A HIERARCHY OF RESEARCH APPROACHES TO THE SUCCESSFUL USE OF "RESOURCE SUBSIDIES" TO IMPROVE PARASITOID PERFORMANCE

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ABSTRACT

This paper reviews recent New Zealand work on Conservation Biological Control and concentrates on the challenges for the future. When resource subsidies, such as flowers, are added to agro-ecosystems to improve the fitness of parasitoid wasps, all or part of a hierarchy of ecological responses would be expected. The most frequent consequence is that parasitoids aggregate on or near the added flowers, while the most difficult outcome to achieve is a reduction in pest populations to below the economic threshold. A key issue is the appropriate selection of floral resources so that agronomic criteria are met and that the parasitoid benefits more than does the pest. Six ways of achieving selectivity in the deployment of resource subsidies are discussed and these are illustrated with recent work.

INTRODUCTION

Conservation biological control of insect pests involves the provision of resource subsidies (Polis and Strong, 1996) such as pollen, nectar, shelter and/or alterative prey or hosts for predators and parasitoids. However, it is important to choose a selective resource which will benefit the parasitoid more than the pest. In this paper, a hierarchy of research approaches for the successful selection and implementation of floral resources to provide pollen and/ or nectar to enhance parasitoid fitness and efficacy are outlined and examples from recent New Zealand work will be used to illustrate this hierarchy.

For decades biologists (Kruess and Tscharntke, 1994; Theis and Tscharntke, 1999) have recognized that habitat diversification results in higher numbers of natural enemies and fewer pests (Landis et al., 2000) and more recently a meta-analysis has confirmed that increasing habitat structure leads to a significant increase in natural enemy abundance (Langellotto, 2004). One way which these systems may be diversified is habitat manipulation. This produces effects that are consistent with the "resource concentration" hypothesis (Root, 1973), which states that pests are less able to find and remain in more diverse systems because of the disruption of cues which are used to find pure stands of crops. These are termed "bottom-up" effects. The idea of "diluting" the crop resource, reducing the contrast between a concentrated crop and the soil, produces a dilution of the visual and chemical stimuli to the pest, resulting in a reduction in damage to the crop (Gurr et al., 2000). Conservation biological control (CBC) generates "top-down" effects, consistent with the "enemies hypothesis" (Root, 1973). This states that the effects of predators and parasitoids are enhanced in a more diverse ecosystem, therefore reducing prey/host populations, due to the provision of resources that may be absent or rare in a less diverse system. These resources may be plant food (nectar or pollen), shelter and/or alternative hosts or prey. Resources such as these are often rare in intensive agricultural systems, due to monocultural cropping practices (Gurr et al., 2000; Landis et al., 2000).

In CBC the provision of these resources can be facilitated through the manipulation of existing vegetation within or around the crop or by adding plant species. The choice of a species for use in this way can be critical to its success (Landis et al., 2000). Plant choice should be based on a good knowledge of the target pest and its natural enemy assemblage. The use of such plants without the proper knowledge of how they affect the natural enemies and the pest may lead to the enhancement of the pest's population in the field (Baggen and Gurr, 1998) or may benefit parasitoids or predators of other natural enemies (Stephens et al., 1998).

Studies in New Zealand over the past decade have shown that by adding floral resources to agricultural systems, greater numbers of natural enemies and greater parasitism and predation rates in the field have resulted (Stephens et al., 1998; Irvin, 1999; Berndt et al., 2002; White et al., 1995). However, the ultimate aim of this CBC work is to determine whether by adding floral resources the five steps in the hierarchy of research outcomes (Gurr et al., 2003) are met. The hierarchy of research outcomes include;

1. Aggregation of parasitoids at or near the flowers
2. An enhancement of the parasitoids' fitness (longevity, fecundity and searching efficiency)
3. An increase in parasitism rate
4. A decrease in pest populations
5. Pest populations are brought below an economic threshold

In order to meet this hierarchy of research outcomes, the successful implementation of added flowers to improve natural enemies' fitness is required. In this paper a hierarchy of research approaches for the successful implementation of cover crops is outlined using examples from recent New Zealand research.

A HIERARCHY OF RESEARCH APPROACHES

Step 1: Choose an agro-ecosystem with relatively depauperate invertebrate communities

Habitat manipulation is more likely to be effective in a system which has a relatively low species abundance and diversity. In an early study of species diversity in complex versus less complex systems, a greater number of arthropod taxa was found in a semi-natural grassland system compared with barley crops (Potts and Vickerman, 1974). Therefore, the authors suggested that higher species diversity in cereals could be accomplished by undersowing these crops with grass or grass-legume mixtures.

Agricultural systems are managed habitats comprising either annual or perennial crops. In annual systems, a single crop may be cultivated throughout the entire season or it may comprise part of a sequence of plantings and harvests of the same or several different crops (Barbosa, 1998). Perennial cropping systems, such as orchards and vineyards, are less likely to change between seasons and therefore potentially provide a more stable environment for the pest and parasitoid. However, both annual and perennial systems can have periods when resources, such as food, alternative hosts and/ or shelter or overwintering sites for parasitoids are unavailable. Orchards and vineyards, for example, are often intensively managed, with high herbicide use and with understories notably absent or comprising of rye-grass (*Lolium* spp.) only. Therefore, the provision of resources for natural enemies in these modified environments is necessary for the conservation of natural enemy species (Barbosa, 1998).

Step 2: Rank candidate flowering plants in the laboratory (against pest and natural enemy) as a first step in enhancing the most appropriate botanical diversity

<u>Choosing the resource subsidy</u>

There are a number of criteria that need to be taken into consideration when choosing the plant species to be added. These have been outlined by Gurr et al. (1998) and include; species which will provide resources required by the natural enemies (food, shelter and/or alternative prey or hosts), the ability of the species to survive with little maintenance, the cost and availability of seed, flowering period, sowing-to-flowering time (Bowie et al., 1995), frost susceptibility and the likelihood of becoming a weed.

<u>Screening plants in the laboratory</u>

Adult parasitoids require nutrients such as carbohydrates in their diet in order to perform biological activities necessary for survival and reproduction (Rivero and Casas, 1999). Adult parasitic wasps which feed solely on plant-associated food sources such as nectar, extra floral nectar and homopteran honeydew acquire carbohydrates from these resources (Jervis et al., 1993) and since nectars affect longevity and fecundity in adult Hymenoptera (Idris and Grafius, 1997) and also sometimes enhance pest fitness (Baggen and Gurr, 1998), it is necessary to screen these plants before introducing a them into an agricultural system.

A number of New Zealand studies have examined the effect of flowering plant species on the parasitoid and pest fitness (Irvin, 1999; Tylianakis, 2004; Berndt, in press; Irvin et al., in press; Lavandero et al., unpublished data) in the laboratory. Berndt and Wratten (in press) demonstrated that the longevity of female *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae) was more than seven times greater when these parasitoids had access to alyssum (*Lobularia maritima* L.) with flowers than to plants without flowers. The number of cocoons (a measure of realized fecundity) produced over the lifetime of *D. tasmanica* was more than seven times greater for parasitoids with access to alyssum flowers than those fed water (Berndt and Wratten, in press). The sex ratio of *D. tasmanica* was also affected by the presence of flowers, where a greater proportion of female offspring was produced when flowers were present (Berndt and Wratten, in press).

In a separate study, Irvin et al., in press examined the effects of alyssum flowers on the fitness of the leafroller pest, *Epiphyas postvittana* (Walker, Lepidoptera: Tortricidae). The results of this study showed that when *E. postvittana* adults were exposed to alyssum flowers, their longevity was increased from 10 days (water only) to 18 days and their total fecundity was increased from approximately 550 eggs laid (water only) to 750 when exposed to alyssum (Irvin et al., in press). These results demonstrate the importance of testing "selective food plants" in the laboratory before planting them in the field as alyssum flowers enhanced the fitness of both the parasitoid and the pest.

Step 3: Interpret rankings

The reasons why flowering plants have diverse effects on parasitoids' fitness have been poorly studied. One possibility is differences in floral architecture.

Floral architecture

The ability of parasitoids to feed on a plant species can be influenced by the plants' floral architecture (Patt et al., 1997). Suitable cover-crop species are often selected because of their shallow corollae or exposed nectaries, which enable a short-tongued parasitoid to access the nectar. *Phacelia tanacetifolia* Benth. (Hydrophyllaceae) is a species commonly used in CBC (Hickman and Wratten, 1996) but it has deep corolla tubes. It also has partly-hidden nectaries and upward pointing hairs on the style (Figure 1). Therefore, some parasitoids may not be able to access its nectaries (Baggen and Gurr, 1998).

This inability to access the nectaries of phacelia may be one explanation of the finding of Lavandero et al. (unpublished data) working on *Diadegma semiclausum* (Helen) (Hymenoptera: Ichneumonidae), a parasitoid of the diamondback moth (*Plutella xylostella* L.) and *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae), a parasitoid of leafrollers. When these parasitoids were provided separately with water only, buckwheat or phacelia, the longevity of *D. semiclausum* was increased by buckwheat and phacelia (Figure 2a), whereas *D. tasmanica* longevity was increased only by buckwheat (Figure 2b). However, the floral architecture of the phacelia flowers may not be the only mechanism influencing the use of phacelia by these parasitoids, and other mechanisms, including nectar quality, are currently being studied in New Zealand.

Fig. 1 Half-flower of *Phacelia tanacetifolia* showing its deep corolla tube, flaps above the nectaries and pointing hairs on the pistils.
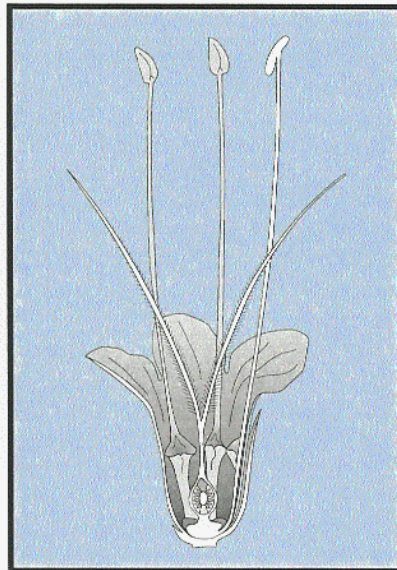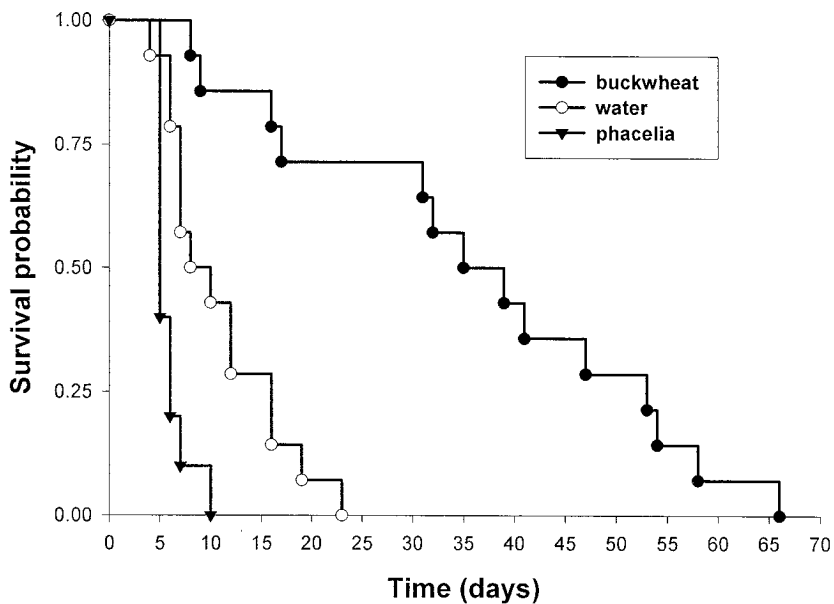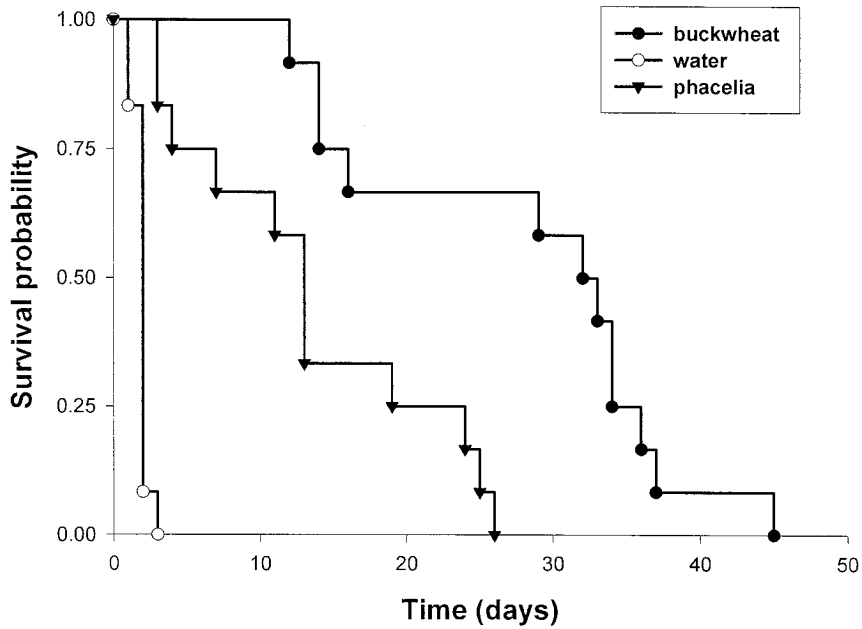
Fig. 2. Survival of the parasitoids a) *D. semiclausum* and b) *D. tasmanica* under different food treatments (see text).

Step 4: Choice experiments in the laboratory

Although choice experiments (offering the parasitoid choice between two flowering plant species) have not been conducted in New Zealand, they may provide valuable insight into the "preference" of a parasitoid for a single flowering plant species during different physiological life stages. For example, a parasitoid may feed on a flowering plant in the laboratory when there is no other food source available and consequently its fitness is increased. However, when introduced into the agricultural system, this plant species may fail to attract the parasitoid, rendering it useless. Evidence for this lack of continuum from laboratory to field is poorly studied due to the difficulties of measuring age and fitness of parasitoids in the field (Jervis et al., in press).

Step 5: Select one or more flowering plant species for the agricultural system under study

Once a flowering plant species has been selected, based on laboratory testing, it can be planted in the system. However, its suitability will be determined by its phenology, duration of flowering, likelihood of becoming a weed, palatability/toxicity to livestock, competitive ability, frost susceptibility etc (see Bowie et al., 1995).

Step 6: Determine appropriate spacing of selected plants

Once a flowering species has been identified, it is necessary to determine the spatial arrangement of these resources in the agricultural system. Floral resources may be added to the system either in close proximity to the crop (by use of cover crops or intercropping) or distant from it (by planting flowers at field borders) (Speight, 1983; Hickman and Wratten, 1996). The distance over which the dispersal of the parasitoid occurs will determine the spatial arrangement of such floral resources.

Dispersal of parasitoids from floral resources into the adjacent crop may be measured using a number of techniques (Hagler and Jackson, 2001). Marking is a common method used to study the dispersal of parasitoids and a review of these techniques will appear in a special issue of the International Journal of Pest Management (Lavandero et al., in press) and in Gurr et al. (in press).

Recent work in New Zealand has used rubidium chloride as a marker to examine the movement of *D. tasmanica* from flowering buckwheat plants in a vineyard. Preliminary results have indicated that the parasitoid disperses at least 30 m from flowering buckwheat plants in a 7-day trapping period. Also, greater numbers of rubidium-marked male *D. tasmanica* than females were caught on yellow sticky traps close to the buckwheat flowers (Figure 3). Although these results are preliminary, they facilitate recommendations to viticulturalists that buckwheat be planted at intervals of approximately 15 vine rows to ensure that parasitoid fitness is enhanced throughout the vineyard.
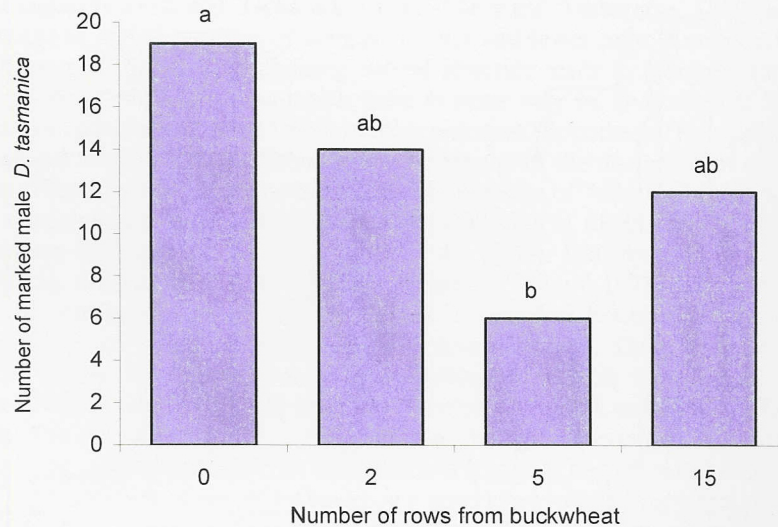

Fig. 3. Number of marked male *D. tasmanica* collected at 0, 2, 5 and 15 rows from the buckwheat. Rows are 2 m apart. Columns sharing the same letter do not differ significantly at $P<0.05$.

A more robust decision on the arrangement of floral resources in the landscape will be influenced by the spatial pattern of each component of the hierarchy (Gurr et al., 2003) given above. Examples of the third step in the above hierarchy come from Berndt et al. (2002), who found significantly more male *D. tasmanica* near buckwheat flowers compared with control areas. Tylianakis et al. (2004) showed that there was a significant increase in parasitism of the aphid *Metopolophium dirhodum* (Walker, Hemiptera: Aphididae) by *Aphidius rhapalosiphi* (De Stefani-Perez, Hymenoptera: Aphidiidae) near buckwheat flowers. Parasitism rates declined exponentially with increasing distance from the flowers, reaching zero beyond 14 m. The latter results demonstrate the profound effect

that a crop monoculture can have on rates of biological control, supporting similar evidence from Kruess and Tscharntke (1994) and Theis and Tscharntke (1999).

Step 7: Further questions

Once a plant species has been selected for use in the system and the appropriate spacing of the plants has been selected, there are some further research questions which may be worth considering when monitoring the effectiveness of the cover crop. Such questions include; does the behavior of the parasitoid differ in the presence of floral resources, are there subtle differences in the behavior of male and female parasitoids in relation to the floral resource, does the physiology of the female or age of the parasitoid have any effect on the use of the resource and finally, what types of trapping methods are best used to measure the effects of the resources on the parasitoids, as some traps (especially colored ones) may be more attractive to a hungry parasitoid. For example, a gravid female parasitoid may have sought out nectar resources when it was an immature adult, but may be more likely to seek hosts rather than nectar in its later life. For this reason, its responsiveness to colored traps may be lower at this stage.

Step 8: Consider the fourth trophic level

Added floral resources have the potential to enhance the fitness and impact of organisms other than species targeted, such as predators and parasitoids of other natural enemy insects. For example, Stephens et al. (1998) caught greater numbers of *Anacharis* sp. (Hym.: Figitiidae), a parasitoid of the predatory brown lacewing (*Micromus tasmaniae* Walker, Neuroptera: Chrysopidae) in areas of apple orchards where buckwheat was planted. Hyperparasitoids of parasitoids may also be affected by added flowers but nothing is known of this potential effect.

Step 9: Consider the effects of floral resources on community structure and food webs

The concept of "indirect resource subsidies" has been recently developed in New Zealand and this explores the idea that both parasitoid and pest may benefit from the resource subsidy, but that the parasitoid gains a greater benefit than does the pest, therefore making it viable to use these resources under these circumstances. A hierarchy of the ways in which resource subsidies may benefit the parasitoid more than the pest is:
1. Parasitoid benefits but pest does not
2. Both parasitoid and pest benefit, but the pest has a higher longevity only (not a higher fecundity)
3. Both parasitoid and pest benefit but the parasitoid benefits relatively more
4. Parasitoid and pest benefit but the improved fitness of the pest leads to a greater benefit to the parasitoid's fitness than to the pest. This could occur because the developing parasitoid larva derives a higher level of nutrients from a host which has fed on nectar/ pollen
5. Parasitoid benefits but its hyperparasitoids do not
6. Parasitoid benefits but natural enemies of other natural enemies do not.

These subtleties associated with adding resource subsidies to agro-ecosystems can be explored via empirical laboratory or field studies, ideally with the support of ecological modeling (see Kean et al., 2003). ·

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