Feeding Strategy, Coexistence and Impact of Insects in Spotted Knapweed Capitula

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Abstract

Although this paper primarily analyses spotted knapweed capitula insects in terms of feeding strategies and value as biological control agents, the conclusions should apply to any thistle species. Seven feeding strategies of seed-head insects are characterized. The most damaging to the host plant are the woody gall formers which create a powerful metabolic sink and sequester nutrients from other parts of the plant. Receptacle feeders displace the woody gall formers and have less impact on the host plant. They are the best choice as biological control agents in the absence of a woody gall former and may also be useful if the host plant is scattered. However, if likely to displace a gall former, they should not be used. Ovary gall formers have good dispersal but are displaced by most other feeding strategies. The ovary feeders oviposit into, and the larvae perish in, capitula attacked by woody gall formers and receptacle feeders. They do, however, have good dispersal and are a useful supplement to attack isolated plants. The achene gall former avoids capitula attacked by the woody gall formers and receptacle feeders and is destroyed by species of most other strategies. Like the ovary gall former, it appears to be broadly oligophagous and becomes locally abundant when populations of other insects are depressed. The soft achene feeders avoid capitula attacked by woody gall formers and receptacle feeders and so supplement their impact. The ripe achene feeders should be avoided as biological control agents except in special cases.

Introduction

There are many stenophagous insects that develop in the capitula of spotted knapweed (Centaurea maculosa Laminack; Asteraceae). Zwölf (1985) reported that in Europe capitula attack increased with up to seven insect species at a site. Attack in Canada with one phytophagous species in the absence of specialized parasitoids is similar to that in Europe with seven insect species (Fig. 1) and the increase by adding two additional species is parallel to the European line.

It appears from Figure 1 that the more species, the better; however, there is competition between them and the per site average was only 3.2 species (Zwölf 1979). It is important for biological control to establish a complex that maximizes impact on the weed. Spotted knapweed is a particularly good species for analysis as it has a rich fauna. It is suggested that the conclusions from this plant species are applicable to any species of Cynareae.

Feeding Strategies of Knapweed Seed-head Insects

Zwölf (1988) identified three feeding strategies of endophagous insects in the seed-heads of Cynareae spp. I suggest that there are seven strategies that affect the seed production, two of which are almost confined to the Centaurea. One additional strategy largely exploits residual flower head tissues and hence is of no interest to biological control.

The strategies (Table 1) in approximate order of attack on the flower-heads are: a) the formation of woody galls; b) receptacle feeding; c) the formation of non-woody ovary galls; d) ovary feeding; e) formation of achene galls; f) feeding on well developed but still soft achenes; g) feeding on mature achenes and preying on insect species in the previous strategies. It is suggested that seed destruction in the absence of parasitoids is maximized by establishing a community with only an a, d and f strategy insect.
It is apparent from Table 1 that there are several insect species with the same feeding strategy and there are more than shown. Normally only one insect species of a strategy occurs at a site. For example, the receptacle feeder *Xyphosia miliaria* Schr. (Diptera: Tephritidae) was only abundant on *Cirsium heterophyllum* (L.) Hill in the absence of *Tephritus conura* Loew (Diptera: Tephritidae) in northern Sweden (Romstöck 1983). The pattern agrees with the Fox (1987) species assembly theory: there is a high probability that species entering a community will be drawn from different functional groups. In part the insects have different climatic requirements and this should be considered when selecting a species for biological control. The exceptions where two species with the same strategy occur at a site may arise from the reduction of their populations by parasitoids.

![Graph showing the increase in knapweed attack with number of insect species present.](image)

**Figure 1. Increase in knapweed attack with number of insect species present.**

Another generality is that the species in a genus have the same feeding strategy regardless of their host plant. The exceptions (Table 1) are more apparent than real: the receptacle feeding *Larinus longirostris* Gyllenhal (Coleoptera: Curculionidae) is in a different subgenus from *L. minutus* Gyllenhal, which feeds on the soft achenes. Similarly, the gall of *Urophora quadrifasciata* (Meig.) (Diptera: Tephritidae) is so different from those of the woody gall forming species that it could be placed in a different subgenus. Indeed, allozyme studies (Brandl, R., pers. comm. 1988) showed that *U. quadrifasciata* is older than the woody gall formers. The genus *Isocolus* (Hymenoptera: Cynipidae) needs more study to determine whether the woody gall former and the achene gall former are closely related.

**Woody Gall Formers**

Gall formers must attack meristem tissue. The woody gall formers attack at an early capitula developmental stage. Those on spotted knapweed are *Isocolus minutus* Dyack, D'yakonchik (1982) and *Urophora affinis* Frauenfeld (Diptera:Tephritidae). All the woody gall formers that have been investigated (Harris and Shorthouse, unpubl. data) cause
proliferation of the vascular tissue and create a powerful metabolic sink that sequesters nutrients from other parts of the plant. Logistically it is a particularly effective strategy for exploiting plant species that produce many small capitula over a long season. To achieve similar utilization, a non-gall former must attack most of the flower-heads. Possibly this is why woody-gall formers are common in Centaurea, which has many species with small capitula and are rare or absent in genera such as Cynara and Silybum which have a few large capitula.

Table 1. Feeding strategies in spotted knapweed capitula.

<table>
<thead>
<tr>
<th>Flower-head Stage</th>
<th>Gall Formers</th>
<th>Non-gall Formers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immature bud</td>
<td>Woody gall</td>
<td>Receptacle feeder</td>
</tr>
<tr>
<td></td>
<td><em>Isocolus minutus</em> Djack</td>
<td><em>Bangasterna fausti</em> (Reitt.)</td>
</tr>
<tr>
<td></td>
<td>(Hymenoptera: Cynipidae)</td>
<td>(Coleoptera: Curculionidae)</td>
</tr>
<tr>
<td></td>
<td><em>Urophora affinis</em> Frauenfeld</td>
<td><em>Larinus longirostris</em> Gyllenhall</td>
</tr>
<tr>
<td></td>
<td>(Diptera: Tephritidae)</td>
<td>(Coleoptera: Curculionidae)</td>
</tr>
<tr>
<td>Floret growth</td>
<td>Ovary gall</td>
<td>Ovary feeder</td>
</tr>
<tr>
<td></td>
<td><em>Urophora quadrifasciata</em> (Meigen)</td>
<td>Chaetorellia acrolophi White and Marquardt</td>
</tr>
<tr>
<td></td>
<td>(Diptera: Tephritidae)</td>
<td>(Diptera: Tephritidae)</td>
</tr>
<tr>
<td>Achene growth</td>
<td>Achene gall</td>
<td>Soft achene feeder</td>
</tr>
<tr>
<td></td>
<td><em>Isocolus iaceae</em> (Schenck)</td>
<td><em>Larinus minutus</em></td>
</tr>
<tr>
<td></td>
<td>(Hymenoptera: Cynipidae)</td>
<td>(Coleoptera: Curculionidae)</td>
</tr>
<tr>
<td></td>
<td><em>Terelia virida</em> Loew</td>
<td><em>Larinus minutus</em></td>
</tr>
<tr>
<td></td>
<td>(Diptera: Tephritidae)</td>
<td>(Coleoptera: Curculionidae)</td>
</tr>
<tr>
<td>Ripe achene</td>
<td>No niche</td>
<td>Achene feeder - predator</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Metanoria paucipunctella</em> Zeller</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Lepidoptera: Gelechiidae)</td>
</tr>
</tbody>
</table>

The gall has an additional attribute as when hardened, the larvae are protected from most other seed-head insects. A problem faced by the insect is that it has a narrow oviposition window. *U. affinis* attacks flower buds of a particular size (Berube 1980) so that hatching coincides with meristem activity of the upper receptacle. Theoretically plants could escape attack by flowering earlier or later (Weis *et al.* 1988); but the insect forms local races rapidly, apparently assisted by an aggregation pheromone. For example, four years after *U. affinis* release in Canada, the colony increased to a population of 76 million galls all within a radius of 410 m (Harris 1980b).

Late-forming capitula on attacked plants abort because the resources of the plant are channelled to the capitula attacked earlier (Harris 1980a). The buds never reach the stage of having meristematically active upper receptacle and the larvae in them die.

Impact studies have not been made on *Isocolus* spp. However, *Trichologaster acaciaelongifoliae* (Foggatt) (Hymenoptera: Pteromalidae), which induces woody galls in the immature flower buds of *Acacia longifolia* (Andrews) Wildenow (Mimosaceae), forms a powerful metabolic sink that can prevent all tree growth during the summer (Dennill 1987). Total gall weight comprised up to 21% of the above ground biomass of the tree on a dry weight basis. *I. minutus* should have a similar impact on spotted knapweed, although whether it can coexist with an unparasitized population of *U. affinis* is uncertain. Its occurrence in the Ukraine indicated it might be a valuable species to restrict the spread of spotted knapweed onto the Canadian prairies.
The *Urophora* spp. which form woody galls are responsible for the major energy loss from the capitula of Cynareae. Zwölfer (1985) reported that *U. stylata* L. was responsible for up to 95% of the energy loss from the capitula of *Cirsium vulgare* (Savi) Tenore. In the biennial diffuse knapweed, attack of the flower heads reduced above ground biomass by 71% by diverting assimilates normally destined for vegetative growth (Harris 1980a). Unfortunately this has not produced an equivalent reduction in the impact of spotted knapweed on grass. The reason seems to be that the knapweed roots still use the available moisture (the limiting resource) although they make fly biomass rather than knapweed biomass. Seed-destroying insects should not increase grass biomass until seed production is below the number needed for weed replacement.

The impact of *U. affinis* on the perennial spotted knapweed became obvious after several years of attack. Apparently the sink created by the galls competed with the replenishment of root reserves so that fewer and smaller flowering stems were produced in the following year. Most of the decline in flower head production at Chase, British Columbia (Table 2) has been the result of attack by *U. affinis*. Other attributes of woody gall formers are:

(a) Crowding within a capitula has little effect on larval weight (Harris 1980a). The larvae either get enough nourishment or they do not develop at all.
(b) The limited dispersal is helpful in getting establishment of colonies as it reduces dispersion loss. However, *U. affinis* has had to be manually dispersed to other knapweed stands.
(c) Poor dispersal makes the insect dependent on a high weed density. The numbers of *U. affinis* per may decline in Canada as knapweed is reduced to a scattered plant.
(d) Gall formation and hence impact on the plant does not require fertilization of the capitula.

My first choice for a biological control agent among capitula insects for any Cardueae weed is a woody gall former because it is likely to have a greater impact than any other feeding strategy. No other insect should be introduced that will reduce its impact.

**Receptacle Feeders**

Most receptacle-feeding insects also have a narrow oviposition window. Like the woody gall former, the critical time for egg hatch is probably the period of high meristematic activity in the upper receptacle. It was found in *Carduus nutans* L. capitula attacked by *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae) (Shorthouse and Lalonde 1984) and in *C. heterophyllum* capitula attacked by *T. conura* that callus was induced in the upper receptable Romstöck (1987). The callus may prevent bud abortion by maintaining the nutrient flow to the attacked head. The nutrient flow to *T. conura*-attacked heads was similar to that of unattacked heads (Romstöck 1987), so in effect the insect replaces the sink of normal capitular tissue with a callus sink.

If the receptacle feeder attacks too early, the capitula abort and the larvae die; if they attack too late they are displaced by the woody gall former and they have lost any competitive advantage over the soft achene feeders. Angermann (1987) reported a high mortality from capitula abortion in the receptacle-feeding tephritid *X. miliaria* on *Cirsium arvense* (L.) Scopoli and Romstöck (1987) found the same on *C. heterophyllum* attacked by *T. conura*. *T. conura* has formed races on *Cirsium* spp. that flower at different times (Romstöck 1987) and these populations are genetically isolated (Seitz and Komma 1984) apparently by a host plant rendezvous. This allows the fly to synchronize larval hatch with capitulum susceptibility. The *C. heterophyllum* race of *T. conura* has low parasitism (Romstöck 1987), so it is rather like an introduced biological control agent. It maybe coincidence, but there is no woody gall former on *C. heterophyllum* in Europe. On *Cirsium erisithales* (Jacq.) Scopoli, the woody gall former *Urophora congra* Loew is restricted to small regions where *T. conura* does not occur (Müller-Hohenstein 1984).

No other insects survive in spotted knapweed capitula with the receptacle feeding weevil *Bangasterus fausti* (Reitt.) (Coleoptera: Curculionidae) (P.H. Dunn, pers. comm.). Presumably it consumes any *U. affinis* while the galls are still soft. I expect that in North
America, without the depression of the *B. fausti* population by parasitoids, *U. affinis* will be displaced from sites with *B. fausti* sites.

On the other hand, in *C. nutans* heads Zwölfer (1973, 1979) reported that the weevil *R. conicus* was partially displaced by the gall-former *Urophora solstitialis* (L.). This displacement, which must occur before the galls harden, may arise because the gall is a strong metabolic sink which outcompetes the callus sink. The outcome of the competition seems to depend on the timing of the attack. The *C. nutans* strain of *R. conicus* studied by Zwölfer (1979) has not specialized to the same degree as other receptacle feeders, and in North America it attacks *Carduus* spp. and *Cirsium* spp. indiscriminately (Turner et al. 1987). On many of these, such as *Cirsium undulatum* (Nutt.), the attack is mistimed so that most of the capitula abort and the larvae dies. I contend that if the whole attack occurred a few days earlier on *C. nutans*, the weevil would displace *U. solstitialis*, although the bud abortion rate would also increase.

**Table 2. Number of *Urophora* spp. and *Centaurea maculosa* capitula in Chase, British Columbia.**

<table>
<thead>
<tr>
<th>Year</th>
<th>No. capitula per m²</th>
<th>No. <em>Urophora</em>/head</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>affinis</em></td>
</tr>
<tr>
<td>1973</td>
<td>1000</td>
<td>0.0003</td>
</tr>
<tr>
<td>1974</td>
<td>1524</td>
<td>0.01</td>
</tr>
<tr>
<td>1976</td>
<td>560</td>
<td>3.3</td>
</tr>
<tr>
<td>1977</td>
<td>260</td>
<td>4.9</td>
</tr>
<tr>
<td>1978</td>
<td>280</td>
<td>2.5</td>
</tr>
<tr>
<td>1979</td>
<td>204</td>
<td>1.8</td>
</tr>
<tr>
<td>1982</td>
<td>-</td>
<td>0.8</td>
</tr>
<tr>
<td>1985</td>
<td>287</td>
<td>3.6</td>
</tr>
<tr>
<td>1986¹</td>
<td>132</td>
<td>1.9</td>
</tr>
<tr>
<td>1987</td>
<td>24</td>
<td>1.3</td>
</tr>
</tbody>
</table>

¹ Risley et al. (1986).

*R. conicus* achieved a high population density in *C. nutans* in Canada and better dispersal than *U. affinis*. It reduced seed production by about 50% and in most sites with good grass competition, has controlled the thistle. It has been less effective on *Carduus acanthoides* L. which produces small capitula over a long season (Harris 1984). *T. conura* accounted for 90% of the biomass of the primary consumers and utilized 25-50% of the flower head production (Romstock 1987). Dispersal is extremely good in *T. conura* but resulted in a 90% population loss over winter (Romstock 1987). Consequently large numbers would be needed to establish it in a new region. Apart form a possible problem in getting establishment with some species, receptacle feeders can be effective biological control agents.

My concern is that receptacle feeders are likely to displace the woody gall-former. This is not beneficial as their utilization is restricted to the capitula while the woody gall-former can exploit the whole plant. If there are no woody gall formers my choice is a receptacle feeder. I would also use them if the host plant is scattered which is not the case for spotted knapweed in Canada.

**Ovary Feeders**

The eggs of *Chaetorellia acrolophi* White and Marquardt (Diptera: Tephritidae) are laid between the involucral bracts shortly before anthesis (Marquardt 1986). The larvae consume
ovaries, soft achenes and receptacle tissue. The important feature is the time of oviposition. Species with this strategy do not seem to avoid capitula attacked by other insects. For example Romstöck (1987) found that Chaetostomella onotrophese Loew (Diptera: Tephritidae) oviposited into capitula attacked by T. conura and perished as a result. As T. conura attacked a high proportion of C. heterophyllum capitula, C. onotrophes was rare on this plant. Chaetorellia spp. in knapweed seem to be adept at attacking isolated plants. Probably this is the result of aggressive adult behaviour as found by Romstöck (1987) in T. conura. As the woody gall formers tend to be confined to stands of its host, the tephritid should have little competition for the isolated plants.

C. acrolophi is likely to supplement the impact of U. affinis by attacking isolated plants. However, it would add little seed destruction in the presence of a receptacle feeder with good dispersal. Marquardt (1987) found it to be a rare but widely dispersed species in Europe. I think it would have been found more frequently if scattered knapweed plants had been sampled.

I contend the ovary feeder is a valuable addition for biological control if scattered plants are not being attacked; but is a waste of effort if they are well exploited.

Ovary Gall-formers

The ovary gall-former oviposits during the floret growth stage shortly before anthesis. The galls are not woody, there is less consumption per gram of larvae than by the woody gall-former, there is little or no proliferation of vascular tissue, and the sink is restricted to the attacked head (Harris 1980a). The gall-former utilizes the normal nutrient flow to the capitula and cannot survive in unfertilized heads. It is a rare feeding strategy restricted to the Cenautrea, except possibly for one species in the genus Echinops. The gall-former is displaced by most other capitula insects, but in Echinops some of the competition is eliminated by a different capitula construction. In Cenautrea, U. quadrifasciata seems to survive because it is broadly oligophagous and has good dispersal.

U. quadrifasciata avoids heads containing many U. affinis. However, it coexist in heads lightly attacked by U. affinis. U. quadrifasciata is becoming increasingly important in Canada (Table 2) and presently is supplementing the impact of U. affinis (Myers and Harris 1980). However, I expect it to be displaced when we have reduced seed production still further by establishing ovary and ripe achene feeders. Thus, an ovary gall-former is likely to be a waste of effort from a biological control point of view.

Achene Gall-former

Little is known about the biology of Isocolus iaceae (Schenck). It presumably oviposits into enlarging achenes which means that it will avoid capitula heavily attacked by woody and ovary gall formers and those with receptacle feeders. It is likely to be consumed in capitula attacked by the ovary, soft and ripe achene feeders, so it is at a considerable competitive disadvantage. The galled achene is only slightly enlarged and it is unlikely that there is proliferation of vascular tissue. The achene gall formers are restricted to the subtribe Centaurineae and Buhr (1964) suggests that there is one broadly oligophagous species on Cenautrea. The situation is similar to the ovary gall-former U. quadrifasciata.

I. iaceae is locally common in Europe in the black knapweed species group; but rare in spotted knapweed. To achieve a high impact it must attack most achenes. It obviously supplements the impact of other capitula insects in Europe; but I feel that the establishment in Canada of several competitively superior capitula insects without their parasitoids leaves I. iaceae without a niche. Thus, like U. quadrifasciata, it is a waste of effort screening it as a biological control agent.
Soft Achene Feeders

Michaelis (1984) reported that the soft achene feeding Terellia serratula (L.) (Diptera: Tephritidae) tended to avoid capitula of Cirsium vulgare attacked by the woody gall-former U. stylata. Oreilla rufticauda Fabr. tended to avoid heads attacked by the receptacle feeder X. miliaria (Angermann 1987) as well as by T. conura (Romstöck 1983). This is a simple process as soft achene feeders oviposit into the open flower head and those heads heavily attacked by woody gall formers and receptacle feeders do not open. In spotted knapweed, L. minutus and Terellia virens Loew supplement the impact of U. affinis by attacking capitula that it has missed (Sinskon and Marquardt 1987). Thus this strategy avoids the problem encountered by the ovary feeders.

The impact of the soft achene feeder in North America has still to be determined. Marquardt (1978) found T. virens to be common, especially in Hungary and Austria and L. minutus occurred in Romania. Thus they appear to be attractive biological control agents for Canada.

Ripe Achene Feeder/Predator

This strategy is employed by a number of moths and beetles that feed partially on ripe achenes. Most of them also have the ability to consume other insects in the head including those in woody galls although the galls are usually eaten while still soft. Clearly this is undesirable from a biological control point of view. However, the genus Meteneria (Lepidoptera: Gelechiidae) does relatively more damage to its host plant than to other capitula insects and so is a worthwhile biological control agent. Many species are also able to move between capitula, an ability not present in the other feeding strategies.

M. paucipunctella Zeller has added to seed destruction in spotted knapweed in Canada with each larva reducing seed production by about 6 seeds/head. The early instars of M. paucipunctella are spent in the receptacle where all but one larva is destroyed. Around October the larva leaves the receptacle to feed on three seeds located next to the bracts or a Urophora larva if it is encountered. However, U. affinis galls are normally located near the center of the receptacle and are missed. Most of the U. quadrifasciata, which are peripheral, emerge for a second generation before October. At Castlegar, British Columbia, where around 80% of the capitula are attacked, I found up to 10% of the U. affinis and 1% of the U. quadrifasciata galls eaten. I expect the number to decrease as the knapweed and U. affinis density declines.

My feeling is that M. paucipunctella and possible other species in the genus are beneficial as biological control agents; but most ripe achene feeders, such as Homesoma spp., should be avoided.

Capitula Insect Community and Biological Control

The insect community in spotted knapweed and other Cardueae seem to be determined by a number of factors. In part the capitula insects have different climatic tolerances. Obviously for biological control this should be considered. For knapweed control in the interior of British Columbia insect species occurring in Hungary and to the east and north are of most interest.

Some the capitula species within a region survive by evasion tactics. The soft achene feeders largely avoid competitors by oviposition into open flower heads. Similarly the ovule feeders may avoid competitors through aggressive adult behaviour that disperses the population. The result is that attack tends to occur on isolated plants rather than the stands favoured by the woody gall formers and some receptacle feeders. The evasive species is a useful biological control agent as it supplements the impact by the main consumer.

The survival of insect species in Europe that compete directly is partly the result of population depression by parasitoids. In Europe, seven species attack around 60% of spotted
knapweed capitula while in Canada three species attack around 85% (Fig. 1). Clearly competition is greater in Canada.

It is difficult for species that oviposit at the same time to avoid each other and the outcome seems to depend on the timing of attack. I suggest that if the woody gall-former and the receptacle feeder hatch simultaneously, the receptacle feeder will win. For the receptacle feeder to do this consistently, it must specialize so that larval hatch occurs at the start of high meristic activity in the upper receptacle. This appears to be the strategy of *T. conica*. If the receptacle feeder fails to specialize (as is the case with *R. conica*) it will be partially displaced by the woody gall-former. For biological control purposes the woody gall-former is the superior species as it utilizes energy from the plant as a whole and not just that in the capitula. Thus, if available, my first choice is a woody gall-former and care should be taken not to introduce a specialized receptacle feeder, since without parasitoids, it will displace the gall-former and increase seed production of the weed.

The competitively inferior species such as the ovary and achene gall formers survive in Europe by evasion tactics and the gambling strategy of spreading the risk over several host plants. In Europe the increase in the impact on the host plant; but I doubt if there is a niche for them in Canada when the more specialized woody gall-former, and ovary feeder and a soft achene feeder are established.

The biological control value of introducing a ripe achene feeder will depend on whether it is primarily phytophagous as *M. paucipunctella* or preferentially predatory.

The insect community in other thistles and knapweeds is similar to that in spotted knapweed and the conclusions of this study should apply to them all. Thus my choice for the biological control of any *Carduus* species is first a woody gall-former and in its absence a receptacle feeder, but not both. A receptacle feeder is also indicated if the host plant is scattered. Either of these insects should be supplemented with an ovary feeder if isolated plants are not being attacked and with a soft achene feeder to exploit capitula missed by the first insect.

**Acknowledgments**

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**References**


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Lam. (diffuse knapweed) and C. maculosa Lam. spotted knapweed (Compositae) in North America.