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INSECT LIMITATION OF WEEDY PLANTS AND ITS ECOLOGICAL IMPLICATIONS

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INTRODUCTION

The ecological consequences of releasing a genetically modified organism into a novel environment will depend upon its establishment, dispersal, and interactions with other organisms. Establishment and dispersal in the population dynamics of weedy plants are discussed by Jordan (these proceedings). My task is to discuss the known effects of plant-feeding insects on populations of native weedy plants, which provide the best current predictive basis for assessing the potential ecological consequences of the movement of resistance genes from genetically modified crops into their native weedy relatives.

The focus of our research over the last 20 years has been on understanding and predicting the quantitative outcome of plant-feeding by insects on the density, distribution, and lifetime reproductive success of native weedy plants. In the context of this workshop, these data can be used to address: (1) what is the evidence that insect herbivores can limit plant population density, restrict plant distribution, or reduce lifetime reproduction of native weedy plants? (2) under what circumstances is such limitation strongest or most likely? and, (3) when might increased resistance to insects alter the weed status of presently innocuous weedy plants?

Experimental evidence that feeding by insect herbivores can influence the growth, reproduction, and population density of native herbaceous plants has accumulated over the last 25 years (see reviews: Crawley 1983, 1997; Parker 1985; Hendrix 1988; Weis and Berenbaum 1989; Louda 1989, 1995). From these studies it is clear that herbivorous insects, either singly or in combination, often significantly limit both the success of individual plants and the densities of populations of native weedy plants. Increased insect resistance in such cases would result in a reduction in control exerted by insects on plants and would lead to a prediction of increased weediness of the native plant species.

To illustrate the influence of insects on plants and to explore the circumstances under which insect herbivores have been shown to be crucial in limiting plant density, I would like to review the highlights of two of our research projects. The first concerns a native crucifer that is related to canola and wild radish (Brassicaceae). The second project concerns a group of native thistles that are related to sunflower (Asteraceae). In addition, I will review some of the implications of these data for anticipating potential ecological responses to altered insect pest resistance introduced into related weedy native plants. In the absence of direct tests on the role of insects in the dynamics of crop-related weedy native species, these studies can be used as the best models presently available to assess the role of insects and insect resistance in the dynamics of native weed populations.

Before considering the studies in detail, three main points from this work emerge as relevant to the question at hand:

1. Foliage-feeding insects on the crucifer and inflorescence-feeding insects on the thistles altered the growth, reproduction, recruitment, and density of both types of plants in some environments. These results suggest that increasing plant resistance to insects has the potential to increase individual plant performance and

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population density for such species in some portions of the environment.

2. The severity of limitation by insects in these studies depended on the physical and biological environment in which the interaction occurred. Thus, our results suggest that prediction of the quantitative effect of altered plant resistance to insects requires knowing something about the environments under which the native plants grow, or would grow as performance increased.

3. Changes in insect herbivore load associated with the introduction of resistance to one guild of insects can alter total herbivore load and augment the impact of other native insects on plant performance and density. Thus, prediction of the quantitative effects of altered resistance to herbivores such as leaf beetles, in response to a coleopteran specific Bt, will require knowing how other groups of plant-feeding insects respond to the change in plant growth, phenology, and reproductive success.

CRUCIFERS (BRASSICACEAE)

Crucifers, such as canola (*Brassica napus*) and cabbage (*Brassica oleraccea*), are among the crops targeted to receive transgenes conferring increased insect resistance. Our research on bittercress (*Cardamine cordifolia* A. Gray), a potentially weedy perennial crucifer found in the Rocky Mountains, provides a model for the effects of insects on crucifer dynamics. Closely related species are circumboreal, occurring in our northeastern deciduous forests and plains grasslands as well as in the montane environment. Bittercress density is highest in moist, moderately shaded areas. The aim of our studies with this species was to determine experimentally the role of herbivorous insects, especially a particularly damaging chrysomelid leaf beetle (*Phaedon* sp. nr. *oviformis*: Louda 1984), in plant growth, density, and distribution. In addition, we evaluated the role of plant resistance factors, such as the mustard oil defenses, in mediating insect influence. The results of our studies over a decade suggest several points relevant to this workshop.

First, foliage-feeding insects limited the growth and reproduction of bittercress under field conditions (Louda 1984). To determine the overall effect of the foliage-feeding insects, an insecticide check test was used to reduce insect load compared to controls. Since the chrysomelid leaf beetle was the predominant herbivore at the study site, the results are relevant to discussions of the ecological effects of coleopteran specific Bt resistance genes. In addition, this experimental technique could be used with native weedy relatives of crop plants to simulate reduced insect herbivore load associated with increases in plant resistance. Such an experiment could eliminate concern about demographic effects of introgression of the resistance gene, if the insecticide check showed that insects had no significant effect on plant reproduction and recruitment. Alternately, if the insecticide check led to increased plant performance or density, as was the case here, further tests would be merited to assess the relative contribution of a specific insect guild, for example beetles vs. moths. The simplicity of the experimental design, and its ability to eliminate concern if done properly, argue in favor of requiring such an experiment prior to any release of an insect resistance gene into a crop with native weedy relatives.

Second, insect limitation of plant performance and density was much greater in the exposed drier habitat than in an adjacent moister environment (Louda and Rodman 1996). The two experimental protocols used in the study could both be used to quantitatively evaluate the effect of environmental variation on the outcome of insect feeding for the density of weedy native relatives of modified crop plants. Clonal material was transplanted from naturally-occurring plants into plots in an exposed sunny habitat and in a nearby moderately shaded habitat; half in each habitat were protected with insecticide. When plants in the exposed site were protected from insect herbivory, their performance was comparable to plants in the preferred shaded habitat. Also we removed the shade cover over half the shaded plots and quantified both foliage loss to herbivores and change in plant density over three years. Herbivory increased and density decreased dramatically over time when exposure was increased (Louda and Rodman 1996). Over the same three-year period, cumulative levels of insect herbivory in the exposed sunny habitat limited density of plants there, demonstrating that insects restricted the occurrence of this crucifer to the shaded habitat. The implication of this result is that increased resistance to insects in this crucifer, and likely in similar species, would increase plant density within the current preferred habitat and expand the habitat range over which the native weedy relative could become abundant.

Third, in the exposed habitat where insects limited plant density, the variation in the level of impact was determined by the interaction of three factors: lower defensive compound concentrations (glucosinolates, the mustard oil precursors), higher insect abundance, and higher plant stress (Louda and Rodman 1983, 1996). We tested the role of plant physiological status directly in several experiments that manipulated plant water status (see Louda and Collinge 1992, and references therein). In every case, insect feeding damage was greater on plants that exhibited moderate leaf water deficits and higher nitrate-nitrogen concentrations (a symptom of plant water deficit). Clearly, insect impact on plant density, and consequently the potential for increased weediness in response to altered insect resistance, can be severe and can vary among growing environments. These results suggest that realistic, multi-factor models will be needed to predict plant density responses to increases in insect resistance.

THISTLES (ASTERACEAE)

Thistles are members of the Asteraceae family, which also includes cultivated sunflowers, a crop targeted for improved pest resistance. Our work on native thistles, which are characteristic native species in the prairie grasslands of the upper Great Plains, provides data on the role of insects in limiting weedy plants in this family.

The genus *Cirsium* is circumboreal, and plants occur in disturbances in a wide range of habitats in North America and Eurasia. Several species, such as bull or spear thistle (*C. vulgare*) and Canada thistle (*C. arvense* L.), are considered agronomically important weeds in some places. The aim of our studies of these species has been to determine the degree to which insects limit plant performance and contribute to limiting the weed potential of these species under normal conditions. In addition, these studies have fortuitously provided quantitative information on the ecological effects of increased insect herbivore load caused by the host range expansion of an insect deliberately released for the biological control of exotic thistles species (Louda *et al*. 1997; Louda 1998, 1999). The results of our studies over the last 15 years suggest three points that are relevant here.

First, insect herbivores significantly reduce growth and reproduction of thistles under indigenous conditions. Leaf-feeding insects restrict individual growth of both weedy thistles, such as tall thistle (*C. altissimum*) (e.g., Guretzky and Louda 1997) and a federally-listed threatened species, Pitcher's thistle (*C. pitcheri*) (Bevill *et al*. 1999). Inflorescence-feeding insects significantly reduced seed production and seedling establishment in every case we have studied experimentally to date (see references above). For example, using the insecticide check method, we found that inflorescence-feeding insects significantly lowered lifetime maternal fitness and limited population density of Platte thistle (*C. canescens* Nutt.) in the field (Louda *et al*. 1990, Louda and Potvin 1995). The implication of these results is that increased pest resistance that leads to reduced insect herbivore load in native weeds such as these would lead to significant increases in plant density and weediness.

Second, the role of insects in plant density limitation was more obvious, consistent, and important in the more disturbed open habitat than in the nearby grassland (Louda and Potvin 1995). After experimental reduction in insect damage to developing flowers and seeds, seedling recruitment and subsequent plant densities were higher in the disturbed sand prairie (stabilizing blowouts) than in the more heavily vegetated grass-dominated areas. Insects had a significant effect in both competitive environments, but the release from insect suppression was greater where the environment was disturbed. So, the prediction of the magnitude of insect suppression of thistles, in relation to other potentially limiting factors, is related to microenvironment, which is similar to findings described above for crucifers.

The implications of these results are that the quantitative response to increased pest resistance in a population that is being limited by insects will depend on the environment in which reproduction and recruitment are taking place. This is not reassuring for fugitive plant species, such as sunflower, which are well adapted to the disturbances that are a characteristic feature of managed agricultural ecosystems and their adjacent vegetation.

Third, even well-intentioned, planned releases of novel species can have unexpected ecological side effects in complex biological systems (Louda *et al*. 1997), and current protocols for risk assessment fall short of providing a definitive, unambiguous determination of ecological risk (Simberloff and Stiling 1996; Arnett and Louda 1999, in review). Release of a weevil (*Rhinocyllus conicus*) for the biological control of exotic thistles has led to its widespread feeding on native thistles, including species in several national parks and nature reserves (see Louda *et al*. 1997). For native Platte thistle, the effects of this alteration of herbivore load on fitness and population density are quantifiable based on our previous studies. The outcome may model the quantitative effects of increased insect resistance in native species subsequent to the development of insect resistant crops.

The population growth of *Rhinocyllus* on Platte thistle has been exponential since its first discovery in 1993 (Louda 1998), and the weevil population now significantly reduces seed production of this seed-limited species (Louda *et al*. 1997). Native insects alone, which were shown to limit recruitment and density, already reduce seed production by 65% (Louda and Potvin 1995). The weevil, superimposed on the damage by native insects, led to a 94% reduction in seed by 1996 (Louda *et al*. 1997).

The implications of these studies for releases of genetically-modified organisms are two-fold. First, increased resistance to insects by native weedy relatives of crop species could lead to increases in seed production, recruitment, and weediness. Second, it is clear that accurate prediction of ecological risk associated with releases is still in its infancy. We are only now learning what needs to be measured to predict insect feeding and impact on plant performance and dynamics. Nevertheless, the data from native thistles provides testable predictions for native weedy relatives of crop species. Based on what we know now, the plant types most likely to have insect herbivory as a significant determinant in their densities in disturbed areas are larger annuals and short-lived perennial native weeds with fugitive life histories like sunflowers and thistles (see Louda 1989).

CONCLUSIONS

The inferences of these studies for the three main questions posed at the beginning of this presentation are as follows: (1) There is evidence that insect herbivores can limit plant population densities and restrict distributions of native weedy plants. Since many of the native plant species related to crops targeted for improved pest resistance genes are weedy, quantification of the role of insects in limiting their densities are needed in order to have reliable risk assessments. The quantification process should start with insecticide exclusion studies. Manipulation of specific groups of insect herbivores is then merited if the insecticide tests show that seed, seedling, and older plant densities are affected by insect feeding. (2) The importance of insect limitation of weed density varied with environmental conditions. Insects played a significant role in limiting plant populations in open, disturbed, and potentially stressful growing conditions. Since disturbance is characteristic of agricultural fields and their margins, conditions are favorable to facilitate increases in weediness if insect resistance becomes incorporated into the native weedy relatives of genetically modified crops. (3) The studies to date suggest that increased resistance to insects could alter the weed status of presently innocuous weedy plants in disturbances in agricultural and native plant communities when those plant populations are limited by their insect enemies. Further research in this area is merited, and specific studies of native weedy relatives of crop plants are needed.

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