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Experimental evidence for insect impact on populations of short-lived, perennial plants, and its application in restoration ecology

SVATĚA M. LOUDA

Introduction

Successful management of vegetation and the restoration of threatened or endangered plant populations clearly depend on the unambiguous identification of the factors that determine and limit plant abundance and distribution (e.g. Harper 1977, Jordan, Gilpin & Aber 1987). Physical conditions, plant physiological responses, and plant competitive interactions are often important (e.g. Harper 1977, Chabot & Mooney 1985, Pickett & White 1985, Grace & Tilman 1990), and these factors are usually evaluated. However, trophic interactions, such as those involving plant consumption by insects and pathogens, may also be critical in the growth, reproduction, and population dynamics of native plants (e.g. Harper 1969, Whittaker 1979, Rausher & Feeny 1980, Dirzo 1984, Howe & Westley 1988, Burdon 1987, Hendrix 1988, Burdon, Jarosz & Kirby 1989, Louda 1989), but are seldom evaluated in plans for the management or restoration of threatened plant species.

In this chapter, after presenting some background on insect herbivory in plant dynamics, I review several key results from two field experiments that excluded flower- and seed-feeding insects from native plants. I then use these results to: challenge the view that insect damage can be assumed to be irrelevant to plant success, suggest patterns of significant insect damage to seeds of native plants, and make two recommendations involving assessment of insect herbivory to improve the management and restoration of rare and threatened plant species. The evidence suggests that evaluation of insect herbivory is generally warranted. Insect herbivory can be a critical, limiting factor, particularly in determining the abundance and distribution of relatively short-lived, herbaceous, perennial plants. This appears especially true where both insect damage and regeneration failure are observed in declining populations of a rare or threatened plant.

Insect herbivory in plant performance

Analysis of plant growth, reproduction, density, and distribution has traditionally emphasized plant response to variation in physical conditions and resource availability (e.g. Curtis 1959, Weaver 1954, 1965, Harper 1977, Newman 1982, Tilman 1982, 1988). Attempts to understand the consequences of damage by small invertebrate herbivores for individual plants and for populations of plants have accelerated only in the past 20 years or so (Harper 1969, Janzen 1971, Whittaker 1979, Hodkinson & Hughes 1982, Crawley 1983, Dirzo 1984, Hendrix 1988, Louda 1989, Louda, Keeler & Holt 1990a). These attempts have created some controversy, and two opposing schools of thought have emerged.

One school argues that chronic damage by coevolved, adapted insects is seldom a significant factor in plant success (e.g. Owen 1980, Crawley 1989a,b), except possibly under outbreak conditions (Barbosa & Schultz 1987). Several observations are used to support this interpretation. For example, it has been observed that the 'world is green' (Hairston, Smith & Slobodkin 1960; Slobodkin, Smith & Hairston 1967), that chronic insect damage to the foliage of adults of the dominant plant species averages only 5–10% of net productivity (e.g. Odum 1959, Hairston *et al.* 1960), and that there is little evidence of competition among phytophagous insects for food resources (Strong, Lawton & Southwood 1984). Furthermore, most plants have some capacity to compensate for tissue damage or removal (Hendrix 1979, 1984, McNaughton 1983, 1986, Maschinski & Whitham 1989). Also, plant-feeding insects have enemies, which may help reduce herbivore impact (Lawton & McNeill 1979, Strong *et al.* 1984). Finally, seed supply often seems to exceed the numbers required for recruitment, at least at the level of replacement (Harper 1977, Crawley 1990).

The other school, however, points out that such observational evidence is incomplete and inconclusive. For example, to insects the world may actually be colored 'brown and fibrous' or 'chemically noxious' (Ehrlich & Birch 1967, Feeny 1976). Also, chronic insect damage to foliage can be high, even on adults of dominant forest trees (Morrow & LaMarche 1978; Lowman 1984a,b; Fox & Morrow 1983, 1986; Morrow & Fox 1989), and insect damage and its effects are often much heavier on young individuals, especially seeds (see Janzen 1971, Fenner 1985). Also, in spite of some interesting exceptions, possibly including grasses (Belsky 1986, 1987), complete compensation for loss of tissue and seeds to insects generally falls short of complete recovery. Furthermore, the success of plant regrowth and compensation depends directly on the availability of time and resources for regrowth (Cottam, Whittaker &

Malloch 1986, Karban & Courtney 1987, Maschinski & Whitham 1989, Polley & Detling 1989, Louda *et al.* 1990a). Thus, the impact of chronic insect consumption is difficult to discern without experiment.

The accumulating experimental evidence on insect herbivory suggests that the interactions are complex, subtle, and often more important in plant dynamics than suspected (Harper 1969, Whittaker 1979, Dirzo 1984, Marquis 1984, Stamp 1984, Crawley 1985, 1987, Hendrix 1988, Louda 1988, 1989, Louda *et al.* 1990a). Experimental exclusions of insects provide strong evidence with which to estimate the actual effect of insect feeding on plant performance.

The exclusion tests available show that chronic insect herbivory can have a highly significant negative effect on plant survival, growth, flowering, seed set, or successional success (Cantlon 1969; Rockwood 1974; Morrow & LaMarche 1978; Waloff & Richards 1977; Parker & Root 1981; Brown 1982; Louda 1982a,b, 1984, 1989; Hendrix 1984; Kinsman & Platt 1984; Parker 1985; Parker & Salzman 1985; Hendrix, Brown & Gange 1989; Louda, Potvin & Collinge 1990b). Exclusion of insects also illustrates that they can alter plant competitive ability (Windle & Franz 1979; Bentley & Whittaker 1979; Bentley, Whittaker & Malloch 1980; Fowler & Rausher 1985; Cottam *et al.* 1986; Louda *et al.* 1990a).

Insect herbivory that affects the production, maturation, or dispersal of seeds may be especially critical in determining the success of plant reproduction (e.g. Janzen 1971, Fenner 1985, Hendrix 1988, Louda 1989). Reliance on recruitment from seed varies among plant species (Grubb 1977), and contrary to usual expectation, the number of seeds produced may not exceed the number that allows for persistence. Experiments show that inflorescence-feeding insects limited seedling establishment and density for two composite shrubs (Louda 1982a,b, 1983) and for a native thistle (Louda *et al.* 1990b). These tests were done *in situ*, and thus combine desirable aspects of observational data with experimental evidence. If their results are generalizable, they suggest that the population consequences of insect consumption may be generally underestimated, especially for large-seeded, short-lived perennials with a colonizing life history strategy (Louda 1989).

The consequences of insect seed-consumption for seed production or for seedling recruitment cannot be evaluated using estimates of damage levels to seeds. Observational measures of damage generally underestimate the role of insects in reducing viable seed (Anderson 1988). Furthermore, since other factors may restrict seedling establishment even from abundant seed (Harper 1977, Crawley 1990), the seed-to-seedling linkage must be evaluated experimentally (Louda 1982a,b, 1983, 1989). The two main types of experiment that provide data on the role of seed limitation in seedling recruitment and plant

density are artificial seed augmentation and consumer exclusions, both during seed development and after seed dispersal.

Artificial seed augmentation, which involves dispersing seeds by hand into marked quadrats (Harper 1977), is the classical test of the tightness of the seed-to-seedling linkage (see Darwin 1859; Foster 1964 in Harper 1977; Putwain, Machin & Harper 1968; Platt 1975; Werner 1977; Harper 1977; Gross & Werner 1982; Gross 1984; Crawley 1990). Seed augmentation generally results in significant increases in the recruitment of seedlings by large-seeded, nondominant herbaceous perennial plants, especially in open vegetation or disturbance patches.

Consumer exclusion allows a more direct measure of predator effects on the seed-to-seedling linkage. The *in situ* exclusion of consumers is more realistic, and allows assignment of causality, because it examines more natural seed release patterns, seed densities, and timing of seed release, while allowing other processes that influence the linkage to proceed as usual. Thus, such tests measure the direct impact of seed consumers, such as flower- and seed-feeding insects, on seedling densities. If seed-feeding insects significantly affect seedling numbers, then their exclusion should result in increased seedling densities around the parent plant. Few experiments testing this prediction have yet been published (see Fenner 1985, Howe & Westley 1988, Hendrix 1988, Louda 1989).

The results of two series of experimental studies of insect influence on the seed-to-seedling linkage suggest that where plant regeneration and population persistence depend directly on successful seed input, insect seed predation can be the most significant process limiting regeneration of the population. For many threatened plant species that depend on current seed supply for regeneration, seed predation can become a severe hazard as populations decline. Therefore, more attention should be paid to phytophagous insects in the management, restoration, and eventual delisting of threatened plant species.

Case 1: Goldenbushes, mid-successional shrubs in chaparral

Experimental studies of two native goldenbushes, which replace each other along the environmental gradient from coast to mountains in southern California (Fig. 5.1), demonstrate that insects feeding on flowers and developing seed can have significant demographic and distributional effects on the seedling recruitment and population dynamics of their host plant species (Louda 1978, 1982a,b,c, 1983, 1988). The species that predominates near the coast is coastal goldenbush, *Isocoma veneta* Nutt. (Nesom 1989), until recently considered to be *Haplopappus venetus* ssp. *vernonioides* (Nutt.) Hall (Hall 1928, Munz 1974).

Fig. 5.1. Observed frequency of occurrence and replacement of *Isocoma* (*Haplopappus*) *veneta* (broken line and bars) at the coast by *Harzardia* (*Haplopappus*) *squarrosa* spp. *grindelioides* (solid line and bars) in the inland portion of the gradient from ocean to foothills of the coastal mountains in San Diego County, southern California, USA (adapted with permission from Louda 1989). Predispersal seed predation limits viable seed and seedling establishment at all sites for both species (Louda 1982a,b, 1983). Interestingly, the replacement of the two species along the gradient is best explained by differential predation pressure along the gradient: much higher seed losses for *H. squarrosa* caused by inflorescence-feeding insects near the coast (Louda 1982b) plus significantly more intense seedling losses for *I. veneta* caused by vertebrate herbivores inland (Louda 1983).

The species that predominates near the mountains is scaly goldenbush, *Harzardia squarrosa* (H. & A.) Green var. *grindelioides* (D.C.) Clark, comb. nov. (Clark 1977), which had been called *Haplopappus squarrosus* var. *grindelioides* (DC.) Keck (Hall 1928, Munz 1974). These species are quite similar in stature, general appearance, phenology and insect herbivore guilds.

Three results are important here. First, insects feeding on the developing inflorescences limited both the number of viable seeds and the number of seedlings recruited by both species at all study sites (Louda 1982a,b, 1983). Second, the distribution of the inland species, scaly goldenbush, was compressed and displaced away from the coast by more intense predispersal seed predation coastally (Louda 1982b). Third, the distribution of coastal goldenbush was also compressed, but it was displaced toward the coast by the combination of intense seed reduction by insects all along the gradient and by higher consumption of seedlings by vertebrate herbivores in the inland portion of an environmental gradient (Louda 1983). In summary, inflorescence-feeding insects limited the abundance of seedlings of both species of goldenbush all along the gradient, and damage by these insects was the primary factor in sig-

nificantly altering the distribution of scaly goldenbush on the gradient (Louda 1978, 1982a, b, 1988).

Case 2: Platte thistle, a fugitive species in grassland

Grasslands worldwide are generally characterized by the mosaic of a few dominant grasses, interspersed with a surprising diversity of herbaceous perennial forbs (Weaver 1954, 1965, Risser *et al.* 1981). Many characteristic grassland forbs appear to depend on seed recruitment into disturbances for both local and metapopulation persistence (e.g. Platt 1975, Platt & Weis 1977, 1985, Goldberg & Werner 1983, Louda *et al.* 1990b). Many of the forbs of the once-extensive grasslands of the northcentral Great Plains, USA, also have diverse guilds of phytophagous insects (S. M. Louda, personal observation). To better understand such forb-insect interactions, the Platte thistle (*Cirsium canescens* Nutt.; Fig. 5.2A), a short-lived forb of Sandhills prairie, was studied, and the effects of predispersal flower- and seed-feeding by insects, post-dispersal seed predation by vertebrates, and grass interference with seedling survival and growth on its population dynamics were tested (Louda *et al.* 1990b, Louda & Potvin 1994).

Sandhills prairie covers most of central Nebraska, USA (19300 sq. mi.), and forms the largest grass-stabilized continental dune system in the western

Fig. 5.2. Platte thistle, *Cirsium canescens*. (A) upper part of plant with inflorescence, illustrating leaf characters and flowerheads in five stages of development (from bottom: one in small bud, one in large bud, one in partial flower, two in full flower, and terminal one in maturing seed stage) (B) Dissection of a maturing seed stage flowerhead illustrating typical damage and pupae of the tephritid flies that feed on developing flowers and seed, and two or three viable, undamaged seeds at outside edge of head and outside the head.

hemisphere (Bleed & Flowerday 1989). The vegetation of the Sandhills is a special type of 'mixed' grassland (Weaver 1954, 1965), dominated by a distinctive combination of short, mid, and tall prairie grasses and forbs (Keeler, Harrison & Vescio 1980, Kaul 1989). Because the soils are fine sands and the annual rainfall is relatively low, soil moisture deficit stress occurs with some frequency, especially in the heavily vegetated interdune areas (Barnes & Harrison 1982, Barnes & Heinisch 1984).

Platte thistle is broadly, but sparsely, distributed throughout the Sandhills. Its microhabitats include the large disturbances called blowouts or smaller openings among clones of prairie grasses. Platte thistle is closely related to the federal-threatened Pitcher's thistle (*Cirsium pitcheri* [Torrey ex. Eaton] Torrey & Gray), which is endemic to the grassland dunes around Lakes Michigan, Superior, and Huron (Johnson & Iltis 1963, Keddy & Keddy 1984, Loveless 1984, Harrison 1988, Loveless & Hamrick 1988, McEachern, Magnuson & Pavlovic 1989, McEachern *et al.* Chapter 8 of this volume). Based on electrophoretic evidence, Loveless & Hamrick (1988) make a case for Platte thistle as the putative progenitor for Pitcher's thistle. They suggest that populations moved from the Sandhills into similar sand habitats to the northeast after the last glacial retreat, and differentiated relatively recently.

Platte thistle has a perennial, monocarpic life history, and reproduces only from seed. Plants grow as rosettes for two to four years, and then bolt, flower, and die. Insects do some damage to the foliage (W. O. Lamp, personal observation; S. M. Louda, personal observation), but much more striking damage to the developing inflorescences (Fig. 5.2B). Early instars feed on the floral tubes, later instars consume ovules, and both burrow into the receptacle disk; levels of damage to inflorescences average between 35 and 75% of the florets initiated (1977–1979, 1984–1991) (Lamp & McCarty 1979, 1981, 1982, Louda *et al.* 1990b). The insects that cause this damage are two species of picture-winged flies (Tephritidae: *Orellia occidentalis* (Snow), *Paracantha culta* (Wiedmann)), and a moth (*Homeosoma stypticellum* Grote: Pyralidae) related to the sunflower moth (Lamp & McCarty 1979, 1982).

At least three types of biological interaction could potentially influence the population dynamics of fugitive species, such as thistles. First, damage by insects to flowers and developing seeds can limit the success of plant reproduction and subsequent recruitment (Louda 1978, 1982a,b, 1983, Lamp & McCarty 1981, 1982). Second, postdispersal seed consumption by birds and rodents can also limit recruitment from seed, as found for several European species of thistle (de Jong & Klinkhamer 1988a,b, Klinkhamer, de Jong & van der Meijden 1988). Third, such species may be limited more by competition with established grasses than by absolute seed availability (Platt, Hill & Clark

1974, Platt 1975, Harper 1977, Platt & Weis 1977, 1985, Goldberg & Werner 1983, Crawley 1990). Consequently, three concurrent experiments were run to evaluate the influence of these three biotic interactions on the abundance and distribution of Platte thistle. The experiments were done from 1984 to 1990 at Arapaho Prairie, a Nature Conservancy preserve of Sandhills grassland in east-central Nebraska (Louda *et al.* 1990b, Louda & Potvin 1994).

In the first experiment, insecticide (Isotox, Chevron Chemical) was used to reduce the damage caused by insects to the developing flower heads in 1984 and 1985. There were three treatments: localized (flowerhead only) hand application of small amounts (50–100 ml) of insecticide-in-water, water-only, or nothing. The treatments were applied biweekly during the critical oviposition period of the flowerhead insects (May to mid-June, 1984 and 1985; 4 applications per year). The treatments at each location were switched between the two years to control for the effect of microclimatic variation among areas on treatment outcome. Both the development of viable seed within seedheads and the establishment of successful seedlings within grids around the experimental plants in the subsequent year were recorded, and seedlings were marked and followed to maturation. There was no evidence of plant toxicity or pollination reduction with insecticide application (Louda *et al.* 1990b, Louda & Potvin 1994). No significant differences were found in treatment effects between years, and the data are here combined to summarize the outcome.

The plants in all three treatments initiated a similar number of flowers (Fig. 5.3A). Insecticide application reduced insect damage to developing flowers and seeds by over 75%, leading to a significantly greater number of viable seeds (Fig. 5.3B). Thus, flowerhead insects significantly decreased the number of viable seeds that were matured and released by Platte thistle. The reduction in damage by insects and the concomitant increase in viable seed in the insecticide-treated plants led to a four- to six-fold increase in the new seedlings that established, thus increasing the seedling plant population density dramatically (Fig. 5.3C). This increase in seeds and then in seedlings subsequently led to a highly significant increase in the number of adult flowering plants in the next generation, four years later (1988 and 1989; Fig. 5.3D). The experiment thus clearly demonstrates the vital influence that flower- and seed-feeding insects have on seed supply, on seedling recruitment, and eventually on adult plant density of Platte thistle within its characteristic habitat.

Damage to developing flowers and seeds had a greater effect than did post-dispersal predation on seeds by vertebrates. In the vertebrate exclosure experiment, 30 seeds, 15 buried and 15 scattered on the soil surface, were placed within a 30×30-cm plot. This seed density (333 m⁻²) is within the range of potential seed density in the vicinity of an adult plant. Each of the 10 replicates

Fig. 5.3. Summary of the results of the insecticide exclusion of inflorescence-feeding insects from developing flowerheads, 1984–1990, according to insecticide spray, water-only spray, and no spray treatments (see text): (A) number of flowers initiated; (B) number of viable, undamaged (good) seeds for release; (C) average number of seedlings established by each plant; and (D) number of flowering adults that were eventually produced per parent plant (adapted from Louda *et al.* 1990b, Louda & Potvin 1994).

contained three such plots, with either a complete enclosure cage of 1.25 cm (0.5 in.) hardware cloth, a comparable cage that was open on two sides and the top, or no cage. Five replicates were placed within grass vegetation, and five were placed in open areas near a large blowout in September 1984. Seedling emergence, growth, and survival were monitored over the next two years. The results under these experimental conditions show that overall germination rates were low, and that postdispersal seed predation had a small, but significant, effect on seedling recruitment in the open habitat associated with blowouts (Fig. 5.4).

Fig. 5.4. Average number of seedlings surviving per plot in the cage exclusion of post-dispersal vertebrate seed predators, 1985–88, according to total, partial, and no caging (see text): (A) in disturbed blowout areas; and (B) in stabilized grassland vegetation adjacent to the blowout areas (adapted from Louda *et al.* 1990b).

Finally, the effects of competition from established grasses on the survival and growth of new seedlings were tested in a transplant experiment. In each of five sets of six seedlings, three seedlings were planted into an open area within a clone of *Panicum virgatum* and three seedlings, in a comparable spatial array, were planted into the open area between grass clones (Louda *et al.* 1990b). Grass competition greatly decreased seedling survival and growth over the subsequent two years (Fig. 5.5).

Analysis of the three experiments together allows an initial prediction of the relative contribution of the three types of biotic interaction to the dynamics of Platte thistle (*Cirsium canescens*) under natural conditions in Sandhills prairie. The insecticide exclusion experiment showed that flower and seed consumption by insects caused a highly significant reduction in both the number of seedlings established and the flowering plants that eventually resulted. Predispersal damage to flowerheads was responsible for a reduction in individual plant fitness, which led to population limitation. Plant competition and spatial or habitat variation amplified the influence of such interactions on plant demography (Louda *et al.* 1990b). Because these effects occurred with ambient levels of postdispersal seed consumers, because they occurred in grassland as well as in blowouts, because such factors as germination and seedling survivorship were comparable among treatments, and because the levels of insect

Fig. 5.5. Survival of Platte thistle seedlings transplanted into the open areas between grass clones versus into the open areas within grass clones (see Louda *et al.* 1990b).

damage were near average (Louda & Potvin 1994), insect destruction of flowers and developing seed can be considered the most important limiting factor in the recruitment and local abundance of Platte thistle. Moreover, the effects of the biotic interactions were cumulative. Postdispersal seed predation and seedling competition with established grasses augmented the effects of the major decrease in seed caused by the damage inflicted by flower- and seed-feeding insects.

Implications for restoration ecology

From the studies of goldenbushes and Platte thistle, it is clear that flower- and seed-feeding insects can have a highly significant effect on plant recruitment,

abundance, distribution, and persistence. On the basis of these studies, a general methodological recommendation can be made for managing and rebuilding populations of threatened plant species. The recommendation also leads to a specific suggestion for the restoration of declining populations of the threatened Pitcher's thistle (*Cirsium pitcheri*), using experimental results with its nearest relative, Platte thistle (*Cirsium canescens*).

General methodology

The studies to date suggest that a mixed strategy of observational and experimental studies should become standard. Traditional observational studies of the natural history of threatened plant species need to be continued. However, actual tests of the factors that are thought to be important in controlling population dynamics and limiting density and distribution are also critical (see also Pavlik, Chapter 13 of this volume). To do this while minimizing any potential negative impacts on the threatened or endangered species, a comparative approach can be taken. After essential aspects of the ecological similarity are established observationally, a more common, but closely related and ecologically similar, species could be used for the experimental studies. Critical results should then be validated with comparable, but smaller-scale, tests on the protected species. The results would provide a strong conceptual and empirical basis for restoration management.

Positive tests, such as excluding predators suspected of being significant, hold particular promise and merit serious use. Such tests are 'win-win' experiments. The potential for damage to the threatened or endangered species should be low, and the potential for positive effect should be high. The synthesized results of the comparative observations and experiments could then be used to guide management to augment the growth and densities of appropriate populations of the threatened or endangered plant under natural circumstances.

In summary, augmentation and restoration strategies would have a stronger and more scientific basis if the traditional, observational study of a threatened or endangered plant's dynamics and interactions were matched with experimental determination of the relative importance of the factors suspected to be controlling its population demography. Emphasis should be placed on designing 'win-win' experiments and possible strategies of restoration management. Initially, experiments should be restricted to an ecologically similar, closely related, but non-threatened species, if available. Significant experimental results should then be retested in small-scale validation experiments on the threatened species. This process should enhance the effectiveness of restoration, and it should increase the probability of sustainable results after intervention.

A combined observational and experimental approach is also an efficient information-generating design, and can maximize our capacity to detect the really critical processes in the dynamics of rare plant species. Such an approach could be applied without jeopardizing the populations of threatened or endangered plants, and it avoids reliance on inherently tenuous extrapolations of causality from observational data alone. Specifically, experimental information on critical processes in the dynamics of a closely related, ecologically analogous species should provide objective, mechanistically based, specific recommendations for potential manipulations that have a high probability of increasing recruitment and persistence in populations of threatened or endangered plants.

Prediction for Pitcher's thistle

The parallels between the federal threatened Pitcher's thistle (*Cirsium pitcheri*) and its closest known relative, Platte thistle (*C. canescens*), are striking. These include: open sand habitat, early-season-growth phenology, monocarpic life history, comparable or identical flowerhead insects, relatively high levels of observed seed damage, and dependence upon current seed for recruitment (Lamp & McCarty 1979, 1981, 1982; Keddy & Keddy 1984; Loveless 1984; Loveless & Hamrick 1988; McEachern *et al.* 1989; Louda *et al.* 1990b; McEachern *et al.*, Chapter 8 of this volume).

Both species of thistle often have problems producing large numbers of viable seeds; good seeds of both are often difficult to find. The data substantiating this observation for Platte thistle are extensive and consistent among years and studies (e.g. Lamp & McCarty 1979, 1981, 1982; Louda *et al.* 1990b). Furthermore, it is clear that, for Platte thistle, insect damage to flowers and seeds is a major factor in its low levels of viable seed and low population recruitment and density (Fig. 5.3; Louda *et al.* 1990b). Pitcher's thistle also has low levels of seed viability, and good seed is usually scarce (Loveless 1984; Loveless & Hamrick 1988; McEachern *et al.* 1989; M. Bowles, personal communication). Insects and major insect damage in the inflorescences of Pitcher's thistle are often reported (Keddy & Keddy 1984, Loveless 1984, Loveless & Hamrick 1988). The levels of damage observed appear similar to those documented for Platte thistle.

The similarities between these species suggest that the experimental outcomes for the more common, non-threatened Platte thistle should form a reasonable model for biological predictions for the management of Pitcher's thistle. The most obvious prediction is that Pitcher's thistle's production of viable seed and establishment of seedlings could be increased significantly by

restricting the damage caused by its flower- and seed-feeding insects. Increased seedling establishment and subsequently higher population densities within the protected dune habitat should stem the declines in populations of Pitcher's thistle that have recently been documented (McEachern *et al.* 1989, Chapter 8 of this volume) especially at Indiana Dunes National Lakeshore. Because extinction probabilities tend to be inversely related to population densities (Gilpin & Soulé 1986), this intervention, if successful, should increase the probability that self-perpetuating populations can be established in good to excellent protected habitat. Although factors such as rabbit herbivory, trampling, and competition from grasses might interfere with their success, protecting the plants from insect herbivory should at least increase the likelihood of seedling establishment, the base on which other mortality factors operate.

Both the available evidence and the theory of predator-prey interactions support this suggestion. However, the factors affecting Platte thistle in the continental dune system may not have the same relative effect on Pitcher's thistle in the Great Lakes dune system. Thus, a small-scale experimental validation of the effect of insect herbivory on Pitcher's thistles' seedling establishment and plant dynamics is being done (S. M. Louda & A. K. McEachern, unpublished data). As previously discussed, an insect-exclusion experiment is a positive ('win-win') manipulation. It is unlikely that the thistles will be harmed, and there is a high, logically predicated possibility that seed supply, seedling establishment, and plant density of Pitcher's thistle will be enhanced. If larger, and possibly more, populations of Pitcher's thistle result, sustainable population levels might be reached, obviating the need for further intervention.

Conclusions

Recent analyses of the influence of insects on the reproduction and establishment of native plants in several ecosystems suggest that more attention should be paid to insect impact in the management and restoration of threatened plant species. The experimental results presented in this chapter challenge the view that insect damage does not influence the success of native plants and they suggest patterns of interaction effects. The experimental results can be used to make recommendations for the management of threatened or endangered plant species, as illustrated for Pitcher's thistle. As demonstrated, preliminary experiments useful in determining the management of a threatened or endangered species can be carried out on an ecologically similar, non-threatened, close relative, and confirmed in small-scale experiments on the threatened or endangered species itself.

In two species of goldenbush, seedling recruitment by both species was limited by insect feeding on flowers and seeds at all sites along the environmental gradient. The distribution of scaly goldenbush was compressed, with insects essentially excluding it from the coastal area by more intense predispersal seed predation there. Inland, the distribution of coastal goldenbush seedlings was reduced significantly by the combination of intense predispersal seed predation augmented by more intense vertebrate herbivory on seedlings. In the Platte thistle, insect feeding on flowers was responsible for significant reduction of individual plant fitness, population limitation, amplification of the effects of plant competition, and spatial variation in the influence of such interactions on plant demography. Together, these findings show that insect pests can limit recruitment, abundance, and distribution of short-lived herbaceous perennial plants within their usual environment.

The ecological similarity of a threatened native thistle, Pitcher's thistle (*Cirsium pitcheri*), to Platte thistle (*C. canescens*), its putative progenitor, is strong. Such similarities and the experimental results from the more common Platte thistle suggest a scientific approach to the management and stabilization of threatened plants within protected habitats. Based on the results of a series of experiments with Platte thistle, I propose three predictions for the restoration and enhancement of Pitcher's thistle. First, insecticide exclusion of flower- and seed-feeding insects should increase the maturation and release of of viable seed by Pitcher's thistle, as it did for Platte thistle (Fig. 5.2B). Second, the successful production of increased numbers of viable seed by Pitcher's thistle should improve its seedling establishment success, as it did for Platte thistle (Fig. 5.2C). And third, higher seedling recruitment should lead to increased densities of flowering adults in the next generation, as it did for Platte thistle (Fig. 5.2D), at least in open habitats.

In general, I suggest that the management and enhancement of threatened plant species will be improved by comparative experimental analyses of ecologically similar, but more common, plant species. This approach depends on insights gained through parallel observation and experimental analysis of a more common species that is ecologically analogous to the threatened species. Such insights should lead to improved management and predictions for the enhancement and restoration of populations of the threatened species. Information on potentially critical biotic interactions for more common ecological analogs can clearly contribute to our understanding and to our capacity to manage and restore populations of threatened or endangered plant species with consistent and chronic damage by insect pests.

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