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## Oviposition Behavior of Insects Used in the Biological Control of Weeds

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### Abstract

Insect herbivores that irrupt to levels at which they severely damage their host plant tend to lay their eggs in clusters. Egg clumping is common among both forest pest insects and numerically dominant herbivores of goldenrod. Non-outbreak species tend to lay their eggs singly. I hypothesized that successful weed control agents, inasmuch as they can be considered outbreak species on their respective host plants, would, like other outbreak species, tend to lay eggs in clusters. A survey of 39 successful control agents, revealed that this is not the case; biocontrol agents are not more likely than randomly chosen herbivores to lay eggs in clusters.

**Keywords:** biological control, weeds, insect outbreaks, *Solidago*, oviposition behavior

In weed biological control programs using herbivorous insects as agents, success depends on maintaining herbivore populations at levels sufficient to damage the host plant. However, most herbivore species persist at low densities at which they do little damage to the host (Lawton 1979). The question of what maintains most herbivorous insect species at levels far below those at which they deplete their resources has been keeping population ecologists—those of theoretical and empirical bent alike—occupied for decades. Whereas some authors have stressed the importance of external factors such as natural enemies or climatic conditions, others have sought the key to population dynamics in the characteristics of the species themselves. Studies comparing outbreak and non-outbreak herbivores have revealed a variety of life-history traits that are associated with a tendency to erupt (Rhoades 1985, Wallner 1987, Nothnagle and Schultz 1987, Redfearn and Pimm 1988). Probably the most striking pattern to emerge from these studies is a consistent association between outbreaking and gregarious behavior (Rhoades 1985, Nothnagle and Schultz 1987, Hunter 1991, 1995, Hanski 1987, Root and Cappuccino 1992). Females of outbreak species tend to lay their eggs in batches as opposed to scattering their eggs throughout a stand of the host plant. In some extreme cases, the females are flightless and deposit all their eggs in a single mass. Often the larvae feed in groups, sometimes constructing webs or other sorts of group shelters.

If egg clumping is a good predictor of the propensity of herbivorous insects to outbreak, one might expect that it might also be a good indicator of the potential success of species being considered as biological control agents for weeds. I address this question in two ways. First, I consider the fauna associated with the tall goldenrod *Solidago altissima*, a native North American perennial that is now an introduced weed in Europe. Drawing on population abundance data from an earlier study (Root and Cappuccino,

1992), I ask whether egg clustering is characteristic of outbreak species. Secondly, I review examples of weed biocontrol success stories, to determine whether effective agents tend to lay eggs in clusters.

### Materials and Methods:

The tall goldenrod *Solidago altissima* L. is a dominant perennial forb of old field communities throughout eastern North America. Along with two other goldenrods, *S. graminifolia* (L.) and *S. gigantea* Ait., it was introduced to London as an ornamental in the 1700s and is now spreading throughout continental Europe (Weber 1998). In North America, it has a diverse herbivore fauna. In the Finger Lakes Region of New York State, where we conducted a long-term, large-scale census of *Solidago* herbivores (described in Root and Cappuccino 1992), *S. altissima* is host to over 100 insect species. Some of these herbivores do considerable damage to plant fitness (Root 1996, Meyer 1993). From 1981 through 1986, twenty-three species were sampled twice yearly at 22 sites. The species sampled were chosen on the basis of the ease with which they could be identified in the field. Nevertheless, the species chosen for sampling are not random with respect to abundance, since one becomes adept at identifying abundant species more readily than rare ones. Twenty of these species (those for which information on their oviposition strategy was available) are included in the present analysis (Table 1).

Species are generally qualified as "outbreak species" or "pests" when the damage they do reaches an unacceptable economic level. Biocontrol agents are deemed a success if they significantly reduce populations of their host plant. Because goldenrod is not an economically important species, we cannot rely on an economic threshold to determine which herbivore species are the "pests", nor were we able to conduct tests of the impact of each herbivore species on the plant, in order to evaluate species as control "successes". For the purposes of the present analysis, I defined outbreak species in two ways: 1) species that reached a density of one individual per goldenrod stem at least once over the course of the six-year census, and 2) species that attained an herbivore load (biomass per unit stem length) of 1 mg per meter once during the census.

The 20 species fell into two classes of egg-laying strategies: those species that deposit their eggs in clusters of five to 50 eggs and those that lay eggs singly. Unlike tree-feeding Lepidoptera (Hunter 1995), none of the goldenrod-feeders deposits its entire complement of eggs in a single mass, probably because a single goldenrod stem would not be able to support a large number of larvae.

### Biocontrol success stories.

McFadyen (1998) has noted how difficult it is to determine whether biological control agents should be considered a success. For the purposes of the present analysis, I have adopted an economic definition of success; species were considered a success if they were available either from commercial sources or governmental agencies, the rationale being that if some company or organization is willing to invest time and money in collecting and rearing programs, then the species must be effective. Information on the availability of control agents was obtained from two sources, both available online: Hunter (1997) and Weeden *et al.* (1999). Thirty-nine species for which I was able to find information on oviposition behavior were retained for the present analysis (Table 2).

Biocontrol failures are not included in the analysis, since it is difficult to determine the reason for the failure. A species may have the appropriate population dynamics and impact

**Table 1.**  
**Goldenrod-feeding insects, their oviposition behavior and outbreak status.**

SPECIES	FAMILY	GUILD	OVIPOSITION BEHAVIOR	OUTBREAK STATUS*
<i>Corythucha marmorata</i>	Tingidae	sap-feeder, leaves	Clusters	O, O
<i>Trirhabda virgata</i>	Chrysomelidae	leaf-chewer	Clusters	O, O
<i>Microrhopala vitata</i>	Chrysomelidae	leaf-miner/chewer	Clusters	O, O
<i>Ophraella conferta</i>	Chrysomelidae	leaf-chewer, nocturnal	Clusters	O, O
<i>Asteromyia carbonifera</i>	Cecidomyiidae	gall-maker, leaves	Clusters	O, N
<i>Cremastobombycia solidaginis</i>	Gracillariidae	leaf-miner	Single eggs	O, N
<i>Philaenus spumarius</i>	Cercopidae	sap-feeder, stems	Clusters	O, O
<i>Publilia concava</i>	Membracidae	sap-feeder, stems	Clusters	O, O
<i>Exema canadensis</i>	Chrysomelidae	leaf-chewer	Single eggs	N, O
<i>Gnorimoschema gallaesolidaginis</i>	Gelechiidae	gall-maker, stems	Single eggs	N, O
<i>Scrobipalpula sacculicola</i>	Gelechiidae	leaf-miner	Single eggs	N, N
<i>Calycomyza solidaginis</i>	Agromyzidae	leaf-miner	Single eggs	N, N
<i>Eurosta solidaginis</i>	Tephritidae	gall-maker, stems	Single eggs	N, O
<i>Rhopalomyia solidaginis</i>	Cecidomyiidae	leaf-miner	Single eggs	N, N
<i>Asphondylia bifolia</i>	Cecidomyiidae	gall-maker, leaves	Clusters	N, N
<i>Phaneta formosana</i>	Tortricidae	stem-borer	Single eggs	N, O
<i>Adaina montana</i>	Pterophoridae	leaf-chewer	Single eggs	N, N
<i>Agonopteryx pulvipennella</i>	Oecophoridae	leaf-chewer	Single eggs	N, N
<i>Epiblema scudderiana</i>	Tortricidae	gall-maker, stems	Single eggs	N, O
<i>Oidaematophorus homodactylus</i>	Pterophoridae	leaf-chewer	Single eggs	N, N

\* O = outbreak species;

N = non-outbreak species.

First letter refers to outbreak status using only abundance to define outbreak levels; second letter refers to outbreak status when herbivore load is used to define outbreak levels (see Materials and Methods).

**Table 2.**  
**Successful biological control agents and their oviposition strategies.**

Species	Family	Guild	Oviposition behavior*	Reference
<i>Apthona nigriscutis</i>	Chrysomelidae	Root-feeder	S	1
<i>Apthona flava</i>	Chrysomelidae	Root-feeder	S	1
<i>Apthona lacertosa</i>	Chrysomelidae	Root-feeder	S	1
<i>Trichosirocalus horridus</i>	Curculionidae	Borer	S	1
<i>Rhinocyllus conicus</i>	Curculionidae	Flower-, Seed-feeder	C	2
<i>Agapeta zoegana</i>	Cochylidae	Borer, roots	S	3
<i>Cyphocleonus achates</i>	Curculionidae	Borer, roots	S	1
<i>Metzneria paucipunctella</i>	Gelechiidae	Flower-feeder	S	4
<i>Sphenoptera jugoslavica</i>	Buprestidae	Borer, roots	S	5
<i>Urophora quadrifasciata</i>	Tephritidae	Gall-maker	C	1
<i>Apthona cyparissiae</i>	Chrysomelidae	Root-feeder	S	1
<i>Apthona czwalinae</i>	Chrysomelidae	Root-feeder	S	1
<i>Oberea erythrocephala</i>	Cerambycidae	Borer	S	1
<i>Spurgia esulae</i>	Cecidomyiidae	Gall-maker	C	1
<i>Calophasia lunula</i>	Noctuidae	Leaf-chewer	S	1
<i>Longitarsus jacobaeae</i>	Chrysomelidae	Leaf-chewer	S	6
<i>Brachypterolus pulicarius</i>	Nitidulidae	Flower-, seed-feeder	S	7
<i>Tyria jacobaeae</i>	Arctiidae	Leaf-chewer	C	6
<i>Cactoblastis cactorum</i>	Pyrilidae	Leaf-chewer	C	8
<i>Neochetina bruchi</i>	Curculionidae	Borer	C	1
<i>Neochetina eichhorniae</i>	Curculionidae	Borer	S	1
<i>Agasicles hygrophila</i>	Alticinae	Leaf-chewer	C	9
<i>Pterolonche inspersa</i>	Pterolonchidae	Borer	S	5
<i>Chrysolina quadrigemina</i>	Chrysomelidae	Leaf-chewer	S	10
<i>Aplocera plagiata</i>	Geometridae	Leaf-chewer	S	11
<i>Bangasternus orientalis</i>	Curculionidae	Seed-feeder	S	12
<i>Eustenopus villosus</i>	Curculionidae	Flower-feeder	S	13
<i>Urophora cardui</i>	Tephritidae	Gall-maker	C	14
<i>Ceutorhynchus litura</i>	Curculionidae	Miner	S	15
<i>Cystiphora schmidti</i>	Cecidomyiidae	Gall-maker	C	16
<i>Agrilus hyperici</i>	Buprestidae	Borer, roots	S	17
<i>Apion fuscirostre</i>	Curculionidae	Seed-feeder	S	18
<i>Apion ulicis</i>	Curculionidae	Seed-feeder	C	19

Species	Family	Guild	Oviposition behavior*	Reference
<i>Coleophora klimeschiella</i>	Coleophoridae	Leaf-chewer	S	20
<i>Coleophora parthenica</i>	Coleophoridae	Borer	S	21
<i>Leucoptera spartifoliella</i>	Lyonetiidae	Borer	S	22
<i>Microlarinus lareynii</i>	Curculionidae	Seed-feeder	S	23
<i>Microlarinus lypriformis</i>	Curculionidae	Borer, roots	S	23
<i>Urophora sirunaseva</i>	Tephritidae	Gall-maker	C	24

\* S = lays single eggs; C = lays eggs in clusters.

References:

- 1 = Weeden *et al.* (1999);
- 2 = Louda (1998); 3 = Müller *et al.* (1988);
- 4 = Story *et al.* (1991); 5 = Müller (1989);
- 6 = McEvoy *et al.* (1993); 7 = Hervey (1927);
- 8 = Fullaway (1954);
- 9 = Maddox (1968); 10 = Clark 1953;
- 11 = Murray (1949);
- 12 = Maddox, *et al.* (1991);
- 13 = Fornasari *et al.* (1991);
- 14 = Peschken and Harris (1975);
- 15 = Zwölfer and Harris (1966);
- 16 = Caresche and Wapshere (1975);
- 17 = Campbell and McCaffrey (1991);
- 18 = Parnell (1966);
- 19 = Davies (1928);
- 20 = Kahn and Baloch (1976);
- 21 = Hawkes *et al.* (1975); Parker (1964);
- 23 = Andres and Angalet (1963);
- 24 = Zwölfer (1969)

to be an effective control agent but may fail to thrive in the new climatic conditions of its place of release.

Differences in the frequency of egg-clumping among outbreak and non-outbreak species, or between biocontrol success stories and other species, were analyzed using G-tests (Sokal and Rohlf 1981).

## Results and Discussion

Over the course of our long-term, large-scale census of goldenrod herbivores in the Finger Lakes region of New York, eight species reached densities of one individual per stem or higher (Table 1). Of these eight species, seven lay their eggs in clusters, and one lays a single egg per stem. In contrast, only one species of the twelve that did not outbreak lays its eggs in clusters. This association between outbreak densities and egg-clustering is statistically significant (Table 3).

Many goldenrod herbivores, including a large number of Lepidoptera, were not rep-

**Table 3.**  
**Proportion of outbreak and non-outbreak goldenrod-feeders**  
**that lay eggs in clusters.**

**A) Dynamics based on abundance, all species included;**  
**B) Dynamics based on herbivore load, all species included;**  
**C) Dynamics based on herbivore load, excludes stem gall-makers and stem-borers.**

Dynamics	Proportion of species that lay eggs in clusters	Test of independence between dynamics and oviposition strategy
A)		
Outbreak	0.875	G = 14.006
Non-outbreak	0.083	P < 0.001
B)		
Outbreak	0.545	G = 2.226
Non-outbreak	0.222	0.05 < P < 0.10
C)		
Outbreak species	0.857	G = 6.902
Non-outbreak species	0.222	P < 0.01

resented in the census, some because they were difficult to distinguish in the field, others because they were seen so infrequently. Thus the proportion of the entire fauna considered as outbreak species (40%) is probably greatly exaggerated. Likewise, in Hunter's (1992) data set on forest Lepidoptera, as many as 12% were classified as outbreak species. As she notes, however, the true proportion of outbreaking species, based on the large number of rare, undescribed forest Lepidoptera, is probably closer to 2%. In both the forest Lepidoptera data as well as the goldenrod herbivore data set, many of the extremely rare species may be solitary, and would thus greatly increase the count of nonoutbreak species that lay eggs singly.

This association of egg-clumping with high densities fits the general pattern seen in other herbivore communities, such as sawflies (Hanski 1987) and tree-feeding Lepidoptera (Nothnagel and Schultz 1987, Hunter 1992, 1995). In addition, a study of the larviposition behavior of goldenrod-feeding aphids revealed a similar pattern (Cappuccino 1987). *Uroleucon nigrotuberculatus*, an outbreak species, forms large colonies by actively aggregating and depositing large numbers of nymphs on a single goldenrod stem. Its nonoutbreaking congener, *U. caligatum*, moves frequently, leaving a few nymphs on each of many stems.

Defining an outbreak, not by mere density, but by herbivore load (insect mass per unit of host plant) is likely to reflect more accurately the effect of the insect population on the population of the host plant. Using this criterion for outbreaking, three large stem-gall-

makers and one medium-sized beetle move into the outbreak category, whereas small leaf-miners and leaf-gall-makers move out. The association between outbreaking and egg-clustering drops below the threshold of statistical significance (Table 3). Removing the four large stem-gallers and borers, which in any case are constrained to lay eggs singly by their large size relative to a single goldenrod stem, restores the significant association between outbreaking and egg clustering (Table 3).

The two methods used here to assess outbreak status—density and herbivore load—like all classifications of outbreak species or biocontrol successes, are arbitrary, and fall short of capturing the true impact of the insects on goldenrod fields. The most important North American forest pests need no quantification; foresters and lay persons alike can all agree on what constitutes an outbreak species. The spruce budworm, the gypsy moth, the tent caterpillar and the southern pine beetle would make the top ten of most lists. Likewise, *Cactoblastis cactorum* and *Cyrtobagous slavinae* are textbook examples of weed control agents; their impact on the hostplant is visually obvious. Of all the goldenrod insects, only three—*Trirhabda virgata*, *Microrhopala vittata* and *Corythucha marmorata*—have the visually striking effect of major forest pests and unmitigated biocontrol successes. All three species have been observed to cause widespread defoliation, stem death and reduction in flowering and seed set. All three lay their eggs in clusters.

Would outbreaking goldenrod herbivores perform well as control agents? For the purpose of weed control, an herbivore species that outbreaks in one year and then disappears for the next ten would not necessarily provide effective control. However, the egg-clustering, outbreaking goldenrod herbivores did not join the ranks of rare species in the intervals between their major outbreaks. Dominant herbivores, whether defined by numbers or biomass, remained dominant throughout the study (Root and Cappuccino 1992). Likewise, the spruce budworm in non-outbreak years, remains one of the numerically dominant herbivores of balsam fir, even when it is as scarce as one individual per 100 branches (unpublished data).

Many researchers in weed control as well as in the biocontrol of insect pests, have debated the merits of releasing several control agents as opposed to one (e.g., Ehler and Hall 1982). Our results from the goldenrod fauna are pertinent to this discussion as well. We found very little evidence for competition between herbivores, even in sites where a dominant species was defoliating the plants. On the contrary, the total herbivore load of the non-dominant species was positively correlated with the load of the dominant species in every year of the study (Root and Cappuccino 1992). Again, similar evidence comes to us from studies of the spruce budworm: non-outbreaking Lepidoptera have been shown to have higher rates of population growth in years when the western spruce budworm is outbreaking (Mason 1987). Such positive indirect interactions between herbivores may be more common than once thought (Damman, 1993, Cappuccino and Martin 1994).

### Biocontrol success stories.

Of the 39 weed biocontrol agents that are available from government or commercial suppliers, 17 (43.6 %) lay their eggs in clusters and 22 (56.4 %) lay single eggs. The proportion of species laying eggs in clusters is significantly lower than that of forest pests (G-test with William's correction;  $G = 19.81$ ;  $P < 0.001$ ). It is also significantly lower than that of outbreak species on goldenrod defined by abundance ( $G = 42.07$ ;  $P < 0.001$ ) but not significantly different from that of outbreaking goldenrod-feeders defined by herbivore load ( $G = 2.036$ ;  $P > 0.05$ ). If we had information on the oviposition behavior of a random

sample of the herbivores on each of the weed species we could test whether the proportion of egg-clustering species is higher for the control agents than for the randomly selected species. In lieu of these data, one can compare the proportion of egg-clustering species among the successful control agents with the pseudo-random selections of herbivores included in Root and Cappuccino (1992) and Hunter (1995). Egg clustering is not more prevalent among successful biocontrol agents (43.6%) than among goldenrod herbivores (40%;  $G = 0.2$ ;  $P > 0.50$ ) or forest Microlepidopterans (46.3%;  $G = 0.18$ ;  $P > 0.50$ ).

The large proportion of solitary feeders among successful weed biocontrol agents may be partly explained by the large number of species feeding upon plant parts that constitute a small and circumscribed resource with respect to the size of the exploiters. Successful biocontrol agents seem to be drawn disproportionately from the ranks of stem-borers, gall-makers, seed-feeders and root-feeders, perhaps because of the heavy impact of these feeding styles (eg., Harris and Shorthouse 1996) or their specificity to one or a few related hosts. Stems, seeds, and taproots can often only support a single large borer or gall-maker, whereas leaves can support groups of larvae chewing or mining communally.

### **Bet-hedging, risk-clumping and escape from natural enemies**

Although the association between aggregation and eruptive dynamics is a consistent one, the case of biocontrol agents notwithstanding, the mechanisms linking oviposition behavior to population dynamics have rarely been addressed. Several consequences of aggregation by insect herbivores could explain the tendency of egg-clustering species to outbreak, and could also explain why so many solitary species nevertheless perform well as control agents.

Many studies have revealed advantages of group-living for herbivores. Effective defense from natural enemies (Codella and Raffa 1993), effective shelter-building (Damman 1991), and a local safety-in-numbers from enemies (Cappuccino 1987, Turchin and Kareiva 1989) are among the benefits of aggregation. On the other hand, several advantages to solitary feeding have also been proposed, such as the avoidance of induced defenses (Rhoades 1985), density-dependent parasitoids (Brower 1958) and pathogens (Dwyer 1992). Most studies comparing the advantages of group living versus solitary living consider only the average performance of a female's offspring. More important, however, for understanding the link between egg-clustering and eruptive dynamics is the variability in performance. When larval survivorship is variable and unpredictable in space, a female increases the chance that at least some of her offspring will survive by laying eggs singly. By spreading her eggs in space, she is adopting a "bet-hedging" or "risk-spreading" oviposition behavior (Root and Kareiva 1984). Like a timid gambler who places a small amount of money on each several outcomes, the results of risk-spreading are relatively predictable; the gambler cannot win much, but neither does he lose everything. The opposing strategy, that of "risk-concentrating" or placing "all one's eggs in the same basket", yields a more variable outcome. Species that concentrate the risk by clustering their eggs have a greater spatial variability in success, and this spatial variability may translate into increased temporal variability. Hanski (1987) illustrated this with a model of sawfly dynamics, in which the probability of escaping the control of predators increased as a function of the between-group variance in survivorship. In other words, egg-clustering led to boom-or-bust dynamics by facilitating an escape from natural enemies.

Given that biocontrol agents are often released into environments that are relatively free of natural enemies, it is likely that the dependence on egg clumping to achieve high

density breaks down. Bet-hedging species that normally have constant, low densities because they rarely escape the control of predators may become, in the absence of enemies, outbreak species, limited only by the abundance of their resource. The large proportion of solitary species among successful biocontrol agents may also provide insight into the debate on top-down and bottom-up control in natural systems (eg., Hunter and Price 1992). If the mechanism proposed by Hanski—that of risk-clumping to escape the control of enemies—is indeed the key linking aggregation to outbreak dynamics, then the low proportion of risk-clumpers among biocontrol agents (without enemies), coupled with the high proportion of risk-clumpers in natural systems (with enemies), underscores the importance of top-down control of herbivores in the natural systems.

Finally, analyses of the life-history characteristics of successful biocontrol agents, like analyses of the characteristics of outbreak species, are hindered by our limited knowledge of species that do not outbreak and that are not economically important. Studies on the natural history of non-outbreak species are deserving of our attention.

## References

- Andres, L.A., and G.W. Angalet. 1963.** Notes on the ecology and host specificity of *Microlarinus lareynii* and *M. lypriformis* (Coleoptera: Curculionidae) and the biological control of puncture vine, *Tribulus terrestris*. *Journal of Economic Entomology* 56: 333-340.
- Brower, L.P. 1958.** Bird predation and foodplant specificity in closely related procryptic insects. *American Naturalist* 92:183-187.
- Campbell, C.L., and J.P. McCaffrey. 1991.** Population trends, seasonal phenology, and impact of *Chrysolina quadrigemina*, *C. hyperici* (Coleoptera: Chrysomelidae), and *Agrilus hyperici* (Coleoptera: Buprestidae) associated with *Hypericum perforatum* in Northern Idaho. *Environmental Entomology* 20:303-315.
- Cappuccino, N. 1987.** Comparative population dynamics of two goldenrod aphids: spatial patterns and temporal constancy. *Ecology* 68:1634-1646.
- Cappuccino, N., and M.A. Martin. 1994.** Eliminating early-season leaf-tiers of paper birch reduces abundance of mid-summer species. *Ecological Entomology* 19:399-401.
- Caresche, L.A., and A.J. Wapshere. 1975.** The *Chondrilla* gall midge, *Cystiphora schmidti* (Rübsaamen) (Diptera: Cecidomyiidae). II. Biology and host specificity. *Bulletin of Entomological Research* 65:55-64.
- Clark, L.R. 1953.** The ecology of *Chrysomela gemellata* Rossi and *C. hyperici* Forst. And their effect on St. John's Wort in the Bright District, Victoria. *Australian Journal of Zoology* 1:1-69.
- Codella, S.G., and K. F. Raffa. 1993.** Defense strategies of folivorous sawflies, pp. 261-294 *In* M. R. Wagner and K. F. Raffa [eds], *Sawfly life history adaptations to woody plants*, Academic Press, San Diego, CA.
- Damman, H. 1993.** Patterns of interaction among herbivore species, pp. 132-169 *In* N. E. Stamp and T. M. Casey [eds.] *Caterpillars: Ecological and evolutionary constraints on foraging*, Chapman and Hall, New York, NY.
- Damman, H. 1991.** Oviposition behaviour and clutch size in a group-feeding pyralid moth, *Omphalocera munroei*. *Journal of Animal Ecology* 60:193-204.
- Davies, W.M. 1928.** The bionomics of *Apion ulicis* Forst. (gorse weevil), with special reference to its role in the control of *Ulex europaeus* in New Zealand. *Annals of Applied Biology* 15:263-285.
- DeLoach, C.J., and H.A. Cordo. 1976.** Life cycle and biology of *Neochetina bruchi*, a weevil attacking waterhyacinth in Argentina, with notes on *N. eichhorniae*. *Annals of the Entomological Society of America* 69:643-652.

- Dwyer, G. 1992. On the spatial spread of insect pathogens: theory and experiment. *Ecology* 73:479-494.
- Ehler, L.E., and R.W. Hall. 1982. Evidence for competitive exclusion of introduced natural enemies in biological control. *Environmental Entomology* 11:1-4.
- Fornasari, L., C.E. Turner, and L.A. Andres. 1991. *Eustenopus villosus* (Coleoptera: Curculionidae) for biological control of yellow starthistle (Asteraceae: Cardueae) in North America *Environmental Entomology* 20:1187-1194.
- Fullaway, D.T. 1954. Biological control of cactus in Hawaii. *Journal of Economic Entomology* 47:696-700.
- Hanski, I. 1987. Pine sawfly population dynamics: patterns, processes, problems. *Oikos* 50:327-335.
- Harris, P., and J.D. Shorthouse. 1996. Effectiveness of gall inducers in weed biological control. *Canadian Entomologist* 128:1021-1055.
- Hawkes, R.B., R.D. Goeden, A. Mayfield, and D.W. Ricker. 1975. Biological control of Russian Thistle. *California Agriculture* 29:3-4.
- Hervey, G.E.R. 1927. A European nitidulid, *Brachypterolus pulicarius* L. (Coleoptera, family Nitidulidae). *Journal of Economic Entomology* 20:809-814.
- Hunter, A.F. 1991. Traits that distinguish outbreaking and non-outbreaking Macrolepidoptera feeding on northern hardwood trees. *Oikos* 60:275-282.
- Hunter, A.F. 1995. Ecology, life history and phylogeny of outbreak and nonoutbreak species. Pp. 41-64 *In* N. Cappuccino and P. W. Price [eds.], *Population dynamics: new approaches and synthesis*, Academic Press, San Diego, CA.
- Hunter, C.D. 1997. Suppliers of beneficial organisms in North America. <http://www.cdpr.ca.gov/docs/ipminov/bensup.pdf>
- Hunter, M.D., and P.W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724-732.
- Khan, A.G., and G.M. Baloch. 1976. *Coleophora klimeschiella* (Lep; Coleophoridae) a promising biocontrol agent for Russian thistles, *Salsola* spp. *Entomophaga* 21:425-428.
- Lawton, J.H. 1979. Between the devil and the deep blue sea: on the problems of being a herbivore. *Symposium of the British Ecological Society* 20:223-244.
- Louda, S.M. 1998. Population growth of *Rhinocyllus conicus* (Coleoptera: Curculionidae) on two species of native thistles in prairie. *Environmental Entomologist* 27:834-841.
- Maddox, D.M. 1968. Bionomics of an alligatorweed flea beetle, *Agasicles* sp. *In* Argentina. *Annals of the Entomological Society of America* 61:1299-1305.
- Maddox, D.M., D.B. Joley, A. Mayfield, and B.E. Mackey. 1991. Impact of *Bangasternus orientalis* (Coleoptera: Curculionidae) on achene production of *Centaurea solstitialis* (Asterales: Asteraceae) at a low and high elevation site in California. *Environmental Entomology* 20:335-337.
- Mason, R.R. 1987. Nonoutbreak species of forest Lepidoptera. pp. 31-57 *In* P. Barbosa and J. C. Schultz [eds.], *Insect outbreaks*, Academic Press, San Diego, California, USA.
- McEvoy, P.B., N.T. Rudd, C.S. Cox, and M. Huso. 1993. Disturbance, competition, and herbivory effects on ragwort *Senecio jacobaea* populations. *Ecological Monographs* 63:55-75.
- McFadyen, R.E.C. 1998. Biological control of weeds. *Annual Review of Entomology* 43:369-393.
- Meyer, G.A. 1993. A comparison of the impacts of leaf- and sap-feeding insects on growth and allocation of goldenrod. *Ecology* 74:1101-1116.
- Müller, H., D. Schroeder, and A. Gassmann. 1988. *Agapeta zoegana* (L.) (Lepidoptera: Cochyliidae), a suitable prospect for biological control of spotted and diffuse knapweed, *Centaurea maculosa* Monnet de la Marck and *Centaurea diffusa* Monnet de la Marck (Compositae) in North America. *Canadian Entomologist* 120:109-124.
- Murray, D. 1949. *Anaitis plagiata* L. *Entomologist's Record* 61:87-89.

- Nothnagle, P.J., and J.C. Schultz. 1987.** What is a forest pest? pp 59-80 *In* P. Barbosa and J. C. Schultz [eds.], *Insect outbreaks*, Academic Press, San Diego, California, USA.
- Parker, H.L. 1964.** Life history of *Leucoptera spartifoliella* with results of host transfer tests conducted in France. *Journal of Economic Entomology* 57:566-569.
- Parnell, J.R. 1966.** Observations on the population fluctuations and life histories of the beetles *Bruchidius ater* (Bruchidae) and *Apion fuscirostre* (Curculionidae) on Broom (*Sarothamnus scoparius*). *Journal of Animal Ecology* 35:157-188.
- Peschken, D.P., and P. Harris. 1975.** Host specificity and biology of *Urophora cardui* (Diptera: Tephritidae), a biocontrol agent for Canada thistle (*Cirsium arvense*) *Canadian Entomologist* 107:1101-1110.
- Redfearn, A., and S.L. Pimm. 1988.** Population variability and polyphagy in herbivorous insect communities. *Ecological Monographs* 58:39-55.
- Rhoades, D.F. 1985.** Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *American Naturalist* 125: 205-238.
- Root, R.B. 1996.** Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. *Ecology* 77:1074-1087.
- Root, R.B., and N. Cappuccino. 1992.** Patterns in population change and the organization of the insect community associated with goldenrod. *Ecological Monographs* 62:393-420.
- Root, R.B., and P. M. Kareiva. 1984.** The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences of Markovian movements in a patchy environment. *Ecology* 65:147-165.
- Sokal, R.R., and F. J. Rohlf. 1981.** *Biometry*. Second edition. W. H. Freeman and Co., San Francisco.
- Story, J.M., K.W. Boggs, W.R. Good, P. Harris, and R.M. Nowierski. 1991.** *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae), a moth introduced against spotted knapweed: its feeding strategy and impact on two introduced *Urophora* spp. (Diptera: Tephritidae). *Canadian Entomologist* 123:1001-1007.
- Turchin, P., and P. Kareiva. 1989.** Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology* 70: 1008-1016.
- Wallner, W.E. 1987.** Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. *Annual Review of Entomology* 32:317-340.
- Weber, E. 1998.** The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *Journal of Biogeography* 25:147-154.
- Weeden, C.R., A.M. Shelton, and M.P. Hoffman. 1999.** *Biological control: a guide to natural enemies in North America*.  
<http://www.nysaes.cornell.edu/ent/biocontrol/weedfeeders/wdfdrtoc.html>
- Zwölfer, H. 1969.** *Urophora siruna-seva* (Hg.) (Dipt.: Trypetidae), a potential insect for the biological control of *Centaurea solstitialis* L. in California. *Technical Bulletin of the Commonwealth Institute of Biological Control* 11:105-155.
- Zwölfer, H., and P. Harris. 1966.** *Ceutorhynchus litura* (F.) (Col.: Curculionidae), a potential insect for the biological control of thistle, *Cirsium arvense* (L.) Scop., in Canada. *Canadian Journal of Zoology* 44:23-38.