

Seeds as the Target for Biological Control of Weeds

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Abstract

Seeds play an essential role in the maintenance and spread of annual weeds, yet they are vulnerable to pre- and post-dispersal predators, some of which might affect the dynamics of weed populations. We conducted studies to identify pre- and post-dispersal predators of the annual broadleaf weeds giant ragweed (*Ambrosia trifida*) and velvetleaf (*Abutilon theophrasti*), and to determine levels of seed loss caused by these predators in established maize fields. Specialized seed feeding insects were the main pre-dispersal predators of both species. Flies and a moth were important predators of giant ragweed, while the velvetleaf seed beetle (*Althaeus folkertsii*) was the main pre-dispersal predator of velvetleaf. Cage exclusion studies showed that rodents and invertebrates were the main post-dispersal predators of both weeds. Over a 12-month period, up to 88% of giant ragweed seeds were lost to predation, with a maximum monthly predation rate of 19%. Giant ragweed seeds covered with maize crop residue had lower predation by rodents than uncovered seeds, but residue did not affect predation by invertebrates. Velvetleaf seeds were predated at rates ranging from 1.2 to 57% per day. Rates of seed loss were the same in no-tillage and moldboard plow fields. Pre-dispersal predators are probably better candidates for biological control of these weeds, due to host specificity and potential for population augmentation. Preventing seed burial and optimizing habitat for seed predators could reduce seed survival of both weed species, but the impact would be expected to be greater for giant ragweed than for velvetleaf.

Introduction

Seeds are the primary dispersal unit by which annual weeds are spread over space and time. Among the characteristics that distinguish weedy species from crop plants is the production of high numbers of seeds with adaptations for dispersal and long-term survival. Weed seeds are also an abundant and compact source of nutrients that can help supply the food needs of small mammals, birds, and numerous invertebrate organisms. While still attached to the mother plant, weed seeds are hosts to many predators, some of which are quite specific in their food sources. After dispersal, weed seeds generally rest on or below the soil surface, where they are subject to destruction and/or transport by other more generalist organisms.

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Some authors have suggested that seed predation is unlikely to have a significant effect on plant populations because factors other than seed number limit population size (Crawley, 1989; Harper, 1977). However, there are many cases where seed feeding insects have played a significant role in biological control of weedy and invasive plants (Julien, 1992). In some crop plants, pre-dispersal predators are an important problem resulting in the loss of a significant proportion of crop yield (Shade *et al.*, 1987). Even though seed predators alone are unlikely to be effective biological control agents, they can act together with other agents to stress weed populations (Denoth *et al.*, 2002).

Pre-dispersal seed predation is generally attributed to specialist seed feeders, many of which can have a large impact on total viable seed output (Crawley, 2000). However, few studies have been conducted with adequate replication in time and space to help elucidate the dynamic nature of predation. Moreover, there is little information on weed seed predators in maize (*Zea mays*) cropping systems that might indicate whether there is any relationship between seed predation and subsequent seedling density.

Post-dispersal seed predators in agricultural fields are mostly large and small carabid beetles, mice, ants and crickets, with larger animals preferentially consuming larger seeds (Brust 1994; Brust and House 1988; Cardina *et al.* 1996; Cromar *et al.* 1999; Lund and Turpin 1977; Marino *et al.* 1997; Mittelbach and Gross 1984). The omnivorous carabid beetle *Harpalus pennsylvanicus* can feed on small grass weed seeds, whereas the common carabid *Amara cupreolata* feeds on common chickweed (*Stellaria media*) and grass seeds (Barney and Pass, 1986). Five species of carabid beetles common to maize fields fed on small grass and broadleaf weed seeds, but preferred seeds of other host species in a laboratory study (Best and Beegle, 1977). Two species of *Harpalus* fed on relatively large broadleaf weed seeds including sicklepod (*Senna obtusifolia*), jimsonweed (*Datura stramonium*), and common ragweed (*Ambrosia artemisiifolia*) (Brust and House, 1988). In general, there is a positive correlation between predator size and seed size (Brust and House 1988; Hulme 1998; Mittelbach and Gross 1984; Povey *et al.* 1993; Price 1983). Mice select seeds to maximize their net energy intake (Kerley and Erasmus 1991) and prefer large seeds due to the high energetic return per time spent handling individual seeds (Abramsky 1983). Chemical, textural, or nutritional differences may also be the basis for seed preferences (Lund and Turpin 1977).

Giant ragweed is a competitive annual weed of field crops in the U.S. Corn Belt (Harrison *et al.* 2001; Webster *et al.* 1994). It produces relatively few, large, short-lived (<4 yr) seeds that require burial for maximum emergence. Seeds are susceptible to pre-dispersal predation by several insects (Amatangelo 1974; Bazzaz 1984; Harrison *et al.* 2001; Hartnett *et al.* 1987). The dispersal unit of giant ragweed seed is technically an involucre, a fruit consisting of fused, hardened bracts enclosing a single achene (but for sake of simplicity we will use the term “seed” in this paper when referring to this dispersal unit). About 10 to 20% of giant ragweed fruits contain no seeds and thus are considered to be parthenocarpic.

Velvetleaf is a widespread and persistent annual weed whose seeds can remain viable in soil for up to 50 years. Seeds are produced in a multi-celled capsule but are generally dispersed as individual units as capsules split open during dry autumn conditions. Return of seeds from even sparse populations has long-term consequences for future weed management due to high seed production and long-term survival. After a 17-year study with no velvetleaf seed return, 1 to 3 million seeds per

ha remained in soil that originally contained 8 to 16 million seeds per ha (Louda, 1989). Some researchers have concluded that there is no economic threshold for velvetleaf because seed return cannot be tolerated (Mittelbach and Gross, 1984; Platt, 1976).

Given the importance of seeds in maintenance and spread of annual weed populations, and their vulnerability to pre- and post-dispersal predation, it is important to understand which animals are responsible for weed seed loss and to determine what level of seed loss might be expected under normal crop production conditions (i.e. without efforts to artificially augment predator densities). Therefore, we conducted studies with the objectives to identify pre- and post-dispersal predators of giant ragweed and velvetleaf seeds and to determine the impact of seed predation on plant fecundity.

Materials and Methods

Studies were conducted in fields with long histories of maize and soybean (*Glycine max*) production to identify common pre- and post-dispersal seed predators and to estimate rates of seed loss due to predation. Fields used in velvetleaf studies did not have previous velvetleaf populations and were split into two tillage systems: moldboard plowing followed by two diskings in springtime, and no-tillage. Fields used for giant ragweed studies were all no-tillage fields with a 10-year history of giant ragweed infestation. Maize crops were planted using standard hybrid, fertility, planting density, and herbicide recommendations for Ohio (USA) conditions.

Pre-dispersal predators. Identifications of pre-dispersal predators were made for velvetleaf by daily observations of developing capsules and seed collections. Capsules were observed for visiting arthropods for 2 hr each day (different times of day), and suspected predators were captured and caged on individual capsules in mesh cloth bags. Capsules were harvested at maturity, seeds removed, and percent damaged seeds recorded. For giant ragweed, seeds were collected by placing perforated plastic dishes in the field beginning in mid-September. Seeds were recovered from the dishes at weekly intervals, counted, and dissected to identify predators and determine infestation rates.

Post-dispersal predators. Exclosure structures, constructed from wire mesh and consisting of apertures of varying size, served as seed stations for both giant ragweed and velvetleaf, and provided differential access to predators based on size (Cardina *et al.* 1996; Hulme and Borelli 1999). For example, openings of 6.5 cm² restricted the entry of birds and large animals, while allowing mice and invertebrates admission. Openings of 1.6 cm² restricted the entry of all predators, excepting the arthropods. Open access stations had no sides or top and provided unrestricted access to all potential predators, including birds, mammals, and invertebrates. In addition, we captured potential seed predators, including field mice (*Mus musculus*), and various species of slugs and ground beetles (*Amara* spp, *Harpalus pensylvanicus*) and fed them target weed seeds in the laboratory.

Predation over time. Rates of seed loss to post-dispersal granivores in the field were determined using methods similar to those described by Mittelbach and Gross (1984). Seeds (50 for velvetleaf, 250 for giant ragweed) were placed in trays containing field soil to which herbicides had not been applied. Holes in the bottom of each tray allowed for drainage. Trays were buried so that the surface

of soil in the tray was level with that of the surrounding soil. In velvetleaf studies, two additional trays contained plastic beads, similar in size to velvetleaf seeds, to test recovery efficiency. To avoid any cues that might attract or repel predators, care was taken to minimize human contact with seeds and to limit disturbance of row middles where trays were located. Seeds were placed in the field on the first of each month beginning in March for velvetleaf and in November for giant ragweed. Velvetleaf studies were repeated during four growing seasons and giant ragweed for two calendar years. The trays, soil, and remaining seeds were collected periodically and taken to the laboratory, where intact seeds were screened, separated, and counted. Treatments were replicated four times and consisted of a factorial arrangement of three sizes of predator access exclosures, two levels of crop residue cover, and two seed sizes (giant ragweed only).

The rate of predation was computed from the number of intact seeds recovered at the end of each sampling period. Seeds remaining in each experimental unit were counted and then classified as intact, destroyed by predation, or as other-nonviable. Seeds in the other-nonviable category were subcategorized as empty (parthenocarpic – giant ragweed only), seeds with a necrotic embryo, or seeds with embryos destroyed by seed-boring insects. Missing seeds were classified as removed by predators, since rodents frequently remove seeds to consume them elsewhere. Previous experience has indicated that the movement of seeds out of the exclosures via wind or water was unlikely. Data for post-dispersal seed predation at each retrieval time were calculated as the number of missing seeds plus those destroyed by chewing converted to a percentage of the initial number of seeds deposited. The mean daily rate of seed loss over the period (P) was calculated as $P=100 * (1-r^{1/d})$, where r is the average proportion of seeds recovered, and d is the duration of the period in days (5, 15). Tests for data normality and homogeneity of variances indicated that square root transformation satisfied the assumptions of ANOVA better than other transformations. Therefore, the percentage data were transformed to $(P+0.5)^{-2}$ prior to analysis, but non-transformed data are reported. Regression analysis to describe the relationship between seed density and predation rate was conducted using a least squares procedure. Data were subjected to ANOVA and means separated using an LSD at the 5% significance level.

A combined ANOVA was performed for each retrieval date to determine the effects of year (experiment) and exclosure treatment, on giant ragweed and velvetleaf seed predation. The effects of involucre size and crop residue on giant ragweed seed production were also assessed.

Results and Discussion

Pre-dispersal predators. Although many insects and other arthropods visited velvetleaf capsules and exposed giant ragweed involucre, few organisms appeared to use these seeds as a food source. For example, white flies, Japanese beetles, stink bugs, and several small flies were occasional visitors to velvetleaf capsules, but none appeared to make an effort to invade capsules, which offer considerable protection to developing seeds. However, velvetleaf can be considered a true host of two insects (Table 1), the scentless plant bug (*Niesthrea louisianica*), a native species that interacts with fungi to cause significant seed damage (Kremer and Spencer 1989) and the velvetleaf seed beetle (*Althaeus folkertsi*), a member of the seed weevil family (Bruchidae). We consider a true host plant to be one on which an organism can complete its life cycle, and do not consider a plant a host

if it serves as a pollen or nectar source only. The occurrence of the scentless plant bug is fairly common in the central U.S., but is relatively rare in Ohio. The velvetleaf seed beetle infested 10 to 27% of seeds collected in natural populations.

Giant ragweed was visited by insects of several orders and served as true hosts for four insect species: a fruit fly, two weevils, and a moth (Table 1). Positive identification of these species is pending. In all cases, however, there was good evidence of seed destruction by these insects. Larvae apparently burrow into developing seeds and complete their life cycle, rendering seeds non-viable. Dissection of involucre revealed that 13 to 19% of seeds were infested with insect larvae that had consumed all or portions of the embryo. Additional seeds showed signs of prior insect damage, including exit holes, frass, or a partially destroyed embryo.

Post-dispersal predators. We consider the main post-dispersal predators (Table 1) for both of these weeds to be field mice (*Mus* spp.). Mice were caught occasionally in velvetleaf seed-baited traps, but not in unbaited traps, and there was no difference between tillage systems in the number of mice trapped. Mouse activity was evident in and around plots with no exclosures and those with large openings. One characteristic of mouse activity was the presence of seed coats cracked and the contents partially or completely eaten. In springtime, slugs (*Arion subfuscus* and *Derocerus reticulatum*) are possible minor predators of velvetleaf seeds, especially during cool, wet periods, when imbibed seeds are available near the soil surface. The carabid beetle, *H. pensylvanicus*, was a minor predator of giant ragweed but not of velvetleaf seeds, although this insect preferred seeds of other weed species.

Predation over time. In giant ragweed studies, the combined ANOVA for total seed predation at each retrieval time indicated no significant year by treatment interactions, so data were combined over year for subsequent analyses. Significant one-way interactions of involucre size by exclosure treatment and residue by exclosure treatment occurred on two or more retrieval dates.

In the open access and rodent + invertebrate treatments, giant ragweed seed disappearance after 12 months averaged 88%, compared to 66% in the invertebrate-only treatment (Table 2). Birds or large mammals did not consume giant ragweed seeds in the open access treatment. Chewed involucre were similar in appearance to seeds chewed by *M. musculus* and *H. pensylvanicus* in laboratory studies, so rodents and invertebrates were likely the principal predators of giant ragweed seeds. These seeds are of little food value to most birds due to their large size and tough outer covering (Martin et al., 1961). Based on these results, the predicted monthly predation rates ranged from 13 to 19% for the open access and rodent + invertebrate treatments during the first 3 months after seed deposition, and rates declined thereafter (Table 2). The highest monthly seed predation in the treatments with rodent access was in late fall and winter, which are times of busy seed gathering and caching by rodents common in midwestern U.S. agricultural fields (Whelan et al. 1991; Whitaker 1966). Lower predation rates in spring and summer may have been due to decreased seed demand by rodents as other food sources became available, and due to lower seed supplies in the exclosures.

We could not distinguish giant ragweed seed predation by invertebrates from predation by rodents in the open access and rodent + invertebrate exclosure treatments. However, the potential contribution of invertebrates to total seed predation was greatest during the period from 6 to 12 months after seed

deposition. Monthly seed predation rates were 3 to 4% by invertebrates during the first 6 months after deposition, and 8 to 11% per month between 9 and 12 months after deposition. Higher predation rates by invertebrates occurred in late summer and early fall, a time of maximum foraging activity by seed-eating adult carabids (Cromar *et al.* 1999; Dritschilo and Wanner 1980; Lund and Turpin 1977). The results indicate that invertebrates were capable of predated most of the giant ragweed seeds when other predators were excluded and may play a major role in giant ragweed seed predation in habitats where rodent populations are low.

The effects of giant ragweed seed (involucre) size on predation rates were significant in the rodent + invertebrate and invertebrate-only enclosure treatments (Table 2). Initial predation of small seeds occurred at a lower rate than that of large seeds in the rodent + invertebrate treatment ($P=0.007$), whereas large seeds were consumed at a lower rate than small seeds in the invertebrate-only treatment ($P=0.022$). Rodents had consumed about 55% of the large seeds and 35% of the small seeds within 3 months after deposition. There was no effect of seed size in the open access treatment, due to less discrimination by rodents in the absence of a protective enclosure. Results suggest that seed predation by rodents may provide stronger selection pressure for seed morphological traits than predation by insects.

Maize residues reduced initial giant ragweed seed predation rates compared to treatments with no residue, where there was rodent access (Table 3). Where there was open access and rodents + invertebrates were allowed, predation rates during the first 3 months after seed deposition were 18 and 22% per month, respectively, without residue compared to 11% per month for both treatments with residue. Although initial rates of predation by rodents were higher when residues were absent, total predation at the end of the 12-month feeding period for both residue treatments ranged from 82 to 93%. Residue had no effect on seed predation by invertebrates ($P=0.336$).

For velvetleaf studies, the main effect of tillage was not significant in any year, but the tillage-by-date interaction was significant in years 1 and 2. Lack of a tillage effect contradicts several findings of previous studies (Brust and House, 1988; House and Brust, 1989; Reader, 1991). Residue from previous years of continuous no-tillage maize provided habitat for seed predators, and the large (12 m) border between main plots should have hindered movement of predators between high and low residue areas. However, factors that promote and restrict predation in both tillage systems may balance each other. That is, the more favorable predator habitat in the no-till plots may have increased seed predator populations, but also may have increased the abundance and diversity of food sources that predators prefer over velvetleaf seeds. The high residue environment might provide habitat for seed predators but could also be good habitat for wildlife that feeds on them. Exposed velvetleaf seeds on the soil surface of the no-residue plots were an unusually accessible food source to seed predators.

Predation rates varied among years, and ranged from 2% to 25% seed loss per day. (Table 4). Predation was generally low in spring, increased in mid-summer, and decreased as winter approached, but there were periods of high predation in the fall every year. The exceptionally high predation rate in year 3 could have been due to the relatively high rainfall and low temperature conditions during the growing season, which have been shown to favor predator activity (Brust *et al.*, 1986). An alternative explanation could be that the repeated addition of seeds to the soil surface

during the three previous years of the study attracted an unusually high population of predators that year. High levels of variation in predation rates have been reported between replications, observation times within a year, and over years (Brust and House, 1988; Crawley, 1992; Crawley, 1989; Louda, 1989; Mittelbach and Gross, 1984).

In comparable studies, Mittelbach and Gross (1984) reported predation rates of four composite weeds during a single month (August) averaging 6% per day in old fields. Brust and House (1988) reported predation rates averaging 2.4% per day for four annual broadleaf weeds during a 5-wk period in soybean fields. The occasional large change in seed loss from one sample period to another could not be explained by differences in rainfall or temperature. Large variation has been reported for predation rates in non-agricultural environments (Crawley, 2000), and there are too few studies in agricultural situations for comparison at this time.

Maize residues appeared to offer some initial protection against giant ragweed seed predation by rodents at the microhabitat level, but that protection may have been lost as residues degraded or seed supplies dwindled and rodent foraging became more exhaustive. The effect of residue was small, probably due to the ability of rodents to locate food through olfaction, and we have since observed rodent excavation and predation of buried giant ragweed seeds (unpublished). We also observed no difference in total predation of velvetleaf seeds by rodents when seeds were left exposed in conventional tillage plots compared to those covered with maize residue in no-tillage plots.

The two species used in these studies represent different cases of predator acceptability and potential impact. Velvetleaf seeds are relatively well protected from pre-dispersal predators during maturation, although the capsule wall does not deter intrusion by the velvetleaf seed beetle or the scentless plant bug. Giant ragweed seeds are borne more-or-less individually in axils of upper branches, and although they appear to be more exposed than velvetleaf seeds, the protective structures are thick and hard compared to those surrounding velvetleaf seeds. Once dispersed, both seeds rest on the soil surface without any adaptive means of enhancing burial or movement. However, velvetleaf seeds are relatively less protected after dispersal than are giant ragweed seeds. Since seed production is relatively lower in giant ragweed compared with velvetleaf, we would expect that comparable levels of seed predation would have a larger impact on subsequent populations of giant ragweed than velvetleaf.

The methodology for seed predation studies is difficult because of many extraneous factors that can influence results. For example, seed losses could have been caused by factors other than predation in the field experiments, such as the impact of raindrops or by movement of non-predatory animals. Occasionally, trays were disturbed so that seed counts were unreliable. Data for dishes containing beads indicated that recovery efficiency was about 97% (data not shown). However, seed disappearance was variable and should be interpreted with caution due to the many factors that could influence seed-predator interactions (Brust and House, 1988; Crawley, 1989).

At this point, none of the seed predators identified in these studies would be expected to be effective biological control agents by themselves. However, we expect that some of the predators could play a role in an integrated, multiple-tactic approach to biological control of these weeds (Denoth *et al.*, 2002). It is important to recognize that no effort was made to augment the predator populations

directly or indirectly in these experiments. The rates of pre-dispersal predation, which would probably be most useful for biological control, suggest that nearly 30% of seeds can be destroyed at natural predator population levels. More information on the life cycle of these predators is needed to understand possible alternate hosts or overwintering sites that could be manipulated to increase their populations. Studies are especially needed to determine the host specificity of these seed predators and what environmental conditions or cultural practices limit their survival and activity.

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Table 1. Pre- and post-dispersal predators of velvetleaf and giant ragweed in corn fields in Ohio. Only species damaging at least 1% of seeds in feeding trials are included.

Weed species	Pre-dispersal	Post-dispersal
velvetleaf	scentless plant bug <i>(Niesthrea louisianica)</i>	field mice (<i>Mus</i> spp.)
	velvetleaf seed beetle <i>(Althaeus folkertsi)</i>	slugs (<i>Arion subfuscus</i> and <i>Derocerus reticulatum</i> ^a)
	corn earworm	ground beetles (<i>Amara cupreolata</i>) cutworms ^a
giant ragweed	fruit fly (Diptera: Tephritidae)	field mice (<i>Mus</i> spp.)
	2 weevils (Coleoptera: Curculionidae)	ground beetle (<i>Harpalus pensylvanicus</i>)
	moth (Lepidoptera: Gelechiidae)	

^aimbibed seeds only

Table 2. Interaction of seed size and predator exclusion treatments on post-dispersal predation of giant ragweed seeds in a no-tillage maize field over a 12-month period. Data are means of 8 replications.

Predator access	Seed size	Time after seed deposition (months)			
		3	6	9	12
		-----cumulative % predation (±SE) -----			
Open	small	41 (4.9)	59 (5.2)	76 (3.6)	87 (1.8)
	large	43 (6.9)	76 (2.7)	85 (2.6)	89 (1.5)
Rodents + invertebrates	small	39 (6.2)	62 (6.1)	77 (4.2)	86 (2.5)
	large	55 (6.6)	80 (5.1)	82 (3.9)	89 (1.8)
Invertebrates only	small	20 (5.9)	18 (3.3)	46 (3.5)	78 (3.8)
	large	7 (0.8)	17 (5.0)	34 (1.6)	56 (5.8)

Table 3. Interaction of maize plant residue and predator enclosure treatments on post-dispersal predation of giant ragweed seeds in a no-tillage maize field over a 12-month period. Data are means of 8 replications.

Predator access	Residue	Time after seed deposition (months)			
		3	6	9	12
		----- cumulative % predation (+SE) -----			
Open	present	28 (4.7)	60 (4.6)	78 (3.6)	85 (1.7)
	absent	55 (5.1)	75 (3.9)	83 (2.9)	91 (1.4)
Rodents + invertebrates	present	30 (6.2)	56 (6.0)	69 (4.1)	82 (2.0)
	absent	64 (3.8)	86 (2.4)	90 (1.5)	93 (1.2)
Invertebrates only	present	15 (4.3)	11 (1.3)	39 (3.9)	68 (4.9)
	absent	12 (4.7)	24 (5.3)	41 (4.7)	65 (6.3)

Table 4. Effects of enclosure size on post-dispersal predation of velvetleaf seeds in no-tillage and moldboard plow field maize over four years. Data are means of 4 replications. Means followed by the same letter in a column do not differ at the 0.05 significance level according to LSD.

Tillage system	Exclosure	Year			
		1	2	3	4
		----- predation (% per day) -----			
no-tillage	none	7.0 a	7.1 a	7.3 a	23.2 a
	large	5.4 b	6.0 a	8.0 a	20.9 ab
	small	3.3 c	5.8 b	4.4 b	17.7 b
	0	5.3	6.3	6.5	20.6
moldboard plow	none	6.9 a	8.7 a	6.2 a	25.3 a
	large	5.9 b	7.4 a	5.0 a	21.2 ab
	small	2.5 c	4.9 b	2.1 b	19.5 b
	0	5.1	7.0	4.4	22.0