Insect Predation of Seeds and Plant Population Dynamics

Jianxin Zhang
Francis A. Drummond
Matt Liebman
and
Alden Hartke

Insect Predation of Seeds and Plant Population Dynamics

Jianxin Zhang
Research Associate

Francis A. Drummond
Associate Professor

Matt Liebman
Associate Professor

and

Alden Hartke
Graduate Student

Department of Applied Ecology and Environmental Sciences
University of Maine
Orono, Maine 04469-5722

ACKNOWLEDGMENTS

Contents

INTRODUCTION

Seed production is a critical stage in the life history of plants. Seeds contribute to adult replacement and to increases in local population size and function as the means of dispersal to areas distant from the local population (Louda 1982). Predation by animals can be a key factor affecting seed mortality, with consequences for plant abundance, distribution, and evolution (Duggan 1985; Harper et al. 1970; Moore 1978).

Seed predation can be grouped into predispersal and postdispersal predation (Janzen 1971a), or pre-seedfall and post-seedfall predation (Kjellsson 1985). Seed predators and dispersers represent many species of animals including insects, birds, deer, peccaries, squirrels, and mice. Among insects, Coleoptera, Hymenoptera, Diptera, Lepidoptera, and Thysanoptera constitute the major seed predators. Diptera, Thysanoptera, Lepidoptera, and some Coleoptera are predispersal predators; Coleoptera, Hymenoptera, birds, and some mammals are postdispersal predators. Both larval and adult insects can function as seed predators. As an example, both larvae and adults of the carabid beetle, *Harpalus rufipes,* are seed predators in agroecosystems (Zhang 1993). Predispersal predation by insects may cause mortality in up to 80% of the seeds produced in many grassland and forest habitats (Andersen 1988; Janzen 1971a, 1980), while postdispersal predation is often a major determinant of seed survival, plant species distribution patterns, and plant community composition (Ashton 1979; Janzen 1972; Schupp 1988; Wilson and Janzen 1972). Table 1 lists insect seed predator species reported in the literature.

PREDISPERSAL SEED PREDATION

Predispersal seed predation refers to seed attack before the seeds are shed by the parent plant. This type of seed predation by insects is a widespread, often severe source of plant mortality (Bohart and Koerber 1972; Harper 1977; Janzen 1969; Louda 1978; Salisbury 1942). Examples of predispersal seed predation by insects are compiled in Table 1. Many insect seed predators are generalists, and therefore, the seeds of many plant species can be attacked by a complex of taxonomically diverse insect species or a mix of insect, bird, and mammal seed predators. A few plant species appear to have only one species of predispersal seed predator associated.

Table 1. A list of insect seed predator species.

Order	Family	Species	References
Coleoptera	Bruchidae	Acanthoscelides fraterculus*	Green and Palmblad 1975
		*Bruchus atromarius**	Crawley 1992
		*Mimosesta mimosae**	Traveset 1990
		*Mimosesta nubigens**	Traveset 1990
		*Sennius abbreviatus**	Crawley 1992
		Stator vachelliae	Traveset 1990
	Carabidae	*Amara* sp.	Imms 1948
		Amara sp.	Zhang 1993
		Evarthus alternans	Best and Beegle 1977
		Evarthus sodalis sodalis	Best and Beegle 1977
		Harpalus fuliginosus	Kjellsson 1985
		*Harpalus penslylanicus**	Best and Beegle 1977; Manley 1992
		Harpalus rufipes	Zhang 1994
		Omophron sp.	Imms 1948
		Pterostichus chalcites	Best and Beegle 1977
		Pterositichus lucublandus	Best and Beegle 1977
		Zabrus sp.	Imms 1948
	Curculionidae	*Curculio glandium**	Crawley 1992
		Diethusa sp.*	Auld 1986
		*Erytenna consputa**	Neser and Kluge 1985
		Melanterius sp.*	Auld 1983
		*Melanterius acaciae**	Auld and O'Connell 1989
		*Pseudanthonomus hamamelidis**	DeSteven 1983
		*Pseudanthonomus virginiana**	Crawley 1992
		Rhinocyllus conicus	Kok and Surles 1975
		Rhyssomatus lineaticollis	Franson and Willson 1983
Diptera	Anthomyiidae	*Hylemya* sp.*	Hainsworth et al. 1984; Crawley 1992
		*Pegohylemyia seneciella**	Crawley 1992
	Scatophagidae	*Gimnomera dorsata**	Molau et al. 1989
	Tephritidae	*Aethes deutschiana**	Molau et al. 1989
		*Euaresta aequalis**	Hare 1980
		*Neospilota signifera**	Louda 1982
		*Orellia occidentalis**	Lamp and McCarty 1982
		*Orellia ruficauda**	Crawley 1992
		*Paracantha culta**	Lamp and McCarty 1982
		*Trupanea wheeleri**	Louda 1982
		*Urophora formosa**	Louda 1982
		Urophora sp.*	Crawley 1992
Hemiptera	Miridae	*Lygus boralis**	Crawley 1992

Table 1. continued.

Order	Family	Species	References
Hymenoptera	Eurytomidae	*Eurytoma* sp.*	Auld 1986
	Formicidae	*Paratrechina vividula*	Alvarez-Buylla and Martinez-Ramos 1990
		Messor arenarius	Abrahamson and Kraft 1965
		Solenopsis geminata	Risch and Carroll 1986
Lepidoptera	Arctiidae	*Tyria jacobaeae**	Crawley and Gillman 1989
	Carposinidae	*Carposina autologa*	Neser and Kluge 1985
	Cochylidae	unidentified sp.*	Louda 1982
	Coleophoridae	*Coleophora alticolella**	Randall 1986
	Gelechiidae	*Sophronia* sp.*	Louda 1982
	Geometridae	*Eupithecia cimicifugata**	Willson 1983
	Heliodinidae	*Heliodines nyctaginella**	Kinsman et al. 1984
	Incurvariidae	*Tegeticula* sp.*	Keeley et al. 1984
	Noctuidae	*Dioryctyra* sp.*	Merkel 1967
		Barbara sp.*	Koerber 1962
		Hadena sp.*	Pettersson 1991
	Oecophoridae	*Depressaria pastinacella**	Sheppard 1987
	Olethreutidae	*Laspeyresia* sp.*	DeSteven 1983; Kraft 1968; McLemore 1975; Werner 1964
	Pieridae	*Anthocharis cardamines**	Duggan 1985
	Pterophoridae	unidentified sp.	Louda 1982
	Pyralidae	*Homeosoma electellum**	Carlson 1967
		*Homeosoma stypticellum**	Lamp and McCarty 1982
	Tortricidae	*Clepsis peritana**	Louda 1982
		Phaneta imbridana	Hare 1980
		*Epiblema scutulana**	Leeuwen 1983
		*Cydia fagiglandana**	Nielsen 1977; Nilsson and Wastljung 1987
		*Phaneta imbridiana**	Hare 1980
Orthoptera	Gryllidae	*Hygronemobiu* sp.	Alvarez-Buylla and Martinez-Ramos 1990
Thysanoptera	Philoeothripidae	*Haplothrips* sp.*	Louda 1982
	Thripidae	*Frankliniella minuta**	Louda 1982
		*Frankliniella occidentialis**	Louda 1982

* predispersal insect seed predator

Predispersal seed predation of *Cirsium arvense*, Canada thistle, by *Orellia ruficauda* (Diptera: Tephritidae) occurs in 20% to 85% of the seed heads, and the proportion of damaged seeds per attacked head averages 20%–80%, depending on geographical location and sampling date (Forsythe and Watson 1985). Although the impact of this seed predator is not severe enough to result in elimination of this plant from an area where it is common, it is suspected to be an important factor in the population regulation of *C. arvense* (Forsythe and Watson 1985).

Quite often a complex of predispersal seed predators attack plants. Kjellsson (1985) found two species of mice in the myrmecochorous *Carex pilulifera* (Cyperaceae) (plants, dispersed by ants) fields before seed fall. During the night, the mice climb the *Carex* tufts, sometimes rising and reaching out for fruiting spikes. Normally, the culm is bitten just below the spikes, resulting in an oblique cut similar to cuts seen on damaged culms in the field. These mice consume diaspores from 20 to 25 culms over two hours. In addition to seed reduction from the mice, the ant species *Solenopsis flavicollis* is a major harvester of *C. pilulifera* seeds (Kjellsson 1985). It is estimated that *S. flavicollis* can reduce the seed pool by 21.3%.

A northern Swedish population of *Bartsia alpina*, an arctic perennial herb, is found to suffer high levels (normally 40%–50% of the fruits) of predispersal seed reduction from the combined predation by larvae of two insect species: *Aethes deutschinana* (Lepidoptera: Tortricidae) and *Gimnomera dorsata* (Diptera: Scatophagidae), both common seed predators of rhinanthoid Scrophulariaceae plants (Molau et al. 1989). The level of tortricid attack is more or less constant between years, and *B. alpina* seems to be the primary host plant for *A. deutschiana*. The scatophagid attack is lower than the tortricid attack, but more variable between years. This is probably due to the fact that this predator has another plant species, *Pedicularis lapponica*, as its main host. Also, the degree of its attack on *B. alpina* depends on the ability of *P. lapponica* to escape in time by shedding its seeds before adult emergence of this scatophagid (Molau et al. 1989).

The intensity of predispersal seed predation by insects varies with plant individuals. Traveset (1990) investigated two bruchid beetles preying on seed of *Acacia farnesiana*. She found that the intensity of seed predation varies notably among shrubs, without showing any seasonal pattern. Assuming that adult bruchids move among shrubs and that they can live up to three months and have

several generations within the five- to six-month fruiting season, an increase in seed predation might be expected during this period.

Predispersal seed predation by insects can be a key factor determining the distribution of plant populations. Louda (1982) investigated the variation in temperate shrubs *Haplopappus squarrosus* and *H. venetus* over an elevational gradient in the coastal sage scrub vegetation of San Diego County, California. *Haplopappus squarrosus* and *H. venetus* are characteristic of California coastal shrubs, the densities being higher on the coast than inland (Louda 1982; Louda et al. 1989). In San Diego County, they replace each other along an 80 to 100 km gradient from the coast to inland mountains; *H. squarrosus* is found inland, whereas, *H. venetus* predominates in coastal areas. Experimental exclusion of seed predators at sites along a gradient from the coast to inland mountains demonstrates two phenomena related to seed predation. First, predispersal seed predation limits seed input to the soil and subsequently affects local seedling recruitment for both species. Second, the net effect of these losses on adult plant distribution along the gradient changes as the physical conditions and impact of other predators varies. For the inland species, *H. squarrosus*, predispersal seed predation is the most important factor explaining both local recruitment and reproductive age class plant distribution over the gradient. Seedling recruitment is proportional to the number of uneaten seeds; predation lowers seed release differentially and is most severe at the coast. For control plants (with seed predators, without pesticides), the distributions of both seedlings and prereproductive age class plants exhibited the same trend as the observed reproductive plant distribution. But, for plants with seed predators excluded (with pesticides), the distributions of both seedlings and prereproductive age class plants corresponded to the reproductive age class plant distribution along the gradient. Louda (1978) concluded that with *H. squarrosus*, predispersal predators limit local recruitment and confine plant abundance to the inland portion of its potential niche. For the coastal *H. venetus*, seed predators also restrict seedling establishment. In addition, seedling mortality, caused primarily by herbivores and not by seed predators, is disproportionately severe inland. Together, higher seed losses and higher seedling mortality in the inland area restricted the observed distribution of *H. venetus* to the coastal portion of its potential range (Louda 1978).

POSTDISPERSAL SEED PREDATION

After seed has been shed from the parent plant it is available as food for a wide variety of animals including small mammals, birds, and insects. Postdispersal seed predation can occur on the soil surface, in the soil, or on some other substrate. Traveset (1990) found that the bruchid beetle, *Stator vachelliae*, finds seeds of the leguminous *Acacia farnesiana* in the feces of horse, deer, and ctenosaur lizards, the major *Acacia* seed dispersers in Costa Rica. Bruchids attack a greater proportion of seeds at 1 m than 5 m from the edge of a shrub's crown (Traveset 1990). Female bruchids lay eggs in seeds found on the surface of dung balls. The eggs hatch and larvae eat the seeds. Female bruchids have a preference for some seeds over others, and the attack rate varies in time and space. The proportion of seeds attacked is not related to their density in a dung ball.

As with predispersal seed predation, postdispersal seed predation can account for significant natural mortality. For instance, Kjellsson (1985) found that the post-seedfall predation rate of *Carex piluifera* in summer and autumn was 55% of the total seed population in northeastern Zealand, Denmark (Kjellsson 1985). Considerable seed mortality due to predation also occurred in the spring. The *Carex* seed pool was reduced 86% by seed predation (including pre-seedfall predation by mice). Mice and ground beetles reduced the seed pool by approximately 21% and 65%, respectively. Seed predation ranging between 30% and 80%, has been reported for several woodland myrmecochores (Culver and Beattie 1978; Heithaus 1981).

Though insects are known to be important postdispersal seed predators in most terrestrial forests, they also play an important role in marine tidal (mangrove) forests. A survey at 12 sites along the tropical Australian coast showed that between 3.1% and 92.7% of the seeds or propagules of 12 mangrove tree species were attacked by insects (Robertson et al. 1990).

Carabid beetles, ants, and rodents are the most studied postdispersal seed predators. More research has been conducted on ants and rodents as seed predators than on carabids. Predation behavior differs greatly between rodents and ants. A study conducted in the Israeli desert (Abramsky 1983) indicates that predation behaviors were similar to those reported for the same two groups in deserts of North America (Mares and Rosenzweig 1978). Rodents find seeds under the soil surface by olfaction, and are more efficient than ants at finding and harvesting seeds. In contrast,

ants can not find seeds under the soil surface. A second difference relates to the timing of predation behavior: rodents are nocturnal, while ants are mostly diurnal. Large seeds are utilized first by rodents, a shift to small seeds occurs only after most of the large seeds have been utilized. Rodents are primarily seed predators, while ants act also as seed dispersers. The interference of ant predation from rodent predation is minimal as ants continue their foraging even while seeds in trays are replaced (Abramsky 1983). Competition may occur between ants and rodents for seeds in low density *Acacia* stands (Holmes 1990).

Ants show an interesting seed preference behavior. Risch and Carroll (1986) found that in feeding preference field studies, the amount of each seed type removed by ants was strongly influenced by the amount and kinds of other seeds in the immediate area. A strongly preferred seed is removed less frequently if it occurs in the midst of non-preferred seeds. Non-preferred seeds are taken much more readily if they occur with preferred seeds (Risch and Carroll 1986). Studies allowing ants free passage to seeds, but excluding larger seed predators show that seed predation of the tropical pioneer tree, *Cecropia obtusifolia*, was not significantly different from uncovered control seeds, indicating that ants were the primary seed predators. The distribution of seed predation rate by ants after four days of experimentation was bimodal, suggesting once ants discover a dish of seeds, all of them are taken (Alvarez-Buylla and Martinez-Ramos 1990).

Seed predation by the Carabidae was reported as early as the 1880s (Forbes 1880, 1883; Johnson and Cameron 1969; Webster 1880, 1900). Nitzsche (1893) reported that carabid beetles of the genus *Harpalus* destroyed up to 80% of the seed and seedlings in nursery beds. Predation rate by carabids varies with predator and prey species. Lund and Turpin (1977) tested predation by five Carabidae species on six seed species. In a test to determine if beetles would attack weed seeds in the laboratory, *Harpalus pensylvanicus* damaged more seeds than other carabid species. However, the number of seeds damaged varied with the seed species. *Pterostichus chalcites* and *P. lucublandus* damaged similar numbers and species of seeds, but only chickweed, *Stellaria media*, was damaged in high numbers. The carabid *Evarthrus sodalis sodalis* damaged only a few seeds of any species (Lund and Turpin 1977).

Further study of predation by *Harpalus pensylvanicus* showed that predation rate varies with seed species. On the basis of predation preference over a 40- hour period, seed species could be

grouped into three to five categories (Lund and Turpin 1977). Best and Beegle (1977) found that *H. pensylvanicus* and *Evarthrus alternates* feed on many kinds of seeds with preference for smooth dock seeds, barnyard grass seeds, and yellow foxtail seeds. Lund and Turpin (1977) found that *H. pensylvanicus* prefers green foxtail, *Setaria viridis* var. *major*, over other seed species tested. The size of seeds tested might influence the number of seeds damaged in one of two ways. Larger seeds provide more food per seed, and it requires fewer seeds to satiate the animal. Also, the size and shape of the seed might affect the ease with which the beetle can handle and open the seed. Preference for one seed species over another might well be due to the ease of handling and opening of the seed rather than selection based on textural or chemical clues (Lund and Turpin 1977).

Although *H. pensylvanicus* is usually a postdispersal seed predator (Best and Beegle 1977; Lund and Turpin 1977), it may also act as a predispersal seed predator in specific habitats. Manley (1992) found that *H. pensylvanicus* adults have more impact on seed production prior to seed maturity than afterwards. Beetle populations in 1992 were highest prior to seed maturity. Caged adults fed on both individual mature seeds of grasses and developing seed heads. Adults readily fed on inflorescences of crabgrass and fall panicum (whose heads are near or on the soil surface), but not on green foxtail (whose seed heads are distant from the soil surface), though beetles fed on individual green foxtail seeds. This suggests that *H. pensylvanicus* may readily attack immature seeds or seed heads when they are near the soil surface.

Considerable research has been conducted on the postdispersal seed predation of the European carabid *Harpalus rufipes*. This species is primarily a seed predator (Briggs 1965; Curtis 1860; Forbes 1880, 1883; Johnson and Cameron 1969; Luff 1980; Skuhravy 1959; Webster 1880, 1900; Zhang 1993; Zhang et al. 1994; Znamenskii 1926); however, when seeds are in low relative abundance, *H. rufipes* will feed on small insects (Chiverton 1987; Coaker and Wiliams 1963; Cornic 1973; Dempster 1967; Hamon et al. 1990; Rivard 1966; Sunderland 1975; Sunderland et al. 1987; Zhang et al. 1994). Adults have been observed to feed on the seeds of 29 of 38 species of plants in the laboratory (Briggs 1965; Zhang 1993). Preference for seed species is shown by *H. rufipes* adults (Zhang 1993). Grasses are a preferred type of seed along with small seeds such as common lambsquarters, *Chenopodium album*, and dandelion, *Taraxacum officinale*. Seeds of species in the Cruciferae are the least preferred. The mode of feeding is associated with seed

species as is the functional response (Zhang 1993). Adults exhibit a type II functional response (Price 1984) to preferred seeds and a type I response to less preferred seeds.

Larvae of *H. rufipes* are also seed predators. Larvae scrape soil away from the terminal cell of the tunnel with their mandibles and press it into the side of the burrow with the dorsal surface of the head. Seeds are carried in the mandibles before being embedded in the side of the burrow with the head. There is often a closely packed cache of seeds just above the terminal cell where the larvae consume single seeds (Thiele 1977). Luff (1980) found that second instar larvae of *H. rufipes* fed on 18 out of 24 species of seeds offered in a choice test. Eight "favorable" species were eaten by at least six of ten larvae to which they were offered. These species were *Lolium perenne*, *Festuca rubra*, *Chenopodium album*, *Agrostis tenuis*, *Dactylis glomerata*, *Trifolium repens*, *Senecio jacobaea*, and *Medicago lupulina*. The remaining "unfavorable" species were *Brassica rapa*, *Cardamine amara*, *Scabiosa columbaria*, *Brassica oleracea*, *Hypericum perforatum*, *Antennaria dioica*, *Campanula rotundifolia*, *Heracleum sphondylium*, *Sisymbrium officinale*, *Brassica napus*, *Filipendula ulmaria*, *Geum urbanun*, *Hesperis matronalis*, *Scutellaria galericulata*, and *Solanum dulcamara*. When given a choice among six "favorable" seeds offered two at a time, the ranking was similar to that when the same seeds were offered without choice, although a more distinct division appeared between grasses and *C. album*, which were highly preferred, and the remaining two lesser preferred seed species.

Germinating seeds are also damaged by *H. rufipes*. Larvae feed on the endosperm of germinating seeds of perennial rye grass (*Loliu perenne*). The larval growth rate is more rapid with germinating seeds of lambsquarters, *C. album*, groundsel, *Senecio vulgaris*, and the grasses *Agrostis tenuis*, *Festuca ovina,* and *Phleum pratense*, than with those of perennial rye grass and cereals. There are no differences between the feeding rate on germinating and non-germinating seeds of *L. perenne*. The mean numbers of germinating and non-germinating seeds eaten by ten larvae were 2.8 ± 0.4 and 2.8 ± 0.3, respectively (Luff 1980).

H. rufipes is associated with cultivated habitats and is most abundant in small fields as compared to large agricultural fields (Traveset 1991). Another characteristic of fields that may affect *H. rufipes* abundance is "weediness." Speight and Lawton (1976) used an artificial prey to test the effect of the weed *Poa annua* in cereal fields on the abundance of carabids, including *H. rufipes*. Within one field, areas of high weed cover had more predatory ground

beetles, and artificial prey suffered significantly greater 'mortality' than areas with few weeds. Diversity of weed species has been suggested to be important for ground beetle populations (Murdoch et al. 1972; Pimental 1961; Speight and Lawton 1976). The relationship between beetle activity and the frequency and abundance of *Poa annua* is probably complex, but it is likely that the role that the weeds play in protecting the predators from weather extremes, i.e., insolation during the day, and desiccation, both during the day and at night, is important (Speight and Lawton 1976). Rivard (1966) found higher catches of carabids in areas of higher humidity, and Thiele (1964) considers that relative humidity is a key factor in the abundance of the majority of carabids and that microclimate in vegetation is very important. High weed densities provide a high relative humidity. It is also possible that there is an indirect effect of weed density due to the abundance of natural prey, which may be more common in dense weed patches (Speight and Lawton 1976). However, exception to the weediness hypothesis exists. Purvis and Curry (1984) found that none of the dominant carabids they studied respond positively to weediness. Although, the activity of *P. melanarius* appeared to persist longer in weedy plots in September, both this species and *H. rufipes* were equally active in all plots during their peak abundance in August. One possible reason may be the crop (beet) provides shade and high relative humidity even in the absence of weeds.

Cultivation may favor *H. rufipes* because of larval requirements for seeds as food. An open soil surface encourages weed growth, and *H. rufipes* larvae would be short of food in a field kept completely weed free (Luff 1980). After using pitfall traps to investigate the carabid fauna of arable land, Scherney (1960) concluded that certain Carabidae (*H. rufipes* included) were associated with cultivation; the numbers taken in pitfall traps in different habitats were in the following order: wheat fields > barely > potato > clover > grass meadow > densely weed-covered waste ground. Although agricultural monocultures are considered unstable habitats, they may provide stable conditions for species dependent on relatively bare, loose cultivated soil, such as *H. rufipes* (Luff 1980).

Other environmental factors also have an impact on seed predation rate by carabids. Brust and House (1987) investigated weed seed loss in conventional till and no-till soybean agroecosystems. Seeds of four broadleaf weed species (ragweed, pigweed, sicklepod, and jimson weed) and one grain crop species (wheat) were provided in a free choice design with densities of 10,

25, and 50 seeds per 24 cm^3 of soil. Approximately 2.3 times more seeds overall, and 1.4 times more large seeds as a group were consumed in no tillage systems than in conventional tillage systems.

In low-input, no-tillage treatments, large ground beetles (15–25 mm) and mice preferentially fed on the large seed species, while small carabids (< 15 mm), ants and crickets, fed almost exclusively on the smaller seed species. Carabid beetles were responsible for more than half of all seeds consumed (Brust and House 1987). The difference in predation rates between no-tillage and conventional tillage systems can be explained by the differences of the seed predator abundance as a result of soil disturbance. In the southeastern United States, conventional tillage systems (moldboard plow/disk) generally support fewer soil arthropods than no-tillage systems (Blumburg and Crossley 1983; House and All 1981; House and Parmelee 1985). Soil disturbances in natural ecosystems can also depress soil arthropod numbers, resulting in a concomitant reduction in seed predation (Mittelbach and Gross 1984).

SEED PREDATION AND PLANT POPULATION DYNAMICS

Plant Population Recruitment

Seed predation may influence plants at both the population and individual levels. At the population level, potential effects include (a) lower recruitment rate due to reduction in occupancy of "safe sites" (Louda 1978) suitable for germination and establishment, (b) discontinuous recruitment due to periodic or "mast" fruiting and the accompanying satiation of seed predators (Janzen 1971a), and (c) alternation of adult distribution, due to density dependent seed predation (Janzen 1971a). The potential consequences of seed predation at the individual level have been less widely explored. Seed production and spatial location may influence the severity of predispersal predation on different individuals (Moore 1978). The ecological result is that the relative contribution of some adults to successful seed production will be greater than that of others, and may be so consistently, from year to year. If these traits are heritable, the evolutionary result is a selective force upon adult characteristics that confers relative escape from predation (DeSteven 1983).

Evaluation of predation in seed bank dynamics is either trivial or surprisingly difficult. Seed consumption is a major gustatory strategy that causes significant seed losses. So in the trivial sense, seed predation, like any mortality factor causing a consistent loss of young, will influence population ecology and evolution. Consis-

tent losses have a potential impact on plant abundance, distribution, competitive status, life cycle traits, and other adaptations. Differences in damage among individuals or between species can be significant even where the magnitude of the loss is small.

Seed predation rate may be related to seed size. Reader (1993) found adding a cage to reduce seed predation, especially by ants, did not increase seedling emergence significantly for small seeds (0.06–0.14 mg). In contrast, seedling emergence increased significantly for larger seeds (0.15–12.2 mg) (Reader 1993). Seed predation not only affects the number of seeds, but also reduces the seed viability. Andersen (1988) compared two methods of studying insect predation on seeds in Australia. The conventional method (inspecting insect attack symptoms) indicated that insects attacked only 2%, 10%, 28%, and 1% respectively of *Eucalyptus baxteri*, *Leptospermum myrsinoides*, *L. juniperinum*, and *Casuarina pusilla* seeds, whereas bagging experiments indicated that insects reduced seed production by 66%, 64%, 44%, and 83%, respectively. Therefore, if the bagging experiments reflect a more accurate picture of predation, then insect seed predators may cause far greater losses than they appear to (Andersen 1988).

How important is seed predation to recruitment in stable populations of long-lived perennials? The importance of seed losses to population recruitment at any point in time is related to the abundance of "safe sites." Insect seed predation rate can be very high, up to 100% of the seed population (Sallabanks and Courtney 1992). However, these losses do not necessarily have an important impact on population recruitment because (a) in most years predation is not 100%, (b) in most years recruitment appears to be limited by a rarity of safe sites and not by seed supply, and (c) the losses do not prevent the establishment of large seed banks (ranging from 30 to 1,100 viable seeds per m²) potentially capable of exploiting temporary conditions favorable for recruitment (Sallabanks and Courtney 1992).

Seed-feeding insects, as compared with leaf-feeding ones, often destroy a large fraction of their food supply (Janzen 1971a). Although seed predation rate may be high on the average, it is also highly variable (House and Parmelee 1981). The dynamics of a seed-predator system seems to depend primarily on how seed predator populations "track" their variable resources in time and space (Solbreck and Sillen-Tullberg 1986). At present, few seed predation models are available. Reduction of the seed bank through seed predation can be expressed as an exponential decay curve (Boucher 1981):

$$dN / dt = -kN;$$

where N is the seed number in the seed bank, t is time, and k the constant instantaneous removal rate. The number of seeds in the seed bank at any time (t) is

$$N_t = N_0 \exp^{-kt}$$

This relationship may be affected by seed size. Removal rate may decrease with increasing seed size and there maybe a satiation effect (Boucher 1981).

Seed Dispersal

Seed removal has two effects on the seed bank. At high plant densities, seeds can be removed and eaten by all seed-predating and dispersing animals. Therefore, high densities of the seed predators and dispersers will play an important role in reducing the seed bank. At low plant densities, there will be competition between seed predators and seed dispersers. Seed predators such as rodents consume seed where it is found and directly reduce the seed bank. Whereas, a high population of ants (dispersers) will remove seeds from the surface to other locations, where seeds may accumulate for the next generation. At this point, seed dispersers are beneficial to the recruitment of the next plant generation. Holmes (1990) demonstrated this interaction while investigating seed removal in the litter layer of *Acacia* spp. stands at bimonthly intervals throughout a one-year period. He found that both ants (dispersers) and rodents (predators) removed significant quantities of seeds and may compete for seeds in low density stands. Seed removal from artificial depots by invertebrates was greatest prior to seed-fall (September–November) and lowest during seed-fall (January–March). Rodents may consume a large proportion of the annual seed production at low *Acacia* spp. densities, but ants play a critical role in accumulating seed banks.

Spatial Patterns of Plants

Seed predation rates may also determine plant spatial patterns. In two experiments, Alvarez-Buylla and Martinez-Ramos (1990) found that ants (*Paratrechina vividula*) and grasshopper nymphs (*Hygronemobius* spp.) were the dominant seed predators of the tropical pioneer tree, *Cecropia obtusifolia*. Removal rates ranged from 27% to 98% in four days and were significantly higher in gap and mature patches than in building patches. Together with pathogens, predators resulted in low survivorship of the tropical

pioneer tree seeds and a rapid turnover rate of its seed bank (1.02 to 1.07 years) (Alvarez-Buylla and Martinez-Ramos 1990).

Whelan et al. (1990) examined the spatial and temporal patterns of postdispersal seed predation of vertebrate-dispersed plant species (*Cornus drummondii* and *Prunus americana*) in temperate woodland and old-field habitats. Rates of seed loss by all predators including insects varied with microhabitat (near logs, tree trunks, and open forest floor), macrohabitat (old-field, forest), plant species, year, and time of dispersal within a year. The levels of final mortality of seeds did not vary with microhabitat or time of dispersal, but did vary between macrohabitats, plant species, and years.

As discussed previously, a study conducted by Louda (1978) showed that the plant *H. squarrosus* is confined to inland portions of its potential niche due to the seed predation of insects. In turn, the distribution of seed resources may affect seed predation. Seed predation in relation to patterns of pod (and seed) distribution was examined in five samples of the common milkweed (*Asclepias syriaca*), in tests of the "resource-concentration" effect both within and between plants (Franson and Willson 1983). Plants with large clusters of pods produced more undamaged pods, and, by this measure, were more successful than plants with small clusters.

Adaptation

Theoretically, seed predation, like other forms of predation, should cause two types of response by the exploited plant population. The first is adaptation, via selection for morphological, chemical, temporal, and spatial mechanisms of predator avoidance. The second is modification of numerical and spatial occurrence, via elimination and redistribution of better-adapted individuals in the population through differential patterns of attack (Harper 1969; Janzen 1969, 1971a, 1971b; Louda 1978). Although variability in the damage to seeds is generally high, seed predation is thought to represent a strong selective force acting on protective structures (Janzen 1969, 1970; Smith 1975); dispersal phenology (Heithaus 1981; Janzen 1971b; Silvertown 1980); and dispersal method (Beattie and Lyons 1975; O'Dowd and Hay 1980). The dispersal of seeds from the parent plant and its surroundings is often thought to decrease the risk of predation and pathogen attack (Augspurger 1983; Harper 1977; Janzen 1969; Wilson and Janzen 1972). Hence, it has been suggested for several genera (e.g., *Viola*, *Sanguinaria*, *Asarum*) that seed predation has been an important selective force in the evolution of myrmecochory (Beattie 1983, Beattie and Lyons 1975, Heithaus 1981, O'Dowd and Hay 1980).

Seed predation may also be a selective factor influencing the evolution of seed protective characteristics such as spine length and wall thickness of burrs. In a study of *Xanthium strumarium,* predation was found to be more intense in populations with low mean burr length and to decline linearly with increasing burr length (Hare 1980). Ten populations of *X. strumarium* occurred in quite similar habitats in proximity to each other, but showed quite striking differences in burr size and susceptibility to seed predators. Mean burr length varied between 15.4 and 19.5 mm among populations, and the percentage of attacked burrs varied from 3% to 84% among populations in one year. Burr length variation among populations is primarily genetically controlled, and differences in susceptibility among populations persisted when plants were grown under uniform conditions and uniformly exposed to insect attack. The probability of attack declined linearly with increasing burr length under both field and experimental conditions. Susceptibility was negatively correlated with mean burr length among plants when plants from all populations were pooled. Seed predation was also higher in populations with a lower mean burr length. Thus, by attacking smaller burrs, Hare (1980) suggests that these insects can be important natural selection agents for increased burr size. On the basis of oviposition behavior of the two insects, *Euaresta aequalis* (Diptera: Tephritidae) and *Phaneta imbridana* (Lepidoptera: Tortricidae), thicker burr walls and longer burr spines could reduce the insects' ability to penetrate burrs. These characteristics were positively correlated with burr length, thus shorter burrs may be more successfully attacked because they are more easily penetrated (Hare 1980).

Seed predation and the coexistence of tree species in tropical forests were studied by Hubbell (1980). Host-specific seed and seedling predation can explain the coexistence of the large number of tree species in tropical forests (Harper 1977). Janzen (1970) noticed that virtually all seeds underneath the parent are killed by seed predators, and proposed that only those viable seeds that are transported some distance from the parent have any significant chance to escape discovery and germinate. Accordingly, such predation should lead to a low density of, and wide spacing between, adult trees. This would prevent any one species from becoming dominant, provided those seed sources for other species exist to fill the available habitat (Janzen 1970). Connell (1971) argued that predation was a much more likely agent than interspecific competition to prevent single-species dominance in tropical forests. In optimal climates, predator abundance should build until

they are resource limited. He postulated that host-specific herbivores (principally folivores) attracted by adult trees would also discover, defoliate, and kill all seedlings in the vicinity of adult trees. Seedlings are presumably less resistant to defoliation. Again, habitat in the neighborhood of adults of one tree species would be open for colonization by juveniles of other tree species, and diversity would be maintained. Seed density and the probability of seed survival can be expected to change with increasing distance from the parent tree because fewer seeds are expected to be carried to greater distances from the parent (Connell 1971). Regardless of the mode of seed dispersal, the "seed shadow" (seeds per unit area) curve is a monotonically decreasing function of distance from the parent tree (Willson 1992). On the other hand, because seed and seedling predation are greater near the parent, the per capita chance of seed survival to maturity is a monotonically increasing function of distance from the parent. The product of the seed shadow and the per capita chance of seed survival to maturity curves describes the density of offspring that survive to maturity at different distances from the parent tree (Hubbell 1980).

Temporal patterns of plant reproduction may also be a result of seed predation. "Mast seeding" or "mast fruiting" describes the phenomenon of synchronous production of seeds within a plant population in one year followed by an interval when few seeds are set. This is a widespread phenomenon among temperate floras and is common in hardwood trees and conifers (Harper 1977). Seed predators can act as a selective force favoring mast fruiting, due to the excessive seed losses incurred by the asynchronous individuals that fruit in "off-peak" years. High predispersal seed predation in poor fruiting years might also enhance fruiting periodicity, if, by preventing seeds from maturing, the resources that would have been used for maturation are instead stored for use in a subsequent year. The weevil *Pseudanthonomus hamamelidis* is host specific and univoltine on witch hazel (*Hamamelis virginiana*). The fluctuating pattern of fruit production is a key feature in understanding the demographic impact of seed predation on witch hazel (DeSteven 1983). DeSteven (1983) observed that fruit production fluctuated between 1977 and 1980. In poor fruiting years (1977 and 1978), oviposition sites were limited due to low fruit abundance and attack percentages on fruit crops were high. The size of the weevil population appeared to be resource limited in such years, since searching weevils may be unable to find particular individual plants because they are small, have very few fruits, or are extremely isolated from conspecifics. Following poor fruiting years,

the fruit crop in a production year "satiates" the relatively small weevil population, with the result that seed predation intensities are substantially lower, and more seeds escape predation. Continued high fruit production allows an annual increase in weevil numbers and in fruit attack; however, any reduction in fruit production following a good fruiting year lowers weevil population size, and fruit attack increases. The result for witch hazel is a pulse of successful seed survival in the occasional production year that satiates the seed predator population (DeSteven 1983). Similar patterns of high seed predation in years of poor seed production have been observed in a number of forest trees, where fluctuating fruiting patterns also appear to regulate seed predator populations (Abrahamson and Kraft 1965; Gardner 1977; Mattson 1971; Miller 1973).

Ballardie and Whelan (1986) investigated the relationship between masting and seed dispersal, and seed predation in the cycad *Macrozamia communis* and found that the result was different from DeSteven's (1983) study. They found that dispersal of seeds by opossums was poorer from source plants in a masting population than from source plants in an adjacent, non-masting population (Ballardie and Whelan 1986). This resulted in fewer seeds per seeding female plant in the masting plot being dispersed to favorable sites. Predation of seeds over the year of the experiment was much more severe in the masting plot than in the nonmasting plot. Very few seeds were touched by rats in the nonmasting plot. Masting did not allow any escape from predation. The absolute number of seeds eaten in the masting plot was more than ten times greater than in the nonmasting plot. They suggest that the mast seeding observed in *M. communis* may not be adaptive, but is more likely a consequence of other factors, which synchronize flowering within local populations (Ballardie and Whelan 1986).

Plant Community Dynamics

A few studies have shown that seed predation can affect plant community structure. A native fire ant, *Solenopsis germinata*, was observed to harvest small seeds, especially grasses, in disturbed habitats in wet tropical areas of Mexico and Central America (Inouye et al. 1980; Risch and Carroll 1986). If common, this ant can lower overall abundance of many weedy species. When the ant exhibited a strong preference for seeds from one plant species, total plant biomass was significantly lower (by up to 50%) in plots with ants for about the first 50 days after planting. Subsequently, the non-preferred species increased, and 83 days after planting, total plant biomass was about the same in the presence and absence of

ants. Seeds of *Paspalum distichum* were highly preferred by the ants, while *Daucus carota* were rejected. In the absence of ants, *P. distichum* is competitively superior to *D. carota*. Ants reverse the course of plant competition. Thus, *P. distichum* contributed little to total weed biomass. A crop growing with ants can thus benefit from reduced competition early in the season (Risch and Carroll 1986). Due to seed preference, ants may selectively remove dominant small seeds, and as a result, increase the community diversity and evenness (Inouye et al. 1980).

WEED CONTROL WITH SEED PREDATORS

Seed predation provides potential for classical biological control of weeds by seed predators (Julien 1982). Weevils have proven to be good candidates in weed integrated pest management (IPM) programs. *Rhinocyllus conicus*, a thistle-head-feeding weevil introduced from France successfully controlled *Carduus nutans* (musk thistle) at a Virginia release site (Pulaski County) six years after the initial release of 100 adults in 1969. Thistle density was reduced by 95%. In 1974 and 1975, about 90% of the thistles were attacked by the weevil; more than 10% of the terminal heads were aborted. Persistent pressure from increasing weevil population on the thistles brought about dramatic changes in the thistle problem (Kok and Surles 1975). Furthermore, 11 years of inter-species population dynamics study at two release sites, Frederick County and Pulaski County in Virginia, shows that thistle reduction was dramatic after the explosive phase of the weevil build-up during the fifth year after release. This was followed by weevil dispersal and resurgence of plant density. However, the resurgent plants were smaller and produced fewer buds than the thistles prior to weevil release; thus bud density during resurgence was significantly lower than the initial density. Between 1969 and 1980, decline in musk thistle bud numbers was 80% at the Frederick County site and 97% at the Pulaski County site (Kok and Pienkowski 1985). *R. conicus*, when introduced into San Luis Obispo County, California, also played an important role in the control of Italian thistle, although the seed loss was only 55% (Goeden and Ricker 1985).

Neser and Kluge (1985) found an introduced seed predator to show promise in weed control in South Africa. *Hakea sericea* (Proteaceae), a fire-adapted woody plant from Australia, is an important weed in the species-rich vegetation of the Cape Mountains, South Africa. This weed occurred over nearly half a million ha, mainly in mountainous areas in dense, impenetrable thickets.

The seeds remain viable in woody follicles that accumulate on the plant over the years. It was estimated that 75 million seeds/ha may be accumulated on 15-year-old stands. From surveys of natural enemies in Australia, two complementary seed-attacking species were selected and tested for release in South Africa. These are the weevil *Erytenna consputa* (Coleoptera: Curculionidae) whose larvae develop in, and cause the death of, young fruits, and the moth *Carposina autologa* (Lepidoptera: Carposinidae) that develops on seeds inside mature follicles accumulated on living plants. *Erytenna consputa* is strikingly adapted to its host and to surviving fires. The weevil was established in South Africa after the release of small numbers of field-collected adults from different climatic regions in Australia. Climatic matching was not as important as host strain matching in the establishment of the weevil. Following establishment, *E. consputa* has greatly (up to 86% of the total fruit mortality) reduced seed accumulation by *H. sericea* and has started to suppress the dense regeneration of the weed. However, additional agents may be required for an integrated control program against this weed from Australia (Neser and Kluge 1985).

Other insect seed predators that may have potential for classical biological control are the seed beetle *Spermophagus sericeus* (Bruchidae) for control of field bindweed, *Convovulus arvensis* (Rosenthal 1985; Rosenthal and Buckingham 1982); the flower- and seed-feeding weevil *Acallopestus maculithorax* for control of velvetleaf, *Abutilon theophrasti* (Mittelbach and Gross 1984); and two seed predatory weevils, *Ceutorhynchus turbatus* and *C. parvilus*, for control of hoarycress, *Cardaria draba* (Lipa 1974).

Inundative release strategies for temporary (one to five years) reduction of weed seed banks has not become a tactic in IPM programs. This is probably due to the expense and difficulty in rearing the necessary numbers of seed predators for such a management tactic relative to the cost of herbicides (Deloach 1978).

A promising tactic for weed management that has also not been implemented is conservation of existing weed seed predators (Liebman and Janke 1990). This tactic has advantages over classical biological control approaches, which rely on foreign introductions. Considerations such as attack of non-target host plants or competitive exclusion of native insect species are usually not significant concerns (Charudattan and Deloach 1988). Carabids and ants are ideal candidates for conservation in north temperate US agroecosystems (Best and Beegle 1977; Blumburg and Crossley 1983; Brust and House 1987; House and All 1981; House and Parmelee 1985; Johnson and Cameron 1969; Lund and Turpin

1977; Manley 1992; Mittelbach and Gross 1984; Reader 1993; Risch and Carroll 1986; Rivard 1966; Webster 1880; Zhang 1993). Conservation of these seed predators in agroecosystems requires that their life systems be understood in sufficient detail so that IPM programs can be designed that minimize mortality and maximize seed predator population growth, under the constraints of managing insect pests in an agroecosystem (Bird et al 1990). The impact of factors such as tillage (Brust and House 1987; House and Parmelee 1985), cover crops (Reader 1993; Zhang 1993), rotation crops (Zhang 1993), and pesticides (Zhang 1993) on the population dynamics of weed seed predators must be investigated for each insect species targeted for conservation. Landscape features such as field borders, topography, and spatial pattern and aggregation of farm lands and forests have not been studied in regards to the population dynamics of insect seed predators. There have been many field studies conducted that assess removal rates and mortality rates of seeds under field conditions, however, there is a general dearth of information on the quantification of insect seed predator numerical and functional responses and interference rates under field conditions (Zhang 1993). The lack of manipulative field studies of weed management by conservation of insect seed predators probably reflects the limited amount of research that has been conducted in the area of alternatives to herbicide based weed management (Liebman and Janke 1990).

We hope that this review has provided a framework for understanding the mechanisms of insect seed predation, the diversity of insects that prey on seeds, and the ecological and evolutionary consequences of insect seed predation. Insect seed predation can play significant roles in reducing plant population growth, modifying intraspecific and interspecific competition, shifting spatial and temporal distribution, affecting species evolution, and plant community structure, both in natural and agricultural ecosystems. Further study on insect seed predation-plant population dynamics, insect seed predator behavior, and how to economically incorporate insect seed predators into integrated weed management programs are all important areas of investigation with regards to insect predation of seeds. We have found, by reviewing the literature, that there is a lack of research that attempts to link weed or plant population or community dynamics with the population or community dynamics of insect seed predators. Most studies focus solely on either the plant's population dynamics or the insect seed predator's population dynamics. The challenge, therefore, in the future is to develop a theoretical basis for the ecology of seed predation.

REFERENCES

Abrahamson, L.P., and K.J. Kraft. 1965. A population study of the cone moth *Laspeyresia toreuta* Grote in *Pinus banksiana* stands. *Ecology* 46:561–563.

Abramsky, Z. 1983. Experiments on seed predation by rodents and ants in the Israeli desert. *Oecologia* 57:328–332.

Alvarez-Buylla E.R., and M. Martinez-Ramos. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84:314–325.

Andersen, A.N. 1988. Insect seed predators may cause far greater losses than they appear to. *Okios* 52:337–340.

Ashton, D.H. 1979. Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in central Victoria. *Australian J. Ecology* 4:265–277.

Augspurger, C.K. 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *J. Ecol.* 71:759–771.

Auld, T.D. 1983. Seed predation in native legumes of south-eastern Australia. *Australian J. Ecology* 8:367–376.

———. 1986. Variation in predispersal seed predation in several Australian *Acacia* spp. *Oikos* 47:319–326.

Auld, T.D., and M.A. O'Connell. 1989. Changes in predispersal seed predation levels after fire for two Australian legumes, *Acacia elongata* and *Sphaerolobium vimineum*. *Oikos* 54:55–59.

Ballardie, R.T., and R.J. Whelan. 1986. Masting, seed dispersal and seed predation in the cycad *Macrozamia communis*. *Oecologia* 70:100–105.

Beattie, A.J. 1983. Distribution of ant-dispersed plants. In *Dispersal and Distribution,* ed. K. Kubitzki, pp. 249–267. Parey, Hamburg.

Beattie, A.J., and N. Lyons. 1975. The effect of rodent seed predation on four species of California annual grasses. *Oecologia* 33:101–113.

Best, R.L., and C.C. Beegle. 1977. Food preferences of five species of carabids commonly found in Iowa cornfields. *Envir. Ent.* 6:9–12.

Bird, G.W., T. Eders, F.A. Drummond, and E. Groden. 1990. Design of pest management systems for sustainable agriculture. In *Sustainable Agriculture in Temperate Zones,* ed. C.A. Francis et al. pp. 55–110. John Wiley and Sons, Inc., New York.

Blumburg, A.Y., and D.A. Crossley Jr. 1983. Comparison of soil surface arthropod populations in conventional-tillage, no-tillage and old-field systems. *Agro-Ecosystems* 8:247–253.

Bohart, G.E., and T.W. Koerber. 1972. Insects and seed production. In *Seed Biology,* Vol 3, ed. T.T. Kozlowwski, pp. 1–50. Academic Press, New York.

Boucher, D.H. 1981. Seed predation by mammals and forest dominance by *Quercus oleoides*, a tropical lowland oak. *Oecologia* 49:409–414.

Briggs, J.B. 1965. Biology of some ground beetles (Coleoptera: Carabidae) injurious to strawberries. *Bull. of Ent. Res.* 56:79–93.

Brust, G.E., and G.J. House. 1987. Weed seed destruction by arthropods and rodents in low-input soybean agroecosystems. *American J. Alternative Agriculture.* 3(1):19–25.

Carlson, E.C. 1967. Control of sunflower moth larvae and their damage to sunflower seeds. *J. Econ. Entomol.* 60:1068–1071.

Charudattan, R., and C.J. Deloach. 1988. Management of pathogens and insects for weed control in agroecosystems. In *Weed Management in Agroecosystems: Ecological Approaches,* ed. M.M. Altieri and M. Liebman, pp. 245–264. CRC Press, Boca Raton, FL.

Chiverton, P.A. 1987. Predation of *Rhopalosiphum padi* (Homoptera: Aphididae) by polyphagous predatory arthropods during the aphids pre-peak period in spring barley. *Ann. Appl. Biol.* 111:257–269.

Coaker, T.H., and A. Wiliams. 1963. The importance of some Carabidae and Staphylinidae as predators of the cabbage root fly *Erioischia brassicae* (Bouche). *Entomologia Experimentalis et Applicata* 6:156–164.

Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forests. In *Dynamics of Populations*, ed. P.J. den Boer and G.R. Gradwell, pp. 298–312. PUDOC, Wageningen.

Cornic, J.F. 1973. Etude du regime alimentaire de trois especes de carabiques et de sez variations en verger de pomiers. *Annals. Soc. Ent. Fr.* 9:69–87.

Crawley, M.J. 1992. Seed predators and plant population dynamics. In *Seeds, the Ecology of Regeneration in Plant Communities,* ed. M. Fenner, pp. 157–191. C.A.B. International, Wallingford, Oxon.

Crawley, M.J., and M.P. Gillman. 1989. Population dynamics of cinnabar moth and ragwort in grassland. *J. Animal Ecology* 58:1035–1050.

Culver, D.C., and A.J. Beattie. 1978. Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. *J. Ecology* 66:63–72.

Curtis, J. 1860. *Farm Insects.* Glasgow, Blackie.

Deloach, C.J. 1978. Considerations in introducing foreign biotic agents to control native weeds of rangelands. Proc. 4th Int. Symp. Biological Control of Weeds, ed. T.E. Freeman. University of Florida, Gainesville.

Dempster, J. P. 1967. The control of *Pieris rapae* with DDT I. The natural mortality of the young stages of *Pieris*. *J. Appl. Ecol.* 4:485–500.

DeSteven, D. 1983. Reproductive consequences of insect seed predation in *Hamamelis virginiana*. *Ecology* 64 (1): 89–98.

Duggan, A.E. 1985. Predispersal seed predation by *Anthocharis cardamines* (Pieridae) in the population dynamics of the perennial Cardamine pratensis (Brass.). *Oikos* 44:99–106.

Forbes, S.A. 1880. Notes on insectivorous Coleoptera. Ill. *State Lab. Natur. Hist. Bull.* 3:153–160.

———. 1883. The food relationships of Carabidae and Coccinellidae. *State Lab. Natur. Hist. Bull.* 1:33–64.

Forsythe, S.F., and A.K. Watson. 1985. Predispersal seed predation of Canada thistle. *Can. Ent.* 117:1075–1081.

Franson, S.E., and M.F. Willson. 1983. Seed predation and patterns of fruit production in *Asclepias syriaca* L. *Oecologia* 59:370–376.

Gardner, G. 1977. The reproductive capacity of *Fraxinus excelsior* on the *Derbyshire limestone. J. Ecology* 65:107–118.

Goeden, R.D., and D.W. Ricker. 1985. Seasonal asynchrony of Italian thistle, *Carduus pycnocephalus*, and the weevil *Rhinocyllus conicus* (Coleoptera: Curculionidae) introduced for biological control in Southern California. *Environ. Entomol.* 14:433–436.

Green T.W., and L.G. Palmbald. 1975. Effects of insect seed predators on *Astragalus cibarius* and *Astragalus utabensis* (Leguminosae). *Ecology* 56:1435–1440.

Hainsworth, R.F., L.L. Wolf, and T. Mercier. 1984. Pollination and pre-dispersal seed predation: Net effects on reproduction and inflorescence characteristics in *Ipomopsis aggregata. Oecologia* 63:405–409.

Hamon, N., R. Bardner, C. Allen-Williams, and J.B. Lee. 1990. Carabid populations in field beans and their effect on the population dynamics of *Sitona lineatus* (L.). *Ann. Appl. Biol.* 117:51–62.

Hare, J.D. 1980. Variation in fruit size and susceptibility to seed predation among and within populations of the cocklebur, *Xanthium strumarium* L. *Oecologia* 46:217–222.

Harper, J.L. 1969. The role of predation in vegetational diversity. *Brookhaven Symposia in Biology* 22:48–62.

———. 1977. *The Population Biology of Plants*. Academic Press, London.

Harper, J.L., P.H. Lovell, and K.G. Moore. 1970. The shapes and sizes of seeds. *Annual Review Ecology and Systematics* 1:327–356.

Heithaus, E.R. 1981. Seed predation by rodents on three ant-dispersed plants. *Ecology* 62:136–145.

Holmes, P.M. 1990. Dispersal and predation in alien Acacia. *Oecologia* 83:288–290.

House, G.J., and J.N. All. 1981. Carabid beetles in soybean agroecosystems. *Envir. Ent.* 10:194–196.

House, G.J., and R.W. Parmelee. 1985. Comparison of soil arthropods and earthworms from conventional and no-tillage agroecosystems. *Soil Till. Res.* 5:351–360.

Hubbell, S.P. 1980. Seed predation and the coexistence of tree species in tropical forests. *Oikos* 35:214–229.

Imms, A.D. 1948. *A General Textbook of Entomology*. E.D. Dutton and Co., New York.

Inouye, R.S., G.S. Byers, and J.H. Brown. 1980. Effects of predation

and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61 (6): 1344–1351.

Janzen, D. H. 1969. Seed-eaters vs. seed size, number, toxicity, and dispersal. *Evolution* 23:1–27.

———. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104:501–528.

———. 1971a. Seed predation by animals. *Annual Review Ecology and Systematics.* 2:465–492.

———. 1971b. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, time of day, and insularity. *Ecology* 54:687–708.

———. 1972. Escape in space by *Sterculia apetala* seeds from the bug *Dysdercu fasciatus* in a Costa Rican deciduous forest. *Ecology.* 53:350–361.

———. 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. *J. Ecology* 68:929–952.

Johnson, N.E., and R.S. Cameron. 1969. Phytophagous ground beetles. *Annals Entomological Society of America* 62:909–914.

Julien, M.H. 1982. *Biological Control of Weeds, A Catalogue of Agents and Their Target Weeds.* Commonwealth Agricultural Bureaux, London.

Keeley, J.E., S.C. Keeley, C.C. Swift, and J. Lee. 1984. Seed predation due to the Yucca-moth symbiosis. *American Midland Naturalist* 112:187–191.

Kinsman, S., W. Platt, and J. Platt. 1984. The impact of a herbivore upon *Mirabilis hirsuta*, a fugitive prairie plant. *Oecologia* 65:2–6.

Kjellsson G. 1985. Seed fate in a population of *Carex pilulifera* L. II. Seed predation and its consequences for dispersal and seed bank. *Oecologia* 67:424–429.

Koerber, T.W. 1962. Douglas fir cone and seed research. *U.S. Forest Service Pacific Southwest Forest Range Experimental Station Progress Report* 1959:1–37.

Kok, L.T., and R.L. Pienkowski. 1985. Biological control of musk thistle by *Rhinocyllus conicus* (Coleoptera: Curculionidae) in Virginia from 1969 to 1980. Proc. VI Int. Symp. Biological Control of Weeds, Vancouver, Canada, ed. E.S. Delfosse, pp. 805–809. Agric. Can.

Kok, L.T., and W.W. Surles. 1975. Successful biocontrol of musk thistle by an introduced weevil, *Rhinocyllus conicu. Environ. Entomol.* 4:1025–1027.

Kraft, K.J. 1968. Ecology of the cone moth *Laspeyresia toreuta* in *Pinus banksiana* stands. *Annals Entomological Society of America* 61:1462–1465.

Lamp, W.O., and M.K. McCarty. 1982. Predispersal seed predation of a native thistle, *Cirsium canescens. Environ. Entomol.* 11:847–851.

Leeuwen, B.H. van. 1983. The consequences of predation in the population biology of the monocarpic species *Cirsium palustre* and

Cirsium vulgare. Oecologia 58:178–187.

Liebman, M., and R.R. Janke. 1990. Sustainable weed management practices. In *Sustainable Agriculture in Temperate Zones,* ed. C.A. Francis et al., pp.111–143. John Wiley and Sons, New York.

Lipa, J.L. 1974. Survey and study of insects associated with cruciferows plants in Poland and surrounding countries. Final Rep. E21-ENT26-FG-PO-248, Inst. Plant Prot. Lab. Biol. Control Miczurina 20, Poznan Poland.

Louda, S.M. 1978. A test of predispersal seed predation in the population dynamics of Haplopappus (Asteraceae). Ph.D. Thesis, University of California, Riverside and San Diego State University.

———. 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs.* 52 (1): 25–41.

Louda, S.M., K.H. Keeler, and R.D. Holt. 1989. Herbivore influences on plant performance and competitive interactions. In *Perspectives in Plant Competition,* ed. J.B. Grace and D. Tilman. Academic Press, New York.

Luff, M. L. 1980. The biology of the ground beetle *Harpalus rufipes* in a strawberry field in Northumberland. *Ann. Appl. Biol.* 94:153–164.

Lund, R.D., and F.T. Turpin. 1977. Carabid damage to weed seeds found in Indiana cornfields. *Envir. Ent.* 6:695–698.

Manley, G.V. 1992 Observations on *Harpalus pensylvanicus* (Coleoptera: Carabidae) in Michigan seed corn fields. *Newsletter of the Michigan Ent. Soc.* 37 (4): 1–2.

Mares, M.A., and M.L. Rosenzweig. 1978. Granivory in North and South American deserts: rodents, birds, and ants. *Ecology* 59:235–241.

Mattson, W.J. 1971. Relationship between cone crop size and cone damage by insects in red pine seed-production areas. *Can. Ent.* 103:617–621.

McLemore, B.F. 1975. Cone and seed characteristics of fertilized and unfertilized longleaf pines. USDA Forest Service Research Paper, Southern Forest Experimental Station SO-109:1–10.

Merkel, E.P. 1967. Individual slash pines differ in susceptibility to seedworm infestation. *J. Forestry* 65: 32.

Miller, W. E. 1973. Insects as related to wood and nut production. In Black Walnut as a Crop. U.S. Forest Service General Technical Report NC-4, North Central Forest Experiment Station, St. Paul, MN.

Mittelbach, G.G., and K.L. Gross. 1984. Experimental studies of seed predations in old-fields. *Oecologia* 65:7–13.

Molau, U., B. Eriksen, and J.T. Knudsen. 1989. Predispersal seed predation in *Bartsia alpina. Oecologia* 81:181–185.

Moore, L.R. 1978. Seed predation in the legume *Crotalaria*. I. Intensity and variability of seed predation in native and

introduced populations of *C. pallida* Ait. *Oecologia* 34:185–202.

Murdoch, W.W., F.C. Evans, and C.H. Peterson. 1972. Diversity and pattern in plants and insects. *Ecology* 53:819–829.

Neser, S., and R.L. Kluge. 1985. A seed-feeding insects showing promise in the control of a woody, invasive plant: the weevil *Erytenna consputa* on *Hakea seriea* (Proteaceae) in South Africa. Proc. VI Int. Symp. Biological Control Weeds, ed. E.S. Delfosse, pp. 805–809. Agriculture Canada

Nielsen, S.G. 1977. Beech seeds as an ecosystem component. *Oikos* 29:268–274.

Nilsson, S.G., and U. Wastljung. 1987. Seed predation and cross-pollination in mastseeding beech (*Fagus sylvatica*) patches. *Ecology* 68:260–265.

Nitzsche, H. 1893. Ein neuer Fall von Saatlampbeschadigung durch Laufkafer Forst naturw. *Zeitschr.* 2 (48).

O'Dowd, D.J., and M.E. Hay. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. *Ecology* 61:531–540.

Pettersson, M.W. 1991. Flower herbivory and seed predation in *Silene vulgaris* (Caryophyllaceae): Effects of pollination and phenology. *Holarctic Ecology* 14(1):45-50.

Pimental, D. 1961. Species diversity and insect population outbreaks. *Annals Entomological Society America* 54:76–86.

Price, W.P. 1984. *Insect Ecology*. John Wiley and Sons, New York.

Purvis, G., and J.P. Curry. 1984. The influence of weeds and farmyard manure on the activity of Carabidae and the ground dwelling arthropods in a sugar beet crop. *J. Appl. Ecol.* 21: 271–283.

Randall, M.G.M. 1986. The predation of predispersed *Juncus squarrosus* seeds by *Coleophora alticolella* (Lepidoptera) larvae over a range of altitudes in northern England. *Oecologia* 69:460–465.

Reader, R.J. 1993. Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *J. Ecology* 81:169–175.

Risch, S., and C.R. Carroll. 1986. Effects of seed predation by a tropical ant on competition among weeds. *Ecology* 67(5): 1319–1327.

Rivard, I. 1966. Ground beetles (Coleoptera: Carabidae) in relation to agricultural crops. *Can. Ent.* 98:189–195.

Robertson, A.I., R. Giddins, and T.J. Smith. 1990. Seed predation by insects in tropical mangrove forests: extent and effects on seed viability and the growth of seedlings. *Oecologia* 83:213–219.

Rosenthal, S.S. 1985. Potential for biological control of field bindweed in California's coastal vineyards. *Agric. Ecosyst Environ.* 13:43-57.

Rosenthal, S.S., and G.R. Buckingham. 1982. Natural enemies of *Convolvulus arvensis* in western Mediterranean Europe. *Hilgardia* 50:1–26.

Sallabanks, R., and S.P. Courtney. 1992. Frugivory, seed predation, and insect-vertebrate interactions. *Annual Review Entomology* 37:377–400.

Salisbury, E.J. 1942. *The Reproductive Capacity of Plants.* Bell, London.

Scherney, F. 1960. Kartoffel kaferbekampfung mit laufkafern (Gattung Carabus). *Pflanzenchutz* 12:34–35.

Schupp, E.W. 1988. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76:525–530.

Sheppard, A.W. 1987. Insect herbivore competition and the population dynamics of *Heracleum sphondylium* L. (Umbelliferae). Ph.D. thesis, University of London.

Silvertown, J.W. 1980. The evolutionary ecology of mast seedling in trees. *Biological J. Linnean Society* 14:235–250.

Skuhravy, V. 1959. Die nahrung der Feldcarabiden. *Acta. Soc. Ent. Cechoslov.* 56(1): 1–18.

Smith, C.C. 1975. The coevolution of plants and seed predators. In *Coevolution of Animals and Plants*, ed. L.E. Gilberg and P.H. Raven. University of Texas Press, Austin.

Solbreck, C., and B. Sillen-Tullberg. 1986. Seed production and seed predation in a patchy and time-varying environment. Dynamics of a milkweed-tephritid fly system. *Oecologia* 71:51–58.

Speight, M.R., and J.H. Lawton. 1976. The influence of weed-cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. *Oecologia* 23:211–223.

Sunderland, K.D. 1975. The diet of some predatory arthropods in cereal crops. *J. Applied Ecology* 12:507–515.

Sunderland, K.D., N.E. Crook, D.L. Stacey, and B.J. Fuller. 1987. A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *J. Applied Ecology* 24:907–933.

Thiele, H.U. 1964. Experimentelle untersuchungen uber die ursache der biotopbindung bei Carabiden. *Zeitschriftfur Morphologie Okologie der Tiere.* 53:387–452.

———. 1977. *Carabid Beetles in Their Environments, A Study on Habitat Selection by Adaptations in Physiology and Behaviour*: Springer-Verlag, New York.

Traveset, A. 1990. Post-dispersal predation of *Acacia farnesiana* seeds by *Stator vachelliae* (Bruchidae) in Central America. *Oecologia* 84:506–512.

———. 1991. Pre-dispersal seed predation in Central American *Acacia farnesiana*: factors affecting the abundance of co-occurring bruchid beetles. *Oecologia* 87:570–576.

Webster, F.M. 1880. Notes upon the food of predaceous beetles. Ill. *State Lab. Natur. Hist. Bull.* 3:149–152.

———. 1900. *Harpalus caliginosus* as a strawberry pest with notes on other phytophagous Carabidae. *Can. Ent.* 32:265–271.

Werner, R.S. 1964. White spruce seed loss caused by insects in interior Alaska. *Can. Ent.* 96:1462–1464.

Whelan, C.J., M.F. Willson, C.A. Tuma, and I. Souza-Pinto. 1990.
    Spatial and temporal patterns of postdispersal seed predation.
    Can. J. Bot. 69:428–436.

Willson, M.F. 1983. Natural history of *Actaea rubra*: fruit dimorphism
    and fruit/seed predation. *Bulletin Torrey Botanical Club*. 110:298–
    303.

———. 1992. The ecology of seed dispersal. In *Seeds, the Ecology of
    Regeneration in Plant Communities,* ed. M. Fenner. CAB
    International, Oxford.

Wilson, D.E., and D.H. Janzen. 1972. Predation on Scheelea palm
    seeds by bruchid beetles: seed density and distance from the
    parent palm. *Ecology* 53:954–959.

Zhang, J. 1993. Biology of *Harpalus rufipes* DeGeer (Coleoptera:
    Carabidae) in Maine and dynamics of seed predation. M.S. thesis,
    University of Maine, Orono.

Zhang, J., F. Drummond, and M. Liebman. 1994. Spread of *Harpalus
    rufipes* DeGeer (Coleoptera: Carabidae) in eastern Canada and the
    United States. *Entomol. Trends in Agric. Sci.* 2:67–71.

Znamenskii, A.V. 1926. *Insects injurious to agriculture. I. Pests of
    grain crops*. Trud. Poltavsk. Sel. Khoz. Op. Stants, no. 50.