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Ten Years of Scentless Chamomile: Prospects for the Biological Control of a Weed of Cultivated Land

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Abstract

In 1988, scentless chamomile (*Matricaria perforata* = *Tripleurospermum perforatum*) was proposed as a new target weed for biological control in Canada. Scentless chamomile is mainly a weed of cultivated land, where it reduces crop yield. But it also forms dense, semi-permanent stands in periodically disturbed sites, such as slough margins, field depressions or roadsides, from which seeds spread into adjacent fields. Biological control is mainly aimed at these populations in uncultivated areas, because chemical and cultural control methods often prove uneconomic or impractical in these habitats, and because biological control agents should be more likely to establish there. Surveys were started in Europe in 1990, and eight potential biocontrol agents have now been investigated. Three of these have been introduced into Canada, three were not specific enough for introduction, and two are still under investigation. Because the plant reproduces only by seed, the first insect to be introduced and established was a seed-feeding weevil, *Omphalapion* (*Apion*) *hookeri* in 1992. This was followed by the stem-mining weevil *Microplontus* (*Ceutorhynchus*) *edentulus* in 1997. Studies on the population biology of scentless chamomile in Europe and Canada suggested that insects which attack the overwintering rosettes of scentless chamomile should be most effective. The gall midge *Rhopalomyia* n. sp., and the agromyzid *Napomyza* sp. near *lateralis* are therefore predicted to be the most successful agents. Both species are multivoltine and attack practically all plant phenostages throughout the growing season. Particularly the overwintering larvae in the rosettes may kill whole plants (*Rhopalomyia*) or developing shoots (*Napomyza*). Field release of *Rhopalomyia* was approved in March 1999, but the taxonomic position and host range of *Napomyza* still need to be clarified. Post-release studies are planned to test our predictions on relative agent effectiveness.

Keywords: *Matricaria perforata, Tripleurospermum perforatum*, scentless chamomile, plant population biology, agent effectiveness, disturbance

Introduction

Scentless chamomile (*Tripleurospermum perforatum* (Mérat) Laínz = *Matricaria perforata* Mérat, Asteraceae: Anthemideae) is a plant of European origin that became naturalized in North America at the end of the 19th-century (Woo *et al.* 1991). Initially, the plant spread slowly, but during the last few decades its range has expanded rapidly (Douglas 1989). Two different cytotypes exist, a diploid ($2n = 18$) which predominates in maritime climates, and a tetraploid ($2n = 36$), with a mainly continental distribution (Kay

1969, Woo *et al.* 1991). The tetraploid cytotype, in particular, has become a serious weed of various agricultural crops in the Canadian prairie provinces of Alberta, Saskatchewan and Manitoba, where it may lead to considerable yield reductions (Cole 1994, Douglas *et al.* 1991, 1992). Scentless chamomile can form dense, semi-permanent monospecific stands on periodically disturbed, poorly drained sites like field depressions and slough margins, from which the seeds spread into adjacent cropland (Peschken *et al.* 1990, Bowes *et al.* 1994). The plant is phenotypically plastic and may grow as an annual, biennial or short-lived perennial (Hegi 1987, Woo *et al.* 1991, Cole 1994). Conventional control methods include chemical and cultural control. Chemical control is difficult because, of the relatively inexpensive and commonly used selective herbicides, only those containing bromoxynil control scentless chamomile, and they are effective only against the seedling stage (Peschken *et al.* 1990). In some crops, such as beans, corn, lentils, peas and potatoes, no product is available at all (Ali 1995). Cultural control methods include tillage, mowing, hand pulling and the establishment of a dense crop which can compete effectively with scentless chamomile (Cole 1994). Tillage is effective against seedlings, but when plants have overwintered, mechanical control is effective only when the soil is dry (Peschken *et al.* 1990). Mowing can prevent seed set, but if carried out too early, scentless chamomile will form secondary shoots with new flowers, and if carried out too late, flower heads contain already viable seeds. Hand pulling is obviously impractical for large infestations.

A further complication is the existence of scentless chamomile populations in non-cultivated areas, such as vacant lots, wasteland, farmyards, fencelines, roadsides or ditches, where chemical or cultural control methods are either impractical or uneconomic, as well as around water bodies such as creeks and sloughs, where herbicide application is prevented by environmental restrictions. However, unless scentless chamomile populations are also reduced in these marginal areas, reservoir populations will continue to produce masses of seed which will infest adjacent fields (Douglas 1989). Therefore, a project aiming at the biological control of scentless chamomile was proposed in 1988 (Peschken *et al.* 1990). The CABI Bioscience Centre Switzerland was contracted to search for and screen host-specific phytophagous insect species associated with scentless chamomile in Europe. The population biology of the weed and its interactions with potential biocontrol agents were also investigated as part of a PhD thesis, with the objective of improving the effectiveness of the biological control project against scentless chamomile (Hinz 1999).

Overview of the project

A survey of the western European literature revealed that 68 phytophagous insect species, 12 fungal and two nematode species are associated with scentless chamomile in Europe, while the plant is attacked by few insects and diseases in Canada, almost all of which are generalists (Woo *et al.* 1991). During field surveys in Europe (Germany, Switzerland, France, Austria, Hungary, the Czech Republic and Serbia) between 1990-1998, 25 phytophagous species were found on scentless chamomile (Freese and Günther 1991, H.L.H. unpublished data). Of these, eight species attacking different plant parts and known to have a restricted host range were investigated: the seed-feeder *Omphalapion* (*Apion*) *hookeri* Kirby, the shoot-mining weevils *Microplontus* (*Ceutorhynchus*) *edentulus* Schultze and *Microplontus* (*Ceutorhynchus*) *rugulosus* (Hbst.), the two root-feeding weevils *Diplapion* (*Apion*) *confluens* Kirby and *Coryssomerus capucinus* (Beck.), the gall midge *Rhopalomyia* n. sp., the agromyzid *Napomyza* sp. near *lateralis* (Fallen), and the anthomyid *Botanophila* (*Pegohylemyia*) *spinosa* (Rondani) (Table 1).

Because reproduction and spread of *T. perforatum* depend exclusively on seeds, the seed-feeder *Omphalapion hookeri* was the first insect that was investigated for its potential as a biological control agent (Table 1). The host-specificity screening was carried out at the Regina Research Station in Saskatchewan. Reports in the literature that *O. hookeri* is monophagous on scentless chamomile were confirmed, and it was released in Canada in 1992 (Peschken and Sawchyn 1993). Since then it has been established in four provinces in western Canada (McClay and DeClerck-Floate 1999).

M. edentulus was the second species reported to be monophagous on scentless chamomile (L. Dieckmann and L. Behne personal communication). Host-specificity tests carried out between 1991 and 1995 confirmed its narrow host range, and permission for field release was obtained in 1997 (Hinz *et al.* 1996). Since then, two shipments of adults collected in the field were made to Canada, where a rearing colony has been established, and the first field releases were made in 1997. Work on *M. rugulosus* was stopped, because it develops on several ornamental plant species in the tribe Anthemideae, and because it preferred the herbal chamomile, *Matricaria recutita* L., to scentless chamomile as a host plant (Hinz and Leiss 1996).

Table 1.
Status of selected phytophagous insect species investigated for the biological control of scentless chamomile at the CABI Bioscience Centre Switzerland between 1990-1999.

Species	Order, family	Status
Omphalapion hookeri [a]	Col., Apionidae	Released in 1992, established
Microplontus edentulus	Col., Curculionidae	Released in 1997, established
Microplontus rugulosus	Col., Curculionidae	Not specific enough
Diplapion confluens	Col., Apionidae	Not specific enough
Coryssomerus capucinus	Col., Curculionidae	Not specific enough
Rhopalomyia n. sp.	Dipt., Cecidomyiidae	First field release in April 1999
Napomyza sp. near *lateralis*	Dipt., Agromyzidae	Still under investigation
Botanophila spinosa	Dipt., Anthomyiidae	Still under investigation

[a], host-specificity tests carried out at the Regina Research Station in Saskatchewan

In 1993, the two root-feeding weevils *D. confluens* and *C. capucinus* were selected as potential agents, in order to add another attack strategy to the biocontrol agent complex.

These two weevils were reported to be specific to plant species within the tribe Anthemideae. However, host-specificity tests showed that they are able to develop to mature larva or adult on several ornamentals and one plant species, indigenous to North America, which makes them unsuitable for introduction (Hinz 1999).

In autumn 1993, galls of a cecidomyid species were discovered on winter rosettes of scentless chamomile in Eastern Austria. The species was tentatively determined by two german cecidomyid taxonomists as *Rhopalomyia hypogaea* (F. Loew), a gall midge usually described from wild chrysanthemums (Hinz and Hunt 1994). However, host specificity tests revealed that the specimens reared from scentless chamomile do not develop on chrysanthemums. Dr. Marcela Skuhravá (Prague, Czech Republic), a cecidomyid specialist, confirmed that it is a new species, and is presently preparing a description for publication. Subsequently, *Rhopalomyia* n. sp. has proven to be specific to the genus *Tripleurospermum* (Hinz 1998), and permission for field release was obtained from the Canadian and United States regulatory authorities in 1999. Galls were shipped to Canada, where a rearing colony has been established, and first field releases were made in April 1999.

The agromyzid *Napomyza* sp. near *lateralis* was chosen as a further potential agent, because it is one of the most common and widespread species on scentless chamomile (Hinz and Leiss 1996). Although records in the literature for *N. lateralis* indicated a broad host range (Spencer 1976), specificity tests carried out from 1996 onwards yielded promising results. Under multiple-choice conditions, specimens originating from scentless chamomile only developed on a restricted number of plant species in the tribe Anthemideae (Hinz and Leiss 1996, Hinz 1997, Hinz and Kirkpatrick 1998).

In 1998, investigations started on the anthomyid *Botanophila spinosa* Rondani, which was reared from larvae mining in the developing shoots of scentless chamomile in spring in Switzerland (Hinz and Kirkpatrick 1998). Unfortunately, mortality of adult flies was high, and oviposition very limited so far in captivity. The larval biology and host plant of this fly were unknown prior to this study (V. Michelsen, personal communication). However the “same” species has recently been proposed as a biological control agent for *Onopordum* spp. (Asteraceae) (Vitou *et al.* 1999). No morphological differences between *B. spinosa* specimens from *Onopordum* and scentless chamomile could be detected, but other species in the genus have only been found on a single plant species or a few very closely related species (V. Michelsen, personal communication). Because of the apparent difficulties to rear this species, it might not be further considered as a potential agent.

Although host specific pathogens have been recorded from scentless chamomile (Woo *et al.* 1991), and damage caused by pathogens was observed in the field, they have so far not been considered in the biological control project against this weed. Seedlings of scentless chamomile for instance were observed to be killed by fungal attack. Rosettes and flowering plants in the Rhine Valley and at the institute frequently showed signs of pathogen attack, which resulted in distorted shoots and stunting. Different pathogens were isolated, including *Colletotrichum gloeosporioides*. It would now be neccessary to determine which of the identified species caused the observed symptoms, and whether they would have potential as biological control agents. The development of a bioherbicide or a classical biological control approach using pathogens is assumed to further increase the chances for successful control of scentless chamomile, especially in crop situations.

Suitability and potential effectiveness of the herbivores investigated

Host-specificity

The prerequisite for any introduction of an exotic natural enemy to control a naturalized weed is a narrow host range. The two root herbivores *Diplapion confluens* and *Coryssomerus capucinus* and the stem-miner *Microplontus rugulosus* proved to be specific to species in the tribe Anthemideae. However, choice and open-field tests revealed that they are able to develop on several ornamentals and one indigenous plant species within the tribe Anthemideae (Hinz and Leiss 1996, Hinz 1999). *Diplapion confluens* accepted the herbal chamomile, *Matricaria recutita*, to the same extent as the target weed, and *M. rugulosus* even preferred *M. recutita* over scentless chamomile. *Matricaria recutita* is not currently grown on a commercial scale in Canada, but is considered a potential future crop (C. Richter, personal communication). Although the ability of an agent to develop on a non-target species may not be a problem shortly after release when host plants are numerous, it may become critical later when the density of the target weed is reduced (Crawley 1986). Therefore, *D. confluens*, *C. capucinus* and *M. rugulosus* were regarded as unsuitable for field release in North America. In contrast, the gall midge *Rhopalomyia* n. sp., like other gall formers, as well as the seed-feeding weevil *Omphalapion hookeri*, have a very narrow host range, restricted to species in the genus *Tripleurospermum*, which makes detrimental effects unlikely (Peschken and Sawchyn 1993, Hinz 1998). The stem-miner *Microplontus edentulus* occasionally developed on *Anthemis* or *Matricaria* spp. under confined conditions. Its field host-range however also seems to be restricted to *T. perforatum* (Hinz *et al.* 1996). No issues of non-target effects are expected to arise with these species.

Host-specificity tests with *Napomyza* sp. near *lateralis* have been hampered by the fact that different species, subspecies or host races seem to be comprised under the species concept of *lateralis*. Several new distinct species have recently been separated and described from the *lateralis*-group (Zlobin 1993, 1994). The "same" species is also being studied as a potential biocontrol agent for Russian knapweed, *Acroptilon repens* (L.) DC, an Asteraceae in the tribe Cardueae (Schaffner and Kovacs 1997). No morphological differences were found between specimens originating from Russian knapweed and scentless chamomile (von Tschirnhaus, personal communication). However, their host range is clearly distinct (Hinz 1997). DNA analysis is now being used by Dr. Sonja Scheffer (USDA, Beltsville, MD) to assess the level of genetic differentiation between these populations.

To carry out host-specificity tests with potential agents under controlled conditions it is essential that the insects can be reared under laboratory or semi-natural conditions. Host-specificity tests with the anthomyid *Botanophila spinosa* could not be carried out so far, because oviposition only occurred once so far in captivity. Sometimes species therefore have to be rejected as biocontrol agents. Species that are difficult to rear may also be difficult to establish in the exotic range of the target plant. Agents often have to be reared for one generation in captivity before field release, to eliminate parasitoids or they are mass reared to speed up establishment.

Life-cycle and biology

A high intrinsic rate of increase that may lead to outbreak densities is considered one of the most important characteristics of a potentially successful biocontrol agent (Crawley 1989, Gassmann 1996). It is considered more likely for insects with small body size and high fecundity that produce several generations per year (Crawley 1986). In this regard, the two multivoltine fly species *Rhopalomyia* n. sp. and *Napomyza* sp. near *lateralis* should be more successful than the univoltine coleopteran species (Table 2). For instance, while the population of *Rhopalomyia* n. sp. increased up to 150-fold during two generations (Hinz 1998), maximum population increases for *O. hookeri* were 17-fold from one year to the next (McClay and DeClerck-Floate 1999). A multivoltine life cycle also results in prolonged attack over the whole vegetation period, which is regarded as another characteristic of effective agents (Harris 1973). In contrast to the univoltine weevil species and the anthomyid, which attack scentless chamomile only during a restricted time period, *Rhopalomyia* and *Napomyza* develop on scentless chamomile practically all year round (Table 2). They may even damage the plant over winter, because their larvae overwinter in the rosettes. This reduces the chances of the plant to compensate for attack or to escape attack. In addition, the flies do not depend on the availability of a specific phenostage of the plant, because they are able to develop in different plant parts (Table 2). This is probably particularly useful for the control of a plant with a variable life cycle such as scentless chamomile, which grows at unstable, periodically disturbed sites.

It has been suggested that insects which are widespread and abundant in their area of origin will establish more easily within exotic environments and will be the most successful agents (Crawley 1987, Crawley 1989). However, other authors have proposed that competitively inferior species, heavily attacked by parasitoids or predators should be given priority, because (a) the plant has not evolved defence mechanisms against these insects, and (b) once released from their competitors and natural enemies, the agents will build up high population densities (Harris 1973, Zwölfer 1973, Myers 1992). Of the three species that have already been released, *O. hookeri* should therefore be most successful according to the first theory, because it is both widely distributed and abundant (Freese 1991), whereas *M. edentulus* and *Rhopalomyia* n. sp. have a restricted distribution (Bacher 1993, Hinz 1998). According to the second theory, *Rhopalomyia* n. sp. should be particularly effective, because it was usually rare in the field (Hinz 1998). Only close monitoring after release will verify one or the other prediction.

Good dispersal ability is another important feature for potentially effective agents, particularly against a weed of relatively unstable habitats (Reznik 1996). *Omphalapion hookeri* has dispersed at a rate of over 1 km/yr from the initial release site at Vegreville, Alberta (A.S.M. unpublished data). *Napomyza* sp. near *lateralis* has been observed to quickly infest isolated populations of scentless chamomile in Europe (H.L.H. unpublished data). The dispersal abilities of *Rhopalomyia* n. sp. and *M. edentulus* are as yet unknown.

Most of the potential agents prefer larger plants for oviposition (Hinz 1999). This should result in an increased attack of overwintering rosettes of scentless chamomile (see also Sheppard *et al.* 1990), which is expected to be advantageous, because these are more competitive and contribute disproportionately to seed output (Hinz 1999, A.S.M. unpublished data).

Impact on individual plant level

Each individual of *O. hookeri*, the first agent to be introduced into North America, reduces the seed production in a head by 11 - 21 seeds (Freese 1991, McClay and DeClerck-Floate 1999). The stem-miner *Microplontus edentulus* reduces both seed output and biomass of scentless chamomile (Bacher 1993). Attack by the gall midge *Rhopalomyia* n. sp. decreases the number of seed heads produced and the height of plants (Hinz and Müller-Schärer 2000). At high attack rates, seedlings or rosettes may be killed, especially in combination with adverse weather conditions over winter (e.g. frost, excess or shortage of water) (H.L.H. unpublished data). In a controlled impact experiment, the two root-feeding weevils, *D. confluens* and *C. capucinus*, alone or in combination, had no effect on the growth or reproduction of scentless chamomile, which was presumably due to low attack rates and because attack occurred too late in the growing season (Hinz 1999). At high densities, *C. capucinus* was observed to stunt plants and provoke premature death (Bacher 1994), while *D. confluens* may kill shoots, thus preventing seed production (pers. observ.). The agromyzid fly *Napomyza* sp. near *lateralis*, which is still being investigated, can kill developing shoots in spring, and larvae that mine in the receptacle occasionally damage seeds (H.L.H. unpublished data). The impact of larvae mining in the shoots of bolting or flowering plants during the growing season is unknown. The anthomyid *Botanophila spinosa* also destroys developing shoots in spring. Shoots are in general readily replaced by side shoots, particularly when killed early in the season. However, these are usually less vigorous.

In summary, the herbivores either reduce the seed output of scentless chamomile, or its biomass. The gall midge *Rhopalomyia* n. sp. was the only species observed so far that is able to kill whole plants. However, the aim of classical biological weed control is not necessarily the death of plants, but rather to reduce their vigour, and thus to weaken their competitive advantage over native plants or crop species and to lower seed production to reduce soil seed banks and dispersal. Because of the variable life-cycle of scentless chamomile, its high regenerative ability and prolific seed production, we do not believe that one single species will be able to control the plant successfully. Instead, a complex of agents attacking different plant parts at different times of the year are being released (also see Harris 1991). It could be argued that the gall midge comprises exactly these characteristics. However, the species may not establish equally well in all habitats or climatic regions, and native parasitoids may compromise its impact over time (Harris and Shorthouse 1996).

Potential impact on plant population level

The impact of herbivores on individual plants needs to be clearly distinguished from their impact at the plant population level. A factorial field experiment was carried out over a three year period in the area of origin of scentless chamomile to estimate the effect of natural levels of herbivory and a reduction in interspecific competition on scentless chamomile populations (Hinz 1999). Permanent plots were established and two treatment factors applied, regular application of insecticide, and disturbance (once a year). The population of scentless chamomile only increased (i.e. yearly rate of population increase, λ, > 1), in the presence of disturbance, irrespective of insecticide applications. However, on disturbed plots, a reduction in herbivory nearly doubled λ, mainly through an increase in the number of seedlings that established, but also through an increase in the number of biennial rosettes that survived. An elasticity analysis showed that the number of seeds

Table 2.

Specificity, number of generations per year, phenostages attacked and spatial and temporal larval feeding niches of potential biological control agents against scentless chamomile.

Species	Specificity	Number of generations	Phenostage Attacked	Spatial niche	Temporal niche
Omphalapion hookeri	M	1	F	seed	June - July
Microplontus edentulus	Ro	1	B – F	shoot	May - July
Microplontus rugulosus	O	1	B – F	shoot, receptacle	April - June
Diplapion confluens	O	1	B – F	root crown, root	April - July
Coryssomerus capucinus	O	1	B – F	root crown, root	April - July
Rhopalomyia n. sp.	M	4	S, R, B, F	apical meristem, leaf axils, flowers	January - December[a]
Napomyza sp. near *lateralis*	Ro (?)	3-4	R, B, F	root crown, shoot, receptacle	January - December[a]
Botanophila spinosa	(?)	1	R, B	developing shoot tips	March - May

m, monophagous (= specific to species in genus Tripleurospermum);
ro, restricted oligophagous (= specific to a restricted number of genera in tribe Anthemideae);
o, oligophagous (= specific within tribe Anthemideae);
S, seedling;
R, rosette; B, bolting plant;
F, flowering plant;
?, not exactly known;
[a], development/feeding during winter will depend on temperature.

being incorporated into the soil seed bank per reproducing plant, as well as the number of plants developing from seeds in the soil seed bank were of minor importance for population growth. Thus, agents reducing the seed production of scentless chamomile will rather have a long term effect, by decreasing the number of seeds added to the seedbank, reducing the spread of scentless chamomile (Paynter *et al.* 1996) and/or stabilizing the population dynamics (Sheppard *et al.* 1990).

The analysis also showed that in insecticide treated, disturbed plots the transitions from biennial rosettes to reproducing plants and from reproducing plants to rosettes were most critical for population build up of scentless chamomile (Hinz 1999). Small changes in these transitions will thus lead to relatively large changes in λ. If we assume that the conditions in these plots (periodic disturbance, reduced herbivory) are similar to those in Canada, agents which reduce the survival and vigour of biennial rosettes of scentless chamomile should be the most successful. Data from permanent plots in Canada indicate that most overwintering rosettes are biennials. Similar to the results of this study they contributed disproportionately to seed output (A.S.M. unpublished data).

Potential integration of biocontrol with conventional control measures

Traditionally, classical biological weed control has been practised against biennial or perennial weeds in relatively stable habitats, with a low disturbance regime, such as pastures, rangeland or natural areas (Goeden 1988). In crop situations, control needs to be rapid and effective over the entire weed population (Andres *et al.* 1976), which is difficult to achieve with the classical approach alone, because of the time lag before control is achieved and the unpredictability of success (Gassmann *et al.* 1996). Although weedy annuals in disturbed areas have been successfully controlled with phytophagous insects (Huffaker *et al.* 1983, Chippendale 1995, Scott and Yeoh 1996), Reznik (1996) concluded that biocontrol agents will then have to exhibit similar properties as pest species (i.e. tolerance against disturbance and chemical treatments). Another argument used against biological weed control in crop systems is that the natural enemies employed are, by definition, specific to one or a very restricted number of plant species, whereas usually a complex of weed species is present in field situations (Bernays 1985). However, situations exist, in which scentless chamomile forms monospecific stands, and is thus the predominant weed species that needs to be controlled (e.g. field depressions). It has also been proposed that classical biological control may be successful in arable land, when the weed is widespread outside the cropping system, and a pool of colonizing individuals of biocontrol agents can be maintained between harvest periods (Bernays 1985), as would be the case for scentless chamomile.

An integration of biological control with existing control measures can be in space or time (Andres 1982, Watson and Wymore 1990). Integration in space is the use of conventional control measures in one area and the use of biological control in other areas, while integration in time is their alternate use at the same infestation site. For scentless chamomile an integration in space could simply mean using biological control in areas where conventional control methods are uneconomic or impracticable, such as farmyards, wasteland, and riparian areas, and to use chemical or mechanical control in crops, where biocontrol agents will presumably be less effective. An integration in space could also require that infestations in field depressions or slough margins are deliberately not sprayed to leave corridors or reservoir areas in which the agents can survive and multiply and from where they can disperse to adjacent infestations (Adair and Edwards 1996, Findlay and Jones 1996). An integration in time could include (a) the initial application of herbicides prior to agent release to get on top of large infestations (Flanagan *et al.* 1996, Hoffmann *et al.* 1998), (b) the application of chemical control measures at a time when the insects are present in the pupal stage inside the plant or in the soil, where they would be relatively protected (Trumble and Kok 1982), or (c) the use of herbicides early in the season, when agents are not active (Lym *et al.* 1996, Julien and Storrs 1996). In the case of scentless chamomile, an integration in time would primarily apply if the agents are released or disperse onto scentless chamomile infestations at field edges, in field depressions or slough margins, i.e. habitats likely to receive spray drift. In these situations, cultural control practices will also have to be well integrated, e.g. harvest should be at a time when insects have already left the plants. During our surveys in Europe, nearly all agents were also found on plants growing at field edges. Thus, they seem to withstand chemical and cultural control measures at least to some degree.

Conclusions and outlook

We suggest that to successfully control scentless chamomile, (1) areas such as slough margins and field depressions in which the weed can form monospecific stands should be left undisturbed to provide a reservoir of biological control agents; (2) tillage or chemical control should be used where possible to remove emerging seedlings within fields, and (3) agents that attack the rosettes of scentless chamomile should preferentially be released as biocontrol agents. The gall midge *Rhopalomyia* n. sp., and the agromyzid *Napomyza* sp. near *lateralis* are therefore considered the most promising agents.

Predictions derived from pre-release studies, and their subsequent verification or rejection by post-release studies, are regarded as an important tool to improve the effectiveness of biocontrol projects (Blossey 1995). Once all agents are securely established in Canada, evaluation of their impact will begin with studies of their effects singly, and in combination, on plant-level parameters such as biomass, seed output and overwinter mortality. In this respect it will also be important to investigate whether the released agents will influence each other negatively. It is expected that competition between agents will be of minor importance, because of their quite separate feeding niches. During rearing at Delémont, the agromyzid and the gall midge emerged in large numbers from the same plants. *Omphalapion hookeri, M. edentulus* and *N.* sp. near *lateralis* were found to infest the same plant or even shoot in Eastern Austria (H.L.H. unpublished data). However, scentless chamomile plants heavily attacked by the gall midge, for instance, may become less attractive to the stem-miner *M. edentulus*, because attacked plants tend to be shorter and have thinner shoots than unattacked plants.

Studies in Canada to evaluate the long-term impact of biocontrol agents on scentless chamomile at a population level will be more complicated, because of the strong influence of periodic disturbance on the population development of the plant. Disturbance (i.e. a reduction in interspecific competition) is the most important factor for population build up of scentless chamomile. Without disturbance, the plant will be outcompeted by perennials within 2-3 years, independent of the presence of herbivory. It might therefore be necessary to include disturbance as a additional treatment in post-release studies. A regional approach such as aerial photography to map the extent of flowering populations may be a useful tool to assess the impact of the biocontrol agents over a wide scale.

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