suggests that the λ of *C. pitcheri* will decrease from 0.99 to 0.87 and the time to halve the population will decrease from 66 to 5 years. These studies point to the potential negative effects of *R. conicus* on the persistence of a rare native plant (80, 81). Long-term monitoring will be necessary to test the predictions of these models.

In the early 1920s, a successful biological control program introduced the *Cactoblastis cactorum* moth from South America to the *Opuntia* cactus in Australia. The moth was later introduced to the Caribbean. From there, it accidentally spread to North America and is now established in Florida, from where it has spread to North Carolina as well as west toward areas of rich cactus diversity in southwestern United States, Mexico, and Central America (52). One of the reasons *C. cactorum* was a successful agent is that it can kill attacked plants. In addition it has a broad host range among *Opuntia* cacti, and it has begun attacking some rare *Opuntia* species in Florida (79). A recent study found a relatively high attack by *C. cactorum* on two of the more common cactus species in Florida, *Opuntia stricta* and *O. humifusa*. Survival and growth of attacked plants were, however, relatively high (60). The authors thus challenged the assumption that *C. cactorum* will always have severe negative effects on populations of *Opuntia* spp.

Although introduced insects potentially threaten some nontarget, rare plant species, they have not been shown to cause plant extinction. In some cases, the introduced exotic insect will become common only when the targeted host plant is still common and spill over to the rare species can occur. This occurred with rangeland weed, hounds tongue, *Cynoglossum officinale*; a European root-feeding beetle, *Mogulones crucifer*; and a low-density nontarget host, *Hackelia micrantha* (20). The initial beetle outbreak on hounds tongue was accompanied by attack of *H. micrantha* for several years. Populations of *M. crucifer* declined following the decline of the host plant, and the nontarget attack ceased.

Although introduced biological control agents sometimes attack nontarget species that may be rare, this attack is not always detrimental to the densities of the rare species. More long-term studies will help to evaluate these situations. Unlike the examples above of accidentally introduced species that have had dramatic impacts on forest trees, species introduced for biological control have had less impact on nontarget species, perhaps because they are more specialized on the target weeds.

IMPACT OF HERBIVORES ON POPULATIONS OF RARE PLANT SPECIES

If insect herbivores have sufficient population-level effects on host plants, they can be of critical importance to the conservation of rare, endangered, or threatened plants. Systematic assessment of the effects of herbivory on rare plant populations could advance successful conservation efforts for at-risk species. For example, an assessment could suggest the best timing for an intervention to mitigate insect herbivory.

Herbivory can pose a particular threat to rare plants that have narrow geographic ranges, restricted habitat preferences, small population sizes, or low genetic diversity (12, 66). Using 37 studies, Ancheta & Heard (2) assessed the effects of 63 insect herbivore species on 35 rare plant populations. Only 3 of the studies directly quantified the effects of insect herbivory on plant population size or growth rate; instead, the vast majority extrapolated from vital rates to population size. The effects of insect herbivory on rare and endangered plants may vary among populations; along environmental gradients; or among habitats, including habitats with different disturbance histories (67, 86, 88). Furthermore, herbivores may exacerbate the impacts of biotic and/or abiotic stresses on rare plants (2). For example, Schöps (134) found that the flightless weevil *Hadramphus spinipennis* could drive its host plant, *Aciphylla dieffenbachia*, extinct locally. Persistence depended on populations being fragmented. Seed predators may have a greater effect on species with metapopulation structures that depend on seed dispersal.

Because studies of rare plants are scarce, researchers have extrapolated knowledge about the impacts of herbivory on common plants onto them. However, the trajectories of common and rare host-plant populations are not necessarily parallel. Rare plants, especially those that are persistently rare in evolutionary time, may not experience the same degree or kind of herbivory as do their common relatives, and they may not respond in the same way (2). For instance, the costs of searching for a rare host are likely to prevent insect herbivores from specializing on rare host plants (cost-benefit scenario) depending on, for example, patch size and fragmentation distance (121). Specialist herbivores are less likely than generalists to be present in small host populations because of their higher probability of extinction and lower rate of colonization (32, 99).

In 1976, Feeny (40) proposed the optimal defense theory that rare or less apparent plants should allocate resources to qualitative rather than quantitative defenses. This should favor attack by specialists rather than generalists (but see 100 for evidence against defense syndromes and trade-offs). Studying seed predation by a specialist and a generalist insect, Boieiro et al. (15) found that predispersal seed loss from both seed predators was higher and varied more from year to year on the rare species of *Euphorbia*: When seed production was low compared with the previous year, seed predation was higher. Specialist herbivores do exist on rare plants (66, 134), and when they have population-level effects on their hosts, they pose a challenge to balancing the conservation of the host plant and herbivore.

Rarity is complicated. Native insect herbivores that specialize on rare plants are often also rare and have a high probability of local extinction. An excellent example of one such system is the endangered grassland plant *Gentiana cruciata* and its specialist herbivore, the endangered butterfly *Maculinea rebeli*. Kéry et al. (66) studied the relationships between *G. cruciata* and *M. rebeli* in 29 plant populations, which ranged in size from 1 to 337 genets. They found 18 populations supported *M. rebeli*. Insects were more common on larger plants and in larger plant populations. Large plants produced more seeds than small ones, but the difference was less pronounced when insect herbivores were present. Genets of plants in large populations suffered more from fruit herbivory, which reduced the number of developed seeds per fruit by more than 50%. The effect on plant density, however, was not clear.

Plant species might be rare because they suffer more insect attacks than do common congeners. Combs et al. (25) tested this hypothesis by using a rare species of *Astragalus* and two common, widespread congeners. Seed production was lower and seed predation higher on the rare species, and one seed predator attacked seeds of only the rare plant species. Martin & Meinke (91) studied two populations of another rare *Astragalus* species, *Astragalus peckii*, in Oregon to determine the impact of the microlepidopteran herbivore *Sparganothis tunicana* on vital rates and population growth. Matrix models showed that growth rates of the two populations were close to or slightly above 1, and the matrixes varied little with or without the inclusion of herbivory; surprisingly, λ was higher in the population with greater herbivory. Combs et al. (25) reviewed studies of seed predators in rare species and concluded that the results were too variable to generalize about impacts. Similarly, in the literature reviewed by Martin & Meinke (91), no strong pattern exists with regard to insect herbivores reducing populations of rare plant species.

An experimental approach to evaluating the impacts of insect herbivores on rare plants is to exclude them. Bevill et al. (12) used this approach to evaluate the impact of insect herbivores on the endangered Pitcher's thistle, *C. pitcheri*. Protecting juvenile plants from herbivores increased seed production tenfold and improved survival by 50%. Baron & Bros (8) used an insect-exclusion experiment to assess the effects of microlepidopteran larvae (an undescribed species of *Aroga*) on the endangered robust spineflower *Chorizanthe robusta* var. *robusta*. Excluding *Aroga* larvae increased seed production by 30% but failed to change plant survival or seed/flower ratios. Again, population-level impacts were not evaluated over time.

We conclude that the conservation of rare species requires specific study and that no generalizations about the role of insect herbivores can be made. The numbers and impacts of generalist and specialist herbivores will likely vary with plant density. The factors that cause plant species to be rare will need to be taken into consideration in conservation programs, and unless for some reason insect herbivores become more common, it is unlikely that they will be a measured threat.

INFLUENCE OF CLIMATE CHANGE ON INSECT-PLANT INTERACTIONS

Climate models project that by 2100 Earth will warm by approximately 3–6°C, with relatively small changes in precipitation levels (95). Climatic change will be most notable at high latitudes and in continental interiors. These changes will affect plant populations directly and also indirectly, by affecting their herbivore consumers. Two particularly important relationships that climate change will influence are (*a*) the phenological events of plants (budburst, fruiting, and flowering) and insects (egg hatch, diapause break, and larval development) and (*b*) range distributions of plants and insects.

Phenological Effects

Considerable research has focused on whether altered phenology may decouple the dynamics of interacting consumer and resource species (155, 158). Consensus is emerging that phenological responses will differ in plants, insects, and vertebrates (115, 156). Particularly interesting is the association between the emergence of spring-active insect defoliators and the budburst of their host plants (16, 114, 139). Synchrony between these two events enables insects to feed on newly flushed young leaves that are generally nutritionally superior to older foliage. Shifts in synchrony can affect insect outbreaks (153) and, thus, populations of host plants and associated species.

Two studies recently used experimental warming to investigate this situation. When researchers warmed the western tent caterpillar, *Malacosoma californicum pluviale*, and its host, the red alder, *Alnus rubra*, significant shifts in synchrony occurred, but these shifts did not translate into differences in insect fitness (68, 131). By contrast, warming of aspens (*Populus tremuloides*), birches (*Betula papyrifera*), and forest tent caterpillars (*Malacosoma disstria*) caused closer synchrony between egg hatching and budburst, and faster larval growth resulted. Yet warming did not influence pupal size (58). Mismatch of egg and leaf phenology may not be as detrimental as originally thought if insects have adapted to variable conditions over evolutionary time (1, 139).

Climate change could alter patterns of spatial/temporal synchrony between insect seed predators and mast-seeding plant species that use temperature as a cue. Mast seeding occurs when perennial plants produce no seeds for multiple years and then flower in synchrony with local conspecifics, thus overwhelming seed predators (64). Mast seeding is typical of many trees and shrubs in temperate and tropical ecosystems (111). Seed predators can exert strong selection pressure against unsynchronized flowering (5). Global warming could cause more regular seeding, allowing specialized seed predators to build up large populations (73, 92), which in turn could affect tree populations and recruitment.

Range Expansion

Climate change has been linked to range expansions and retractions for many native insect herbivores (149, 161) and could influence plant populations in insects' new habitats. In Britain, warmer conditions have allowed the brown argus butterfly, *Aricia agestis*, to expand its geographical range northward by 79 km in just 20 years. As a result, the butterfly is feeding on the more widespread plant species *Geranium molle* instead of its historic host, *Helianthemum nummularium* (116). Differential herbivory along such gradients could cause the replacement of some plant species and thus alter plant populations.

The mountain pine beetle, *Dendroctonus ponderosae*, native to western North America, has had devastating and widespread impacts on its hosts (17, 76). The latitudinal and elevational range of mountain pine beetles in western Canada is not restricted by the availability of suitable host trees. Indeed, lodgepole pine (*Pinus contorta*) extends east into much of Alberta and north into the Yukon and Northwest Territories, whereas Jack pine (*Pinus banksiana*) extends even farther east. The potential for mountain pine beetles to expand east and north may be limited only by climate (159). Under global warming, formerly hostile habitats could become hospitable for the mountain pine beetle, resulting in its range expansion (75).

Climate change can also favor the spread and establishment of insect herbivores both directly and indirectly. For example, a warming climate can provide new areas suitable for invasive herbivores (82), enable insects to shift their geographic range (54, 115, 116), and allow insects to cross barriers that previously limited their natural range (124). Of particular interest is the potential spread of the pine processionary moth, *Thaumetopoea pityocampa*, in Europe; with climate warming, the moth has reduced growth, reproduction, and survival in two relict populations of Scots pine, *Pinus sylvestris*, in Spain (54, 127).

Cyclic populations of forest Lepidoptera often defoliate large expanses of their host trees, but the trees are usually able to refoliate later in the summer. In subsequent years, as the insect population declines, forests recover, perhaps even benefiting from nutrients released in frass by the defoliating insects (107). Population outbreaks of the autumnal moth, *Epirrita autumnata*, and winter moth, *Operopthera brumata*, in Fennoscandia demonstrate such outbreak dynamics (147), but their outbreak densities and feeding can kill the host trees (148). Outbreaks of *E. autumnata* alone have been observed to kill up to 90% of the branches of the mountain birch *Betula pubescens* in northern Sweden, and trees had not fully recovered after 30 years. Recently, the northern range extension of winter moth has increased the overlap with populations of autumnal moth such that outbreak densities and defoliation can last 5 to 6 years. In the most defoliated areas in northern Fennoscandia, up to 95% of mountain birch trees died following the prolonged outbreak from 2002 to 2006 (59). In this situation, the range shift of winter moth increased the length of defoliation as well as the mortality of the host trees, and the effects also cascaded down to modify the densities of the understory plants.

Terrestrial native and non-native insects respond in similar ways to climate change (140). Warmer temperatures accelerate insect growth and reproduction (103, 131) and improve winter survival (7; but for evidence of disruption of developmental cycles, see 6). They also allow greater numbers of generations over a summer and, thus, higher population densities (61, 75, 76, 83). In addition, increased CO_2 levels can modify a plant's defensive chemistry (112), and modified wind speeds can affect top-down control of insect herbivores (9). Consequently, these factors could lead to higher rates of the spread and establishment of non-native herbivores as well as a higher probability of outbreaks of both native and exotic species, with consequences for plant populations (30). A 1°C increase in average annual surface temperature in mainland China from 1900 to 2005 was associated with an increase in the establishment rate of invasive alien insects of approximately 0.5 species per year (56). Information on the fundamental biology and ecology of invasive herbivores and their host plants is needed before meaningful risk assessments can be performed in the context of our changing climate.

INSECT RESPONSES TO HOST-PLANT DENSITY

Insect herbivores can influence the densities of their host plants, but do they respond to host plants in a density-dependent manner? Even if insect density varies with plant density, it is hard to determine whether the insect is driving plant density or whether plant density is driving insect dynamics (104). Two hypotheses have been proposed for how insects might be distributed among food plants. The resource concentration hypothesis (125) predicts that insect herbivores preferentially choose large patches of their host species for feeding and reproduction. Evidence for this hypothesis varies among studies (46). One study that supported this hypothesis involved the native chrysomelid beetle *Trirhabda virgata* feeding on the meadow goldenrod *Solidago altissima* in an old-field setting. The specialist herbivore concentrated on high-density patches of goldenrod and reduced their biomass. This increased species diversity in the area (77).

Carson et al. (18) formed a general rule predicting that native specialist insect herbivores will respond to host-plant density and reach outbreak densities at which point they have a top-down effect through the increased mortality of the host plants. They listed a number of examples of insect outbreaks that defoliate and potentially kill host plants. Plant density is likely to recover eventually, but depending on the species and the extent of mortality, this could be slow. An example of this situation is the mountain pine beetle mentioned above that kills trees over vast areas. Even here, however, it is a fungus transmitted by the beetles that actually kills the trees. A meta-analysis by Jactel & Brockerhoff (57) found that specialist insect herbivores were almost always less common in mixed forests, whereas forest species diversity had less impact on the response of generalist insects.

The resource dilution hypothesis (113) predicts the opposite of the resource concentration hypothesis: greater herbivore load in areas of low host-plant density. A recent example of resource dilution is the introduced emerald ash borer that attacks ash trees in northern Midwest United States and across the border in Canada. Tree mortality is faster in low-density stands (69). What determines whether insect species demonstrate resource concentration or resource dilution patterns is not known but could be associated with the mechanisms they use to identify hosts (e.g., visual, olfactory, touch) (3).

In a review of the impact of insect herbivores on rare plant species, Ancheta & Heard (2) found four studies showing resource concentration patterns of density-dependent responses of insect herbivores, but these lacked long-term dynamics to demonstrate the temporal impact of the insects. They also claimed that successful biological control programs in which densities of invasive species are reduced imply density-dependent regulation. As shown in **Figure 3**, however, variation in plant population growth can continue to be high after control and likely reflects a strong environmental signal determining the population dynamics even when the biological control agent is present.

The potential impacts of resource concentration and resource dilution on plant populations were recently explored with a model that varied the numbers of plants per patch and the distribution of insect attack in three ways: resource concentration, a linear increase with plant density, and resource dilution (143). In the model, plant populations declined more rapidly with either weak resource dilution or directly proportional insect distribution patterns. Resource concentration slowed the decline in plant population density as the variance in insect load increased, leaving refuges of unattacked plants. These results were compared with the distributions and impacts of two insect species introduced as biological control agents on diffuse knapweed. For a successful agent, *L. minutus*, density was proportional to plant density. An unsuccessful agent, *U. affinis*, showed a resource concentration pattern. If insect attack is largely restricted to high-density patches, host plants in low-density patches will continue to grow and populations will persist.

The variable behavior of insect herbivores in terms of oviposition and travel patterns can influence their potential to stabilize plant populations (50). Regulation depends on a positive insect response to plant densities and a negative plant response to insect damage. To demonstrate this requires long-term studies that measure the densities of insects and plants as well as the impacts of insect herbivores over time. There are few studies of this nature.

POSITIVE INFLUENCES OF INSECT HERBIVORY ON PLANTS

Insect feeding damage is usually considered to be a negative influence on individual plants and plant populations. However, in some situations insect attack can be a positive influence on hosts over time. For example defoliation by eastern spruce budworm, *Choristoneura fumiferana*, can kill the preferred host balsam fir, *Abies balsamea*, while white spruce *Picea glauca*, is more tolerant of attack. In regeneration after an outbreak of spruce budworm, preferential recruitment of balsam fir results in this species becoming dominant yet again. Thus outbreaks of spruce budworm rejuvenate forests in which balsam fir becomes overmature and in the long run benefits populations of its host tree (10). Pine bark beetle, *Dendroctonus ponderosae*, also has a role in rejuvenating forests by killing the overmature pine trees which promotes fire and recruitment of young pines (138).

As mentioned above specialist insects can increase the diversity of nonhost plants in a community by reducing the dominance of their host species (77). Generalist insects such as grasshoppers can also benefit plant communities through increasing nutrient cycling, nitrogen levels and plant abundance (11). Richie et al. (123) propose two conflicting hypotheses on how insect herbivores could influence nutrient cycling and plant abundance: They could increase or decrease it. Their herbivore experiments that combined both small mammal and insect exclusion supported the hypothesis that small herbivores decelerate nitrogen cycling by removing plant tissue that is high in nitrogen. More recently Metcalf et al. (97) found that insect herbivores make large contributions to nutrient cycling in both productive and unproductive systems as observed in 30 boreal forest stands with different histories since fire disturbance. Fluxes were greatest however in stands with the longest history since fire.

In conclusion, feeding damage by insects can have positive effects on plant communities through enhancement of nutrient cycling and promotion of plant succession. In this manner insect herbivores can be beneficial to populations of their food plants and to the diversity of plants in communities. The influences of insect herbivore are not consistent, however, and are likely to be context dependent.

CONCLUSIONS

Insect herbivores can influence the densities of their host plants, as shown by experiments involving the removal of insects with insecticides, the addition of herbivores as biological control agents of invasive weeds, detailed studies of the impacts of herbivores on native and introduced plants, the devastation caused by some accidentally introduced insects, and life-table analyses. However, not all insect species influence the populations of their host plants, and what allows some and not others to have measurable impacts remains a question. Given the high level of context dependency and the potential influences of environmental stochasticity, predictions of future plant population densities based on short-term life-table studies must be made cautiously. Carrying out studies over time and habitat gradients is important. Results from spatial and temporal population studies can be helpful for the development of strategies to conserve rare and endangered species and for predicting future distributions of plants in the face of climate change.

Finally, the world is green because plant communities respond to reductions of individual species. For example, successful biological control of diffuse knapweed resulted in expansion of another exotic, cheat grass, *Bromus tectorum* (142), and the rangeland remained green. In addition, defoliation and plant or tree death might be viewed in the short term to be a negative impact on host population density. In the long term, however, this rejuvenation of host plant populations is advantageous for future populations of the insect herbivore. Scaling up from populations to communities and ecosystems in changing environments and over evolutionary time presents a

Herculean challenge for ecologists trying to answer the question of whether insect herbivores limit or regulate host plant populations.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Andrea Stephens, Dawn Bazely, Stephen Heard, and Jenny Cory for their helpful comments on this article. We also thank the Natural Science and Engineering Research Council for funding our research. J.H.M. thanks Svata Louda, in particular, for her many contributions to this area of research and for great discussions over the years.

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