UNDERSTOREY MANAGEMENT FOR THE ENHANCEMENT OF POPULATIONS OF A LEAFROLLER (LEPIDOPTERA: TORTRICIDAE) PARASITOID (*DOLICHOGENIDEA TASMANICA* (CAMERON)) IN CANTERBURY, NEW ZEALAND APPLE ORCHARDS

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Plate 1. Buckwheat growing in the inter-row sward of a pear and apple orchard for the enhancement of natural enemies of leafroller. Note: release sleeve and yellow sticky traps.

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UNDERSTOREY MANAGEMENT FOR THE ENHANCEMENT OF POPULATIONS OF A LEAFROLLER (LEPIDOPTERA: TORTRICIDAE) PARASITOID (*DOLICHOGENIDEA TASMANICA* (CAMERON)) IN CANTERBURY, NEW ZEALAND APPLE ORCHARDS

N. A. Irvin

This study investigated understorey management in Canterbury, New Zealand, apple orchards for the enhancement of populations of *Dolichogenidea tasmanica* (Cameron) (Braconidae) for leafroller (Lepidoptera: Tortricidae) biological control. The first objective was to determine the influence of understorey plants on the abundance of *D. tasmanica* and leafroller parasitism, and to investigate the mechanisms behind this influence. The second was to determine the most suitable understorey plants in terms of their ability to enhance parasitoid abundance, leafroller parasitism, parasitoid longevity, parasitoid fecundity and its ability to not benefit leafroller.

Results from three consecutive field trials showed that buckwheat (*Fagopyrum esculentum* Moench), coriander (*Coriandrum sativum* L.), alyssum (*Lobularia maritima* (L.) Desv), and, to a lesser extent, broad bean (*Vicia faba* L.), enhanced parasitoid abundance and leafroller parasitism. The mechanisms behind the effects of understorey plants had previously been unexplored. However, results here showed that it was the flowers of the buckwheat that 'attracted' the parasitoid to the plant and not the shelter, aphids or microclimate that the plant may also provide. Providing flowering plants in the orchard understorey also increased immigration of parasitoids and enhanced parasitoid longevity and fecundity in the laboratory. In contrast, the understorey plants had no influence on the female:male ratio of *D. tasmanica*.

Although coriander enhanced leafroller parasitism three-fold in field experiments compared with controls, it failed to enhance the longevity of both sexes of *D. tasmanica* in the laboratory compared with water-only. Broad bean significantly enhanced parasitoid abundance three-fold and significantly increased parasitism from 0% to 75% compared with the controls on one leafroller release date. However, laboratory trials showed that broad bean enhanced the longevity of male *D. tasmanica* but it did not enhance female longevity. Also, female *D. tasmanica* foraging on broad bean produced a total of only three parasitoid cocoons, but this result was based on an overall 6.5% survival of larvae to pupae or to parasitoid cocoon. Furthermore, results suggested that extrafloral nectar secretion decreased as the plants matured.

Phacelia (*Phacelia tanacetifolia* Benth.) did not significantly enhance parasitism rate in the field compared with controls, and numbers of *D. tasmanica* captured by suction sampling were significantly lower in phacelia treatments compared with alyssum, buckwheat and control plots. Also, laboratory experiments showed that survival of *D. tasmanica* on phacelia flowers was equivalent to that on water-only and significantly lower than on buckwheat. These results suggest that phacelia does not provide nectar to *D. tasmanica*, only pollen, and therefore is not a suitable understorey plant for *D. tasmanica* enhancement in orchards.

Buckwheat and alyssum showed the most potential as understorey plants for the enhancement of natural enemies. Buckwheat not only increased numbers of *D. tasmanica* seven-fold, but also increased numbers of beneficial lacewings (*Micromus tasmaniae* (Walker)) and hover flies (Syrphidae) captured on yellow sticky traps compared with the controls. It significantly increased leafroller parasitism by *D. tasmanica* from 0% to 86% compared with the controls (on one date only), and in the laboratory enhanced *D. tasmanica* longevity and increased fecundity compared with water-only. Similarly, alyssum significantly increased parasitism rate compared with controls, and two-fold more *D. tasmanica* were suction sampled in these plots compared with controls. It also enhanced longevity of both sexes of *D. tasmanica* compared with water, and showed the most favourable characteristics in terms of being of no benefit to leafrollers. This is because it was not preferred over apple by leafroller larvae and when they were forced to feed on it, it

caused high mortality (94.3%) and low pupal weight (15 mg). Furthermore, alyssum did not enhance the number of fertile eggs produced by adult leafrollers compared with water-only. However, further research is required to address the overall effect of buckwheat and alyssum on crop production and orchard management, including effects on fruit yield and quality, frost risk, disease incidence, soil quality, weeds and other pests. Also, research into the ability of these plants to survive in the orchard with little maintenance, and into the optimal sowing rates, would be useful.

Sampling natural populations of leafroller within each treatment showed that damage from leafrollers and the number of leafroller larvae were respectively 20.3% and 29.3% lower in the flowering treatments compared with the controls. Furthermore, field trials showed up to a six-fold increase in leafroller pupae in controls compared with buckwheat and alyssum. This suggests that increasing leafroller parasitism rate from understorey management in orchards will translate into lower pest populations, although neither larval numbers/damage nor pupal numbers differed significantly between treatments.

Trapping *D. tasmanica* at a gradient of distances showed that this parasitoid travels into rows adjacent to buckwheat plots, indicating that growers may be able to sow flowering plants in every second or third row of the orchard, and still enhance leafroller biocontrol while minimising the adverse effects of a cover crop. Sowing buckwheat and alyssum in orchard understoreys may enhance biological control of apple pests in organic apple production and reduce the number of insect growth regulators applied in IFP programmes. However, the challenge still remains to investigate whether conservation biological control can reduce leafroller populations below economic thresholds.

Keywords Leafroller, Tortricidae, parasitoid, *Dolichogenidea tasmanica*, understorey management, apple orchard, enhancement, *Phacelia tanacetifolia*, *Fagopyrum esculentum*, *Coriandrum sativum*, *Lobularia maritima*, *Vicia faba*, conservation biological control.

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1. INTRODUCTION

1.1 THE APPLE INDUSTRY IN NEW ZEALAND

New Zealand apples are marketed by ENZA New Zealand (International) which ensures uniformly high quality fruit standards regarding pest damage, quarantine, and pesticide residues. The New Zealand apple industry is small by world standards, accounting for about one third of the Southern Hemisphere crop and about 1% of world production (McKenna *et al.*, 1998; Schupp *et al.*, 1999). However, in 25 years, New Zealand production has tripled to over 20 million cartons/year (Schupp *et al.*, 1999) and New Zealand apple yields are typically 90-100 tonnes/ha, which are amongst the highest in the world (Anon., 1999). Recently, the World Apple Report newsletter rated New Zealand as the best place on earth to grow apples (Schupp *et al.*, 1999) and New Zealand emerged with the highest score amongst the major apple producing countries when surveyed on production efficiency, industry infrastructure and inputs, and financial and market factors (O'Rourke, 1996).

The New Zealand apple export business aims for the premium market (O'Rourke, 1996). Therefore, a high degree of pest control is required to meet the standards of fruit quality and quarantine standards demanded by overseas markets. The main insect pests of apple in Canterbury, New Zealand are leafrollers (Tortricidae) and codling moth (*Cydia pomonella* (L.)) with the following secondary pests: European red mite (*Panonychus ulmi* (Koch)), two-spotted spider mite (*Tetranychus urticae* Koch), oystershell scale (*Quadraspidiotus ostreaeformis* (Curtis)) apple leafcurling midge (*Dasineura mali* Kieffer), Froggatt's apple leafhopper (*Edwardsiana crataegi* (Douglas)) and woolly apple aphid (*Eriosoma lanigerum* (Hausmann)) (Tomkins, 1984). This study concentrates on one of the main apple pests, leafroller.

1.2 Leafroller Biology And Life History

There are several species of leafroller in New Zealand, five of which are of particular significance in fruit production. Lightbrown apple moth (LBAM) (*Epiphyas postvittana* (Walker)) is of Australian origin, whereas the brownheaded leafrollers (*Ctenopseustis obliquana* (Walker) and *C. herana* Felder & Rogenhofer) and the greenheaded leafrollers (*Planotortrix excessana* (Walker) and *P. octo* Dugdale) are native species. All are found throughout the country with some species dominant in certain regions. For example, LBAM is most important in the South Island, particularly in Nelson, whereas brownheaded leafroller dominates in the northern North Island (Penman, 1984).

Leafrollers are pests of a range of plants of economic importance and attack more than 265 host species in New Zealand (Thomas, 1989). The host range of LBAM encompasses 34 plant families (Tomkins, 1984) and includes deciduous tree fruits, subtropical fruits, berry fruits, ornamentals and forest and shade trees (Penman, 1984). Leafrollers overwinter as larvae in all instars in mummified fruits, on ground cover or on evergreen host plants. Adults developing from these larvae fly in spring and lay eggs. There are five or six larval instars, after which the prepupal larva spins a brown silken cocoon between folded leaves either on the tree or on foliage beneath the tree (Penman, 1984).

1.3 Economic Importance And Damage

In New Zealand apple orchards, leafroller populations peak during the fruit ripening period and in unsprayed situations 30% of the fruit may be damaged (Wearing *et al.*, 1994). Leafrollers can cause economic loss in orchards by feeding on the fruit surface, producing fruit of poor quality, which is unsuitable for export. Leafroller damage may also expose the fruit to later infections and cause direct damage to buds and foliage. The latter reduces photosynthetic rate, can deform the growth pattern, lead to general tree weakness and sometimes to tree death, especially in younger trees. Despite these potentially important effects of leafroller feeding, leafrollers have a high pest status in apple production mainly because of the zero tolerance of their presence in fruit destined for the export markets and the high requirement for blemish-free fruit (Lo *et al.*, 1997; Walker *et al.*, 1997).

1.4 Methods For Managing Leafroller Populations

Control of leafrollers is the main factor determining the number of insecticide applications in commercial orchards. Export apple growers had applied in the past between three and eleven post-bloom applications per season (Wearing *et al.*, 1991) and broad spectrum organophosphate sprays have been used in New Zealand for about 30 years (Wearing *et al.*, 1993). These insecticides allow the simultaneous control of several pest species with a single spray application (Sicbaldi, 1994) and although targeted against immature pest stages, the good contact activity of many broad-spectrum insecticides allows them to kill all life stages, including the adults and eggs. However, the overlapping generations within and between leafroller species complicate the application of sprays and most of the life cycle of leafrollers is spent in webbed shelters, so larvae are not exposed to insecticide. Also, more recently, the negative effects of intensive pesticide usage have become the focus of major concern for the pipfruit industry. For example, control of leafroller using insecticides has lead to resistance. Localised resistance of lightbrown apple moth to azinphos-methyl in Mariri, near Nelson, has been confirmed (Suckling *et al.*, 1984). Wearing (1995) reported similar resistance of the greenheaded leafroller in central Otago. More recently Lo *et al.* (1997) reported resistance of greenheaded leafroller in Twyford, Hawke's Bay. There are also many other potentially adverse effects of intensive insecticide usage. For instance, pesticides can:

- result in environmental toxicity by contaminating soils, water systems and food chains (MacIntyre *et al.*, 1989; Deedat, 1994; Sicbaldi, 1994);
- be harmful to 'non-target organisms', including domestic animals, honey bees and other pollinators, wildlife and natural enemies (the latter sometimes resulting in secondary pest outbreaks and pest resurgence) (Debach and Rosen, 1991; Sicbaldi, 1994);
- leave residues on produce, therefore decreasing overseas market access;
- be detrimental to human health and can lead to cancer, sterility and death (Debach and Rosen, 1991). There is some debate about the human health risks involved from conventional pesticide use (see review by East and Holland, 1991); however, pesticide poisonings are estimated at three million per year worldwide, with about 220,000 of these resulting in death (WHO, 1990).

Consumers are becoming aware of the negative effects of pesticides and are demanding lower pesticide residues on fruit, or pesticide-free fruit. For example, a survey of New Zealand consumer perception of pesticide use and residues on fruit found that 92% of those surveyed had some level of concern about the presence of pesticide residues in fruit (Wilson-Salt, 1993). This trend has also developed overseas so that now, one of the specifications being applied by some British supermarkets is that exporters from all over the world, including New Zealand, must produce agricultural products under environmentally-friendly practices. It is very likely that other retailers within Europe will follow the same lead (Batchelor, 1996). It is very important for the New Zealand apple industry to meet these criteria because 25% of New Zealand exports are to the United Kingdom (Anon., 1998a). Furthermore, the range of pesticides available is rapidly shrinking, pesticide registration costs are rising, and permissible spray residue levels continue to be reduced (Wearing *et al.*, 1993; Anon., 1999). Therefore, it is apparent that the fruit industry needs to move towards a more sustainable management approach.

Alternative methods of controlling leafroller include pheromone trapping, *Bacillus thuringiensis* Berliner (*Bt*) sprays and insect growth regulators (IGRs). Pheromone trapping to monitor adult populations can identify periods of low adult activity when spraying may not be necessary, thereby reducing the number of sprays applied per season (Suckling *et al.*, 1990b). Mating disruption using pheromones has been a successful technique with resistant populations of LBAM at Mariri (Suckling *et al.*, 1990a) and may have the potential to replace late-season spray applications, hence reducing insecticide residues at harvest. However, it is unlikely that mating disruption will ever replace insecticides for leafroller control due to the wide host range of the pest and the immigration of mated females into the orchard (Suckling *et al.*, 1990b). They also may attract males from long distances (Suckling *et al.*, 1994) and may not accurately reflect within-orchard leafroller populations (Stevens *et al.*, 1995).

Bacillus thuringiensis is a bacterial insecticide which stops caterpillars feeding after ingestion, and death occurs after 5-6 days (Anon, 1997a). Despite the high toxicity of *Bt* to leafrollers, replicated trials over the past six years with a variety of formulations and strains of *Bt* have failed to obtain control consistently below 3% fruit damage (Suckling *et al.*,

1993). This may be because *Bt* is susceptible to ultra-violet light and rainfall, has a short persistence, is effective only against the younger instars, and there is also a need for complete spray coverage and ingestion of *Bt* by caterpillars. *Bt* genes are being inserted into genetically modified plants for insect control. This is causing increasing concern that the persistent expression of *Bt* protein in plants will increase selection pressure for pest resistance (Wigley and Chilcott, 1994).

Insect growth regulators are selective compounds that interfere with the physiology of insects by disrupting growth processes, reproduction or other critical systems. These compounds are extremely safe to beneficial arthropods. In fact, several years of IGR use in European apple orchards have shown that biological control of many apple pests by arthropod predators and parasitoids is greatly enhanced (de Reede *et al.*, 1984; Blommers *et al.*, 1987). Tebufenozide (Mimic®) is an IGR which disrupts the moulting process in lepidopteran larvae by mimicking the action of the insect moulting hormone, ecdysone. Upon ingestion, the larvae cease feeding, undergo a premature and incomplete moult and subsequently die. This compound is more persistent than either azinphos-methyl or chlorpyrifos (Suckling *et al.*, 1996b) but is specific to lepidopteran pests and so should achieve sufficient levels of leafroller control while having no direct effect on natural enemies. However, leafroller resistance to tebufenozide has already occurred in New Zealand (Wearing, 1998).

Although pheromone trapping, *Bt* sprays and IGRs are a step towards reducing chemical pesticide dependence in apple production, each of these methods alone is insufficient. They may have problems coinciding with leafroller phenology, with persistence or obtaining consistent control, with application or spray coverage and with possible resistance occurring. One strategy to combat the development of pest resistance is to reduce or diversify the selection pressure by using a variety of controls (Wigley and Chilcott, 1994). Therefore, the New Zealand pipfruit industry is moving towards integrated fruit production.

1.5 Integrated Fruit Production

Integrated fruit production (IFP) aims to improve the long-term sustainability of pest control and to minimise the health and environmental hazards associated with the use of pesticides (Wearing *et al.*, 1993). It bridges the gap between 'organic' and 'conventional' growing methods and covers all aspects of fruit production, from plant nutrition to tree pruning and spraying (Anon., 1997b). IFP programmes are already internationally accepted, with 35% of all apples consumed in Europe grown under such programmes (Anon., 1997b). The New Zealand pipfruit industry has been implementing integrated pest management practices since the 1970s with the development of insecticide-tolerant biological control agents. The best known example is the predatory mite, *Typhlodromus pyri* (Scheuten) and its use against spider mites (Wratten *et al.*, 1998). As a result of integrated mite control, the European red mite and twospotted spider mite have become relatively minor pests for most New Zealand apple growers (Early, 1984). Since 1996, ENZA and The Horticultural and Food Research Institute of New Zealand Ltd (HortResearch) have developed and introduced an integrated fruit production programme for pipfruit (Batchelor *et al.* 1997). ENZA aims at having all growers operating under the IFP programme by 2001 (Anon., 1997b). This programme was described by Batchelor *et al.* (1997) and requires growers to use monitoring procedures and action thresholds to determine when pesticide application is essential. It strongly favours the use of IGRs and the reduction of broad-spectrum insecticides. In fact, growers using IFP have cut their insecticide use by 50% in the last three years (Anon., 1999). Not only will this programme allow New Zealand to maintain its status as a preferred supplier for United Kingdom retailers (Batchelor, 1996) but the introduction of the selective IGRs, such as tebufenozide, into IFP programmes has allowed an opportunity for utilising natural enemies for the biological control of leafrollers. Research is now required on enhancing biological control to augment the effects of tebufenozide. This is the rationale behind this study.

1.6 Natural Enemies Of Leafroller

Leafrollers are attacked by a variety of natural enemies including predators, pathogens and parasitoids. Little research has been carried out on natural enemies of the native leafrollers but predacious lacewing larvae, *Micromus* spp. are voracious consumers of LBAM eggs

and larvae (Nicholas *et al.*, 1994), while other predators feed mainly on the larval stages. These include a range of spiders, vespid wasps, birds (Thomas, 1965; Collyer and van Geldermalsen, 1975), hover flies (Miller and Wratt, 1915), the predatory shield bugs *Oechalia schellenbergii* (Guērin), and *Cermatulus nasalis* (Westwood) (Ramsay, 1963), and the European earwig *Forficula auricularia* L. (Danthanarayana, 1983). A fungal pathogen, *Entomophthora* sp., causes sporadic mortality among LBAM infestations when weather conditions are favourable (Thomas, 1989) and Dumbleton (1935) reported the presence of nematodes in larvae of LBAM. Nuclear polyhedrosis virus infection has also been noted in LBAM (Collyer and van Geldermalsen, 1975).

There is a complex of parasitoids that attacks leafrollers in New Zealand. The larvae of parasitoids feed exclusively on the body of another arthropod (its host), eventually killing it. Only a single host is required for an individual parasitoid to complete development, and often a number of parasitoids develop gregariously in the same host. Leafroller parasitoids in New Zealand are either endemic or introduced, either accidentally with their host or deliberately to enhance leafroller control. In New Zealand, leafroller parasitoids are mainly either in the order Hymenoptera, belonging to the families Braconidae, Trichogrammatidae, Bethylidae, Eulophidae, Ichneumonidae, and Pteromalidae, or in the order Diptera, belonging to the family Tachinidae (see Table 2 in Stephens, 1996).

Some parasitoid species were introduced from Australia between 1967-1969 for leafroller control. *Glabridorsum stokesii* (Cameron) and the yellowbanded leafroller parasitoid (*Xanthopimpla rhopaloceros* Krieger) attack leafroller pupae, while the tachinid fly *Trigonospila brevifacies* (Hardy) attacks older larvae (Penman, 1984). There is no evidence in the literature that these introduced parasitoids have had a significant impact on leafroller populations in New Zealand. However, no quantitative studies have examined the contribution of introduced parasitoids to control leafroller populations (Thomas, 1989). Early (1984) reported from subjective assessments that leafroller infestations are now much lower in many areas than they were before the introduction of these parasitoids. More detailed reviews of New Zealand leafroller parasitoids are provided by Early (1984), Thomas (1989) and Wearing *et al.* (1991).

Dolichogenidea (formerly *Apanteles*) *tasmanica* (Cameron) (Braconidae) is widespread throughout New Zealand. It has been reported to be the most common parasitoid of leafrollers in Canterbury (Thomas, 1965; Suckling *et al.*, 1996a), Nelson (Dumbleton, 1935) and Hawke's Bay (Charles *et al.*, 1996). This parasitoid attacks all five main species of leafroller but there is some evidence that it prefers LBAM (Wearing *et al.*, 1991). *D. tasmanica* is thought to be self-introduced from Australia at the same time as LBAM (Dumbleton, 1935). It belongs in the family Braconidae and is a solitary parasitoid which attacks early-instar leafroller. It emerges from the fourth instar to spin and pupate in its silken cocoon. One generation takes approximately two months, ten days fewer than the time taken for production of a generation of LBAM at the same time of year (Dumbleton, 1935). There are probably 2-3 generations per summer and it overwinters within overwintering leafroller larvae (Early, 1984).

The role of parasitoids in regulating leafroller populations has so far not been examined in any New Zealand crop (Charles *et al.*, 1996). Most studies report levels of parasitism by *D. tasmanica* to be 20-30% (Collyer and van Geldermalsen, 1975; Green, 1984; Suckling *et al.*, 1996b). However, levels of parasitism by *D. tasmanica* of up to 46% of LBAM larvae in apple orchards have been recorded (Early, 1984; Tomkins, 1984). This suggests there may be some potential for using leafroller parasitoids for biological control in orchards. Unfortunately, little research has been carried out on methods to enhance populations of parasitoids in New Zealand orchards to achieve greater biological control of leafrollers. This study concentrates on the parasitoid *D. tasmanica* and investigates its population enhancement through conservation biological control.

1.7 Conservation Biological Control

Biological control or biocontrol can be defined as the utilisation of natural enemies (parasites, predators and pathogens) to reduce the damage caused by noxious organisms to tolerable levels (Debach and Rosen, 1991). It is increasingly viewed as the best way forward for weed, pest and disease control in the light of problems with pesticides (Field 1997, Williams, 1997). This trend is illustrated in New Zealand by the increasing number of papers on biological control and the reducing number on chemical control published by

the New Zealand Plant Protection Society (Popay, 1997). When biocontrol is effective, it can be a sustainable, inexpensive and, most importantly, a virtually hazard-free method of controlling pest populations.

There are three main approaches to biological control; classical, inundative and conservation biological control.

A. Classical

Many pests were accidentally introduced into new areas without their complement of natural enemies so classical biocontrol involves the search for exotic natural enemies, often in the pest's native country, and the rearing and introduction into new environments. See Clausen (1978) and van Driesche and Bellows (1996).

B. Inundative

Inundative releases consist of releasing large numbers of a natural enemy for an immediate short-term result, in effect, like a biological pesticide (Debach and Rosen, 1991). See also van Driesche and Bellows (1996).

C. Conservation

Conservation biological control or habitat manipulation is the conservation or enhancement of populations of natural enemies by manipulating the environment to enhance their activity against a particular pest or pest complex. Reviews by van den Bosch and Telford (1964), van Lenteren (1987), van Driesche and Bellows (1996), Barbosa and Wratten (1998) and Gurr *et al.* (1998), Landis *et al.* (in press) have explored this extensively.

However, the boundaries between these three forms of biological control may move (Gurr *et al.*, 1998). For instance, *D. tasmanica.*, the main focus of this thesis, was originally self-introduced into New Zealand but recent work (Stephens *et al.*, 1998) and this study are trying to enhance its abundance in New Zealand orchards, through conservation biological control, by manipulating the orchard environment to increase its biological control potential.

Until recently, classical biological control was regarded without question as an environmentally safe and desirable method of pest control. However, it is currently recognised that successful introduction is essentially irreversible and its effects unpredictable so the risk of adverse effects on the environment and 'non-target' organisms is high. Therefore, there is an increasing quantity of research been carried on conservation biological control (Barbosa, 1998; Pickett and Bugg, 1998; Landis *et al.*, in press) and this is illustrated by the increasing number of papers on this field in the CAB Abstracts Database between 1973-1998.

Conservation biological control probably has the least risk of any of the types of biological control because it aims at enhancing natural enemies that have already established and is possibly the only type for which the key effects can be removed totally. It is based on increasing particular aspects of diversity within agricultural and horticultural ecosystems. The 20th century trend in 'western' agriculture is towards extensive monocultures, which has removed diversity from potentially stable natural systems (Altieri, 1991). Recent reviews of the idea that an increase in diversification of agroecosystems may increase their stability show that managed diversification of the vegetational components of agricultural habitats often lowers pest populations (Risch *et al.*, 1983; Russel, 1989; Wratten and van Emden, 1995). Root (1973) proposed two possible hypotheses for these effects: the **resource concentration hypothesis** and the **natural enemies hypothesis**. The former states that herbivores less easily find, stay in and reproduce in diverse systems due to disruption of chemical and visual cues, restricted movement within the crop and an increase in emigration from the crop. It follows that, when the plant resource is concentrated (e.g., regularly-spaced host plants in bare (weed-free) soil), herbivores more easily find their host plants. The second hypothesis states that predator and parasitoid numbers are enhanced through the provision of alternative hosts/prey at times of scarcity, food (pollen and nectar) for adult parasitoids and predators and refuges for over-wintering. This study focuses on the latter.

A review of the literature reveals that conservation biological control can reduce pest populations and has great potential for improving pest control (e.g., van Emden, 1963; Doutt and Nakata, 1973; Powell, 1986; White *et al.*, 1994). For example, 'beetle banks'

have been used to enhance the numbers of predators in field crops by providing shelter and over-wintering sites (Sotherton, 1995; Collins *et al.*, 1996), mixed cropping and inter-cropping have increased parasitism in various crops and beneficial insect populations have been enhanced by providing floral resources in the field.

1.8 Enhancing Parasitoid Populations Through The Provision Of Floral Resources

The importance of pollen and nectar in the life cycles of many natural enemies is well established (Thorpe and Caudle, 1938; Schneider, 1948; Syme, 1975; Zandstra and Motooka, 1978; Takasu and Lewis, 1995; Baggen and Gurr, 1998). Jervis *et al.* (1993) demonstrated the value of flowers for Hymenoptera by a field survey in Britain that demonstrated that 250 species of parasitoids were observed feeding at the inflorescences of 32 plant species. Floral nectars contain sugars, proteins, free amino acids, lipids, antioxidants, alkaloids, phenolics, vitamins, saponins, dextrins, and inorganic substances (Hagen, 1986). Pollen contains various carbohydrates; some contain starch, sterols and essential fatty acids as well as protein/amino acids, triconomes and kairomones associated with parasitoid searching (Barbier, 1970). In some insect groups, these floral resources are a prerequisite for egg maturation, for example, hover flies (Diptera: Syrphidae) (Schneider, 1948) and some parasitic wasps (Hymenoptera) (Jervis and Kidd, 1986), and nectar is often a source of energy for host and mate seeking. Many studies have shown that these food sources can also influence longevity and fecundity, and therefore the efficiency of natural enemies (Lővei *et al.*, 1993b; Baggen and Gurr, 1998).

The introduction of integrated growth regulators (IGR) into IFP programmes has provided an opportunity for utilising natural enemies for leafroller biological control because IGRs are specific to lepidopteran pests, so should achieve sufficient levels of leafroller control while having no effect on natural enemies. The predators described in Section 1.6 may kill up to 90% of newly hatched LBAM caterpillars in spring (Nicholas *et al.*, 1994) and leafroller parasitism rates of up to 46% have been reported (Early, 1984; Tomkins, 1984). However, current control from natural enemies alone is unreliable, especially in orchards with a herbicide-treated orchard floor (Anon, 1997a). Currently, the most common method

of vegetation control in conventional orchards consists of a mown inter-row sward and a herbicide-sprayed strip along the tree-line (Harrington *et al.*, 1992; McCarthy, 1993). Not only does prolonged herbicide use inhibit soil micro-organism activity, limit humus formation, damage soil structure and cause nutrition imbalances (McCarthy, 1993), but it also removes the essential resources such as shelter and/or food required by many natural enemies, making the orchard a less favourable habitat for natural enemies.

Providing flowering plants in the vicinity of crops has been suggested as a way to provide these essential resources. Gardner (1938) found that degrees of parasitism and superparasitism of *Popillia japonica* Newman by *Tiphia vernalis* Rohwer were related to the distance of the host plant from the adult parasitoid's food source. Energy is used by the parasitoid during travel to each site, so a parasitoid arriving at a distant food site is more likely to die of starvation, and one arriving at a distant host site is more likely to superparasitise because starved individuals superparasitise more often (Sirot and Bernstein, 1997). If host and food sites are very distant, then there is also a higher accidental mortality risk associated with travelling between the two. Therefore, providing flowering plants in the vicinity of crops may also reduce superparasitism.

Leaving strips free of herbicide treatment in orchards to encourage weeds has been suggested as a method of providing flowering plants. For example, Leius (1967) found that the presence of wild flowers in apple orchards resulted in a five-fold increase in parasitism of codling moth *Cydia pomonella* larvae. However, the encouragement of weeds in crops would be agronomically unacceptable (Cowgill, 1989) and some weeds have been found to enhance arthropod, nematode, and pathogen pests (Norris, 1986). van Emden (1965a) cited more than 400 pest problems caused by weeds so it may be more useful to select and use plants in an orchard that specifically meet the parasitoids' needs. It may also be possible to choose an understorey plant that increases soil fertility or selectively benefits the natural enemy and not the pest. For example, the longevity of *Copidosoma keohleri* Blanchard, an important parasitoid of potato moth (*Phthorimaea operculella* (Zeller)) was significantly increased on borage flowers, but the pest did not benefit (Baggen and Gurr, 1998).

Batchelor (1996) stated that the New Zealand IFP programme for pipfruit is undergoing continuous improvement and in the 'weed and understorey management section' of the Integrated Fruit Production Programme for Pipfruit, the use of low competition ground cover within the tree rows is encouraged as an alternative to herbicides (Anon., 1998b). It was also stated that research to identify suitable plant species for this purpose is urgently required.

Stephens *et al.* (1998) conducted an experiment to determine the influence of buckwheat (*Fagopyrum esculentum* Moench) as an understorey plant in a Canterbury orchard on the proportion of released leafroller larvae parasitised by *D. tasmanica*. They found that significantly higher levels of parasitism of released larvae were observed in buckwheat plots than in control plots. Also, higher numbers of *D. tasmanica* were captured on yellow sticky traps in buckwheat plots compared with control plots. However, the replicate number and plot sizes used in the study were small and further investigation is needed into other understorey options, the mechanisms behind the increase in parasitoid abundance and the use of the understorey by leafrollers.

The following study investigates the influence of several species as understorey plants on the abundance of *D. tasmanica* and parasitism of leafroller by this parasitoid. The main aims of this study were to:

- determine the influence of understorey plant species on the abundance of *D. tasmanica* and leafroller parasitism in Canterbury, New Zealand, apple orchards;
- investigate the mechanisms behind the influence of understorey plants on parasitoid abundance and leafroller parasitism;
- determine the most suitable understorey plant species for Canterbury apple orchards in terms of its ability to enhance parasitoid abundance, leafroller parasitism, parasitoid longevity, parasitoid fecundity and its influence on leafroller;
- determine the movement of *D. tasmanica* from the understorey plants into the apple canopy.

The field research methods for assessing the influence of understorey plants on parasitoids and their impacts on pests are not well developed. Therefore, a further aim of the study was

to investigate and refine a suitable method for these types of studies. The field experiments are grouped by season in this thesis because over time the protocols for measuring parasitism rate were modified.

2. UNDERSTOREY MANAGEMENT EXPERIMENTS IN 1997

The following chapter investigates the influence of buckwheat (*Fagopyrum esculentum*) (Polygonaceae) and broad bean (*Vicia faba* L.) sown in the understorey on the number of natural enemies captured on yellow sticky traps and leafroller parasitism rate (Section 2.1). It also investigates the influence of trap height and type on captures of natural enemies (Section 2.2), and examines the relationship between leafroller density and parasitism of larvae by *D. tasmanica* (Section 2.3).

2.1 THE INFLUENCE OF BUCKWHEAT AND BROAD BEAN ON NATURAL ENEMY ABUNDANCE AND LEAFROLLER PARASITISM

2.1.1 Introduction

Buckwheat originated in southern China (Ohnishi, 1991; Ohnishi and Onishi, 1992) and has been cultivated extensively in the north-eastern United States since European settlement (Björkman, 1995). It has small white flowers with shallow corollae, so pollen and nectar are available to a wide range of beneficial insects (Lővei *et al.*, 1993b), including short-tongued parasitoids. Buckwheat has a short sowing-to-flowering time in New Zealand (Bowie *et al.*, 1995) and its seeds are inexpensive and widely available. Previous studies have shown that buckwheat can enhance predatory insect abundance in crop systems (Bugg and Dutcher, 1989; Bugg *et al.*, 1990) and effectively suppress weeds (Schonbeck *et al.*, 1991; DeHaan *et al.*, 1994). Russian orchards were reported 20 years ago to be under-sown with buckwheat to provide a food source for adult *Trichogramma* spp. parasitoids, which attack codling moth (*Cydia pomonella*) eggs. Only 3.5% of apples were infested with codling moth larvae when buckwheat was present, compared with 1.5% with full chemical control and 54% with no treatment (Zandstra and Motooka, 1978).

Hodgson and Lővei (1993) used pitfall and sweep-net catches to assess the importance of novel crops as reservoirs of natural enemies in a cereal crop. Buckwheat attracted large numbers of adult hover flies and parasitoid wasps showed a distinct 'preference' for buckwheat over the other crops. The larvae of some New Zealand hover flies not only feed

on aphids but they also prey upon early-instar lepidopterans, for example, white butterfly, *Pieris rapae* (L.), and diamondback moth, *Plutella xylostella* (L.) (Valentine, 1967; Miller, 1971; Ashby and Pottinger, 1974).

Work with buckwheat as an understorey plant in a Canterbury, New Zealand, apple orchard led to significantly higher levels of parasitism by *Dolichogenidea tasmanica* of released larvae in buckwheat plots than in controls (Stephens *et al.*, 1998). Higher numbers of *D. tasmanica* were also captured on yellow sticky traps in buckwheat plots compared with controls. However, the replicate number and plot sizes used in the study were small and further investigation is needed into other understorey options in conjunction with larger plot sizes and an increase in plot replicates, to determine the full potential for enhancing leafroller parasitoid numbers and their effects.

The nectar of the flowers of broad (faba) bean is probably inaccessible to short-tongued parasitoids. However, a rich assemblage of ichneumonids attend extrafloral nectaries of broad bean, including parasitoids of agricultural and forest pests (Bugg *et al.* 1989). Extrafloral nectaries are easily accessible for parasitoids and considerable amounts of extrafloral nectar are available for an extended period throughout the growing season (Butler *et al.*, 1972; Yokoyamma, 1978; Adjei-Maafo and Wilson, 1983). Also, parasitoids are potentially able to search for food more efficiently, because the extrafloral nectar sites are both predictable and detectable (Stapel *et al.*, 1997). Broad bean has the added advantages of being able to be planted at any time of the year in New Zealand and the extrafloral nectaries are present soon after germination when the seedlings are only a few centimetres tall. Therefore, it may be useful for early-spring enhancement of natural enemy populations.

Not all effects of understorey plant may, however, be positive. The abundance of *Anacharis zealandica* L. a parasitoid of Tasmanian lacewing (*Micromus tasmaniae* (Walker)), was enhanced by undersowing buckwheat (Stephens *et al.* 1998). Baggen and Gurr (1998) demonstrated that buckwheat enhanced the fecundity of potato moth, whereas no such benefit occurred when borage (*Borago officinalis* L.) was used. Therefore, it is

important to determine the influence of understorey plants on pest species and on parasitoids of natural enemies.

The following study investigates the effect of sowing buckwheat and broad bean in the understorey of an apple orchard on *D. tasmanica*, lacewing, *A. zealandica* and hover fly abundance and investigates the mechanisms responsible for the influence of buckwheat on populations of natural enemies. The effect of plot size on natural enemy abundance was also investigated.

2.1.2 Methods

2.1.2.1 Small experimental plots

Site description and experimental design

Four replicates of each of four treatments (buckwheat with flowers (Plate 2), buckwheat without flowers (Plate 2), broad beans (Plate 2) and herbicide-treated control (Plate 2)) were set up in a randomised complete block design in an apple orchard at the Lincoln University Horticultural Research Area (LUHRA), Canterbury, New Zealand. Each plot was 8 m x 2 m (containing five trees) and the site consisted of eight rows of eight-year-old apple trees (two rows of cv. 'Braeburn' (block 1) and six rows of cv. 'Royal Gala') spaced at 2 m with 4.5 m between rows (Fig. 2.1).

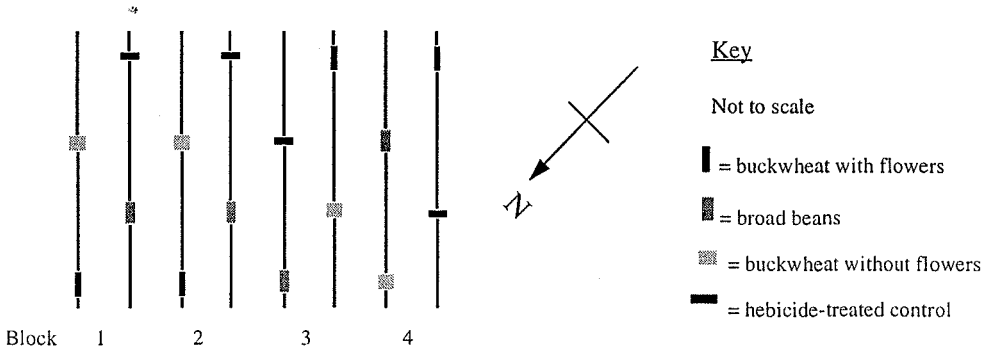


Fig. 2.1 Experimental layout in an apple orchard of the understorey treatments in the 1997 small plot experiment.

Plate 2. Understorey treatments in the 1997 small plot experiment: Top left - buckwheat with flowers treatment; top right - buckwheat without flowers treatment; bottom left - broad bean treatment; bottom right - herbicide-treated control.

Plant agronomy

Simazine 1 kg/ha (Simazine 900DF 900 g/L) had been applied in winter to remove all understorey weeds. To minimise the residual effect of this herbicide, the top 20 mm of soil was removed from each of the areas in which buckwheat seeds were to be sown. Buckwheat (cv. 'Shinano Natsu') seeds were sown in a 50 mm-wide strip at a rate of two seeds/cm^2 on December 6, 1996 and on January 6, 1997 to ensure continual flowering. One row of broad bean seed (cv. 'Exhibition Long Pod') was sown at 30 mm spacings on November 11, 1996 and on January 6, 1997. Seeds were sown at a depth of 30-40 mm on each side of the row. Control understorey plots were re-sprayed in mid-January with simazine 1 kg/ha and glyfosinate-ammonium at 6 L/ha in 400 L water (Buster® 200 g/L). Weeds in the buckwheat treatments were removed by hoeing, and inter-row vegetation (white clover (*Trifolium repens* L.) and ryegrass (*Lolium perenne* L.)) were mown every two-four weeks.

Approximately six weeks after sowing (mid-January, 1997), the buckwheat began flowering and parasitoid trapping and leafroller release began. Flowers in the 'buckwheat without flowers' treatment were removed by hand every 3-5 days until February 26, 1997. By the March 19, 1997, trap collection date there were many flowers present in these plots and therefore they were redesignated as 'buckwheat with flowers' treatments.

On February 14, 1997, the top third of the plants in the first buckwheat drilling in the 'buckwheat with flowers' treatments was removed to encourage lateral flowering and to ensure a longer overall flowering time, while the second drilling was left uncut. On March 13, 1997, the buckwheat was cultivated to determine whether removal of shelter and floral resources led to insect numbers returning to background levels. Consequently, by March 19, 1997 these 'buckwheat with flowers' treatments had been converted into 'controls'.

Parasitoid sampling

One yellow sticky trap ('Trappit', Agrisense-BCS-Ltd, Treforest Industrial Estate, Pontypridd, Mid-Gladmorgan, U. K.) (see Appendix 3 for spectral reflectance) (Plate 3), with a 200 x 245 mm catching surface on each side, was placed 1 m high in the centre of

each plot. Every 9-14 days between January 31, 1997 and April 24, 1997, traps were collected and replaced. The numbers of *D. tasmanica*, Tasmanian lacewing adults (*M. tasmaniae*), lacewing parasitoid adults (*A. zealandica*) and hover fly adults (*Melanostoma fasciatum* (Macquart), *Melangyna novaezelandiae* (Macquart) and *Eristalis tenax* (L).) were counted under a binocular microscope (20x magnification) in the laboratory. The non-aphidophagous species *E. tenax* L. was also included in this investigation because data on this species are useful in understanding the biology of flower-feeding hover flies. Sample specimens of *D. tasmanica* were identified by Jo Berry (New Zealand Arthropod Collection, Landcare Research, Auckland) and reference specimens were lodged at the Entomology Research Museum, Lincoln University.

Plate 3. Yellow sticky trap and nylon sleeve covering an apple branch where leafroller eggs had been released in the broad bean treatment of the 1997 small plot experiment.

Leafroller egg release

Eggs of LBAM (Appendix 1), were placed on a randomly selected branch in the centre of each plot every 15-20 days from January 14 to March 19, 1997. In an earlier study, Stephens *et al.* (1998) released leafroller larvae rather than eggs. However, batches of eggs are easier to count and handle and because they readily hatch under field conditions they may be better acclimatised to the field environment. It is often thought that individuals acclimatised to one environment perform better in that environment than do individuals acclimatised to a different environment (Huey *et al.*, 1999). Eggs laid on paper in the laboratory were divided into batches of approximately 150 eggs by counting the eggs and cutting the paper under a binocular microscope. Paper pieces were stapled to the underside of a leaf of a randomly selected branch on the middle tree in each plot (150 eggs per branch). A closed-ended nylon material sleeve (600 x 200 mm) (Plate 3) was placed over the branch and closed with string to allow hatched larvae to settle and to protect them and the eggs from predators and egg parasitoids, such as *Trichogramma* spp. Larvae hatching from an egg mass disperse rapidly and between 85.1%-93.8% of neonates are lost to predators between egg hatching and establishment of feeding sites (MacLellan, 1973; Geier and Briese, 1980). Sleeves were removed after 2-5 days, leaving the larvae exposed to parasitoids. The branches were removed with secateurs 6-8 weeks after egg placement and the number of parasitoid cocoons and leafroller larvae present were recorded. Parasitism rate was expressed as: [number of parasitoid cocoons recovered/(number of parasitoid cocoons recovered + number of leafroller larvae)] x 100.

Data analysis

Trap catches were divided into 'pre-' and 'post-treatment' phases (pre-treatment: January 31 to March 11, 1997, post-treatment: March 19 to April 24, 1997). Trap catch data were log-transformed ($\log_e(x+1)$) before analysis to stabilise variances and are reported as geometric means in figures. Parasitism rate was not divided into pre- and post-treatment changes because the last leafroller release was March 5, 1997, two weeks before the treatment manipulations. Trap catches and parasitism rates were compared between treatments, treatment manipulations and times using repeated measures ANOVA. When the ANOVA indicated significant main or interaction effects, these were further explored using Fisher's least significant difference test.

2.1.2.2 Large plots

Site description and experimental design

Five sites located at the LUHRA consisting of apple, pear, peach and nectarine orchards were used to create seven blocks each containing both buckwheat and control treatments set up in a randomised complete block design. These plots were each 25 x 9 m.

Peaches and nectarines

Seven-year-old peach trees (cv. 'Fantasia') were spaced 3.4 m apart in rows 4 m apart. Nectarine (cv. 'Flame Crest') trees of a similar age were spaced 2.7 m apart in rows 4 m apart (Plate 4). The recent use of simazine 1 kg/ha in winter had removed all inter-row and understorey weeds. These blocks were cultivated, ripped and flood irrigated to prepare the land for seed drilling.

Plate 4. Buckwheat (left) and control (right) treatments in the nectarine block of the 1997 large plot experiment.

Apples and pears

Apple (cv. 'Taylor's Gold') trees were eight years old and spaced at 2.25 m in rows 4.3 m apart (Plate 5). A block of five-year-old pear (cv. 'Doyenne du Comice') trees were spaced at 3.3 m in rows 4 m apart (Plate 6). The recent use of simazine (1 kg/ha) in winter had removed all understorey weeds.

Buckwheat agronomy

Each block was divided into two treatments plots, buckwheat and control (Fig. 2.2). The inter-row grass strips in the apple and pear buckwheat treatments were sprayed with glyphosate 4 L/ha in 400 L water (Roundup®XTRA 480 g/L) and rotary hoed a week later to prepare the ground for drilling. On December 2, 1996 buckwheat seeds were sown by seed drill in these plots at a mean density of two seeds/cm in the inter-row sward.

Buckwheat treatments were not weeded during the experiment and controls in the apple and pear blocks were mown every 2-4 weeks with an orchard mower. A second application of glyphosate 4 L/ha in 400 L water in the peach and nectarine control plots was made in mid-January.

Plate 5. Buckwheat (background) and control (foreground) treatments in the apple block of the 1997 large plot experiment.

Plate 6. Buckwheat (background) and control (foreground) treatments of the pear block of the 1997 large plot experiment.

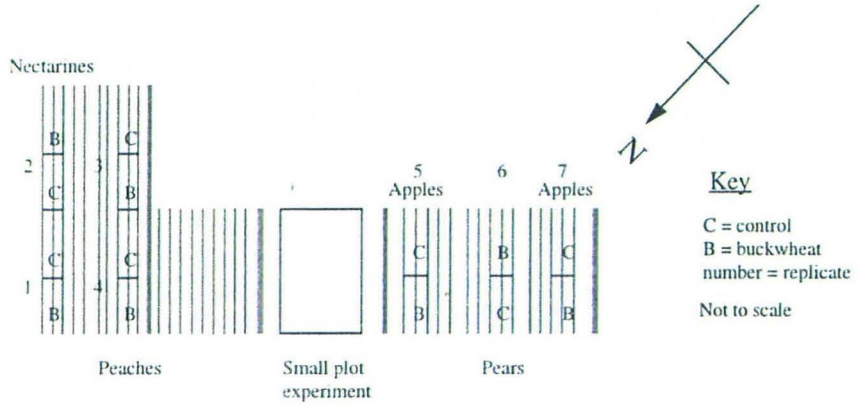


Fig. 2.2 Experimental layout of buckwheat and control treatments in apple, pear, nectarine and peach orchards for the 1997 large plot experiment.

On February 14,1997 the top third of half of the plants on each side of the buckwheat treatments was removed to encourage lateral flowering and to ensure a longer flowering period. From March 14-18, 1997, the buckwheat plants were cultivated to determine whether total removal of pollen, nectar and shelter sources would return parasitoid numbers to those similar in the controls (Plate 7). Consequently, by March 19, 1997, these treatments had been converted into controls.

Plate 7. After cultivation of the buckwheat treatment in the pear block of the 1997 large plot experiment.

Parasitoid sampling

Two sticky traps (see previous description) were placed 1 m high either side of the middle tree of each plot, facing the middle of the row. The traps were collected and replaced at the same intervals as for the previous experiment from January 31, 1997 to April 24, 1997. Traps in the peach blocks were replaced only once due to use of insecticide prior to harvest. The numbers of *D. tasmanica*, *A. zealandica*, *M. tasmaniae* and hover flies were counted under a binocular microscope (20x magnification) in the laboratory.

Leafroller egg release

On January 29 and February 13, 1997 batches of approximately 150 LBAM eggs (Appendix 1) were released on a randomly selected branch of the middle tree in each treatment of the nectarine, apple and pear plots following the protocol described in Section 2.1.2.1. Leafroller release was not conducted in the peach blocks because of the use of insecticides therefore, removing blocks three and four from the original plan (Fig. 2.2). A third release was not undertaken because the larvae were not settling on the nectarine replicates and labour was limiting. After six to eight weeks these branches were harvested and the number of parasitoid cocoons and leafroller larvae present were recorded. Parasitism rate was expressed as: [number of parasitoid cocoons recovered/(number of parasitoid cocoons recovered + number of leafroller larvae recovered)] x 100.

Data analysis

Trap catches were divided into 'pre-' and 'post-treatment' phases (pre - January 31 to March 11, 1997, post - March 19 to April 24, 1997) and data were log-transformed ($\log_e (x+1)$) prior to analysis to stabilise variances and are reported in the figures as geometric means. Trap catches were compared between treatments and times using repeated measures ANOVA. Parasitism rate data were not normally distributed and did not differ significantly between dates (U=34, df=1, $P>0.05$), therefore, data were combined over both release dates and compared between treatments using the non-parametric Mann-Whitney U test. Trap catches from the buckwheat treatment in the large plots experiment and the 'buckwheat with flowers' treatment in the small plots experiment were compared using repeated measures ANOVA to determine whether increasing experimental plot size increases insect catches. This comparison was also conducted between the large and small control plots to determine whether any differences between the buckwheat plot size were due to circumstantial differences between sites.

2.1.3 Results

2.1.3.1 Small plots

Phenology data from control plots

The abundance of *D. tasmanica* decreased from a peak of 0.45/trap/day in late January then remained relatively stable throughout February, March and April, 1997. *A. zealandica* abundance also decreased from a high of 3.13/trap/day in late January but increased again from late March to 2.21/trap/day on April 24, 1997. Lacewing numbers remained low throughout the 1997 summer. Hover fly abundance was low until April when the population increased to a peak of 1.42/trap/day on April 3rd, 1997 (Appendix 2, Fig. 1a).

Dolichogenidea tasmanica

Trap catch data

When data from January 31 to March 11, 1997 were combined, there was an overall significant effect of understorey management treatment on the abundance of leafroller parasitoids (F=7.75, df=3, 9, $P<0.01$). *D. tasmanica* numbers were six- fold higher in the 'buckwheat with flowers' treatment (1.27/trap/day) and almost three-fold higher in the

broad bean treatment (0.52) compared with the control (0.18) (P<0.001) (Fig. 2.3). The 'buckwheat with flowers' treatment enhanced the abundance of leafroller parasitoids significantly more than did the broad beans (P<0.001). There was no significant difference in leafroller parasitoid trap catches between the 'buckwheat without flowers' treatment (0.24/trap/day) and the control (0.18) (P >0.05). There was no significant difference in leafroller parasitoid trap catches between all treatments (Fig. 2.4) when data from March 19 to April 24, 1997 were combined (F=0.810, df=3,9, P>0.05).

When pre- and post-treatment changes were compared, parasitoid abundance was three-fold higher in the 'buckwheat with flowers' treatment before the plants were removed compared with subsequently (F=13.39, df=1,23, P<0.001) (Figs. 2.3 & 2.4). There was a significantly higher number of parasitoids captured after the initial 'buckwheat without flowers' had been converted to a 'buckwheat with flowers' treatment (F=4.853, df=1,23, P<0.05) (Figs. 2.3 & 2.4). *D. tasmanica* trap catches were three-fold greater in the broad beans treatment earlier in the season than later (P<0.05), whereas in the controls, there was no significant difference in the number of *D. tasmanica* captured earlier in the season compared with later (P>0.05) (Figs. 2.3 & 2.4).

Individual date effects over time

On four out of the five trap collection dates before the buckwheat plants were removed, *D. tasmanica* abundance was significantly higher in the 'buckwheat with flowers' treatment compared with the control (P<0.05). After the buckwheat plants were removed, there was no significant difference in trap catches between these plots and the controls (P>0.05). On one of the nine trap collection dates (January 31, 1997), the broad bean treatment significantly increased the number of *D. tasmanica* captured compared with the controls (P<0.05) (Fig. 2.5).

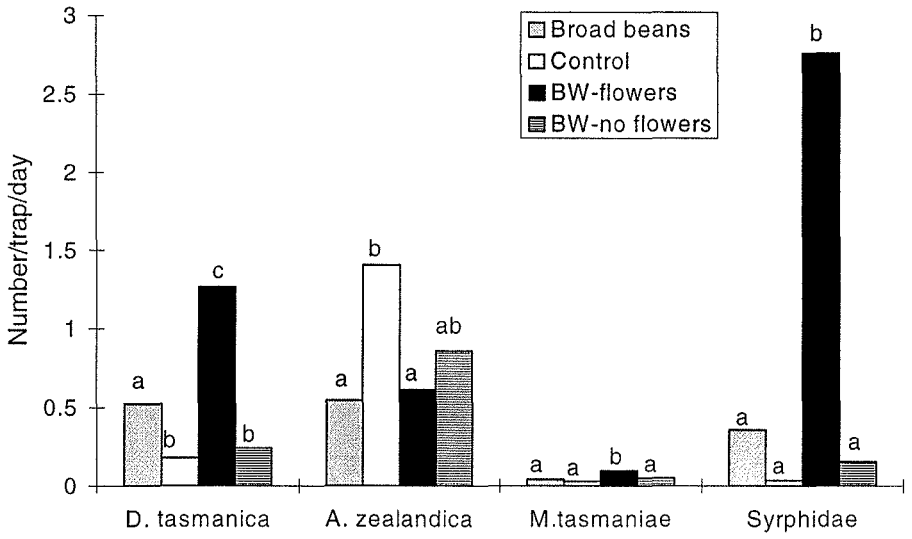


Fig. 2.3 The abundance of insect groups captured from January 31 to March 11, 1997, before treatment changes, in each of the understorey treatments (BW = buckwheat, different letters indicate significant differences between treatments for each insect group (P<0.05)).

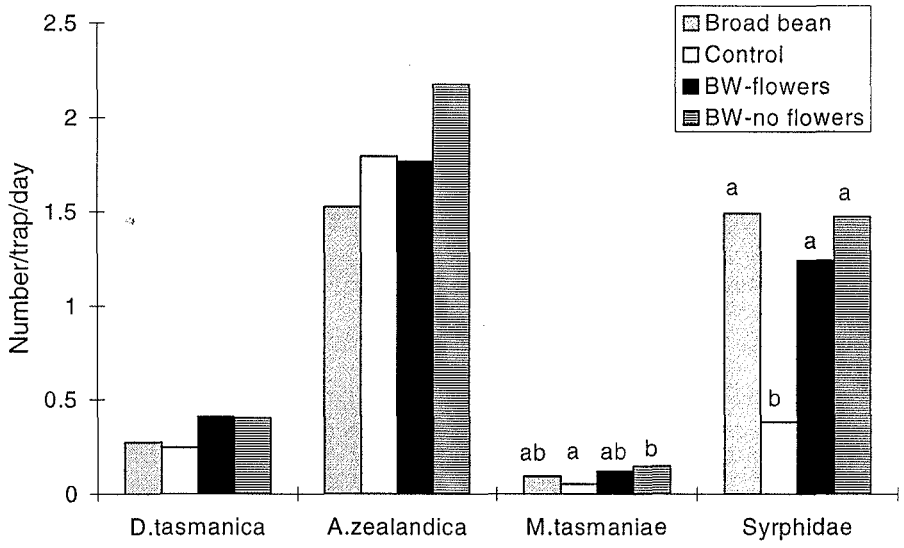


Fig. 2.4 The abundance of insect groups captured from March 19 to April 24, 1997, after plants in the initial 'buckwheat with flowers' treatments were removed and the initial 'buckwheat without flowers' treatments were left to flower, in each of the understorey treatments (see Fig. 2.3).

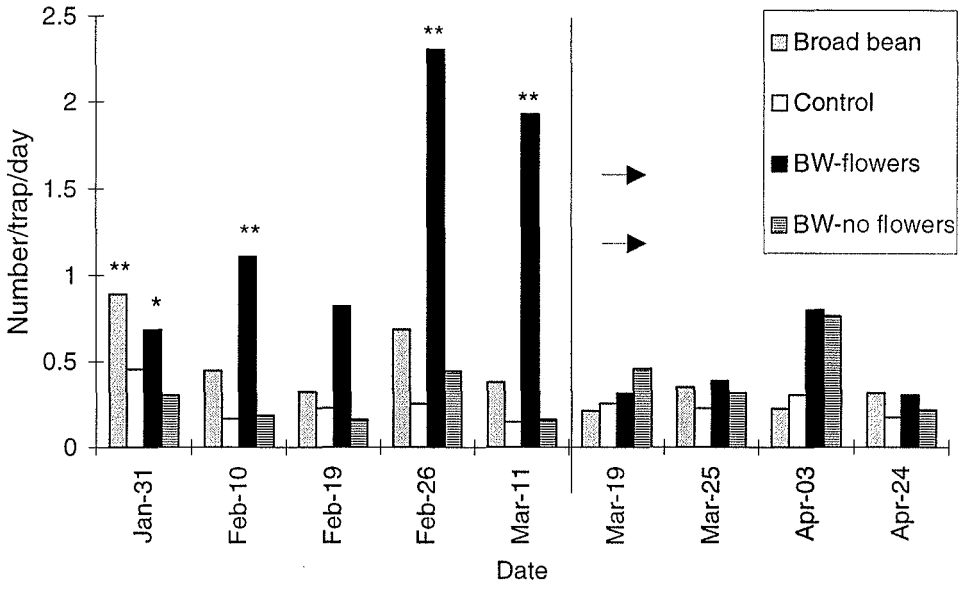


Fig 2.5 The abundance of *D. tasmanica* captured from January 31 to April 24, 1997 for each understorey treatment (arrows indicate period from which treatment manipulations occur, i.e. buckwheat with flowers treatments become controls and buckwheat without flowers treatments were left to flower, * = P<0.05, ** = P<0.01).

Leafroller parasitism rate

On one of the leafroller release dates (February 13, 1997) there was an overall significant effect of treatment on parasitism rate (F=8.32, df=3,6, P<0.05) (Fig. 2.6). There was a significantly higher parasitism rate in the 'buckwheat with flowers' treatment (86%), the broad beans treatment (75%) and the 'buckwheat without flowers' treatment (96%) compared with the control (0%) (P<0.05). These results were based on 34 cocoons and 15 larvae recovered from the February 13, 1997 release date. There was a higher parasitism rate in the 'buckwheat with flowers' treatment compared with the control on the January 29, 1997 and March 5, 1997 release dates; however, these did not reach statistical significance (January 29, 1997, F=2.22, df=3,9, P>0.05; March 5, 1997, F=0.054, df=3,10, P>0.05). Combining all release dates, there were no significant differences in parasitism rate between treatments (F=1.46, df=3,30, P>0.05).

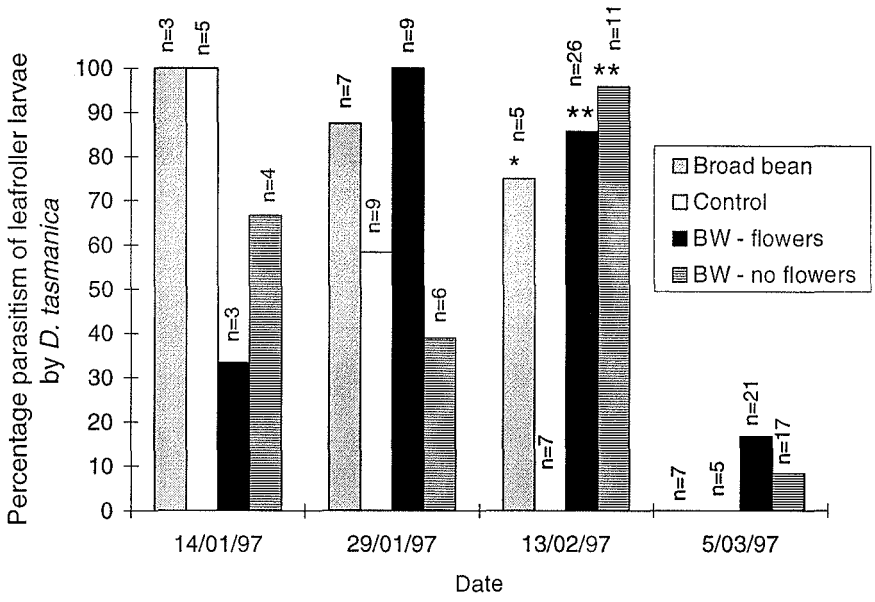


Fig. 2.6 Percentage parasitism of released leafroller by *D. tasmanica* for each understorey treatment on each release date (n = number of parasitoid cocoons + number of leafroller larvae recovered, * = P<0.05, ** = P<0.01).

Anacharis zealandica

Trap catches

When data from January 31 to March 11, 1997, were combined, there was a significantly higher number of *A. zealandica* captured in the controls compared with all other treatments (F=3.22, df=3,9, *P*<0.05) (Fig. 2.3). There were no significant differences in *A. zealandica* abundance between treatments when data from March 19 to April 24, 1997 were combined (F=0.065, df=3,9, *P*>0.05) (Fig. 2.4).

However, when pre- and post-treatment changes were compared, there were more than two-fold more *A. zealandica* captured in the initial 'buckwheat with flowers' treatments after they were converted into controls (F=5.27, df=1,23, *P*<0.05) (Figs. 2.3 & 2.4). In contrast, there were significantly more *A. zealandica* captured in the initial 'buckwheat without flowers' treatments after they were left to flower compared with previously (F=28.51, df=1,23, *P*<0.001) (Figs. 2.3 & 2.4). Also, there was a significantly greater number of *A. zealandica* captured later in the season than earlier in the broad bean

treatments ($P<0.01$). However, in the controls, there was a significantly higher number of *A. zealandica* captured later in the season than earlier ($P<0.05$) (Figs. 2.3 & 2.4).

Individual date effects over time

On one out of the five trap collection dates before the buckwheat was removed, *A. zealandica* abundance was significantly lower in the 'buckwheat with flowers' and 'buckwheat without flowers' treatments compared with the controls ($P<0.05$) (Fig. 2.7). On one out of the nine trap collection dates there was more than twice the number of *A. zealandica* captured in the broad bean treatments (6.17/trap/day) compared with the controls (2.17) ($P<0.01$).

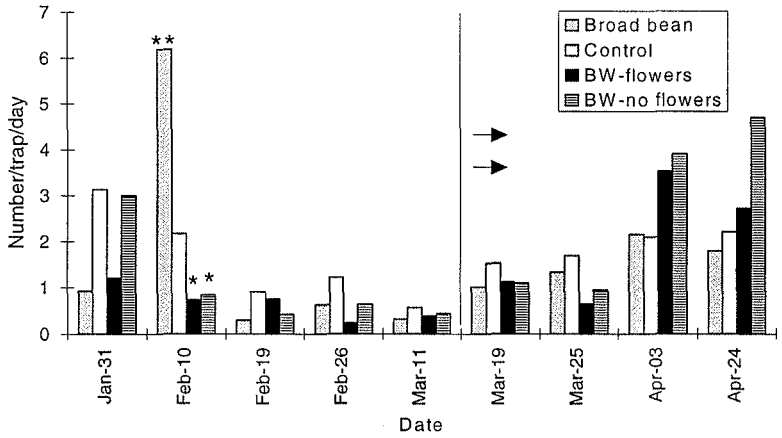


Fig. 2.7 The abundance of *Anacharis zealandica* captured from January 31 to April 24, 1997 for each understorey treatment (see Fig. 2.5).

Micromus tasmaniae

When data from January 31 to March 11, 1997, were combined, significantly more lacewings were captured in the 'buckwheat with flowers' treatments compared with controls ($P<0.05$) (Fig. 2.3). When data from March 19 to April 24, 1997 were combined, numbers of lacewings were three-fold in previously non-flowering buckwheat plots which, by that time, had been allowed to flower, than in controls ($P<0.05$) (Fig. 2.4).

When data from pre- and post-treatment changes were compared, there were three-fold more lacewings captured in the original 'buckwheat without flowers' treatment after they were left to flower (F=8.86, df=1,20, P<0.01) (Figs. 2.3 & 2.4). There were no significant differences in lacewing trap catches between treatments for individual trap collection dates (P>0.05) (Fig. 2.8).

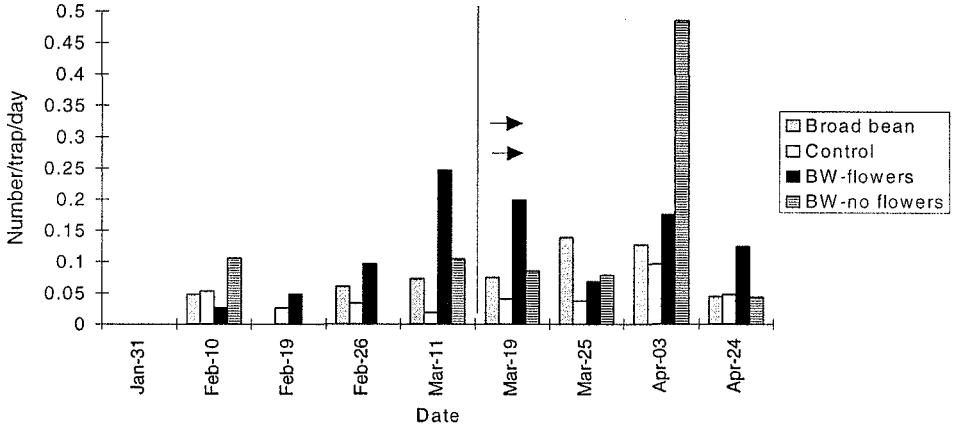


Fig. 2.8 The abundance of *Micromus tasmaniae* captured from January 31 to April 24, 1997 for each understorey treatment (see Fig. 2.5).

Syrphidae

Trap catches

When data from January 31 to March 11, 1997, were combined, seven-fold more hover flies were captured in the 'buckwheat with flowers' treatment compared with all other treatments (P<0.001) (Fig. 2.3). When data from March 19 to April 24, 1997 were combined, there were significantly fewer hover flies captured in control plots compared with all treatments (P<0.05) (Fig. 2.4).

When pre- and post-treatment changes were compared, numbers of hover flies were ten-fold in the 'buckwheat without flowers' plots after they were left to flower compared with previously (F=23.2, df=1,20, P<0.001) (Figs. 2.3 & 2.4). Similarly, there were more than twice as many hover flies captured in the 'buckwheat with flowers' treatment before the plants were removed compared with subsequently (Figs. 2.3 & 2.4). However, this

difference was not statistically significant ($P>0.05$). Hover fly trap catches were significantly higher later in the season than earlier in the broad bean treatments ($P<0.01$). However, in the controls, hover fly abundance was also significantly higher later in the season than earlier ($P<0.05$) (Figs. 2.3 & 2.4).

Individual date effects over time

On two out of the five trap collection dates before the buckwheat plants were removed, the 'buckwheat with flowers' treatment had a significantly higher hover fly abundance compared with controls ($P<0.05$) (Fig. 2.9). After the buckwheat plants were removed, there was no significant difference between these plots and controls ($P>0.05$).

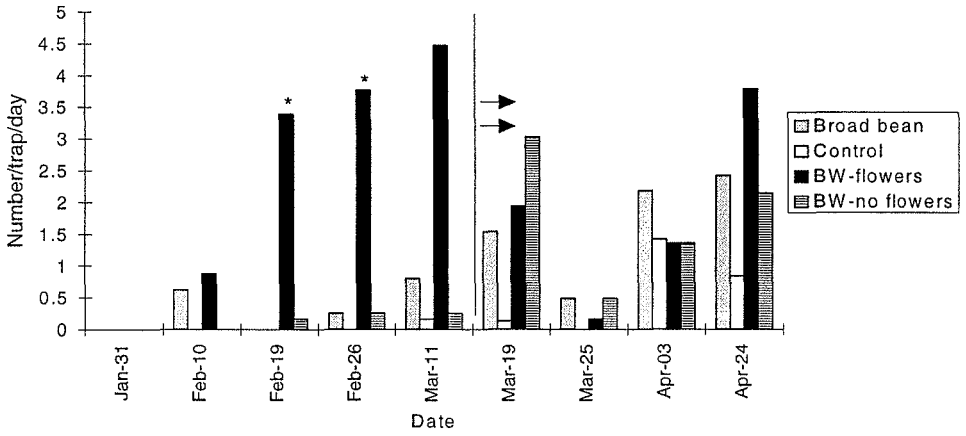


Fig. 2.9 The abundance of Syrphidae captured from January 31 to April 24, 1997 for each understorey treatment (see Fig. 2.5).

2.1.3.2 Large plots

Phenology data from control plots

D. tasmanica and hover fly abundance remained low and stable throughout the summer. *A. zealandica* trap catches decreased from late January then increased in March to a peak of 9.56/trap/day. Lacewing abundance remained stable at a density of approximately 1/trap/day until late March from which it decreased (Appendix 2, Fig. 1b).

Dolichogenidea tasmanica

Trap catch data

When data from January 31 to March 11, 1997, were combined, leafroller parasitoid numbers were more than twice as high in the buckwheat treatments than in the controls ($P<0.001$) (Fig. 2.10). After the buckwheat plants were removed, there was no significant difference between these plots and controls ($P>0.05$) (Fig. 2.11). In fact, when pre- and post-treatment changes were compared, there was more than two-fold more *D. tasmanica* were captured in the buckwheat treatments before the plants were removed compared with subsequently ($P<0.001$) (Figs. 2.10 & 2.11). By contrast, there was no significant difference in trap catches when comparing pre- and post-treatment changes in controls ($P>0.05$) (Figs. 2.10 & 2.11).

Individual date effects over time

On one out of the five trap collection dates before the buckwheat plants were removed, the buckwheat treatments had a significantly higher *D. tasmanica* abundance compared with controls ($P<0.05$) (Fig. 2.12). After the buckwheat plants were removed, there was no significant difference between these plots and controls ($P>0.05$).

Leafroller parasitism rate

Parasitism rate was almost two-fold greater in the buckwheat treatments compared with controls (Fig. 2.13). However, this difference was not statistically significant ($U=30.5$, $df=1$, $P=0.580$).

Anacharis zealandica

When data from January 31 to March 11, 1997 were combined, no significant difference in *A. zealandica* numbers between buckwheat and control plots occurred ($P>0.05$) (Fig. 2.10). When pre- and post-treatment changes were compared, there were more than two-fold more *A. zealandica* captured in the buckwheat treatments after the plants were removed compared with previously ($P<0.001$) (Figs. 2.10 & 2.11). However, there was also a significantly higher number of *A. zealandica* captured later in the season in the controls ($P<0.001$) (Figs. 2.10 & 2.11). There was no significant difference between treatments at

any individual trapping date (P>0.05) (Fig. 2.14). However, this figure shows the trend of an increase in *A. zealandica* over time.

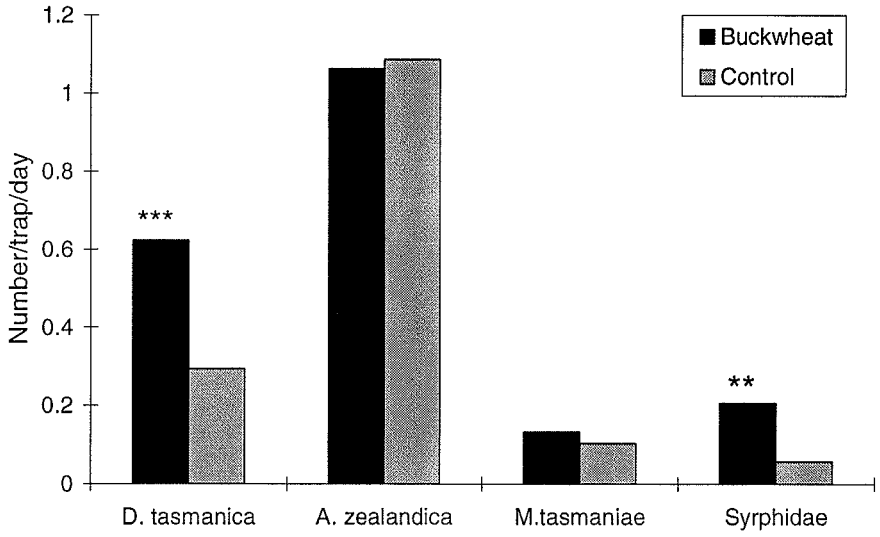


Fig. 2.10 The abundance of insect groups captured from January 31 to March 11, 1997, before treatment changes, in buckwheat and control plots (* = P<0.05, ** = P<0.01, *** = P<0.001).

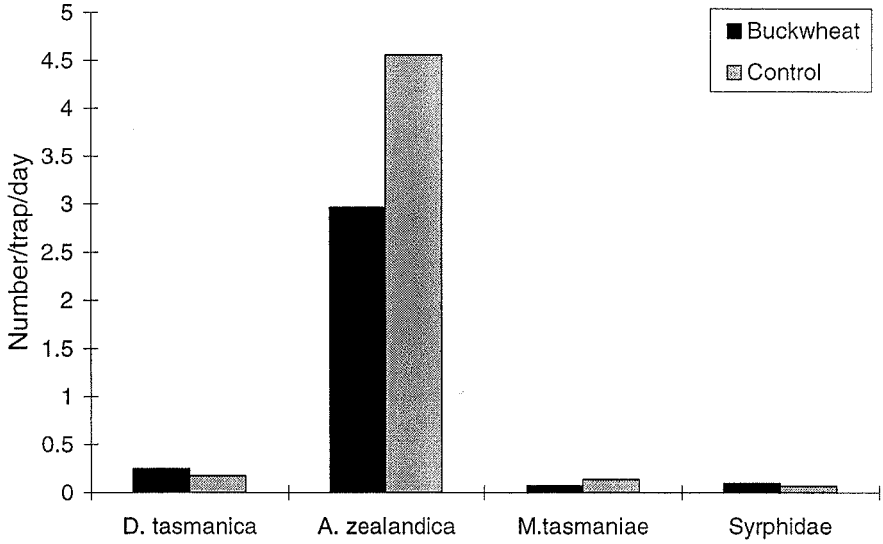


Fig. 2.11 The abundance of insect groups captured from March 19 to April 24, 1997, after the buckwheat plants were removed, in buckwheat and control plots (see Fig. 2.10).

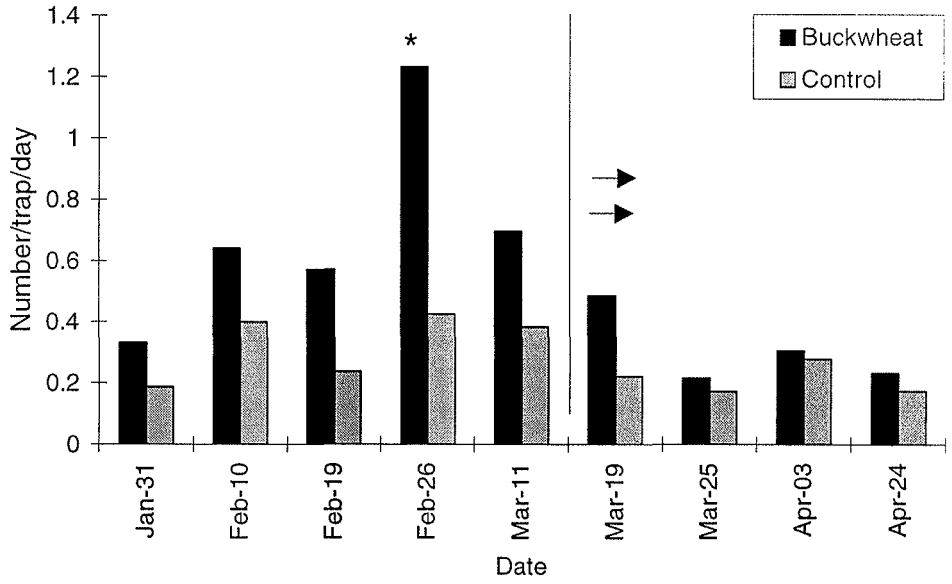


Fig. 2.12 The abundance of *D. tasmanica* captured from January 31 to April 24, 1997 for buckwheat and control plots (see Fig. 2.5).

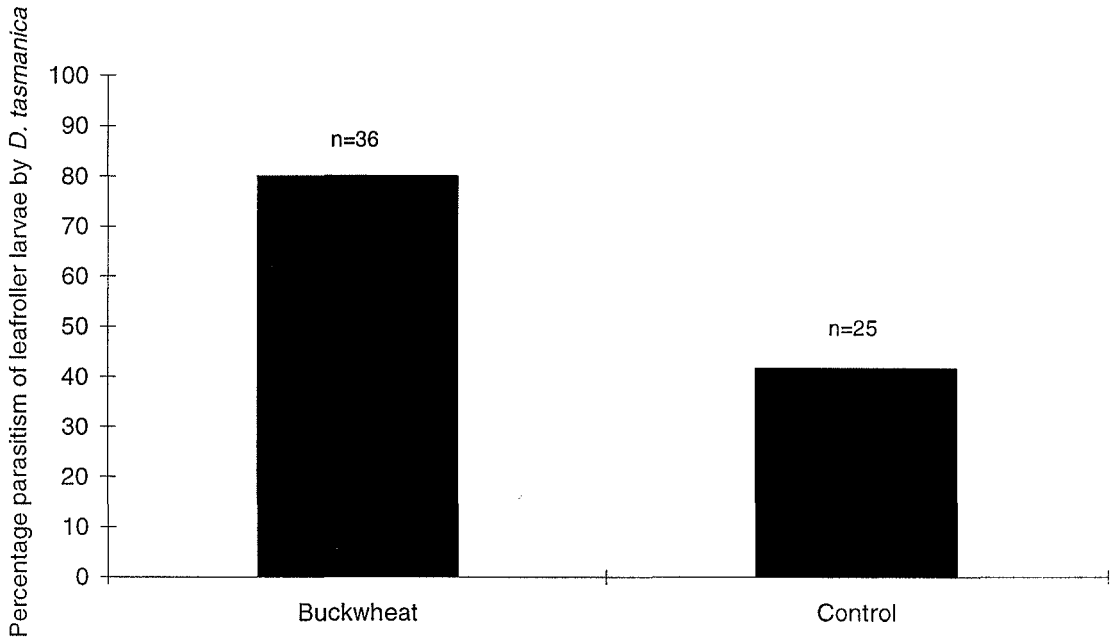


Fig. 2.13 Percentage parasitism by *D. tasmanica* of released leafroller for buckwheat and control plots over both release dates (n = number of parasitoid cocoons + number of leafroller larvae recovered, see Fig. 2.10).

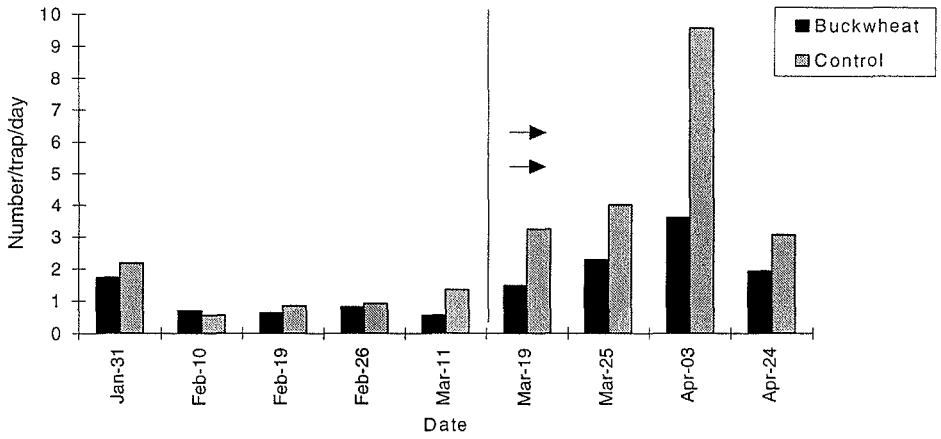


Fig. 2.14 The abundance of *Anacharis zealandica* captured from January 31 to April 24, 1997 for buckwheat and control plots (see Fig. 2.5).

Micromus tasmaniae

There was no significant difference in the number of lacewings present between buckwheat and control plots when data from different sampling dates were combined or between any treatment combinations ($P>0.05$) (Figs. 2.10 & 2.11). There was no significant difference between treatments at any individual trapping date ($P>0.05$) (Fig. 2.15).

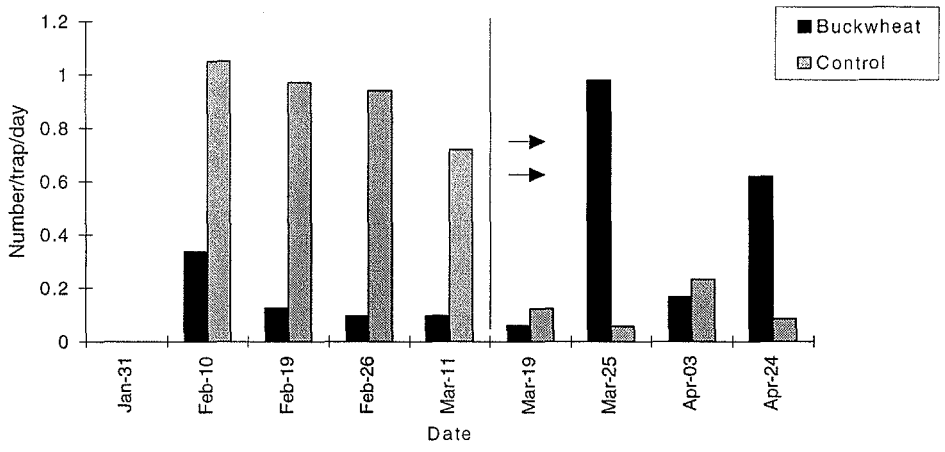


Fig. 2.15 The abundance of *Micromus tasmaniae* captured from January 31 to April 24, 1997 for buckwheat and control plots (see Fig. 2.5).

Syrphidae

When data from January 31 to March 11, 1997, were combined, hover fly abundance was over three-fold greater in buckwheat treatments compared with controls ($P<0.01$) (Fig. 2.10). After the buckwheat plants were removed, no significant difference between these treatments and controls was detected ($P>0.05$) (Fig. 2.11).

When pre- and post-treatment changes were compared, significantly more hover flies were captured in buckwheat treatments, before the plants were removed, compared with subsequently ($P<0.01$) (Figs. 2.10 & 2.11), whereas there was no significant difference between pre- and post-treatment changes in controls (P>0.05) (Figs. 2.10 & 2.11).

On one out of the five trap collection dates before the buckwheat plants were removed, the buckwheat treatments had a significantly higher hover fly abundance compared with controls ($P<0.05$) (Fig. 2.16). After the buckwheat plants were removed, there was no significant difference between these plots and controls ($P>0.05$).

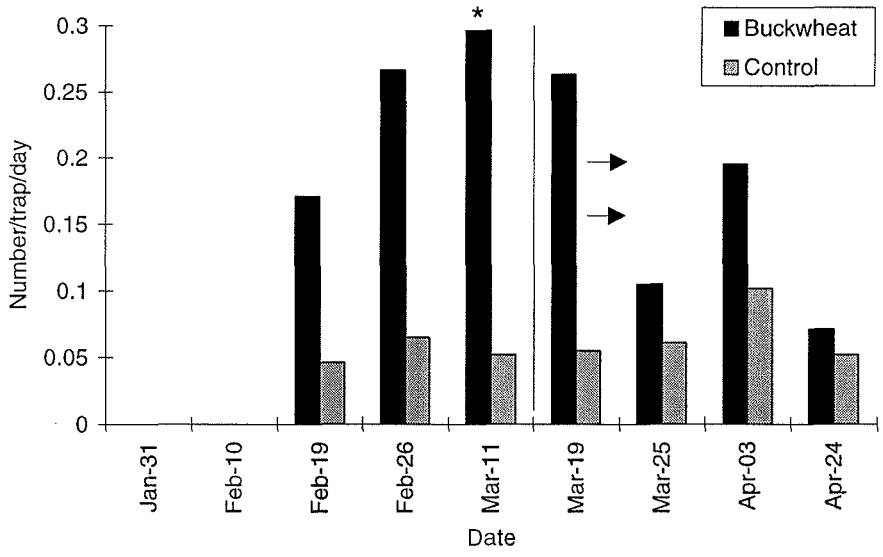


Fig. 2.16 The abundance of Syrphidae captured from January 31 to April 24, 1997 for buckwheat and control plots (see Fig. 2.5).

2.1.3.3 Effect of plot size

Hover fly abundance was 20-fold greater in the small buckwheat plots compared with the large buckwheat plots (F=10.31, df=1,9, $P<0.05$) (Fig. 2.17). Results also showed a strong trend that *D. tasmanica* abundance was two-fold higher in small buckwheat plots compared with large buckwheat plots (Fig. 2.17), although this was not statistically significant (F=4.799, df=1,9, $P=0.056$). There was no significant difference in hover fly and *D. tasmanica* trap catches between the large and small control plots (hover fly: F=0.008, df=1,9, $P>0.05$; *D. tasmanica*: F=2.004, df=1,9, P>0.05) (Fig. 2.18).

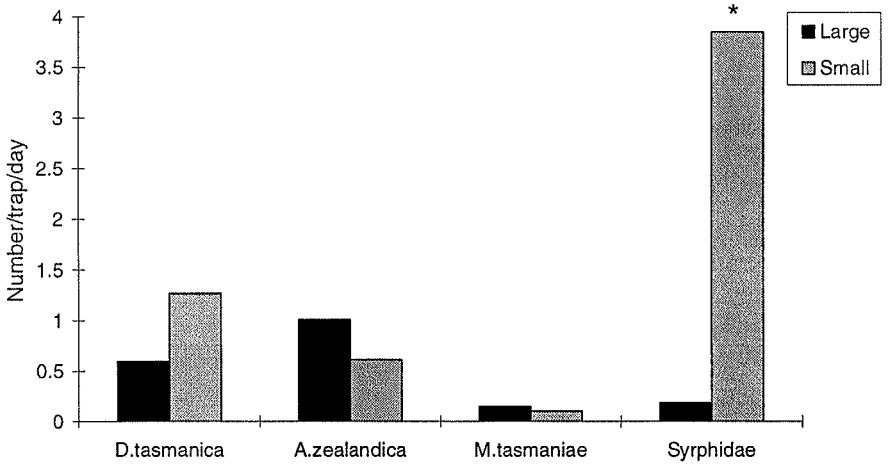


Fig. 2.17 The abundance of insect groups for small and large buckwheat plots (see Fig. 2.10).

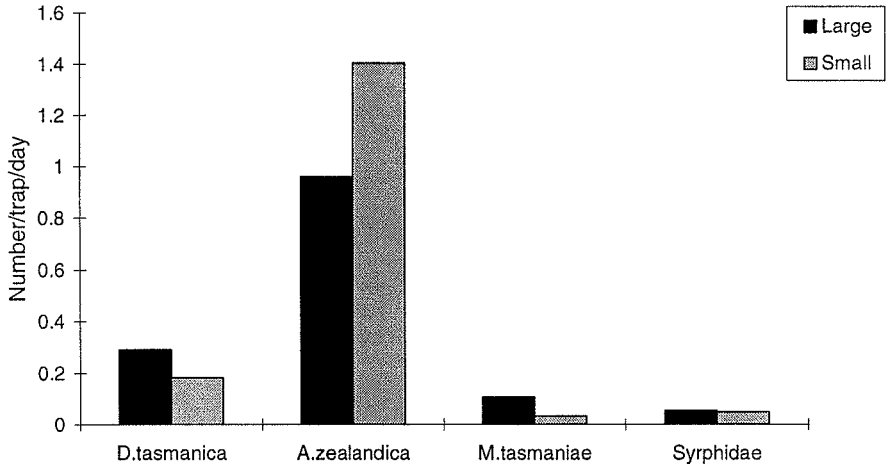


Fig. 2.18 The abundance of insect groups for small and large control plots (see Fig. 2.10).

2.1.4 Discussion

Phenology data from control plots

Leafrollers have three generations per year in Canterbury (Penman, 1984); however, the last generation is the main concern for apple growers because at this time fruit harvest occurs, so the leafrollers can cause major quality and quarantine problems. Therefore, it would be essential for *D. tasmanica* to synchronise well with the phenology of leafrollers if effective control were to be achieved. *D. tasmanica* trap catches remained stable throughout the season suggesting the good potential of *D. tasmanica* as a biocontrol agent throughout the summer.

Hover fly abundance increased in the small control plots after March 19, 1997. On this date the buckwheat was removed by cultivation which may have dispersed flies into the other plots, including controls. Small and large control plots showed that *A. zealandica* populations peaked in April, and in the large plots, this increase was correlated with a decrease in lacewing abundance. *A. zealandica* therefore may have contributed to a decline in its host's population in April.

Dolichogenidea tasmanica

Trap catches

More than seven times as many leafroller parasitoids were trapped in the buckwheat plots compared with controls and similar results from the large plot trial and from manipulating the 'buckwheat with flowers' and 'buckwheat without flowers' treatments were also found. These results support the work of Stephens *et al.* (1998) and suggest that buckwheat shows potential as an understorey plant to enhance *D. tasmanica* abundance for leafroller biocontrol in Canterbury, New Zealand, apple orchards.

The 'buckwheat with flowers' treatment significantly enhanced parasitoid numbers compared with the controls, whereas there was no significant difference between control plots and 'buckwheat without flowers'. This suggests that it is the buckwheat floral resources that lead to enhanced parasitoid numbers, and not the shelter (Taylor, 1920), alternative hosts (Kelly, 1987; Liang and Huang, 1994), microclimate (Thomas *et al.*,

1992), or aphid honeydew (Idris and Grafius, 1995; Landis and Marino, 1997), which the buckwheat may also provide to some natural enemies.

Broad beans also enhanced parasitoid abundance, although to a lesser extent than buckwheat. This may be because buckwheat flowers (with their shallow corollae) provide both pollen and nectar to the parasitoid (Lővei *et al.*, 1993b), whereas broad bean plants provide only nectar, via extra-floral nectaries, because their flowers are too large for short-tongued parasitoids to gain access to floral nectar or pollen (Bugg *et al.*, 1989). It also may be attributed to the differences in quality between extrafloral nectar and nectar from the flower as the concentration or composition may differ between the types of nectar. For example, Vansell (1939) found the sugar concentration of extrafloral nectar of two kinds of vetch (*Vicia* spp.) to be twice as high as that of the flowers on the same plants. The greater concentration of the extrafloral nectar could have been due to its full exposure to the evaporative influences of the sun and wind. This may increase viscosity of the nectar, therefore causing it to be too viscous for parasitoids to imbibe. Furthermore, diurnal and seasonal nectar flows may differ between broad bean extrafloral nectaries and buckwheat floral nectaries.

D. tasmanica abundance was higher in the broad bean treatment earlier in the season compared with later. This difference was not due phenology because there was no significant difference in *D. tasmanica* trap catches between early and late season in the controls. In most cotton species, extrafloral nectar secretion is limited to the period of new growth and the secretion ceases as the leaves mature (Stapel *et al.*, 1997). This could explain the results from the current study which showed a decrease in *D. tasmanica* abundance in the broad bean treatments over time, as the plants matured.

Leafroller parasitism rate

Broad beans significantly enhanced parasitism by up to 75 % compared with the control This supports research conducted by Altieri and Schmidt (1985; 1986) who found that over a two year period, codling moth infested 36.1% of apples in a Californian orchard with a cover crop of *V. faba*, whereas a nearby cultivated orchard suffered a 45.0% fruit loss from

this pest. *V. faba* has been reported to attract *Coccygomimus aequalis* L., a parasitoid of codling moth (Bugg *et al.*, 1989).

Buckwheat significantly enhanced leafroller parasitism from 0% to 86% compared with the control, indicating that the control potential of these parasitoids may be high. However, this significant effect occurred on only one date in that experiment; also, when dates were combined, there was no significant effect overall. In the large plot experiment (see Fig. 2.13) there was also a strong suggestion (although not significant in this case either) that the presence of buckwheat enhanced parasitism rate. In fact, Zandstra and Motooka (1978) showed that only 3.5% of apples were infested with codling moth larvae where buckwheat was present, compared with 1.5% with full chemical control and a 54% with no treatment. Twenty years ago orchards in Russia were commonly undersown with buckwheat because its flowers are a food source for adult *Trichogramma* spp., which attack codling moth eggs (Zandstra and Motooka 1978). For *D. tasmanica*, Dumbleton (1935) found that parasitism in Nelson, New Zealand, ranged from 20 to 50%, and Thomas (1965) found rates ranging between 4 and 28% in unsprayed Canterbury orchards. The differences between the current study and the cited studies may be accounted for by the differences in the methods of leafroller release and the techniques for calculating parasitism rate. For instance, the current study released larvae in the field to calculate parasitism rate, whereas the cited studies sampled natural leafroller populations for *D. tasmanica* parasitism.

In the current study parasitism rate data were variable and most leafroller parasitism rates did not statistically differ between treatments. On the release date where treatments did differ, all treatments were significantly different from the control. For example, the 'buckwheat without flowers' treatment appeared to give parasitism rates as high as those for the 'with flowers' plots. This is probably an artefact associated with the methodology. The high dispersal rates of the leafroller larvae (Penman, 1984) will tend to make recovery of parasitoid cocoons from the release sites variable, making it difficult to detect differences between treatments. Of those cocoons and larvae that were recovered, a high proportion had been parasitised, giving high apparent parasitism rates. MacLellan (1973) reported that mature LBAM larvae frequently leave their feeding sites and prepare a special site for pupation. High parasitism rates in the current study may have been because those

larvae that were not parasitised were more likely to disperse or drop to the ground to pupate, whereas those that have been parasitised may be less mobile. Research is required into the mechanisms behind poor parasitism rate data and into a more reliable and accurate method of measuring parasitism rate. This is explored further in Sections 3.1, 3.2 and 4.1, and Chapter 6.

Releasing larvae at such un-naturally high densities may not make it possible to determine a realistic parasitism rate for *D. tasmanica*. Parasitism rates of up to 86% in buckwheat plots were found in this study compared with 20-30% parasitism recorded for naturally occurring populations (Collyer and van Geldermalsen, 1975; Green, 1984; Suckling *et al.*, 1996a). Information on the extent of density-dependent searching by *D. tasmanica* is unknown. A fixed number of eggs were released per branch on each occasion, therefore minimising such effects. However, a high proportion of the leafroller larvae that were parasitised had 100% parasitism, suggesting that once *D. tasmanica* finds a patch of larvae it may parasitise all larvae present. Therefore, it may be useful to determine the relationship between *D. tasmanica* parasitism rate and leafroller density to determine whether release densities are realistic. This is explored further in Section 2.3. It may also be useful to determine parasitism of natural populations of leafroller instead of releasing high densities of larvae on to one branch for calculating parasitism rate. High parasitism may not necessarily translate into adequate pest management, so sampling natural populations for leafroller larvae and leafroller damage with parasitism rate would be very useful. This is explored further in Section 4.3.

The large plot experiment showed that parasitism rate was higher in the buckwheat treatments compared with the controls; however, this was not statistically significant. Although large experimental plots and increased replicates were used to extend the research of Stephens *et al.* (1998) and reduce parasitoids lost to the 'edge effect', data were more variable because replicates were over a variety of orchard species, in turn making it difficult to detect small differences in parasitism rate between treatments. There was a large variation in replicates ranging from 0-100% in each treatment.

Anacharis zealandica

A. zealandica trap catches were significantly higher in the controls compared with all other treatments and significantly more *A. zealandica* were captured in the initial 'buckwheat with flowers' treatment, after it was converted into a control, than previously. These results contrast with those of Stephens *et al.* (1998) who found that in the 1994-95 season there were up to ten times more *A. zealandica* in the buckwheat plots compared with the controls. However, in this study there was no significant difference in *A. zealandica* numbers between treatments in the 1995-96 season. The current study showed that there was a greater number of *A. zealandica* captured after the 'buckwheat without flowers' treatments were left to flower which supports the Stephens *et al.* (1998) data. However, there were also higher trap catches later in the season compared with earlier in the controls, and *A. zealandica* numbers were higher in broad bean treatments later in the season compared with earlier. Therefore, these results may have been due to the circumstantial increase in *A. zealandica* throughout the season as shown in the controls.

The contrasting results of *A. zealandica* abundance between treatments and studies may indicate that *A. zealandica* abundance is determined by a number of factors, such as presence of hosts, presence of the hosts' prey, mate seeking, microclimate and abundance of pollen and nectar resources. Also, sticky traps may be more apparent in control sites due to the lower amount of vegetation and a reduction in competition with flowers (MacLeod, 1999). In fact, J. Hickman (unpublished data) showed that a larger number of hover flies were captured in more conspicuous traps than in those which were more concealed. They suggested that because hover flies perceived yellow traps as floral food, other available food sources in the vicinity compete with the traps, which in turn underestimate the numbers of flies present.

Micromus tasmaniae

The results suggested that buckwheat enhanced the abundance of lacewings, which may have been attracted to the nectar supplied by the buckwheat as they require this resource for survival. For example, McEwen and Kidd (1995) investigated the influence of different components of artificial food on lacewing longevity and fecundity and found that the insects provided with sugar lived significantly longer than those without.

Lacewing populations may have been higher in the initial 'buckwheat with flowers' treatments compared with the controls because *A. zealandica* abundance was lower in these plots compared with the controls. *M. tasmaniae* is a general insect and mite predator (Leathwick, 1989), so the buckwheat may also have harboured prey for them, which would attract them into these plots. For example, Stephens *et al.* (1998) suction-sampled buckwheat and control plots for the presence of insects. They found that the dominant groups of species caught were weevils, mites, aphids and flies. Both *A. zealandica* and predatory lacewings were caught in very low numbers. It may have been useful to sample the buckwheat during the course of the current study for the presence of lacewing prey, to further speculate on *A. zealandica*/lacewing/prey interactions. This is explored in Section 4.2.

M. tasmaniae is one of the most abundant invertebrate predators in Australasia and has high potential for use in integrated pest management (Leathwick, 1989; Schroeder and Clifford, 1996; Rumpf *et al.*, 1998). The current research indicates that sowing buckwheat in the orchard understorey may increase the abundance of this species, therefore further enhancing its biocontrol potential of orchard pests.

Syrphidae

The hover fly results support many United Kingdom and New Zealand studies which have shown that buckwheat attracts large numbers of aphidophagous hover flies when compared with other candidate plant species (Lővei *et al.*, 1992; MacLeod, 1992a; Hodgson and Lővei, 1993). The larvae of these predators in New Zealand feed not only on aphids but also on early-instar lepidopterans, e.g., white butterfly, *P. rapae*, and diamondback moth, *P. xylostella* (Valentine, 1967; Miller, 1971; Ashby and Pottinger, 1974). There is evidence that hover flies disperse into crops after feeding on pollen and nectar offered in field margin strips (Powell, 1986) and several studies have demonstrated an association between the presence of syrphid larvae and the cessation of aphid population growth (Dean, 1974; Chambers *et al.*, 1983; Holmes, 1984; Entwistle and Dixon, 1990). Therefore, incorporating buckwheat strips into orchards may enhance hover fly populations for woolly apple aphid (*Eriosoma lanigerum* (Hausmann)) and leafroller biocontrol. Woolly apple

aphid is one of the most economically important and most widely distributed pests of apple (Hill, 1983; Eastop, 1966) and has overcome plant host resistance in several parts of the world (Giliomee *et al.*, 1968; Rock and Zeiger, 1974; Sen Gupta and Miles, 1975). Outbreaks of woolly apple aphid have been created around the world as a result of pesticide applications that have reduced populations of biological control agents (Penman and Chapman, 1980; Jenser, 1983). For example, two chemicals used in conventional spray programmes, chlorpyrifos and carbaryl, are highly toxic to *Aphelinus mali* (Haldeman) (Bradley *et al.*, 1997), the most important parasitoid of this species (DeBach, 1964). It is not known whether these New Zealand hover fly species prey on woolly apple aphid; however, Asante (1997) suggested that predators such as Syrphidae and Chrysopidae may contribute effectively to the management of *E. lanigerum* if they could be conserved and augmented in apple orchards.

Although there were twice as many hover flies captured in the 'buckwheat with flowers' treatment before the plants were removed compared with later, this was not significant. However, in the controls, hover fly abundance was significantly higher later in the season than earlier, therefore this may have underestimated the difference between treatment manipulations. Also, hover fly trap catches were higher in the broad bean treatments later in the season compared with earlier. This may have also been caused by the same factors as the increase in hover fly abundance later in the season as shown in the controls. However, it may also be due to an increase of prey populations in these plots as the broad bean plants matured.

Understorey management potential and future work

Buckwheat, and to a lesser extent broad beans, show potential as understorey plants for the enhancement of natural enemies such as *D. tasmanica*, lacewings and hover flies for leafroller and aphid biocontrol. Buckwheat shows good agronomic performance for incorporation into integrated pest management programmes. It germinates easily, has a short sowing to flowering time and in Canterbury, New Zealand, it flowers from November for up to three months (Bowie *et al.*, 1995). Its seed is also cheap and readily available (Wratten *et al.*, 1995). It has a shallow flower structure providing both nectar and pollen to natural enemies. In contrast, broad bean plants provide only nectar to natural enemies via

extra floral nectaries. Pollen is required by many natural enemies for sexual maturation (Schneider, 1948; Jervis and Kidd, 1986), therefore while broad beans may enhance natural enemy abundance by increasing longevity and attracting them from surrounding areas, it may not be as beneficial as buckwheat for maximising fecundity. Also, results suggest that secretion of nectar from extra floral nectaries ceases as the plant matures (Stapel *et al.*, 1997), therefore broad beans may not provide a large enough window for natural enemy enhancement. Additional experiments are required to determine whether buckwheat is the best candidate for understorey management for natural enemy enhancement. This is explored further in Chapters 3 and 4.

The mechanisms by which buckwheat may enhance leafroller parasitoid abundance and increase parasitism rates of leafrollers are unknown. Results from this study indicate that it is the flowers that influence *D. tasmanica* abundance and parasitism rate. However, the question remains whether providing buckwheat in the orchard understorey influences other factors, such as increasing the 'fitness' of the parasitoids. Field and laboratory trials are required to investigate the influence of floral resources on the sex ratio of emerging parasitoids, fecundity and longevity. These aspects are explored further in Sections 4.1 and 5.1.

Results show that planting flowers in the orchard understorey enhances Syrphidae populations seven-fold but increases *D. tasmanica* abundance only two-fold (Fig. 2.3). This may suggest that hover flies rely more on flower resources than *D. tasmanica* or that buckwheat is not the most suitable resource for optimising *D. tasmanica* fecundity and longevity. It also may be an artefact of the trapping method used in these studies because the spectral reflectance may not be optimal for capturing *D. tasmanica* or the sticky polybutene-based insect trap adhesive used on these traps may repel them. This is investigated in Section 2.2.

Effect of plot size

Stephens *et al.* (1998) used relatively small experimental plots which may not have been large enough to prevent parasitoids moving between all plots and treatments and therefore influencing results. Studies have also shown that small experimental plots can

underestimate insect densities compared with large experimental plots because more insects are lost to the 'edge effect'(Duffield and Aebischer, 1994; Brown and Lightner, 1997). Also, small plot sizes have been reported to have contributed to experimental failures (Vickers *et al.*, 1998). However, the current research shows that *D. tasmanica* trap catches did not differ significantly between small (8 x 2 m) and large (25 x 9 m) buckwheat plots. In fact, hover fly trap catches were 20-fold higher in the small buckwheat plots compared with the large. Trap catches of *D. tasmanica* also showed this trend but it was not statistically significant. These results were not due to differences in insect abundance between sites because there was no significant difference in hover fly and *D. tasmanica* abundance between small and large control plots. This contradicts studies that show that hover flies are highly mobile. For example, Cowgill (1991) marked 2910 *Episyrphis balteatus* DeGeer over a 23-day period and less than one percent of the total marked were recaptured. However, the experimental design in the current study was not set up specifically to test the influence of plot size on insect abundance, therefore sites differed in terms of vegetation, with large plots consisting of apples, pears, nectarine and peaches and small plots consisting of apples only. Future research is required to determine how far *D. tasmanica* flies from a nectar source to help determine optimum experimental plot sizes and buffer zones between treatments. This would also be useful for the practical use of buckwheat in understorey management by determining the number, size and spacing of the plots of conservation biocontrol plantings (Landis *et al.*, in press). These aspects are investigated in Section 3.3.

2.2 THE INFLUENCE OF TRAP HEIGHT AND TYPE ON NATURAL ENEMY ABUNDANCE

2.2.1 Introduction

The use of a single trap design may bias results towards insects in a particular physiological condition, i.e., individuals with certain nutritional or reproductive requirements (J. Hickman, unpublished data), towards a particular species or cohort within a species (Haslett, 1989), or towards a particular age of insect (Southwood, 1966). Therefore, insect traps may be ecologically selective by attracting a particular 'type' of insect (Kirk, 1984). Manipulation of trap variables such as colour and height may alter the ecological selectivity of the trap and result in the capture of a different section of the insect population. For example, Mackie (1996) conducted a study on hover flies investigating the influence of water trap height and colour on the abundance, species and cohort of hover flies in New Zealand. He concluded that high yellow water traps capture the greatest percentage of individuals of all three hover fly species studied and that gravid females of *M. fasciatum* and *M. novaezealandiae* captured in high yellow water traps had a lower pollen load, i.e., they were more 'hungry' than those captured in the low yellow traps. These points illustrate that it is important to select a trap type which captures the desired cohort of individuals studied and is representative of the species populations.

It is also important to match the species captured with the species carrying out the biological control. For example, a study in Oregon, USA, used water traps to capture hover flies in alyssum (*Lobularia maritima* (L.) Desv.) and control treatments set up in a broccoli field. They also collected eggs laid among aphid colonies from the broccoli plants and reared them to adults in the laboratory. They found that 148 hover flies were captured in the water traps but only 2% of these individuals were the hover fly species which laid its eggs in the field (J. Luna *et al.*, unpublished data).

The following experiment was set up to determine the height and trapping method that is the most effective at capturing *D. tasmanica* and several other beneficial arthropods for future experiments. It compares three heights of yellow sticky 'Trappit' traps used in the previous study, two heights of water traps used in research conducted by Stephens *et al.*

(1998) and two heights of 'sticky-water' traps. The latter trap design is similar to the water trap but has a sticky acetate sheet as the trapping surface (see description below) and therefore will help determine the influence of water on the abundance and diversity of insect species captured. Lacewings, *A. zealandica* and hover flies have been studied in the previous experiment and therefore were also included in this study to determine which trapping method is most effective for these insect species and to look at the interaction between the lacewing and its parasitoid.

2.2.2 Methods

Site description and experimental design

The site used for the large plot experiment in Section 2.1.2.1 was also used for this trap height and type experiment (Fig. 2.2). On January 22, 1997, seven treatments were set up in a randomised complete block design in the outer four trees of the nectarine, peach and apple blocks, each with six replicates. The treatments were three heights (0, 1, 2 m) of yellow 'Trappit' sticky traps (see previous description), two heights (0 and 0.5 m) of yellow water traps (16 x 16 cm) and two heights (0 and 0.5 m) of yellow sticky-water traps (16 x 16 cm). The water traps consisted of a green, 2.0 litre ice-cream container with a yellow (see Wratten *et al.* (1995) for spectral reflectance) ice-cream container inside and were filled three-quarters full with water, 5 g of the preservative sodium benzoate and a few drops of detergent (Plate 8). 'Sticky-water' traps consisted of a green, 2.0 litre ice-cream container with 25 mm of the base of a yellow (same spectral reflectance as above) ice-cream container stapled into the top so that the surface of the yellow ice cream container base was equal to the surface of the water in the water traps. On to this surface a disposable sticky plastic transparent sheet was stapled (Plate 9).

Insect sampling

Traps were collected and replaced or refilled every seven days from January 22 to March 3, 1997. Water traps were emptied through a sieve into gauze material and later in the laboratory, placed into 70% ethanol to await analysis. Traps in each replicate were replaced except those in the peach block due to insecticide use before harvest. Trap contents were analysed in the laboratory under a binocular microscope for the presence of *D. tasmanica*,

M. tasmaniae, *A. zealandica* and hover flies. Sticky traps were scraped down and re-glued with a sticky polybutene-based insect trap adhesive for re-use.

Plate 8. Water traps placed at ground level (left) and 1 m above ground level (right).

Plate 9. Sticky-water traps placed at ground level (left) and 1 m above ground level (right).

Data analysis

Trap catches were compared between the three heights of traps over all dates combined, for each trap type separately using repeated measures ANOVA. There were no significant differences between heights within each trap type (maximum F=2.462, df=1,5, $P>0.05$). Therefore, heights were combined and compared between trap types using repeated measures ANOVA. Hover flies were analysed as individual species because it has been suggested that the different species could occupy different strata within the habitat (Gilbert, 1985; Wratten *et al.*, 1995).

2.2.3 Results

Sticky traps and sticky-water traps showed an increase in *A. zealandica* abundance over time whereas this trend was not so apparent in the water traps (Appendix 2, Figs. 2a & 3a). Sticky traps showed a decrease in lacewing abundance over time (Appendix 2, Fig. 2b) and *D. tasmanica* numbers increased over the summer period, peaked in late February to a high of 6.04/trap/week and decline again in March, 1997 (Fig. 2.19). *M. fasciatum* and *M. novaezealandiae* abundance peaked on March 3, 1997 for each trap type (Appendix 2, Figs. 2c,d, 3c,d & 4c,d.).

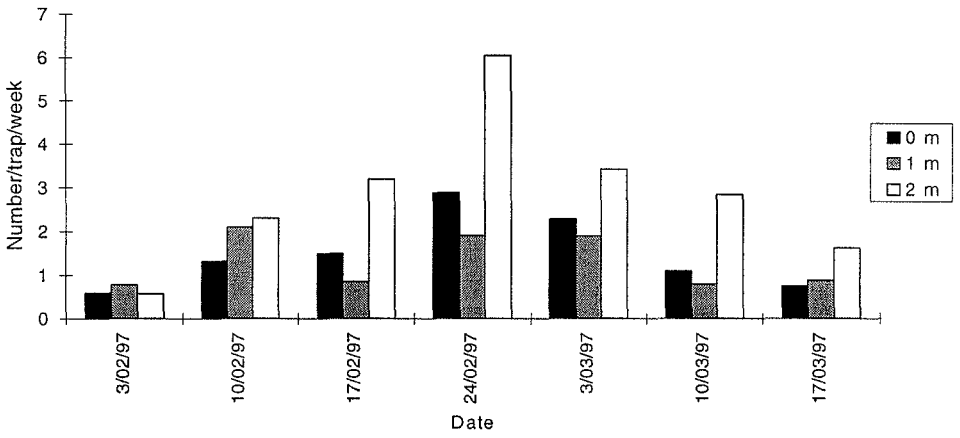


Fig. 2.19 The abundance of *D. tasmanica* captured on three heights of yellow sticky traps from February 3 to March 17, 1997 (there were no significant differences between heights at any date).

There was no significant difference in insect abundance between heights of trapping types at any individual date or over all trapping dates combined ($P>0.05$) (Figs. 2.19, 2.20, 2.21 and Appendix 2, Figs. 2-4), and no significant height x date interaction (maximum $F=1.208$, $df=12,54$, $P>0.05$). However, combining low and medium heights and comparing trap type showed that *D. tasmanica* abundance was significantly higher on sticky traps compared with the other trap types ($F=5.031$, $df=2,15$, $P<0.05$) (Fig. 2.22a). Although trap catches of the other insect species did not significantly differ between trap types ($P>0.05$) (Fig. 2.22b-f), *A. zealandica* abundance showed a similar trend to that of *D. tasmanica* in that there were higher numbers captured on sticky traps compared with the other two trap types (Fig. 2.22b).

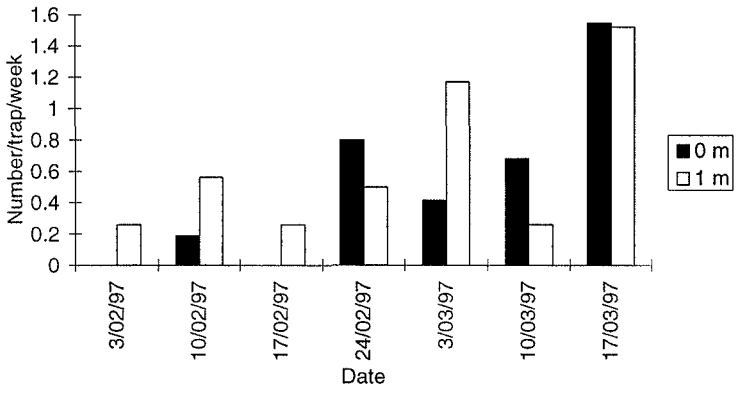


Fig. 2.20 The abundance of *D. tasmanica* captured on two heights of yellow sticky-water traps from February 3 to March 17, 1997 (see Fig. 2.19).

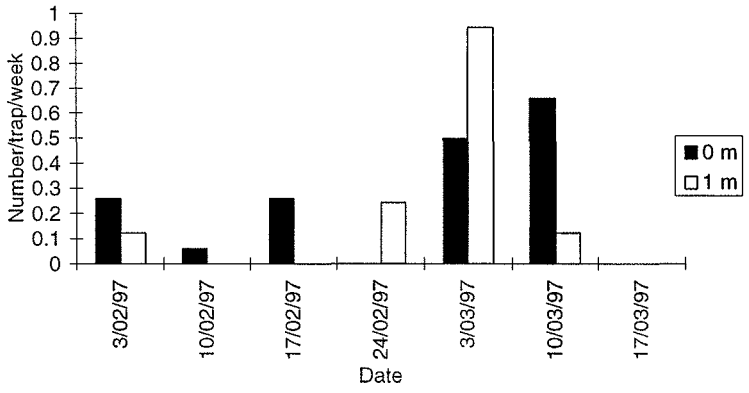
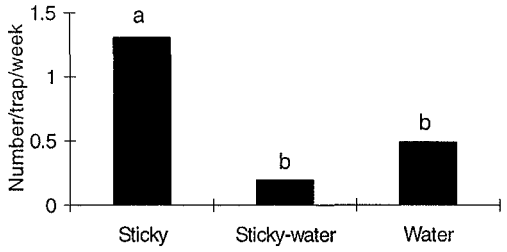
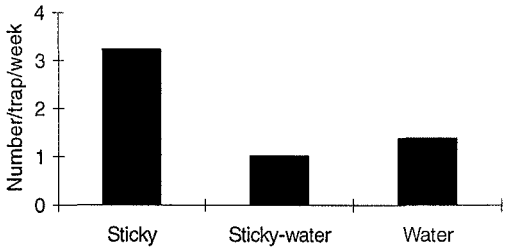


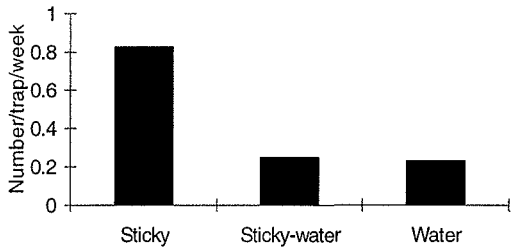
Fig. 2.21 The abundance of *D. tasmanica* captured in two heights of yellow water traps from February 3 to March 17, 1997 (see Fig. 2.19).



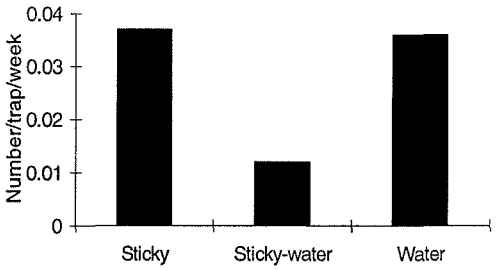
a) *Dolichogenidea tasmanica*



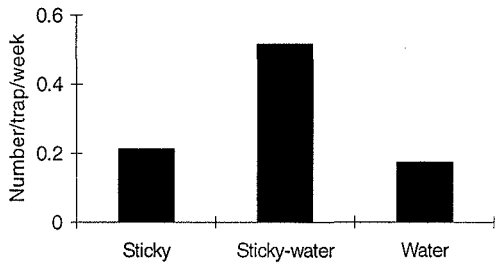
b) *Anacharis zealandica*



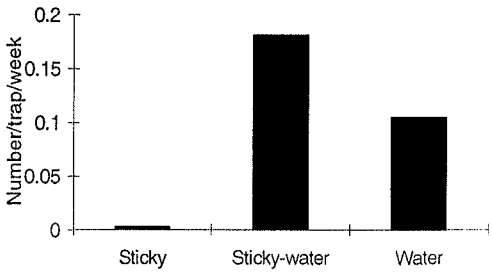
c) *Micromus tasmaniae*



d) *Eristalis tenax*



e) *Melanostoma fasciatum*



f) *Melangyna novaezelandiae*

Fig. 2.22 The mean abundance of insect groups for each trap type from February 3 to March 17, 1997 (different letters indicate significant differences between trap heights ($P<0.05$)).

2.2.4 Discussion

Sticky traps and sticky-water traps showed an increase in *A. zealandica* abundance over time, whereas this trend was less apparent with the water traps (Appendix 2. Figs. 2a, 3a, 4a). This emphasises how trap type can influence phenological data. The phenology of *A. zealandica* shown here supports the increase in *A. zealandica* abundance over the summer period that was shown in Section 2.1.3.2 (Fig. 2.14). Sticky traps also showed a decrease in lacewing abundance over time which suggests that an increase in the *A. zealandica* population may have contributed to a decline in lacewings.

The number of *M. novaezealandiae* and *M. fasciatum* did not significantly differ between heights of the trap types. This contrasts with studies by Wratten *et al.* (1995) and Gilbert (1985) who suggested that hover fly species occupy different strata within the habitat. *M. novaezealandiae* is thought to spend more time higher in the crop, near the upper canopy, compared with *M. fasciatum*. This experiment was set up in the buckwheat treatments of the large plot trial (Fig. 2.2) because it was hypothesised that these plots would have higher insect abundance. However, the flowers may have competed with the traps, therefore underestimating the numbers of insects present and minimising any effects. The experiment was also set up over a variety of crop types (peaches, nectarines, apple and pears), therefore the obtained data were variable, making it difficult to detect differences between treatments. Analysis showed that there was a strong replicate effect on the abundance of most insect species studied for each trap type. Also, the time the experiment was conducted may not have been the optimum time for catching peak numbers of these insect species, therefore low numbers were captured making it difficult to detect small differences between treatments.

Significantly higher numbers of *D. tasmanica* were captured on sticky traps compared with the other two trap types and the catches of *A. zealandica* were also lower in water and sticky-water traps compared with sticky traps. This indicates, especially for *D. tasmanica* (because the difference for *A. zealandica* was not significant), that the yellow sticky traps are better at capturing these parasitoids and measuring their abundance. This could be an artefact of spectral reflectance or trap position. For example, water and sticky-water traps were positioned underneath the tree, whereas sticky traps were placed in the tree canopy.

Also, the former trap types had a horizontal catching surface and could be detected by the insect only when it was flying above the trap, whereas sticky traps had a vertical catching surface and were more conspicuous to insects flying above, below and to the sides of the trap. Therefore, sticky traps may draw insects from all heights compared with the other trap types which only trap insects flying directly above them. Also, leaves in water and sticky-water traps would have reduced the spectral reflectance and catching surface, respectively, therefore reducing the number captured compared with vertical sticky traps.

Results from this study were not significant, however, trends showed that the abundance of the insect species studied differed between trap type and trap height. The trap types used in this study were yellow (although two types had differing spectral reflectances) but Kirk (1984) stated that insects that are not particularly associated with foliage through feeding or oviposition, such as predators and parasitoids, would not be expected to show the positive response to yellow alone that many phytophagous insects do. Weseloh (1981) showed that some tachinid parasitoids are caught particularly by white and yellow traps and Disney *et al.* (1982) showed that adult Phoridae are more numerous in white than in yellow traps. Therefore, it may be beneficial to investigate trap colour and height on *D. tasmanica* abundance, sex ratio, gravidity and pollen load to determine whether yellow sticky traps are the most optimal trap type for monitoring *D. tasmanica* populations and whether they bias the cohort of individuals captured. This has important implications for the interpretation of results of previous and future investigations.

2.3 DENSITY DEPENDENT SEARCHING BY *D. TASMANICA*

2.3.1 Introduction

Information is not available on the extent to which searching by *D. tasmanica* for leafroller is density dependent (Barlow and Wratten, 1996). In previous studies, a fixed number of eggs per branch have been released on each occasion, therefore minimising any such effects. However, it is not known whether release densities used in the previous studies achieve maximum parasitism. Although a fixed number of eggs were released on each occasion, the number of batches of eggs released varied. Once *D. tasmanica* finds a patch of high larval density (i.e., a release site), it may parasitise all the larvae, therefore giving high apparent parasitism rates. Understanding density-dependent searching by *D. tasmanica* is important for deciding egg densities in future release studies and investigating whether *D. tasmanica* has potential to respond to low larval densities required in crops grown for export markets. Therefore, this experiment was set up to determine whether the relationship between *D. tasmanica* parasitism and leafroller larval density is density dependent.

2.3.2 Methods

Experimental design and site description

Apple cultivars 'Fuji' and 'Royal Gala', planted in 1989 on M9 rootstock, were spaced 2 m apart in rows 2.5 m apart. The orchard had a history of biological pest control, with no pesticide use. Five replicates of three treatments (leafroller densities 200, 100 and 40 eggs/branch) were set out in a randomised complete block design in an apple orchard at the Biological Husbandry Unit at Lincoln University using every second row and avoiding the end of rows (Plate 10). The understorey was mown every 3-4 weeks and no irrigation was applied for the duration of the experiment.

Leafroller release

LBAM eggs (Appendix 1), laid on sheets of paper, were counted under a binocular microscope and divided (by cutting the paper) into batches of approximately five replicates each of 40, 100 and 200 eggs. On January 31 and February 13, 1997, five replicates of the

appropriate density was released on to a random branch of the treatment trees following the protocol described in Section 2.1.2.1. After 6-8 weeks these branches were harvested and the numbers of parasitoid cocoons and leafroller larvae present were recorded.

Plate 10. Different leafroller densities released on to apple branches covered with nylon sleeves. Note: The trees had been grafted onto dwarfing rootstock and the understorey was not mown or sprayed with herbicide, therefore the understorey often reached into the lower canopy.

2.3.3 Results and discussion

Only eleven parasitoid cocoons and seven leafroller larvae were found over all release dates and treatments, therefore the data were not statistically analysed. The extremely low numbers of larvae and cocoons recovered may have been influenced by the site used. Neonate larvae prefer actively growing tissue to feed so they are usually found on the upper half of the tree (Tomkins, 1984). The apple trees in the current study had been grafted onto

a dwarfing rootstock, therefore influencing tree height, shape, growth rate of foliage, sap composition and nutritional value. They may not have been a favourable host for leafroller larvae, in turn reducing larval establishment on the branches. Populations of hyperparasites of *D. tasmanica* may have been high at this site because of its biological background, reducing *D. tasmanica* abundance and leafroller parasitism. For example, *Hemiteles* sp. and *Elachertus* sp. are hyperparasites reared from *D. tasmanica* collected in Nelson (Dumbleton, 1935). *Hemiteles* sp. parasitised 15% of *D. tasmanica* cocoons in a season. Furthermore, the understorey was not mown at this site and it often reached into the canopy (Plate 10). Larvae may have been more inclined to drop to the ground into this dense understorey because it may have provided a more sheltered environment and favourable host plants.

Density-dependent searching by *D. tasmanica* is a fundamental biological question about this parasitoid and whether it would be suitable as a biological control agent for leafroller biological control. It would be essential for *D. tasmanica* to be able to operate under very low larval densities due to the low threshold for leafroller allowed in export crops (Wratten *et al.*, 1998). Also, this information would aid future decisions regarding release densities. However, given the time and labour restrictions in later field seasons this experiment was aborted.

3. UNDERSTOREY MANAGEMENT EXPERIMENTS IN 1998

The following chapter investigates the influence of buckwheat and coriander (*Coriandrum sativum* L.) on numbers of *D. tasmanica* captured on yellow sticky traps and leafroller parasitism rate (Section 3.1). It determines the influence of sleeve type on parasitism rate data (Section 3.1) and estimates the establishment rate of leafroller larvae at sleeve removal (Section 3.2). Finally, it investigates the movement of *D. tasmanica* from a buckwheat plot into the apple canopy (Section 3.3).

3.1 THE INFLUENCE OF BUCKWHEAT AND CORIANDER ON *D. TASMANICA* ABUNDANCE AND LEAFROLLER PARASITISM

3.1.1 Introduction

Coriander, like buckwheat, has small white flowers with shallow corollae allowing short tongued beneficial insects access to nectar and pollen. Trials conducted in New Zealand showed that coriander and buckwheat, which were two of four plant species tested, were the preferred food plants of *M. fasciatum* and *M. novaezealandiae* (Lővei *et al.*, 1992). A study in the USA investigating the effects of intercropping potatoes with flowers on predator abundance demonstrated that numbers of coccinellids were significantly higher in fields interplanted with coriander than in the controls (Patt *et al.*, 1997a). Therefore, coriander was included in this field trial to determine whether sowing this plant in the orchard understorey would enhance parasitism of leafroller by *D. tasmanica*. This work extended the 1997 field season's work and helped to determine whether buckwheat was the best annual plant species for understorey management in apple orchards.

During the 1997 field season, parasitism rate was expressed as: [number of parasitoid cocoons recovered/(number of parasitoid cocoons recovered + number of leafroller larvae recovered)] x 100. However, the number of leafroller larvae recovered from the field were low, causing 'parasitism rate' to be high. Therefore, during this field season, the number of leafroller webbed shelters was recorded as a measure of initial field leafroller density or

initial larval establishment after egg release, to give a potentially more robust expression of parasitism rate ((number of cocoons/number of webbed shelters) x 100).

High rates of leafroller larval dispersal and low establishment may also have caused low parasitoid cocoon and leafroller recovery in the previous field season. Therefore, the leafroller release technique was also investigated to determine which technique maximised leafroller establishment and parasitoid cocoon recovery. Stephens *et al.* (1998) released leafrollers onto apple branches using open-ended sleeves to allow ingress of parasitoids. In the 1997 field season, it was hypothesised that closed sleeves would ensure a higher rate of leafroller establishment. However, parasitism data obtained in the 1997 field season were inadequate, so the 1998 field season used both open-ended and closed sleeves to determine the most effective method of releasing leafrollers into the field to obtain the highest leafroller establishment and the most realistic parasitism rate. Open sleeves (Plate 11) were left on the branches for a longer period of time (8-14 days) than closed sleeves because this sleeve type allowed the parasitoid access to the larvae; however, the open end also gave larvae means of dispersal. Closed sleeves (Plate 11) were removed after 5-9 days, to allow exposure of the larvae to the parasitoid.

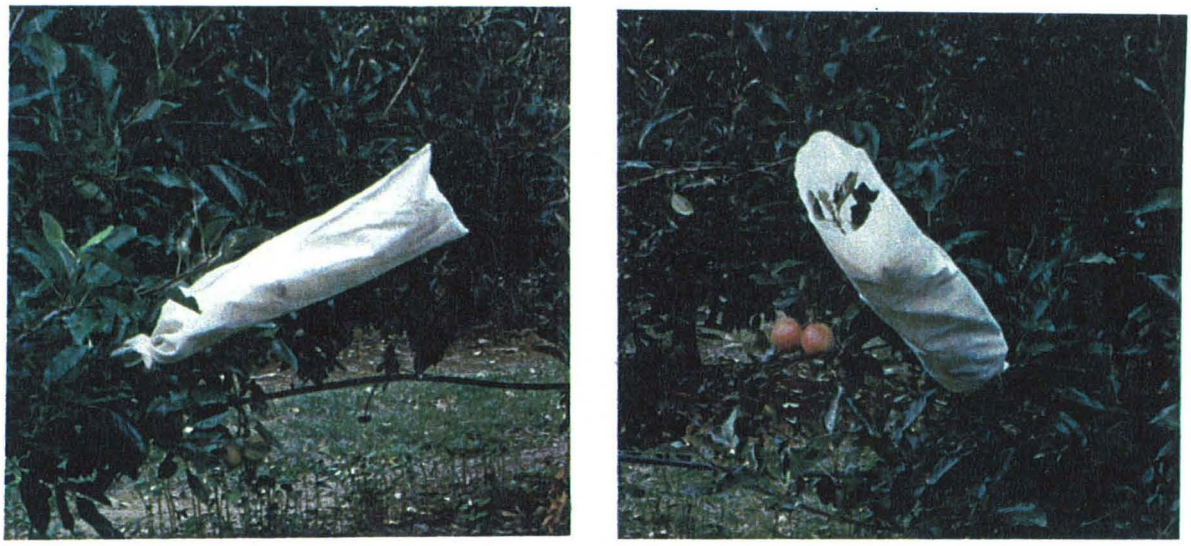


Plate 11. Leafroller eggs released onto an apple branch, covered with a closed (left) or open (right) nylon sleeve.

3.1.2 Methods

3.1.2.1 Site description and experimental design

This experimental site was located at the LUHRA and was the same as that described in Section 2.1.2.1 (refer to this section for site history and description). The use of simazine (2 kg/ha) in mid-August had removed all understorey weeds. However, germination tests revealed that this also inhibited coriander and buckwheat emergence. Therefore, the top 100 mm of the soil was removed from these plots, and 50 mm of non-contaminated soil was brought in to prepare a seed bed. Five replicates of each of three treatments (buckwheat, coriander and a herbicide-treated control, were set up in a randomised complete block design using every second row and avoiding end rows. Each replicate was 8 m long and 2 m wide and consisted of five trees (Fig. 3.1).

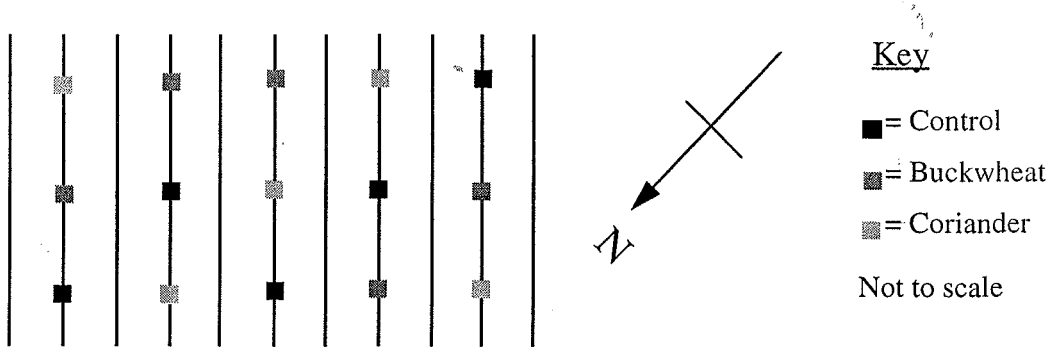


Fig. 3.1 Experimental layout of coriander, buckwheat and control understorey treatments for the 1998 field season.

3.1.2.2 Plant agronomy

Buckwheat (cv. 'Shinano Natsu') and coriander (*Coriandrum sativum* var. *microcarpum*) seeds were sown on December 9, 1997 and re-sown in rows adjacent to the initial sowing site on January 28, 1998 and January 9, 1998, respectively, to ensure continual flowering. In these plots, a 50 mm wide strip of buckwheat or coriander was sown each side of the

tree row at a density of c. 2 seeds/cm^2, and 30 mm of non-contaminated soil was then placed over them.

Weeds in the buckwheat and coriander treatments were removed by hoeing and inter-row strips between the apples were mown every 2-4 weeks. Control plot understoreys were sprayed on January 23, 1998 with simazine (1 kg/ha) and glufosinate-ammonium (1 kg/ha). Irrigation was supplied via mini-sprinklers (1.5 m radius throw, 80 L/hr) on 16 mm lateral pipes, four mini-sprinklers per plot. The plants were irrigated every 2-4 days to ensure water was not a limiting factor.

After approximately 5-6 weeks (mid-January) the buckwheat began to flower and leafroller release began. Coriander and buckwheat were both flowering by the third release date (early-February). On February 11 and 26, 1998 the top third of the buckwheat plants was cut off to encourage lateral flowering and ensure a longer flowering time.

3.1.2.3 Egg release and release method

Two releases per treatment, one for each sleeve type, were conducted on each release date (January 15, January 28, February 10, February 25 and March 11). Sleeves (600 x 200 mm) were made of nylon material and were either open-ended or closed design (Plate 11). Batches of approximately 200 LBAM eggs (Appendix 1) were released following the protocol described in Section 2.1.2.1. A sleeve was placed over the branch, with sleeve treatments being selected randomly, and was tied. Open and closed sleeves were left for 8-14 days and 5-9 days respectively before removal, to provide some protection while the larvae hatched and settled.

Branches were harvested with a pair of secateurs six weeks after egg placement and the number of parasitoid cocoons and leafroller-webbed shelters present were recorded. The March 11, 1998, release date was not harvested as it was too late in the season and had poor larval establishment.

3.1.2.4 Data analysis

Parasitism rate was expressed as: (parasitoid cocoons/webbed shelter) x 100 and log-transformed ($\log_e (x+1)$) to normalise distributions before analysis; data are reported here as geometric means. Data from January 28 to February 25, 1998, were used for analysis as this is the period during which both plant species were flowering. ANOVA for repeated measures was used to compare understorey and sleeve treatments and time effects. Where the ANOVA indicated significant main or interaction effects, these were further explored using Fisher's least significant difference test.

3.1.3 Results

There was no significant effect of the understorey treatments on parasitism rate over all dates and both leafroller release techniques (F=0.29, df=2,8, $P>0.05$). There was also no significant difference in parasitism rate between understorey treatments over all dates for closed sleeves (F=0.93, df=2,8, $P>0.05$). However, there was a significant difference in parasitism rate between the treatments over all dates for open sleeves (F=4.884, df=2,8, $P<0.05$) and no significant interaction between treatment and time (F=0.637, df=4,22, $P>0.05$). Parasitism rate was three-fold higher in the coriander treatment (36%) compared with the control (13%) ($P<0.05$) (Fig. 3.2). Buckwheat (21%) also appeared to enhance parasitism rate compared with the control, but this two-fold increase was not significant ($P>0.05$) (Fig. 3.2). Parasitism rate was significantly higher when using closed sleeves (48%) compared with open ones (29%) (F=7.126, df=1,12, $P<0.05$).

3.1.4 Discussion

A three-fold increase in parasitism occurred in the coriander plots compared with controls, suggesting that coriander shows potential for enhancing leafroller parasitism in apple orchards. This is similar to other studies that demonstrate that coriander enhances natural enemy populations (Lővei *et al.*, 1992; MacLeod, 1992a; Patt *et al.*, 1997a; Baggen and Gurr, 1998). However, coriander seeds did not germinate quickly and it competed poorly with weeds. Buckwheat and coriander are annual plants and would therefore have to be re-sown each year. Self-seeding is not a viable option as these plants are frost-tender (Bowie

et al. 1995) and pre-emergent herbicide use in the understorey would inhibit germination. Also, annual-plant understorey species may not suit some orchard growers. Therefore, research into a perennial understorey species is required. This is investigated in Section 4.1.

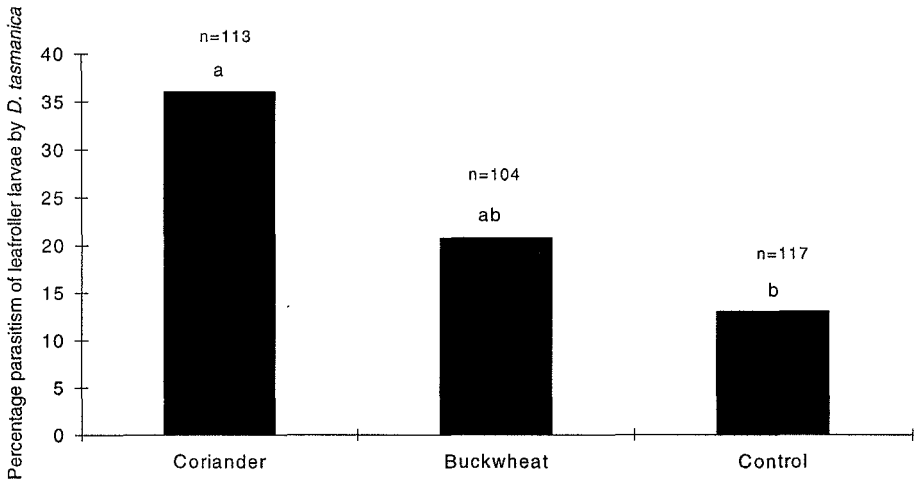


Fig. 3.2 Percentage parasitism of released leafroller by *D. tasmanica* for each understorey treatment (different letters indicate significant differences between treatments ($P<0.05$), n = number of leafroller shelter sites).

Results from this study showed that using closed sleeves for leafroller release resulted in a higher parasitism rate. This may be because the larvae were enclosed during hatching and therefore did not disperse. Neonate leafroller larvae disperse by spinning a silken thread and dropping down to the lower canopy or the ground cover, or they become airborne and disperse great distances (Chapman, 1973). Using closed sleeves may reduce dispersal and increase larval establishment, therefore increasing the number of cocoons recovered.

Although buckwheat did not have a significant effect on parasitism rate in this study, Stephens *et al.* (1998) found higher levels of parasitism in buckwheat plots than in controls and higher numbers of *D. tasmanica* were captured on yellow sticky traps in buckwheat plots. Also, Section 2.1 showed that seven-fold more leafroller parasitoids occurred in the buckwheat plots compared with controls and showed that buckwheat significantly enhanced leafroller parasitism from 0% to 86%, although on one occasion only. The

differences between studies may be accounted for by the differences in method of leafroller release and the techniques for calculating parasitism rate. For instance, different leafroller release densities, sleeve types and leafroller developmental stages may have affected establishment. For example, Stephens *et al.* (1998) released larvae, whereas the present study released eggs. Eggs were used in the current study instead of larvae because larvae that hatch in the field could be better acclimatised to field conditions. It is often thought that individuals acclimatised to one environment perform better in that environment than do individuals acclimatised to a different environment (Huey *et al.*, 1999).

Furthermore, the study in Section 2.1 used [cocoons/(cocoons + leafroller larvae recovered)] x 100 as a measure of parasitism rate whereas the current study used (number of cocoons/shelter site) x 100, therefore influencing the calculated parasitism rate. The high dispersal of leafroller larvae (Penman 1984) will tend to make recovery of parasitoid cocoons from the release sites variable, potentially making it difficult to detect significant differences between buckwheat and control treatments. Also, there could have been a bias introduced by the methods used in the current study if unparasitised and parasitised larvae behaved differently. For instance, the rate at which larvae left the release branch may have differed between parasitised and unparasitised larvae. This aspect is explored further in Chapter 6.

Releasing larvae at such un-naturally high densities may not make it possible to determine a realistic parasitism rate for *D. tasmanica*. The study in Section 2.1 gave parasitism rates of up to 86% in buckwheat plots compared with 20-30% parasitism recorded for natural populations (Collyer and van Geldermalsen, 1975; Green, 1984; Suckling *et al.*, 1996a). Using shelter sites for calculating parasitism rate in the current study produced rates of up to 36%, which is closer to those in natural populations. However, recovery of parasitoid cocoons from the release site was still low, possibly due to low larval survival, high predation rate after sleeve removal, or high larval dispersal. It would be useful to investigate the mechanisms behind low cocoon recovery and to determine a more reliable release method. These issues are examined in Section 3.2 and Chapter 6, and Section 4.1, respectively.

3.2 LARVAL ESTABLISHMENT RATE AT SLEEVE REMOVAL

3.2.1 Introduction

The study in Section 3.1 investigated the effect of sleeve type on parasitism rate. However, it is important to determine the mechanisms behind the low recovery rate of parasitoid cocoons from larval release sites the field. One hypothesis is that there is high mortality of hatching larvae due to competition at high densities, before the sleeve is removed. Therefore, this study was conducted to determine the number of larvae that hatch and establish after egg release that are exposed to the parasitoid after the sleeve is removed.

3.2.2 Methods

On March 11, 1998, ten replicates, each of 200 LBAM eggs (Appendix 1), were established on a randomly-selected branch in a row of apple (cv. 'Braeburn') trees, using every second tree and following the protocols described in Section 2.1.2.1. A closed sleeve was placed over the branch and after five days the sleeve was removed and the branch placed into a polythene bag. The number of larvae on the branch was counted in the laboratory and a mean calculated over the ten replicates.

3.2.3 Results

The mean number of larvae/branch was 39.5. This is an establishment rate of 20% from the 200 larvae released per branch.

3.2.4 Discussion

MacLellan (1973) stated that the highest larval mortality occurred immediately after egg hatching and before larval spin-down and accounted for up to 87% mortality. This may explain the low larval establishment rate in the current study. Larvae were enclosed in a closed sleeve, therefore they could not disperse and were protected from predation from outside the sleeve. Therefore, the high mortality rate during hatching and settling may be

due to infertility of eggs (Danthanarayana, 1983), competition between larvae, predation from inside the sleeve, and disease incidence. Danthanarayana *et al.* (1982) demonstrated that in laboratory experiments larval crowding, even at low densities, caused an increase in mortality to larvae. Furthermore, unsettled larvae may have been left on the inside of the sleeve at removal, hence being removed from the release site.

The number of cocoons recovered from previous field seasons was still much lower than the mean larval establishment shown here and was sometimes zero/release branch. Therefore, some larvae must disperse, drop to the ground or be preyed upon after sleeve removal. A release method is required that allows adequate time for realistic exposure to *D. tasmanica* but which minimises dispersal after sleeve removal to maximise the recovery of larvae which have survived and established. This is explored further in Section 4.1.

3.3 MOVEMENT OF *D. TASMANICA* FROM A BUCKWHEAT PLOT

3.3.1 Introduction

Although the plot size used in the previous studies was increased to extend the work of Stephens *et al.* (1998), it may not have been large enough to prevent parasitoids moving between nectar/pollen resources and between all plots/treatments. The plot size experiment in Section 2.1.3.3 indicated that there was no difference in *D. tasmanica* abundance between large and small experimental sites and, in fact, the abundance of *D. tasmanica* and hover flies was higher in the smaller plots compared with the larger plots. This suggests that *D. tasmanica* may not travel far from a nectar source. However, it is important to investigate the scale of movement of *D. tasmanica* from a nectar source to determine whether it would disperse into surrounding areas of an orchard for biological control. This would also help determine the number, size and spacing the understorey plants required in a practical apple production situation (Landis *et al.*, in press) and determine the optimal plot size and buffer zones between treatments for future experiments. Therefore, this experiment was set up to determine how far *D. tasmanica* travels to feed, and to parasitise larvae, from a buckwheat plot, along the row and across adjacent rows.

3.3.2 Methods

3.3.2.1 Site Description and Experimental Design

This experimental site was located at the LUHRA and eight-years-old apple (cv. 'Taylor's Gold') trees were spaced at 2.25 m in rows 4.3 m apart. This orchard had a history of standard commercial spraying but no insecticides were used during the course of this study. The inter-row spaces were predominantly grass/clover sward and the recent use of simazine (1 kg/ha) in winter had removed all understorey weeds. However, germination tests revealed that this also inhibited buckwheat emergence. Therefore, the top 100 mm of soil was removed from these plots using a ripper and 50 mm of non-contaminated soil was brought in to prepare a seed bed.

Four replicate plots, each with sticky traps and leafroller release placed at seven distances down the row (middle of the buckwheat plot, edge (3.5 m from middle) of the plot, 1 m, 2 m, 5 m, and 10 m from the plot edge, and in the adjacent row (Fig. 3.3)) were established, avoiding rows on the perimeter. Each buckwheat plot was 8 m long and 2 m wide.

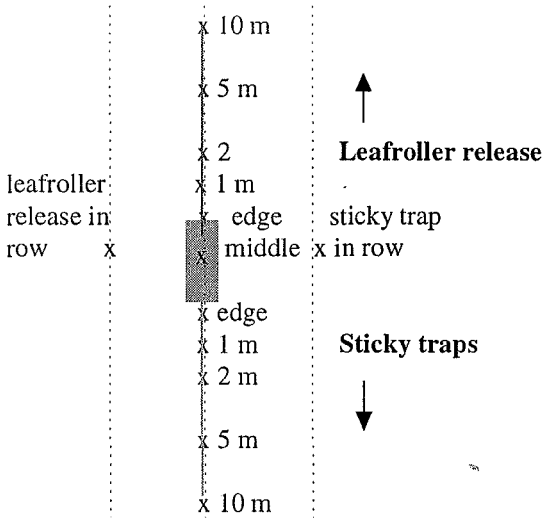


Fig. 3.3 Sticky traps and leafroller egg release at different distances along rows of apple trees from, and adjacent to a buckwheat plot (grey box).

3.3.2.2 Plant agronomy

Buckwheat (cv. 'Shinano Natsu') seeds were sown on December 9, 1997 and re-sown on January 19, 1998, to ensure continual flowering. In these plots, a 50 mm wide strip of buckwheat was sown each side of the trees at a density of 2 seeds/cm^2 and 30 mm of non-contaminated soil was placed over them. Weeds were removed by hoeing and inter-row strips between the apples were mown every 2-4 weeks. The surrounding understorey was sprayed on January 23, 1998 with simazine (1 kg/ha) and glufosinate-ammonium (2 kg/ha). Irrigation was supplied via mini-sprinklers (see previous description) on 16 mm lateral pipes with two mini-sprinklers per plot. The plants were irrigated every 2-4 days to ensure that water was not a limiting factor.

The buckwheat began to flower in mid-January and both parasitoid trapping and leafroller egg release began. Flowers declined in abundance in mid-March, 1998; therefore, the first and last trap catch date and the first leafroller release date are excluded from the data analysis. On February 11 and 26, the top third of the buckwheat plants was removed to encourage lateral flowering and ensure a longer flowering time.

3.3.2.3 Parasitoid trapping

One yellow 'Trappit' trap (see previous description), which had been scraped and reglued with a sticky polybutene-based insect trap adhesive, was placed 1 m above ground level at each of seven distances (described above), facing the middle of the row. Traps were collected and replaced from January 15 to March 12, 1998, every two weeks. In the laboratory, the number of adult *D. tasmanica* was counted under a binocular microscope. Traps were scraped and re-glued for re-use.

3.3.2.4 Leafroller release

Batches of approximately 200 LBAM eggs (Appendix 1) were released at each distance described above on January 15, January 29, February 11, February 26 and March 12 following the protocol described in Section 2.1.2.1. This leafroller release gradient was in the opposite direction to the sticky trap gradient and was randomly selected (Fig. 3.3). A closed-ended sleeve was placed over the branch, tied and left for 5-9 days to protect the larvae while they hatched and settled.

Branches were harvested six weeks after egg placement and the number of parasitoid cocoons, leafroller webbed shelters present were recorded. The last release date was not harvested because of poor larval establishment.

3.3.2.5 Data analysis

Data from collection dates January 29 to February 25, 1998 were used for analysis because this was the period during which the buckwheat was flowering. Parasitism rate was expressed as: (number of parasitoid cocoons/webbed shelters) x 100. Trap catch data and

parasitism rate data were log-transformed ($\log_e(x+1)$) to normalise distributions before analysis and are presented here as geometric means. ANOVA for repeated measures was used to compare distance treatments and time effects. Where the ANOVA indicated significant main or interaction effects, these were further explored using Fisher's least significant difference test.

3.3.3 Results

There was no significant (F=0.68, df=6,42, $P>0.05$) effect of distance from the buckwheat plot on parasitism rate and no significant date x distance interaction (F=0.810, df=12,24, $P>0.05$). However, there was an overall significant effect of distance from the buckwheat plot on parasitoid trap catches over all flowering dates (F=4.296, df=3,18, $P<0.01$). Least significant difference tests revealed that there was a significantly higher number of *D. tasmanica* captured on sticky traps in the middle, at the edge and 1 m from the edge of the flowering buckwheat plot compared with 5 m and 10 m from the plot edge ($P<0.05$). There was no significant difference between numbers of *D. tasmanica* trapped in the middle, at the edge and 1 m from the buckwheat plot edge ($P>0.05$) (Fig. 3.4). *D. tasmanica* abundance was significantly higher at 1 m (mean = 0.103 *D. tasmanica*/trap/day) compared with 2 m from the edge of the buckwheat plot (0.093) ($P<0.05$). There was no significant difference in numbers of *D. tasmanica* between the edge, 1 m and 2 m from the plot, and the adjacent row ($P>0.05$) (Fig. 3.4).

3.3.4 Discussion

Results show that trap catches were significantly higher at 1 m compared with 2 m from the edge of the buckwheat plot. This supports results obtained from the plot size experiment discussed in Section 2.1.4 and indicates that *D. tasmanica* may not travel far from a pollen and nectar source. Results from the current study also showed that higher numbers of *D. tasmanica* were captured in the middle, edge and 1 m from the plot compared with 10 m away. This suggests that small experimental plots with buffer zones of 10 m may be adequate for future work to minimise parasitoids moving between treatments and plots.

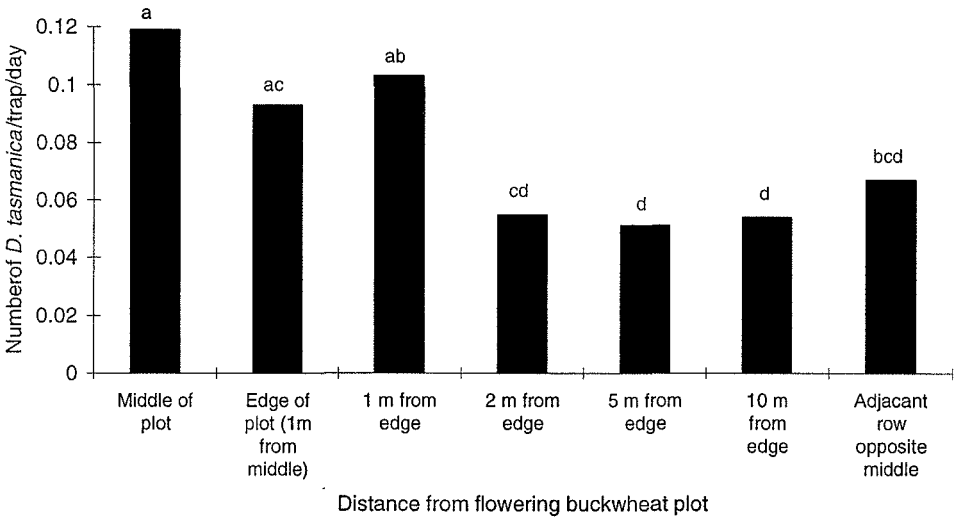


Fig. 3.4 The mean abundance of *D. tasmanica* captured on yellow sticky traps at a gradient of distances from a buckwheat plot (see Fig. 3.2).

Structural diversity in landscapes may sometimes impede natural enemies' movement between fields (Frampton *et al.*, 1995; Mauremootoo *et al.*, 1995) although, for others, it may also facilitate natural enemies' movement (Burel and Baudy, 1990). Results presented here showed that for *D. tasmanica* there was no difference in parasitoid abundance between the edge and 1 m from the plot, and the adjacent row. This indicates that growers may be able to sow flowering plants in every second or third row of the orchard and still enhance leafroller biocontrol while minimising the adverse effects of a cover crop such as competition with the crop, complicating machinery movements, increased humidity and increased frost risk, the latter through lower temperatures and reduced wind speeds (Miller *et al.*, 1989). However, as the parasitoids were not marked it remains unknown how many individuals at each distance actually had been influenced by the buckwheat, i.e., to what extent 'dilution' of the numbers on the traps occurred via captures of individuals from the 'background' population in the orchard. The numbers trapped from the 2 m distance and beyond may, indeed, represent that background population. The hypothetical pattern of decline would have been expected to have been exponential, because of the radial spread of dispersing insects (Hickman, 1990).

Trap catch data were obtained from yellow sticky traps placed at different distances from a buckwheat plot. Those traps closer to the buckwheat plot would have competed with the flowers for insects, therefore underestimating trap catches and effects between distances (MacLeod, 1992b). Results showed that there was no significant difference in *D. tasmanica* abundance between the middle, edge and 1 m from the nectar source. These traps represent 'food' for parasitoids and capture a cohort of 'hungry' parasitoids (Wäckers, 1994; MacLeod, 1999). It can be hypothesised that parasitoids captured 1 m from the buckwheat plot have left the nectar source in search of another food source because they are drawn to the trap. This may suggest that *D. tasmanica* requires a number of sugars, proteins and amino acids for tissue maintenance, survival, energy for mate seeking and egg maturation, therefore they may require more than one flowering plant species. This is explored further in Sections 4.1 and 5.1.

Parasitoids commute between nectar sources and the crop (Powell, 1986; Lővei *et al.*, 1993a). MacLeod (1999) found that providing additional resources slowed the rate of dispersal of *E. balteatus* by over three times compared with the control. The reduction in dispersal rate indicates that rich floral patches may act as a 'sink' for ovipositing females therefore negatively affecting integrated pest management programmes. Although numbers of *D. tasmanica* in the current study were significantly lower in the middle compared with 10 m from the buckwheat plot, some parasitoids were still captured 10 m away. This indicates that *D. tasmanica* may move into the crop for leafroller biocontrol. However, this experiment used yellow sticky traps to capture *D. tasmanica* so may have represented only 'hungry' parasitoids captured, rather than gravid females searching for hosts. Therefore, some mark/release/recapture work with *D. tasmanica* may be beneficial to establish whether *D. tasmanica* can move between food-containing areas and host-containing areas.

Using yellow sticky traps may have also influenced the results of the current study because they are attractive to parasitoids (MacLeod, 1999) so may have influence *D. tasmanica* behaviour and movement. The use of transparent sticky traps may have been better as this would have given a more realistic representation of parasitoid movement from a buckwheat plot into surrounding areas. This is investigated in Section 4.4.

4. UNDERSTOREY MANAGEMENT EXPERIMENTS IN 1999

The following chapter investigates the influence of alyssum (*Lobularia maritima* (L.) Desv.; Brassicaceae), buckwheat and phacelia (*Phacelia tanacetifolia* Benth.) on leafroller parasitism rate (Section 4.1), the sex ratio of *D. tasmanica* (Section 4.1), the number of *D. tasmanica* sampled by Vortis suction sampling (Section 4.2) and the abundance of *D. tasmanica* cocoons, leafroller larvae and leafroller damage (Section 4.3). It also investigates an alternative method of calculating parasitism rate (Section 4.1) and examines the movement of *D. tasmanica* from a buckwheat plot using transparent sticky traps (Section 4.4).

4.1 THE INFLUENCE OF ALYSSUM, BUCKWHEAT AND PHACELIA ON LEAFROLLER PARASITISM RATE

4.1.1 Introduction

This study determines the influence of sowing buckwheat, phacelia and alyssum in the orchard understorey on parasitism rate of leafroller. It also investigates a new technique of measuring parasitism rate and explores the effect of understorey plant on sex ratio of subsequent progeny of *D. tasmanica*. Buckwheat was included in this study because it has good agronomic characteristics for incorporation into integrated pest management programmes (Bowie *et al.*, 1995; Wratten *et al.*, 1995) and shows potential for increasing parasitism of leafroller (Sections 2.1 and 3.1). Coriander and broad bean were not included because coriander does not germinate or establish well and is a poor competitor with weeds, and broad bean provides only extrafloral nectar to parasitoids. Although broad bean enhanced parasitoid abundance (Section 2.1), parasitoid numbers were significantly lower compared with the buckwheat treatment and results suggested that nectar secretion may cease as the plant matures (Section 2.1). Furthermore, extrafloral nectars tend to be sucrose-rich and are more attractive than floral nectar to adult Lepidoptera (Handel *et al.*, 1972), implicating broad bean in enhancing leafroller adult populations in the orchard.

Buckwheat is an annual, the regular sowing of which may not suit some orchard growers. It would have to be re-sown each year because the plant is frost-tender (Bowie *et al.* 1995) and pre-emergence herbicide use in the understorey would inhibit germination. Therefore, research into a perennial plant for natural enemy enhancement in perennial crops, such as apples, is necessary. One candidate may be alyssum. Twenty-two flowering plant species, including phacelia, buckwheat and coriander, were recently ranked for their potential use as in-field insectaries in lettuce crops in California (Chaney, 1998). Alyssum showed the greatest potential because no other plant tested flowered as quickly when sown from seed or attracted as many beneficial insect species. Therefore, alyssum was included as a treatment in the following study to determine its potential for enhancing leafroller parasitism by *D. tasmanica.*

Phacelia, coriander and buckwheat cultivars have been compared with respect to their sowing-to-flowering times and susceptibility to low temperatures in Canterbury, New Zealand (Bowie *et al.*, 1995). Phacelia proved to be the most reliable species tested in terms of its resistance to low temperatures and frost. Phacelia seed is inexpensive and widely available in New Zealand and seeds sown in Canterbury during November still flowered in June of the following year (Wratten and van Emden, 1995). However, short-tongued insects, such as parasitoids and hover flies, probably cannot gain access to the nectaries as the flower has a deep corolla (MacLeod, 1992a; Holland *et al.*, 1994). This characteristic has apparently not prevented the use of this plant in biological control experiments. For example, Chumakova (1960) sowed phacelia in Soviet apple orchards and recorded higher levels of parasitism by *Aphytis proclia* (Walker) of San José scale (*Quadraspidiotus perniciosus* Comstock) in test plots than in controls. Three successive plantings increased parasitism of scale from 5% in cultivated orchards to 75% where phacelia was grown. Telenga (1958) also reported increased aphid parasitism by *Aphelinus mali* and increased *Trichogramma* activity due to sowings of phacelia and the umbellifer *Eryngium* sp. in apple orchards. Phacelia has been included in this study as an understorey plant because of its known potential to enhance parasitoid populations (Telenga, 1958; Chumakova, 1960). It was not known whether *D. tasmanica* would be attracted to this plant in the field.

Sections 2.1 and 3.1 showed that parasitism rates of up to 100% are obtained when leafroller larvae were released on apple branches in sleeves, whereas naturally-occurring parasitism in apples is approximately 20-30% (Collyer and van Geldermalsen, 1975; Green, 1984; Suckling *et al.*, 1996a). It is hypothesised that this may be because parasitised larvae are less likely to disperse than unparasitised larvae (see Chapter 6). Leafroller larvae disperse by spinning a silken thread and dropping to the lower canopy or the ground cover, or they drift in air currents and disperse great distances (Chapman, 1973). Also, male larvae frequently leave their webbed shelters and prepare a special site for pupation, usually on a lower part of the tree (MacLellan, 1973). Therefore, a high proportion of larvae that are released in the field in experiments to estimate parasitism rate between treatments will probably disperse from the release branch. A release method is therefore required that allows sufficient time for exposure to *D. tasmanica* to occur, but minimises larval dispersal after the sleeve is removed. The following experiment compares the recovery of released larvae after two and four weeks.

Field work in Sections 2.1 and 3.1 showed that providing flowering plants in the orchard understorey enhanced *D. tasmanica* abundance and increased parasitism of leafroller larvae. The mechanisms by which buckwheat may aid leafroller biocontrol have been largely unexplored. Results from Section 2.1 suggest that it is the flower of buckwheat that attracts *D. tasmanica* to the plant and not the shelter, microclimate or presence of aphid honeydew, that the buckwheat may also provide. However, a question still remains to whether any other factors contribute to the increase in parasitism rate seen in the field. Floral resources can also influence parasitoid searching ability, primary sex ratio, generation time and egg viability (Jervis *et al.*, 1996), therefore, the following study also investigated the influence of understorey plant on the sex ratio of *D. tasmanica*.

4.1.2 Methods

4.1.2.1 Site description

This understorey management experiment was set up in the Integrated Fruit Production (IFP) area established in 1995 at the LUHRA. This experiment, jointly conducted by HortResearch and Lincoln University, consisted of three approaches to apple production:

conventional (CFP), integrated (IFP) and biological fruit production (BFP). However, due to the current trends in apple production away from CFP (mainly chemical control) and towards IFP (monitoring and use of selective chemicals), the CFP treatment was converted in 1999 into an IFP treatment with an understorey management component. The trial consisted of three replicates, each of seven treatments (IFP, BFP, alyssum, buckwheat, phacelia, control and USM (the intersection of the flowering treatments) (Plate 12)), set up in a randomised complete block design. The IFP, BFP and USM plots comprised 17 trees per row in 10 rows (50 m x 50 m) of four-year-old 'Braeburn' apples trained to a central leader system. The alyssum, buckwheat, phacelia and control plots were located within the USM plots so were 25 m x 25m in dimension (Fig. 4.1). No control tactics against lepidopteran pests were used during the period of the trial (from November-April). Treatments were as below:

Integrated Fruit Production (IFP)

Glyphosate 4 L/ha in 400 L water and glyfosinate-ammonium 6 L/ha in 400 L water were applied to a one-metre-wide strip below the tree line. The inter-row sward consisted of ryegrass, which was frequently mown with the cut grass directed into the tree line. One application of 2% mineral oil (D-C-Tron® 991 ml/L) and of dodine 1 L/100 L (Dodine400 400 g/L) were applied to the trees in September for scale, mite and aphid control, and blackspot and powdery mildew control, respectively. One application of myclobutanil 30 g/100 L (Systhane®40W 400 g/kg) was applied in October for control of blackspot and powdery mildew.

Biological Fruit Production (BFP)

Pea straw was used as a mulch to reduce weed growth in the tree lines. The inter-row sward consisted of a mixed herb ley (including ryegrass, plantain (*Plantago lanceolata* L.) and white clover). The inter-rows were alternately mown to maintain long growth to reduce blackspot inoculum and provide a refugia for beneficial insects. The cut grass was directed into the tree line. One application of 2% mineral oil and two of sulphur 3 L/1500 L (Lime sulphur 15%) were applied in September for control of scale, mites, aphids, blackspot and powdery mildew. Three applications, each of copper hydroxide 250 g/L (Kocide®DF 400 g/kg) at 5 L/ha and lime 1.6 kg/100 L were made in October with a fourth application in

November. Pruning to open up the canopy was also carried out to improve disease management.

Buckwheat (foreground) and phacelia (back ground).

Control.

Buckwheat - Note: second sowing on the left of plants.

Alyssum.

Integrated fruit production .

Biological fruit production.

Plate 12. Understorey treatments in the 1999 field season (the seventh treatment was the intersection of the flowering treatments).

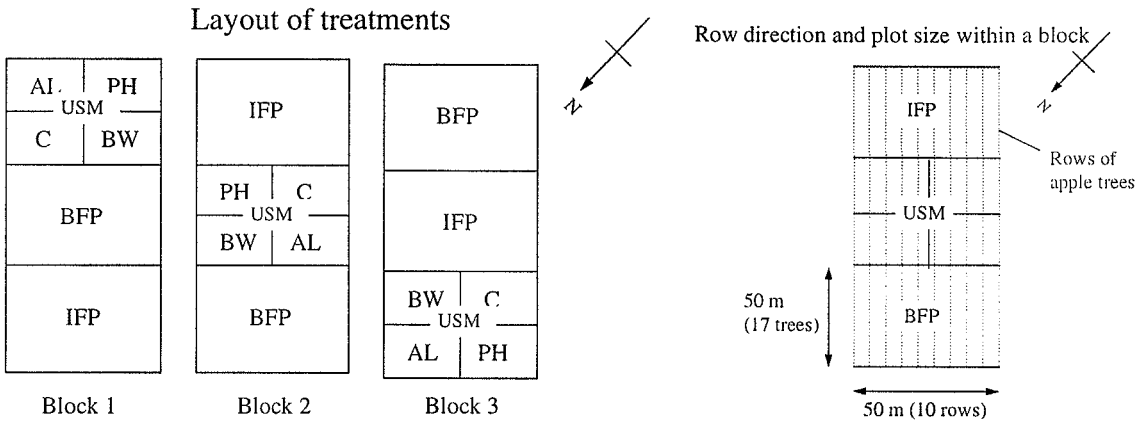


Fig. 4.1 Experimental layout of buckwheat (BW), alyssum (AL), phacelia (PH), control (C), understorey management (USM), biological fruit production (BFP), and integrated fruit production (IFP) plots in 1999.

Understorey management (USM)

The tree line was mulched with bark (*Pinus* sp.) and the inter-row sward consisted of ryegrass that was mown frequently and the cut grass was directed into the tree line. The spray programme and pruning strategy was identical to that of BFP. This treatment was divided into four different understorey treatments; alyssum (cv. 'Carpet of Snow'), phacelia (cv. 'Balo'), buckwheat (cv. 'Shinano Natsu') and a herbicide-treated control (see Fig. 4.1).

4.1.2.2 Plant agronomy in USM blocks

To prepare the understorey for sowing the north-east side of the tree line was sprayed with glyphosate 4 L/ha in 400 L water on September 18, 1998, and with glyfosinate-ammonium 6 L/ha in 400 L water on September 22, 1998. On October 26, 1998, alyssum, phacelia (both commercially coated to standardise the seed size for the seed drill) and buckwheat were drilled in six lines below the outer tree canopy at a rate of 20 kg/ha, 20 kg/ha and 100 kg/ha, respectively. The alyssum seeds did not germinate, possibly due to being drilled too deeply, so these plots were sprayed with glyfosinate-ammonium 4 L/ha in 400 L water on November 27, 1998, and one row of flowering alyssum transplants was planted approximately 30 cm apart on December 2, 1998. Also, a row of alyssum seed was sown 1 cm deep beside the alyssum transplants and raked over on December 3, 1998. On

November 27, 1998, half of the buckwheat and phacelia was pulled out by hand and by hoeing, respectively, to allow room for another sowing. The bare halves of these plots were sprayed with glyfosinate-ammonium 3 L/ha in 300 L water on December 3, 1998, and redrilled on December 7, 1998. This staggered plant development and prolonged the flowering period. On January 6, 1999, the top two thirds of the plants in the first drilling of phacelia and buckwheat were removed to encourage lateral growth and prolong flowering.

4.1.2.3 Leafroller release

By mid-January 1999, the first drilling of buckwheat and phacelia was flowering and leafroller release began. Batches of approximately 150 LBAM eggs (Appendix 1), laid on sheets of paper, were placed on a randomly selected apple branch using the middle three trees in each plot on January 15, January 29, February 12, February 26 and March 15. Egg batches were placed randomly in the alyssum, phacelia, buckwheat and control plots using trees four, five and six of row two and placing them on the side of the row that the flowers were situated. Egg releases were made in the IFP, BFP and USM treatments, using trees eight, nine and ten of row five and placing them on alternating sides for different dates. Nylon mesh closed-ended sleeves (600 x 200 mm) were placed on the release branch and were removed after 4-8 days exposing the larvae to parasitoids. Two egg releases were conducted on each date in each treatment; one of these releases was collected after two weeks and the other after four weeks. All leaves from the release branch were removed and inspected for larvae. These were removed and placed individually into diet tubes (Appendix 1). They were reared through to adult moth or adult parasitoid stages at 16.5°C with a 2°C range, and the numbers of leafroller pupae, parasitoid cocoons and sex of the emerging parasitoids were recorded.

4.1.2.4 Data analysis

The number of larvae collected were log-transformed ($\log_e(x+1)$) to normalise the distribution and compared between collection methods (two and four weeks), treatments and collection times using repeated measures ANOVA. Significant results were further explored using Fisher's least significant difference test. Parasitism rate was expressed as (the number of cocoons/number of larvae collected) x 100. Percentage leafroller pupae was

expressed as (the number of pupae/number of larvae collected) x 100 and log-transformed ($\log_e(x+1)$) before analysis to stabilise the variance and normalise the distribution. Percentage females of emerged parasitoids from the diet tubes was also calculated. Parasitism rate, percentage leafroller pupae and percentage females were compared between treatments and times using ANOVA and significant results were further explored using Fisher's least significant difference test.

4.1.3 Results

When all treatments were pooled the number of leafroller larvae collected after two weeks (mean=10.0 larvae/branch) was almost four-fold higher than the number collected after four weeks (2.86) ($F=112.78$, df=1,170, $P<0.001$). There was no significant collection x treatment interaction for parasitism rate ($F=1.883$, df=6,170, $P>0.05$). Overall, there was a significant effect of treatment on leafroller parasitism rate by *D. tasmanica* ($F=6.88$, df=6,12, $P<0.01$) (Fig. 4.2) and no significant treatment x date interaction ($F=0.836$, df=24,135, $P>0.05$). Least significant difference tests showed that phacelia and the control produced a significantly lower parasitism rate than all other treatments ($P<0.05$) (Fig. 4.2).

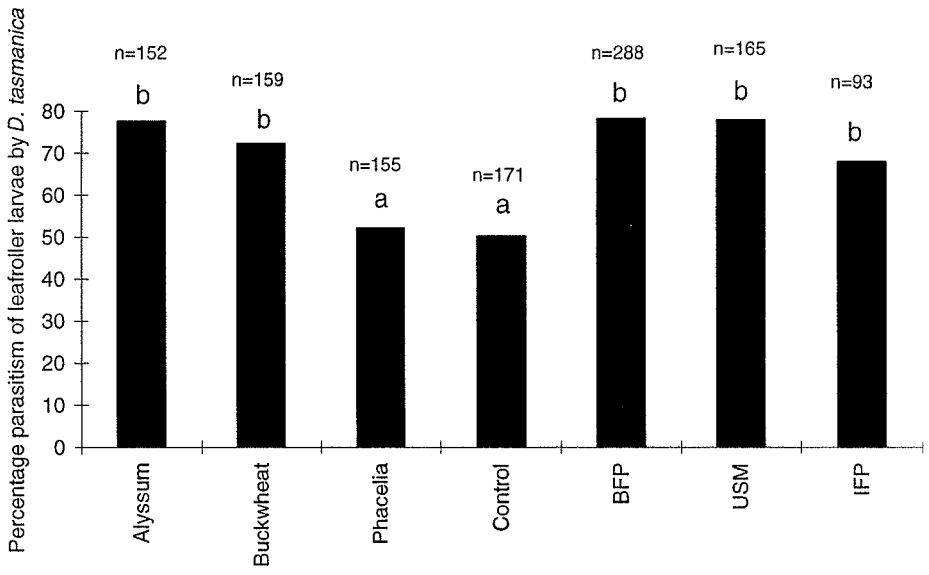


Fig. 4.2 Percentage parasitism of released leafrollers by *D. tasmanica* for each understorey treatment (n = number of leafroller larvae; different letters indicate significant differences between treatments ($P<0.05$); see Fig. 4.1).

The number of larvae recovered from the leafroller release sites was significantly different between treatments (F=5.12, df=6,12, $P<0.01$). Numbers were 39-67% lower in the IFP treatments compared with all other treatments ($P<0.05$) (Fig. 4.2).

Leafroller pupae were three-fold and six-fold lower in the buckwheat and alyssum treatments, respectively, compared with the controls (Fig. 4.3). However, this trend was not significant (F=2.947, df=6,12, $P>0.05$) and there was no significant treatment x collection date interaction. (F=0.759, df=24,135, $P>0.05$).

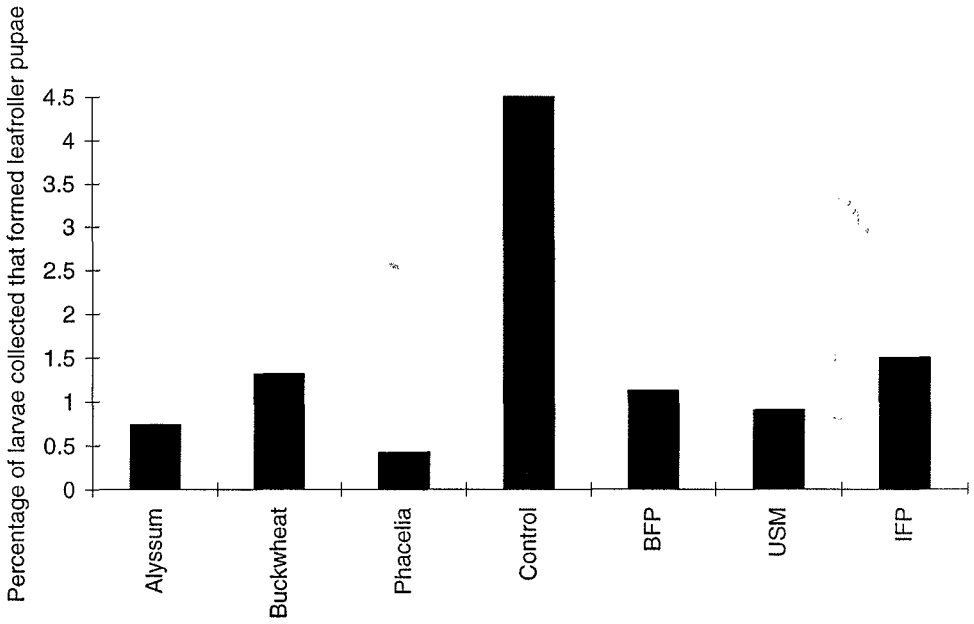


Fig. 4.3 Percentage of leafroller larvae collected that formed leafroller pupae for each understorey treatment (see Fig. 4.2).

Percentage female *D. tasmanica* that emerged from the diet tubes did not significantly differ between treatments (Fig. 4.4) or collection dates (treatment: F=1.22, df=4,8, $P>0.05$; date: F=1.89, df=6,12, $P>0.05$) and there was no significant collection date x treatment interaction (F=1.14, df=24,113, $P>0.05$).

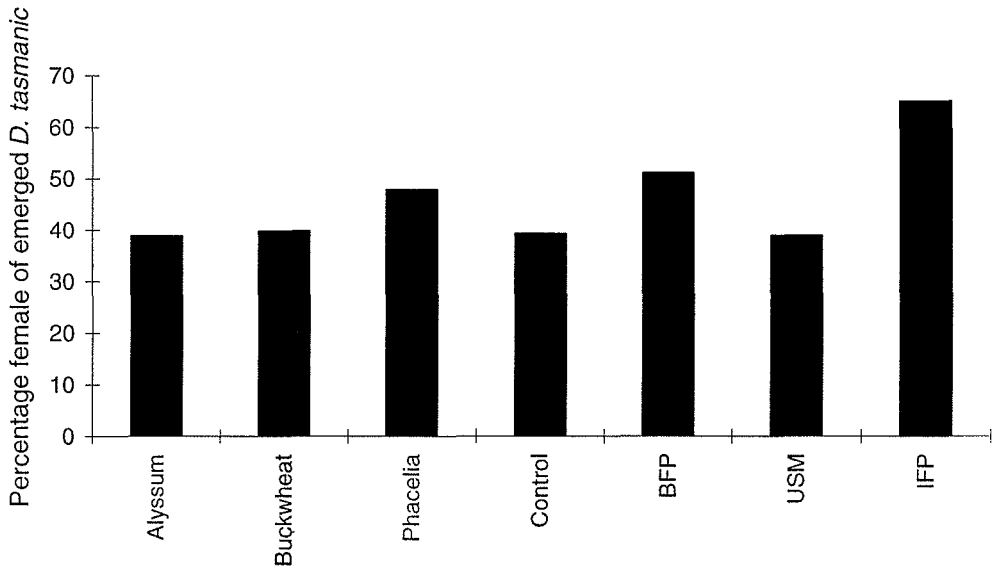


Fig. 4.4 Percentage female *D. tasmanica* that emerged from cocoons collected from the field (see Fig. 4.2).

4.1.4 Discussion

The number of released leafroller larvae collected after two weeks was almost four-fold higher than that collected after four weeks. Tomkins (1984) stated that third instar leafrollers move to new feeding sites. Therefore, removing larvae two weeks after release in the field would reduce the number of larvae lost from the branch from dispersal at the third instar. However, collecting larvae and placing them into individual diet tubes still produced parasitism rates of up to 78.2%, whereas natural levels of parasitism by *D. tasmanica* are approximately 20-30% (Collyer and van Geldermalsen, 1975; Green, 1984; Suckling *et al.*, 1996a). This may be because larvae that are parasitised by *D. tasmanica* are less mobile than unparasitised larvae so a higher proportion of larvae that are collected would be parasitised, giving high parasitism rates. This hypothesis is explored in Chapter 6. Also, the unusually high larval densities caused by artificial release may increase encounter rates by *D. tasmanica*. Therefore, it may be beneficial to sample natural populations of leafroller in each treatment to determine natural leafroller damage, the presence of leafroller larvae and *D. tasmanica* parasitism. This may provide a more

realistic representation of the influence of understorey plant on these parameters. This is explored in Section 4.3.

Leafroller parasitism was 35.2% and 30.4% lower in controls compared with alyssum and buckwheat treatments, respectively. This supports previous field experiments (Sections 2.1 and 3.1) which showed that buckwheat enhanced parasitism of leafroller and indicates that alyssum may have potential perennial understorey for apple orchards. Grossman and Quarles (1990) also showed an increase in parasitism of green pea aphid (*Myzus persicae* Sulzer) by the wasp *Diaeretiella rapae* McIntosh, when lettuce fields were interplanted with alyssum. Results for percentage leafroller pupae between treatments were not significant; however, there were 90.7% and 83.9% less leafroller pupae found in the alyssum and buckwheat treatments, respectively, compared with controls. This may suggest that the effect of providing flowering plants in the understorey on increasing leafroller parasitism, leads to a decrease in pest abundance .

Phacelia did not significantly enhance leafroller parasitism compared with the control. Although this plant is potentially a good source of nectar (Crane *et al.*, 1984), the flowers have deep corollae probably making the nectar inaccessible to short-tongued parasitoids (Holland *et al.*, 1994). Results from this study indicate that, unlike some other braconids, *D. tasmanica* may not have elongated mouthparts that are used to feed on flowers that have deep corollae (Jervis *et al.*, 1996) and that *D. tasmanica* may not crawl down the corollae of phacelia flowers to exploit nectar. This suggests that phacelia would not be a good understorey plant; however, laboratory experiments would be needed to confirm that *D. tasmanica* cannot obtain nectar from phacelia flowers. This is explored in Section 5.1.3.

Providing three flowering species (USM) did not further enhance parasitism rate compared with alyssum and buckwheat alone. This may be attributed to the buckwheat and alyssum treatments already producing parasitism rates of up to 77.53%, therefore making it difficult to further enhance leafroller biocontrol. These high parasitism rates re-emphasise the need to sample naturally occurring leafroller populations as described in Section 4.3. Laboratory studies are also required to determine whether providing *D. tasmanica* with two plant

species synergistically enhances parasitoid longevity, for instance by providing a wider range of amino acids and proteins. This is explored in Section 5.1.1 and 5.1.2.

The addition of flowering plants to the apple management block (USM) would be expected to increase parasitism compared with block BFP. However, parasitism rates were similar between the two treatments (Fig. 4.2). BFP had a mixed herb ley in the inter-row sward consisting of ryegrass, plantain and white clover, and rows were mown alternately to maintain long growth. Therefore, some of the plants in the inter-row sward would have flowered and in turn, provided pollen and nectar to *D. tasmanica*. IFP had a frequently-mown inter-row sward of ryegrass, and the understorey was sprayed with herbicide. This may explain the lower parasitism rate in IFP (67.8%) compared with BFP (78.2%) and USM (77.9%), although this was not significant. The flower treatments in USM blocks may not have significantly enhanced parasitism rate over that in the BFP and IFP blocks because the USM blocks were previously managed using a conventional spray programme that included the organophosphate insecticides chlorpyrifos and diazinon. Therefore, natural enemy populations may not have fully recovered.

BFP blocks may have increased parasitism rate compared with the control in USM because of the presence of flowering plants in the inter-row sward and the presence of pea straw which was used as a mulch in the tree line. Studies show that mulches such as straw tend to have higher soil temperatures in the morning and lower soil temperatures in the afternoon compared with bare soil (Hartley and Rahman, 1994; Hartley *et al.*, 1996). This reduction in temperature fluctuations is advantageous in reducing temperature extremes (Hartley and Rahman, 1994) which may have benefited *D. tasmanica* survival and parasitism. Furthermore, some insects exploit reflectance of light from soil and vegetation surfaces to locate host plants (Harrington and Barbosa, 1978; Barbosa and Benrey, 1998) so the straw mulch may have influenced *D. tasmanica* behaviour.

Buckwheat and alyssum showed potential as annual and perennial understorey plants, respectively, for the enhancement of *D. tasmanica* and results showed that a mixed herb ley and a straw mulch may be an alternative option for enhancing leafroller biological control. However, further research is still required into their influence on pest populations and on

overall crop production, for example, tree yield, fruit quality, nutrient availability, and weed and pest complexes.

The number of larvae recovered from release sites was 39-67% lower in IFP treatments compared with all other treatments. This may be due to the use of the fungicides dodine and myclobutanil in this treatment which may have influenced leafroller survival. For example, dodine has reduced egg hatching of *Amblyseius fallacis* (Garman) (Phytoseiidae: Acari) in Quebec apple orchards (Bostanian *et al.*, 1998).

Providing floral resources in the understorey did not appear to have any effect on the sex ratio of *D. tasmanica* emerging from cocoons collected from the field. This may indicate that like most Hymenoptera and most *Apanteles* spp. (Allen and Smith, 1958), *D. tasmanica* has arrhenotokous ovaries in that haploid eggs develop into males if not fertilised, and into females if fertilised. Therefore, the sex ratio of progeny from *D. tasmanica* may be more strongly determined by whether the females are mated, than by food supply.

4.2 ABUNDANCE OF *D. TASMANICA* IN ALYSSUM, PHACELIA, BUCKWHEAT AND CONTROL TREATMENTS USING VORTIS SUCTION SAMPLING

4.2.1 Introduction

A study in Oregon, USA, used water traps to capture hover flies in alyssum and control treatments set up in a broccoli field (Luna *et al.*, unpublished data). They also collected eggs laid among aphid colonies from the broccoli plants and reared them to adults in the laboratory. Of the 148 hover flies that were captured in the water traps, only 2% were the hover fly species which laid its eggs in the field (J. Luna *et al.*, unpublished data). These results illustrate the importance of not relying on one method of sampling to investigate the influence of providing flowering plants for biocontrol.

In the current study, the past three field seasons have used yellow sticky traps to capture adult *D. tasmanica* to measure abundance, and have measured parasitism rate by releasing leafroller larvae into the field. The use of a single trapping method may bias results towards collecting insects in a particular physiological condition, i.e., individuals with certain nutritional or reproductive requirements (J. Hickman, unpublished data), towards a particular species or cohort within a species (Haslett, 1989), or towards a particular age of insect (Southwood, 1966; Kirk, 1984). Therefore, additional methods of measuring parasitoid abundance are required. The following experiments investigated the use of Vortis suction sampling to estimate *D. tasmanica* abundance in each treatment.

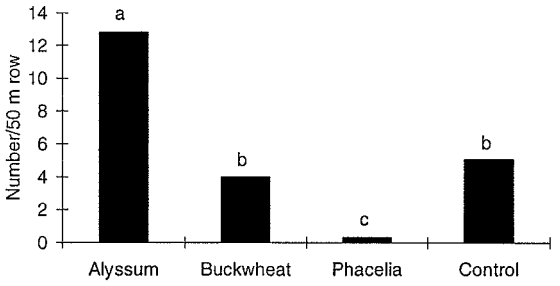
4.2.2 Methods

Sampling using a Vortis suction sampler (Arnold, 1994) was carried out on February 19, 1999, on the north-east side of each row of all three replicates of the alyssum, phacelia, buckwheat and control plots. One sample consisted of walking down the entire row length at a constant speed, sampling the flowering part of the plant (for the control and alyssum treatments this height was lower than for phacelia and buckwheat treatments). The Vortis sampler delivered the catch into a 350 ml cup which was removed and closed with a lid. The cups were placed into a freezer to kill the insects; the contents were then placed into 70% ethanol to await sorting under a binocular microscope in the laboratory. The presence

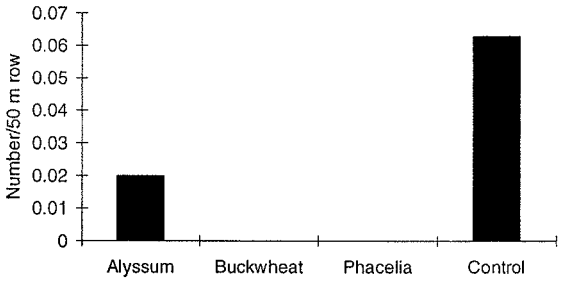
of *D. tasmanica* adults and other parasitoids and predators including lacewing parasitoid adults (*A. zealandica*), Tasmanian lacewing adults (*M. tasmaniae*), hover fly adults (*M. fasciatum*, *M. novaezelandiae* and *E. tenax*), aphids (Aphididae), bees (*Apis mellifera* L.) and bumble bees (*Bombus* spp.) were recorded. Insect abundance data were log-transformed ($\log_e(x+1)$) and differences between treatments were compared using ANOVA and Fisher's least significant difference test.

4.2.2.1 Results

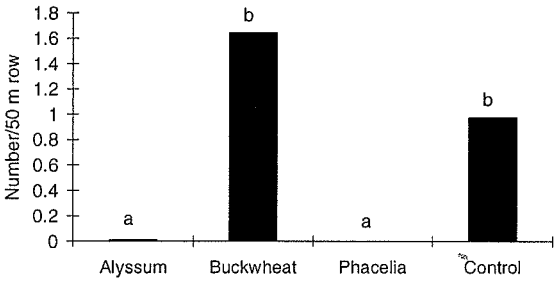
There was a highly significant effect of understorey treatment on *D. tasmanica* abundance ($F=60.16$, df=3,5, $P<0.001$) (Fig. 4.5). Least significant differences tests revealed that *D. tasmanica* abundance was significantly higher in alyssum compared with all other treatments ($P<0.01$). The number of *D. tasmanica* captured in the phacelia treatment was significantly lower than all other treatments, including control ($P<0.001$). Understorey treatments had a highly significant ($F=16.02$, df=3,5, $P<0.001$) effect on aphid abundance and least significant difference tests revealed that buckwheat and controls significantly harboured more aphids than did alyssum and phacelia ($P<0.05$) (Fig. 4.5). There was an overall significant effect of understorey treatment on the number of bees and bumble bees (bees: $F=34.11$, df=3,5, $P<0.01$; bumble bees: $F=26.40$, df=3,5, $P<0.01$). The abundance of both was significantly higher in the phacelia treatments compared with all other treatments ($P<0.01$). There was no significant difference in hover fly and *A. zealandica* abundance between treatments (hover fly: $F=0.95$, df=3,5, $P>0.05$; *A. zealandica*: $F=0.83$, df=3,5, $P>0.05$) (Fig. 4.5). However, *A. zealandica* was found only in the control and alyssum treatments and three times as many were found in the controls compared with alyssum. No leafroller larvae were found in any treatments.



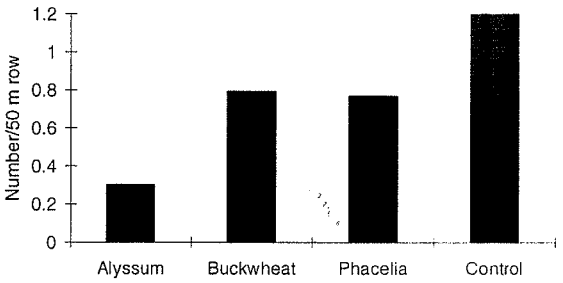
a) *Dolichogenidea tasmanica*



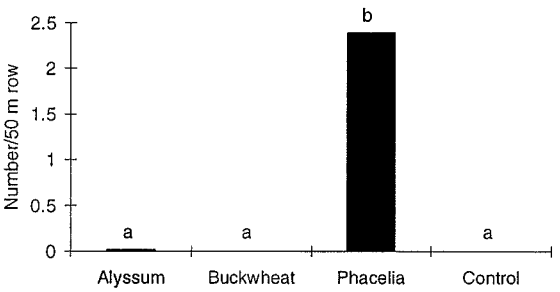
b) *Anacharis zealandica*



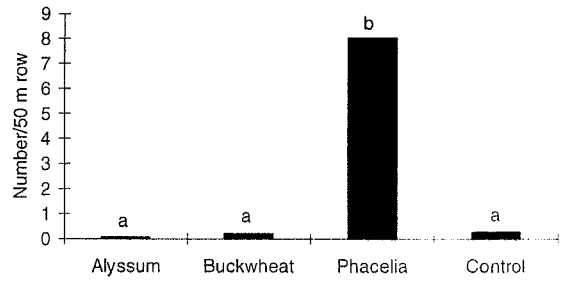
c) Aphididae



d) Syrphidae



e) *Bombus* spp.



f) *Apis* spp.

Fig. 4.5 The mean number of insects captured by Vortis suction sampling of the flowers in alyssum, buckwheat, phacelia and control plots on February 19, 1999 (different letters indicate significant differences between treatments for each insect group ($P<0.05$)).

4.2.2.2 Discussion

The abundance of *D. tasmanica* was over two-fold higher in the alyssum treatment compared with buckwheat, phacelia and control. These results are similar to those shown in Section 4.1 which showed that planting alyssum in the orchard understorey increases leafroller parasitism compared with phacelia and the control. Buckwheat also enhanced leafroller parasitism compared with the latter treatments in Section 4.1, whereas in the current study, it did not enhance *D. tasmanica* abundance. This may be attributed to the Vortis suction sampler not sampling the buckwheat and phacelia treatments as effectively as it did the alyssum and control treatments. The greater height of buckwheat and phacelia made it difficult to hold the suction sampler and increased the angle from which they were sampled. Also, the control may have contained some flowering weeds from the edge of the inter-row sward, such as white clover. Parasitoids can gain access to floral nectar of white clover through holes in the corollae of previously bitten by other insects, such as bees (Newton and Hill, 1983) and ichneumonds (Idris and Grafius, 1997). Therefore, the presence of white clover in the controls may have led to there being more *D. tasmanica* in this treatment.

Section 2.1 showed that buckwheat enhanced lacewing abundance three-fold compared with controls. This may have been due to a higher number of prey in buckwheat plots; however, the current study showed that aphid numbers were similar in both treatments. Therefore, it was probably the flower that attracted the lacewings to the buckwheat plots in Section 2.1, and not alternative prey.

Alyssum may be a suitable perennial understorey option for apple growers because it attracted more *D. tasmanica* than all other treatments and resulted in higher parasitism rates than controls (Section 4.1). It would be beneficial to conduct experiments to determine whether these results are due to the parasitoid exploiting the floral resources, leading to increased parasitoid longevity and fecundity. This is explored in Section 5.1.2. In the current study, alyssum also had the additional benefit of harbouring significantly less aphids than buckwheat and control plots. However, the species of aphids were not identified so it is not known if they were orchard pests. If apple was not a host of the aphid

species found then they may have been beneficial by providing alternative prey and honeydew as additional food sources for natural enemies.

Alyssum did not attract large numbers of bees which may interfere with manual operations around the orchard due to worker allergies and phobias. Furthermore, *A. zealandica* abundance was three times lower in alyssum plots compared with control. *A. zealandica* is a parasitoid of the Tasmanian lacewing (*M. tasmaniae*) which is a general insect and mite predator (Leathwick, 1989). This is similar to field trials (Section 2.1) which showed that sowing buckwheat in the orchard understorey does not enhance numbers of *A. zealandica* but contradicts research by Stephens *et al.* (1998), who found that in the 1994-95 field season there were up to ten times more *A. zealandica* in the buckwheat plots compared with the controls.

Lower numbers of *D. tasmanica* were captured in phacelia plots compared with all other treatments, supporting results reported in Section 4.1. These studies suggest that *D. tasmanica* does not exploit flowers that have deep corollae, such as phacelia. Parasitoids can learn to recognise a particular flower odour following feeding experience on that flower (Patt *et al.*, 1999), therefore *D. tasmanica* may not visit phacelia plants after an initial encounter because there is no reward. However, laboratory studies would be needed to confirm this hypothesis (Section 5.1.3).

No leafroller larvae were found in any treatments. This supports Suckling *et al.* (1996b) who showed that suction sampling did not represent leafroller larvae numbers even though they were present. It may have been beneficial to conduct hand searching of the understorey plants to determine whether they harboured leafroller. This concept is explored further in Section 5.2 with laboratory trials that investigate whether these understorey plants are suitable hosts for leafroller.

4.3 NATURAL INSECT POPULATION SAMPLING

4.3.1 Introduction

Releasing larvae in the field to estimate parasitism produced unrealistically high parasitism rates. The study in Section 2.1 produced parasitism rates of up to 86% (significantly so on one date) in buckwheat plots, whereas natural levels of parasitism by *D. tasmanica* in apple orchards are approximately 20-30% (Collyer and van Geldermalsen, 1975; Green, 1984; Suckling *et al.*, 1996a). This may be because larvae that are parasitised are less mobile than unparasitised larvae or are less prone to predation. This hypothesis is examined in Chapter 6. Information on density-dependent searching by *D. tasmanica* is unknown. However, in the study described in Section 2.1.3.1 a high proportion of the leafroller larvae that were parasitised had 100% parasitism, suggesting that once *D. tasmanica* finds a patch of larvae, it parasitises all that are present. High parasitism may not necessarily translate into adequate pest management, and leafroller releases in the field may overestimate parasitism and the potential for *D. tasmanica* to control leafroller. Therefore, the following experiment samples the natural populations of leafrollers in the alyssum, phacelia, buckwheat and control plots and records the presence of damage on apple foliage, and the numbers of leafroller larvae and pupae and parasitoid cocoons present.

4.3.2 Methods

On February 15, 1999, four trees in each of the alyssum, phacelia, buckwheat and control treatments were sampled in each of the three replicates. These trees were randomly located by tree number and row number, but trees which had been used for leafroller release in Section 4.1 were avoided. A three-minute search of apple foliage was conducted at a height of 1-2 m, in a band around the tree. The number of leafroller larvae and pupae, *D. tasmanica* cocoons and the number of leaves showing leafroller feeding damage was recorded. Data were log-transformed ($\log_e(x+1)$) to normalise distributions and treatments were compared using ANOVA. The data were also grouped based on whether the tree sampled was on the perimeter, non-perimeter or central part of the block (see Fig 4.1). To determine whether more insects were found on the perimeter of the blocks, leafroller

damage, the number of leafroller larvae and the number of *D. tasmanica* cocoons were compared between these groups. Only one pupa was recovered from the trees sampled.

4.3.3 Results

There was no significant difference between any of the understorey treatments and controls in terms of leafroller damage and numbers of leafroller larvae and parasitoid cocoons (leafroller damage: F=1.37, df=3,42, $P>0.05$; larvae: F=0.338, df=3,42, $P>0.05$; parasitoid cocoons: F=1.58, df=3,42, $P>0.05$). However, leafroller damage and the number of leafroller larvae present were respectively 20.3% and 29.3% lower in the flowering treatments compared with controls (Fig. 4.6). Also, the number of *D. tasmanica* cocoons was more than twice as high in the alyssum and buckwheat treatments compared with controls (Fig. 4.6). Only one leafroller pupa was found over the 48 trees sampled and it was in a control plot. There was no significant difference in leafroller damage, number of leafroller larvae and number of parasitoid cocoons between the three perimeter groupings (damage: F=0.550, df=2,40, $P>0.05$; larvae: F=1.24, df=2,40, $P>0.05$; cocoons: F=0368, df=2,40, $P>0.05$).

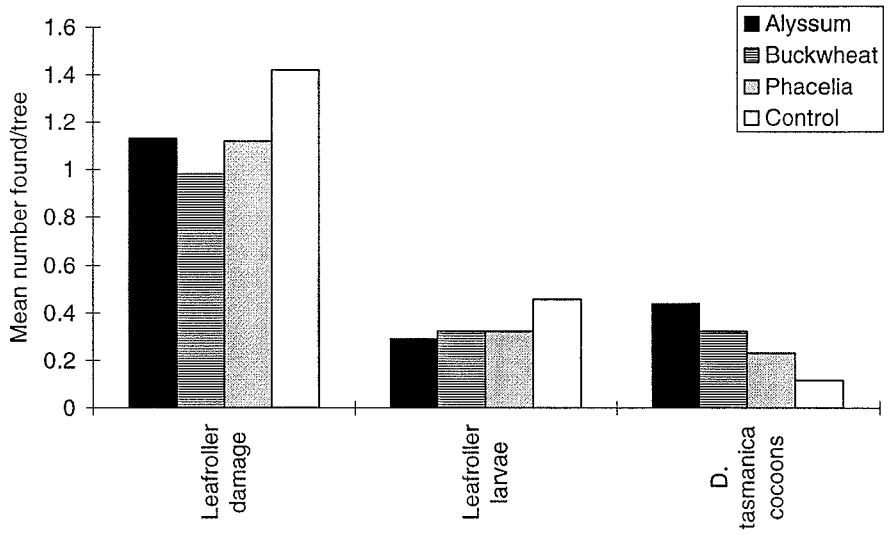


Fig. 4.6 The mean number of leafroller damage, leafroller larvae and parasitoid cocoons found per tree in the alyssum, buckwheat, phacelia and control plots on February 15, 1999 (there were no significant differences between treatments ($P>0.05$)).

4.3.4 Discussion

No significant results were obtained from sampling natural leafroller populations, possibly due to the small number of replicates and the low leafroller population present. This illustrates why it was necessary to make leafroller releases in previous field work to increase the leafroller population and make it easier to detect significant differences in parasitism rates between treatments. However, trends here showed that the number of parasitoid cocoons were over twice as high in the alyssum and buckwheat treatments compared with controls. This supports the results from Section 4.1 which showed that leafroller parasitism was 35.2% and 30.4% lower in alyssum and buckwheat treatments, respectively. In the current study, leafroller damage was 20.3% (but not significantly) lower in the flowering treatments compared with the control, indicating that increasing leafroller parasitism rate may translate into an increase in pest control and a decrease in damage to apple foliage. In fact, the number of larvae found in the flowering treatments was 29.3% lower than controls, providing further supporting evidence. However, it is not known how many of these larvae were parasitised by *D. tasmanica*.

The number of leafroller larvae found in the phacelia treatment was equivalent to those found in the buckwheat treatment. This contradicts field work which showed that phacelia reduced leafroller parasitism 27.8% compared with buckwheat (Section 4.1). Also, Vortis sampling the understorey treatments suggested that phacelia contained 92.4% less *D. tasmanica* than did buckwheat (Section 4.2.). Although the number of leafroller larvae were equivalent in both treatments in the current study, the number of *D. tasmanica* cocoons found in phacelia was 28.5% lower than those found in buckwheat. This suggests that counting leafroller larvae as a measure of the success of biocontrol may not be a suitable parameter because the proportion of these larvae which are parasitised is not known. For example, although the same number of larvae were found in the buckwheat and phacelia treatments, a lower proportion of these may have been already parasitised in the phacelia treatment. Therefore, it may be beneficial to randomly collect larvae over all trees and branches in each treatment, place them into individual diet tubes and calculate the proportion parasitised. If parasitised larvae are more mobile than unparasitised ones (see Chapter 6), this method may give more realistic parasitism rates, compared with releasing larvae in the field.

Male larvae frequently leave their webbed shelters and prepare a special site for pupation, usually on the lower portion of the tree (MacLellan, 1973). This may explain why only one leafroller pupa was found after sampling 48 trees because a 1-2 m band of the apple canopy was surveyed during the study. Therefore, larvae which left to disperse to the lower portion of the tree, or dropped to the ground to pupate, would not have been sampled.

There was no significant difference in leafroller damage or the number of leafroller larvae or *D. tasmanica* cocoons between the three perimeter groupings. This supports results of Lawson *et al.* (1996) who found no edge effect of the activity of the obliquebanded leafroller *Choristoneura rosaceana* (Harris) around perimeters of commercial apple orchards blocks. However, there is often an edge effect where LBAM eggs are found in higher numbers along the ends of rows or in sheltered locations (Clancy, 1997).

4.4 DIRECTIONAL TRAPS TO DETERMINE THE MOVEMENT OF *D. TASMANICA*

4.4.1 Introduction

As discussed in Section 4.1, it is important to determine the mechanisms responsible for increased parasitoid abundance in the presence of flowering plants. Field work showed that it is the flower which attracts the parasitoid to the buckwheat plant (Section 2.1), and laboratory experiments will investigate the influence of floral resources on parasitoid longevity and fecundity (Sections 5.1). Section 4.1 showed that providing floral resources in the understorey appeared to have no significant effect on the sex ratio of subsequent progeny. Jervis *et al.* (1996) reported that providing flowering plants increased immigration of parasitoids and decreases those lost through emigration. However, questions still remain to where the parasitoids are attracted from and whether they will move to the apple canopy to exert biocontrol of leafroller. Searching for food resources and hosts involves metabolic costs to the parasitoid, therefore it is advantageous to be able to feed and breed on the same plant (Eijs *et al.*, 1998). Also, Geervliet *et al.* (1994) showed that *Cotesia rubecula* (Marshall), a parasitoid of the white butterfly *P. rapae.*, searched for hosts on the same host plant in which they were reared and rich floral patches may act as a 'sink' for ovipositing females, in turn negatively affecting integrated pest management programmes. For example, MacLeod (1999) found that providing additional resources slowed the rate of dispersal of the syrphid *E. balteatus* by over three times compared with the control. Therefore, parasitoids feeding on understorey plants may not move into the apple crop to parasitise leafroller. The following experiment investigates the movement of *D. tasmanica* to and from a buckwheat plot.

4.4.2 Methods

'Directional traps' consisted of a sheet of perspex (210 x 297 mm) clipped with two bulldog clips in between two steel rods pushed into the ground (Plate 13). On each side of the perspex and acetate sheet covered with a sticky polybutene-based insect trap adhesive was positioned and fastened at the bottom with a paper clip. On February 15, 1999 one directional trap was placed in the middle of rows three and four of each replicate of the

buckwheat and control plots in the USM block (Fig 4.1). In the buckwheat plots, the trap was positioned between the tree and buckwheat plants. In the controls, the traps were placed in the same relative position. Traps were positioned 1 m above the ground (half way between the buckwheat and tree canopy), running south-east to north-west (see Fig 4.1). After two weeks they were collected and the number of *D. tasmanica* on each side of the trap was counted under a binocular microscope in the laboratory. An ANOVA for repeated measures was conducted on the data to determine the difference in *D. tasmanica* abundance between the north-east and the south-west side of the traps within the buckwheat and control plots.

Plate 13. Transparent sticky trap placed between apple tree and buckwheat strip.

4.4.3 Results

Twenty six percent less *D. tasmanica* were captured on the north-east side of the traps in the buckwheat pots than on the south-west side (Fig. 4.7). In contrast, 34.6% less *D. tasmanica* were captured on the south-west side of the traps in the control plots than on the north-west side (Fig. 4.7). However, these differences were not significant (buckwheat: $F=1.79$, $df=1,5$, $P>0.05$; control: $F=0.28$, $df=1,5$, $P>0.05$).

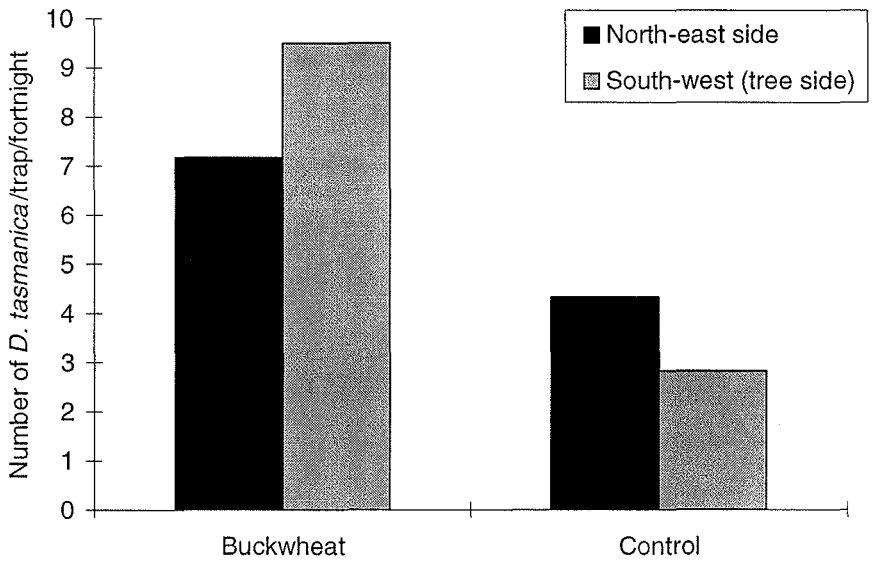


Fig. 4.7 The mean number of *D. tasmanica* per fortnight captured on each side of transparent sticky traps placed in the middle of buckwheat and control plots on February 15, 1999 (see Fig. 4.6).

4.4.4 Discussion

Although the results were not significant, more *D. tasmanica* were captured on the north-east side of the traps in the control plots, whereas this trend was reversed for traps placed in buckwheat plots. Surface wind at Lincoln is highly directional as a result of channelling, with prevailing north-easterly (22%) and easterly (18%) winds, typically averaging 3.8-4.4 m/sec (at 6 m) for February (Ryan, 1987). These strong prevailing winds may have blown parasitoids on to the north-east side of the trap, hence explaining why a higher number of *D. tasmanica* were captured on this side in the controls compared with south-west. However, in the buckwheat plots this trend was reversed so that a higher number were captured on the tree side (south-west) of the trap compared with the buckwheat side (north-east). This may be attributed to a higher cohort of parasitoids flying from the tree to the buckwheat plants for floral resources, compared with those flying from the buckwheat flowers into the apple canopy. For example, male, gravid female and non-gravid female

parasitoids would fly from surrounding areas, even against the prevailing wind, to the buckwheat for floral resources and possibly mate seeking. However, only gravid females would fly from the buckwheat flowers in to the tree canopy to seek hosts. Wind direction may not have influenced the movement of *D. tasmanica* in the buckwheat plots compared with the control because there was a source of nectar influencing their behaviour. However, the buckwheat may also have sheltered parasitoids from the wind. These interpretations must remain tentative, however, because of the lack of statistical significance pointed out at the beginning of this section.

There was a suggestion of higher number of parasitoids captured on the tree side of the traps compared with the buckwheat side suggesting that *D. tasmanica* migrates to the buckwheat strip, even up wind, to use floral resources or shelter. However, results were not significant and it is not known whether *D. tasmanica* would mate on floral strips or in the apple canopy after emergence or what sex or condition the individuals on each trap side were. Therefore, firm conclusions on whether gravid females fly from the buckwheat into the crop for leafroller biological control are not warranted. Section 3.3 showed that *D. tasmanica* travels into rows adjacent to buckwheat plots and Powell (1986), Lővei *et al.* (1993a) and Long *et al.* (1998) have found that parasitoids commute between nectar sources and the crop. Therefore, it is possible that *D. tasmanica* flies into the apple canopy after feeding, but it would be beneficial to repeat this experiment, sexing *D. tasmanica* captured and dissecting adults for gut fullness and egg load, so that conclusions regarding the direction the movement of different cohorts could be drawn. Also, some mark/release/recapture work would help track the scale of movement of *D. tasmanica* from the flowering strips to the apple canopy.

5. PARASITOID AND LEAFROLLER BIOLOGY

The following chapter describes laboratory experiments carried out to investigate the influence of floral resources on the fitness of adult *D. tasmanica* and adult leafroller. It also determines whether the understorey plants used in previous field season are suitable hosts of LBAM.

5.1 THE EFFECT OF FLORAL RESOURCES ON PARASITOID FITNESS

It is important to investigate the mechanisms behind the increase in parasitoid abundance and parasitism rate shown in the previous field work. Results from Section 2.1 suggest that it was buckwheat flowers which attracted the parasitoid to the plant and not the shelter which the plant also may have provided. However, the question remains as to what effect the understorey flowers have on parasitoid fitness.

Floral and extrafloral nectar are significant sources of nutrients for most adult Hymenoptera (House, 1977). They maximise longevity and fecundity (Hagley and Barber, 1992; Wäckers and Swaans, 1993; Idris and Grafius, 1995; Baggen and Gurr, 1998), searching activity (Takasu and Lewis, 1995) and parasitism (Treacy *et al.*, 1987; Somchoudhury and Dutt, 1988), and Jervis *et al.* (1996) concluded that "food availability and/or quality influences parasitoid fecundity, survival, various key foraging decisions, searching efficiency, primary sex ratio, egg viability, the incidence of diapause among progeny, the likelihood of flight initiation, the timing of flight, host and parasitoid population dynamics, competitive interactions and niche partitioning among parasitoid species, productivity in parasitoid cultures, the probability of establishment in classical biocontrol, and the ability of parasitoids to control pest populations." However, not all nectars are beneficial to parasitoids (Elliot *et al.*, 1987), therefore it is essential for conservation biological control to determine those that are.

Host feeding has been recorded in the females of 17 families of parasitoid Hymenoptera (Jervis and Kidd, 1986) and Diptera (Clausen, 1940; Nettles, 1987). The majority of these species consume haeomolymph secreted from an ovipositor puncture or from a puncture made specifically for the purpose, either with the mouthparts or with the ovipositor (Jervis

et al., 1996). It is not known whether *D. tasmanica* feeds on its host; however, this is unlikely because *D. tasmanica* parasitises leafroller larvae which are sheltering under webs in rolled leaves (Dumbleton, 1935). Therefore, the head of *D. tasmanica* probably does not come in direct contact with the larva. This means that floral resources are probably important for this parasitoid because it cannot obtain the nutrients required for tissue maintenance and egg production via host feeding. Some parasitoids of concealed hosts construct feeding tubes that connect a puncture in the host with the exterior (Jervis *et al.*, 1996). However, if *D. tasmanica* feeds, then floral resources would still probably be important for survival and reproduction. For example, Heimpel *et al.* (1997) showed that in the absence of honey, host feeding had no significant effect on the longevity and fecundity of *Aphytis melinus* DeBach.

It is not known whether *D. tasmanica* is proovigenic or synovigenic. Proovigenic parasitoids emerge with their full lifetime complement of eggs, so do not require materials for egg production, but still require carbohydrates for tissue maintenance. Synovigenic parasitoids mature their eggs during adult life, so they require materials for egg production as well as maintenance (Jervis and Kidd, 1986; van Lenteren *et al.*, 1987). It is likely that *D. tasmanica* is a synovigenic parasitoid (P. Cameron, pers. comm.), therefore increasing longevity would increase the potential to produce more eggs over time and enable more leafrollers to be parasitised. If *D. tasmanica* is proovigenic, increasing longevity will still increase the likelihood of finding suitable hosts over its life span, decreasing superparasitism.

High fecundity is considered necessary for parasitoids to be able to reproduce more rapidly than the pest's population and to respond to changes in the abundance of the pest (Sweetman, 1958; Waage and Hassell, 1982; Waage, 1990; Ehler, 1995). Parasitoids with a higher fecundity have a greater frequency of success in biocontrol and there is a significant positive relationship between the outcome of biocontrol and parasitoid fecundity for Lepidoptera (Lane *et al.*, 1999). Therefore, it may be possible to choose an understorey plant which not only attracts the parasitoid into the desired crop but also maximises *D. tasmanica* survival and fecundity, in turn offering greater control of leafroller. The following experiments investigated the influence of floral resources on *D. tasmanica*

fitness in the laboratory and to determine which understorey plant species maximise longevity and fecundity.

5.1.1 The influence of buckwheat, coriander and broad bean on parasitoid fitness

5.1.1.1 Introduction

The following experiment compares the understorey plant species used in the 1997 and 1998 field seasons to determine which was optimal for fecundity and longevity. Plants trialed during these field seasons were buckwheat, broad bean and coriander. The nectar of the flowers of broad bean is probably inaccessible to short-tongued parasitoids but a rich assemblage of ichneumonids attend extrafloral nectaries of broad bean (Bugg *et al.* 1989). Section 2.1 showed that sowing broad bean in the orchard understorey significantly enhanced *D. tasmanica* abundance, although, significantly less so than buckwheat. *D. tasmanica* has been seen feeding on the extrafloral nectaries of *Acacia longifolia* (Andr.) Willd. and *A. leprosa* (Collyer and van Geldermalsen, 1975). Broad bean was included as a treatment in the following experiment to examine the use of its extrafloral nectaries by *D. tasmanica*. Honey/water solution was included because it is often used as an energy supplement when culturing this parasitoid (Dumbleton, 1935) and other insects (Lee *et al.*, 1996; Loomans *et al.*, 1997; Thompson, 1999). Coriander and buckwheat were also combined as one treatment to determine whether providing two plant species would further enhance parasitoid fitness.

5.1.1.2 Methods

Five replicates, each of six treatments (water, 50:50 honey/water solution, buckwheat (cv. 'Shinano Natsu'), broad bean (cv. 'Exhibition Long Pod'), coriander (var. microcarpum) and buckwheat and coriander combined) were set up in a randomised complete block design under a 16:8 L/D photoperiod, at 16.5°C with a 2°C range. The water and honey/water treatments were contained in a 40 mm x 15 mm vial filled and sealed with a

cotton wool plug. A water-filled vial was placed in each treatment to prevent dehydration. Plant treatments consisted of a 5 cm length of flowering stem(s) placed in a similar water-filled vial and sealed with a cotton wool plug. All treatments were topped up with water or honey/water solution as necessary. Plant material was not replaced. Vials were covered with a cylindrical acetate sheet with netting glued on one end (similar to Plate 14).

Five diet tubes, each with five first instar LBAM larvae were placed in each treatment (Plate 14). These diet tubes had been inverted for 24 hours before use to settle the larvae and minimise their dispersal. The diet tubes containing the leafroller larvae were removed and replaced every five days. Larvae which strayed were removed with a small paint brush and placed into one of the diet tubes. They were then placed into an airtight container and incubated at 25°C with a 2°C range.

Plate 14. One replicate of the seven floral resource treatments from Section 5.1.2, with diet tubes containing leafroller larvae. Treatments were (from left): broad bean, buckwheat, alyssum, buckwheat without flowers, buckwheat and alyssum combined, water and 50:50 honey/water.

A pair of newly-emerged adult *D. tasmanica* was placed in each treatment. Parasitoids were obtained from a culture of *D. tasmanica* from LBAM larvae reared on potted crab apple trees (*Malus* ex 'Crimson Red) into a Perspex box (55 x 50 x 50 cm) lined with damp tissue paper. This box was maintained under a 16:8 L/D photoperiod at 16.5°C with a 2°C range. A 50% honey/water solution was supplied as a source of 'nectar' to the adult

parasitoids. Some parasitoids were used for laboratory experiments while enough were left to continue the culture. Four generations of *D. tasmanica* were produced before the culture became unproductive.

Parasitoid longevity (measured in days) for both sexes was checked daily on most occasions and when not, every second day. Males were not replaced once dead. Survival curves were compared between treatments using a the log rank test and Kaplan Meier estimates of mean survival were calculated (Kaplan and Meier, 1958).

5.1.1.3 Results

There was an overall effect of floral treatment on male and female longevity (male: X^2=24.9, df=5, P<0.001; female: X^2=21.647, df=5, P<0.01). Individual Kaplan Meier estimates between pairs revealed that the water-only treatment resulted in the shortest longevity of both female and male *D. tasmanica*, which was significantly lower than all other treatments, except coriander (P<0.05) (Figs. 5.1 & 5.2). Longevity of parasitoids in the honey/water treatment was significantly greater than in the coriander treatment for adult *D. tasmanica* (P<0.05). No other treatment combinations differed significantly for female *D. tasmanica* (P>0.05) (Fig. 5.2). However, for males the honey/water treatment (mean=21.1 days) also gave a significantly greater longevity than did buckwheat (10.2) (P<0.05) (Fig. 5.1). Combining buckwheat and coriander flowers gave a significantly higher longevity than those for buckwheat or coriander alone, for male *D. tasmanica* (P<0.05) (Fig 5.1). The diet tubes eventually became contaminated with fungi, so the number of cocoons produced, and hence fecundity, could not be measured.

5.1.1.4 Discussion

The longevity of female and male *D. tasmanica*, being significantly lower in the water-only treatment compared with all other floral treatments (except coriander) even in the presence of hosts, may be even more significant in the field since the parasitoid would have far greater energy requirements (for mate searching, host searching and oviposition) in the natural habitat. Results indicate that *D. tasmanica* may not host feed and that floral resources are vital for survival. Baggen and Gurr (1998) similarly found that longevity of

Copidosoma koehleri Blanchard, a parasitoid of potato moth, *Phthorimaea operculella*, was significantly increased when adults were caged on flowering plants of dill (*Anethrum graveolens* L.) and borage, compared with these species without flowers. Many other laboratory studies have also shown that in the absence of food, longevity of both sexes of parasitoids is significantly reduced (Hagen, 1964, 1986; Jervis and Kidd, 1986; van Lenteren *et al.*, 1987).

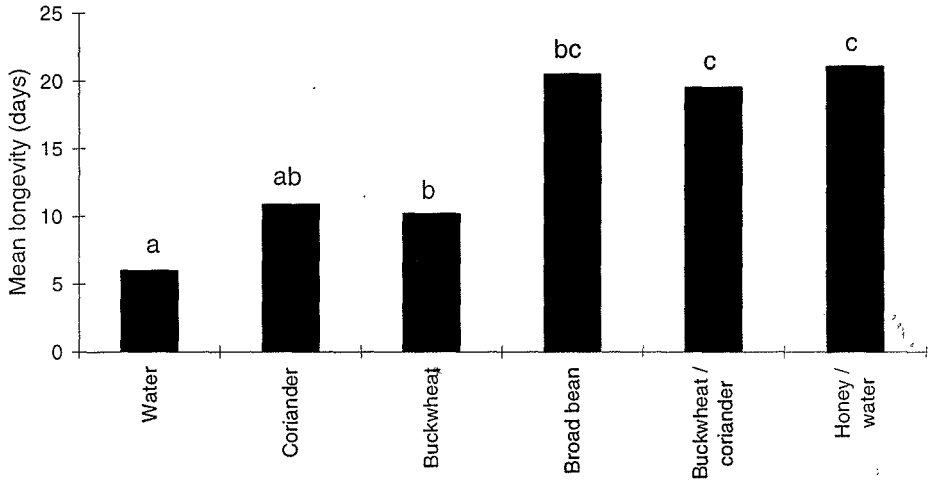


Fig. 5.1 Mean longevity (days) of male *D. tasmanica* provided with different food sources in the laboratory at 16.5°C (different letters indicate significant differences between treatments ($P<0.05$)).

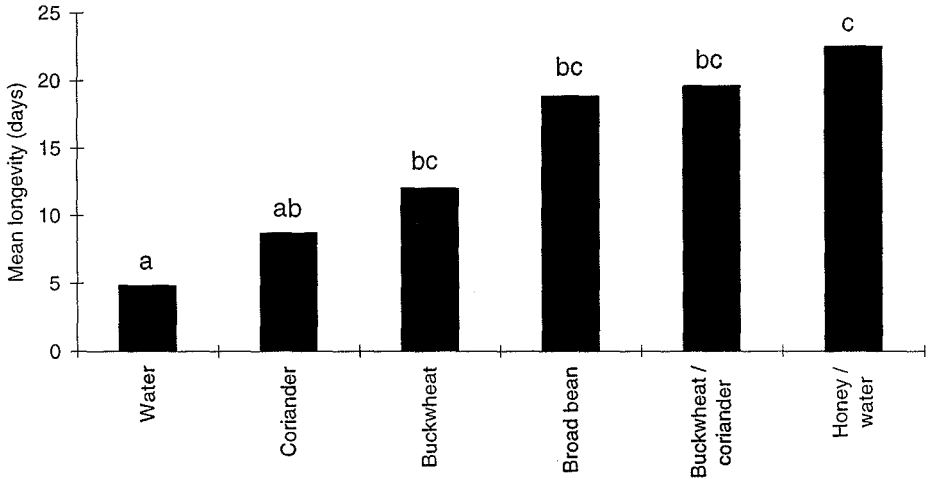


Fig. 5.2 Mean longevity (days) of female *D. tasmanica* provided with different food sources in the laboratory at 16.5°C (see Fig. 5.1).

Buckwheat enhanced longevity of both sexes of *D. tasmanica* compared with water. This may explain results from Section 2.1 which showed that planting buckwheat in the orchard understorey attracted parasitoids to the vicinity of flowers and increased leafroller parasitism on one leafroller release date. Sirot and Bernstein (1997) reported that parasitoids with a longer life expectancy are less likely to superparasitise.

Coriander did not enhance parasitoid longevity compared with water-only. This contradicts results from Section 3.1 which showed that coriander sown in the orchard understorey enhanced parasitism more than three-fold compared with controls. Also, studies have shown that coriander was one of the two most preferred floral resources by hover flies in the United Kingdom and in New Zealand (MacLeod, 1992a; Lővei *et al.*, 1993b), and Baggen and Gurr (1998) found that longevity of *C. koehleri* was significantly increased when adults were caged on flowering coriander compared with coriander without flowers. Floral features such as colour, depth of corolla tube, and nutritional value of pollen and nectar are believed to be important factors influencing use of flowers by hover flies (MacLeod, 1992a). This may suggest that *D. tasmanica* cannot access the flowers of coriander. This is consistent with Patt *et al.* (1997b) who showed that *Edovum puttleri* Grissell (Eulophidae) had great difficulty gaining access to the nectar of coriander which has partially exposed nectaries. They attributed this to the head width of *E. puttleri* (0.47 mm) being much larger than the size of the gap between the stamen and petals of coriander (0.23 mm).

The discrepancies between studies may also be attributed to not replacing plant material during the current study, whereas Baggen and Gurr (1998) used intact flowers. Using cut stems in water instead of intact flowers may have influenced the quality, quantity and duration of nectar supplied. Also, the rate at which the cut stems deteriorate may differ between species. For example, ethylene, gibberellins and cytokinins influence a number of plant processes, such as cell death, petal wilting and flower opening (van Doorn and Woltering, 1991). Therefore, plant species which differ in their ability to produce these hormones or in their ability to uptake water once cut will differ in 'vase life' or flower quality (Brandt and Woodson, 1992; Wernett *et al.*, 1996). Coriander may therefore perform poorly once cut and placed in water.

Longevity of female and male *D. tasmanica* on the honey/water solution was greater than in all other floral treatments. This suggest that honey/water may be a suitable resource for increasing *D. tasmanica* longevity when culturing this species. However, to be certain, its influence on fecundity would also have to be determined. This is explored in Section 5.1.2. Results from the current study were similar to those of Rechav (1978) who showed that adults of the braconid *Chelonus inanitus* L. offered honey/water lived significantly longer than those offered fresh flowers. This highlights the inability to apply results from artificial food experiments to the field situation. However, in the current study, results may have been influenced by the fact that the honey/water solution was a constant food source in terms of quality, in contrast to the plant material, which was not replaced and may have deteriorated during the experiment. Furthermore, the honey/water solution may have increased humidity in the cages of this experiment and may have influenced parasitoid survival. For example, Allen and Smith (1958) showed that female *Apanteles medicaginis* Mues. survival was increased from 18.4 to 28.2 days when humidity was increased from 30 to 55%. They concluded that humidity is an important factor in parasitoid longevity. Also, Hodgson *et al.* (1993) stated that high humidity was important for the survival of *Microctonus hyperodae* (Loan). The effect of honey/water solution on humidity is explored in Section 5.3.

Broad bean enhanced *D. tasmanica* survival compared with water for both sexes. Large numbers of *D. tasmanica* have been seen feeding on the extrafloral nectaries of *Acacia longifolia* and *A. leprosa* (Collyer and van Geldermalsen, 1975). Results here indicate that *D. tasmanica* can forage nectar from broad bean extrafloral nectaries and that nectar quality is sufficient to sustain parasitoid survival. These results support research by Bugg *et al.* (1989) who discovered 20 species of Icheumonidae feeding at the extrafloral nectaries of this plant. Broad beans may show potential as an understorey plant species for natural enemy enhancement as extrafloral nectaries are easily accessible and, unlike flowers, they provide abundant food throughout the growing season (Stapel *et al.*, 1997). However, field work suggested that nectar production stopped once the plant had matured (Section 2.1). Also, if parasitoids cannot access the flowers of broad bean, this plant will not provide pollen. Pollen is thought to be required for sexual maturation of some natural enemies such

as hover flies and parasitoids (Schneider-Orelli, 1945; van Emden, 1963); however, fecundity could not be investigated here because the diet tubes containing larvae exposed to the parasitoids became infected with fungi. The influence of broad bean on parasitoid fecundity is explored further in Section 5.1.2.

For male *D. tasmanica*, a combination of buckwheat and coriander gave a significantly greater longevity than either species on its own. The provision of two pollen and nectar sources may synergistically enhance parasitoid longevity, possibly by providing a wider range of amino acids and proteins required by the parasitoid. Also, the increase in leaf area from having two flowering stems in this treatment compared with one may have increased humidity, prolonging parasitoid survival. These two plants may have different peaks in nectar production, therefore enhancing longevity by supplying nectar over a longer period of time. Furthermore, one plant may have provided nectar and the other pollen, which may have led to a greater resource for the parasitoid.

Field trials need to be conducted to determine whether a combination of two different flowering species in an orchard's understorey further enhances parasitism by *D. tasmanica* or reduces leafroller abundance. The objective of conservation biological control is to ensure that the occurrence of as many essential parasitoid resources coincides in time and space (Barbosa and Benrey, 1998). Therefore, determining the daily variation in nectar production times of the plants used before implementation may also be beneficial as it could be possible to provide two species with opposite peaks in nectar production, thereby supplying nectar to natural enemies throughout the day. For example, Björkman (1995) reported that anthers of buckwheat were open only between 8.30-9.30 am and that by 11.00 am pollen was scarce. It may be possible to find a plant where pollen was available during the afternoon, therefore extending the period which it is available to natural enemies. Furthermore, if the activity and feeding period of *D. tasmanica* was determined, then an understorey plant could be chosen with a nectar and pollen production matching with the parasitoid's peak activity. For example, Bennett and Beg (1970) found that adult *Jaynesleskia jaynesi* Aldrich flies were most numerous and fed frequently at flowers from 7.30-9.30 am.

Parasitoids used during this experiment were sourced from a culture of *D. tasmanica* which, after four generations became unproductive. This sudden decline in progeny may have been due to inbreeding and suggests that the individuals used for this experiments may not have been of high genetic quality. Many studies reported inbreeding problems arising from insect cultures which led to increased mortality or decreased vigour (Breene *et al.*, 1989; Lawson and Morgan, 1992; Zheng *et al.*, 1993). In the current study, a decrease in vigour may have influenced results because parasitoids may not have been as resilient to stressful conditions, such as the water-only treatment.

Fecundity data could not be obtained from this experiment. The diet tubes containing larvae which had been exposed to the parasitoids in each treatment were placed in an airtight container and incubated at 25°C to speed up development. An airtight container was used to prevent the diet from drying out (Clare *et al.*, 1987). Although the diet contained a fungicide (A. Barrington, pers. comm.), this temperature caused excessive mould growth causing loss of data. The Insect Rearing Unit (Insect Science Group, HortResearch, Auckland, New Zealand) successfully rear larvae in individual diet tubes at 20°C (A. Barrington, pers. comm.). Reducing the temperature at which the tubes were incubated and decreasing the number of larvae per tube may reduce mould growth.

This experiment needs to be repeated, modifying the fecundity protocol, using parasitoids reared from the field and renewing plant material more regularly to provide a constant nectar and pollen supply. This is investigated in the following Section.

5.1.2 The influence of alyssum, buckwheat and broad bean on parasitoid fitness

5.1.2.1 Introduction

As discussed in Section 5.1, it is important to understand the mechanisms behind the increase in parasitoid abundance shown in the field and to determine the effect of understorey plants on parasitoid fitness. The following experiment extends the previous one on the effect of floral resources on parasitoid fitness by including alyssum and by measuring fecundity. In the previous experiment the fecundity data were lost because of fungal contamination. Therefore, to reduce this risk the diet tubes were not placed in an airtight container before incubation, the temperature at which they were incubated was decreased and the number of larvae per diet tube was reduced. Foliage was also renewed during this experiment to provide a more constant food source.

Phacelia was trialed in the 1999 field season but was not included in the following investigation because it was not flowering over the duration of the experiment. However, work on phacelia is described in Section 5.1.3. Coriander was not included in this study because Section 5.1.1 showed that it did not enhance parasitoid longevity compared with water-only and, in the field, seeds did not germinate quickly and it competed poorly with weeds. Buckwheat and alyssum were combined as one treatment to see if this further enhanced longevity, as was demonstrated in the previous experiment when combining coriander and buckwheat.

Some parasitoids use aphid honeydew as a source of sugar (Idris and Grafius, 1995; Landis and Marino, 1997). This can increase the longevity of some species (Hagley and Barber, 1992). In the current study, a 'buckwheat without flowers' treatment was included to determine whether the increase in longevity in the buckwheat treatment, as demonstrated in the previous experiment, was a result of an increase in humidity from transpiring leaves, aphids from the greenhouse on the plant material, or the flowers themselves.

5.1.2.2 Methods

Seven replicates, each of seven treatments (water, 50:50 honey/water solution, buckwheat (cv. 'Shinano Natsu') with flowers, 'buckwheat without flowers', flowering alyssum (cv. 'Carpet of Snow'), non-flowering broad bean (cv. 'Exhibition Long Pod') and buckwheat and alyssum combined (Plate 14)) were set up in a randomised complete block design under a 16:8 L/D photoperiod, at 16.5°C with a 2°C range. Water, honey/water and plant treatments were set up as described in Section 5.1.1.2. All treatments were topped up with water or honey/water solution as necessary and plant material was replaced every six days.

In all treatments five diet tubes each with three first instar larvae, were present (Plate 14). These tubes had previously been inverted for 24 hours to settle the larvae and minimise dispersal. The larvae were removed and replaced every three days and placed into incubation at 16.5°C with a 2°C range to develop. After eleven food renewals (36 days), larvae were not supplied because fecundity decreases with increasing parasitoid longevity (Howell, 1981).

A pair of newly-emerged adult *D. tasmanica* was placed in each treatment. Parasitoids were obtained from adults emerging from the diet tubes containing field-collected larvae (see Section 4.1). Replicates were set up over time, randomising treatments and finishing one replicate before starting another. The number of parasitoid cocoons and leafroller pupae were recorded and parasitoid longevity (measured in days) for both sexes was checked daily on most occasions and when not, every second day. Males were not replaced.

Survival curves were compared between treatments, including all replicates using a log rank test, and Kaplan Meier estimates of mean survival were calculated (Kaplan and Meier, 1958). There was low survival of larvae and low production of leafroller pupae and parasitoid cocoons in the later replicates. Therefore, they were excluded from the analysis. The parasitoid cocoon data were not normally distributed and log-transformation did not normalise the distribution; therefore, a Kruskal Wallis non-parametric ANOVA was conducted. Leafroller pupal data were log-transformed ($\log_e(x+1)$) to stabilise variances before ANOVA. Where the ANOVA indicated significant effects, these were further explored using Mann-Whitney U tests or Fisher's least significant difference test.

5.1.2.3 Results

Parasitoid survival

There was a strong significant effect of treatment on longevity for female and male *D. tasmanica* (male: X^2=32.27, df=6, P<0.001; female: X^2=32.27, df=6, P<0.001). Individual Kaplan Meier tests revealed that for male *D. tasmanica*, all floral treatments except 'buckwheat without flowers' resulted in a significantly greater parasitoid longevity than water (P<0.05) (Fig. 5.3). Buckwheat produced a significantly longer survival time than alyssum, buckwheat/alyssum, broad bean and 'buckwheat without flowers' treatment (P<0.05). Honey/water did not produce the greatest longevity out of the floral treatments (Fig. 5.3).

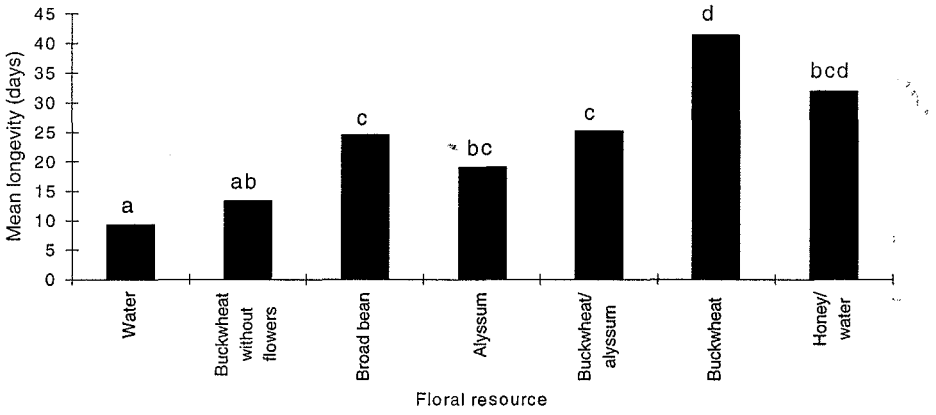


Fig. 5.3 Mean longevity (days) of male *D. tasmanica* provided with different food sources in the laboratory at 16.5°C (see Fig. 5.1).

For female *D. tasmanica*, all floral treatments except broad bean and 'buckwheat without flowers' produced a significantly greater longevity than water (P<0.05) (Fig. 5.4). Buckwheat resulted in a significantly (P<0.01) longer survival than 'buckwheat without flowers', and the honey/water, buckwheat and buckwheat/alyssum treatments significantly enhanced longevity compared with broad bean (P<0.05) (Fig. 5.4).

There was no significant (X^2=2.37, 1, P>0.05) gender effect on longevity over all treatments (male mean = 23.6, female = 29.0).

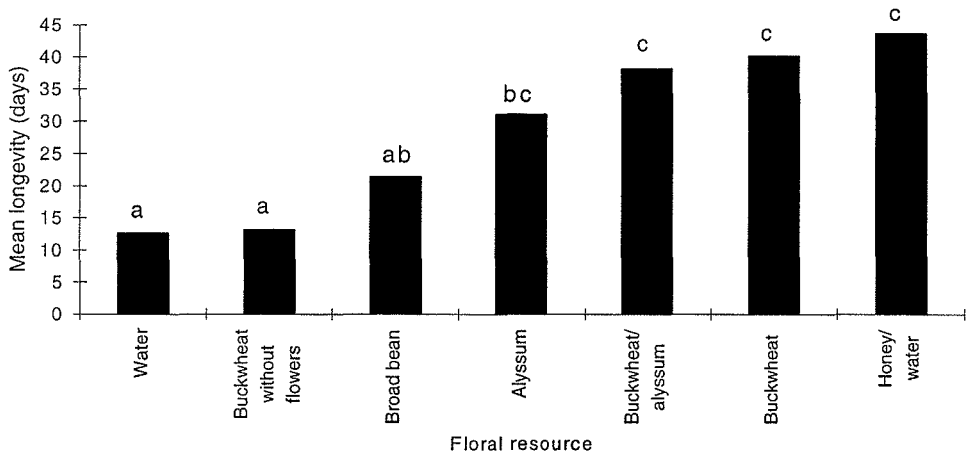


Fig. 5.4 Mean longevity (days) of female *D. tasmanica* provided with different food sources in the laboratory at 16.5°C (see Fig. 5.1).

Leafroller diet tubes

The total number of parasitoid cocoons and leafroller pupae produced was 45 and 128 respectively. Leafroller larval survival in the diet tubes was only 6.5%. Of those larvae that survived, 35.2% were parasitised. The median number of parasitoid cocoons produced from larvae exposed to the parasitoids did not significantly differ between treatments (X^2=6.556, df=6, P>0.05) (Fig. 5.5). However, almost four times as many parasitoid cocoons were produced in the honey/water (total=15) and buckwheat/alyssum (16) treatments compared with the other floral treatments.

There was an overall effect of floral treatment on the number of leafroller pupae produced (F=2.79, df=6,24 P<0.05). Least significant difference tests revealed that the mean number of leafroller pupae produced was significantly higher in the broad bean, buckwheat and buckwheat/alyssum treatments compared with water-only (P<0.05) (Fig. 5.5). Buckwheat/alyssum produced a significantly higher mean number of leafroller pupae than did 'buckwheat without flowers' and the honey/water treatment (P<0.05) (Fig. 5.5). The total number of larvae surviving to leafroller pupae or parasitoid cocoons was lower in the water treatment (total=5) compared with honey/water (29), buckwheat (28), 'buckwheat without flowers' (14), buckwheat/alyssum (57), alyssum (20) and broad bean (20) treatments.

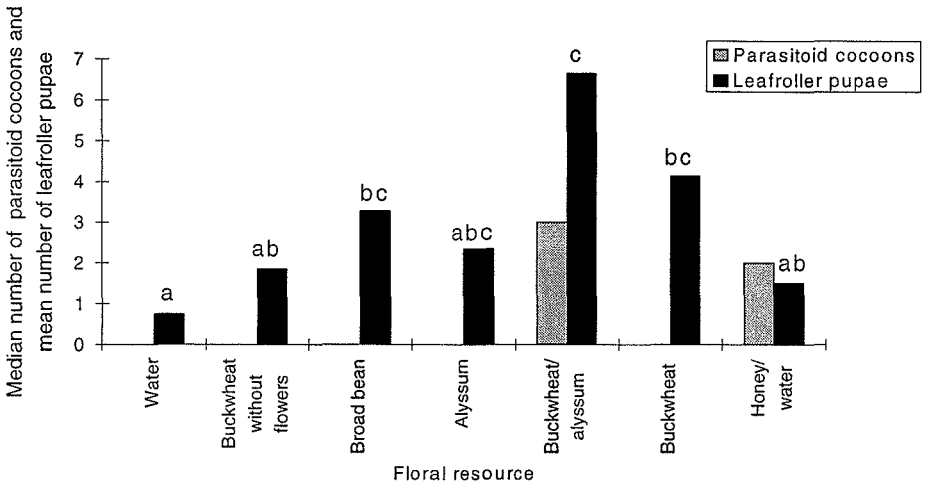


Fig. 5.5 The median number of parasitoid cocoons and the mean number of leafroller pupae produced by female *D. tasmanica* provided with different food sources in the laboratory at 16.5°C (different letters indicate significant differences in numbers of leafroller pupae between treatments ($P<0.05$); number of parasitoid cocoons did not significantly differ between treatments ($P>0.05$)).

5.1.2.4 Discussion

The buckwheat, alyssum, buckwheat/alyssum and honey/water treatments resulted in a higher parasitoid longevity than did water. This re-emphasises that floral resources are extremely important for *D. tasmanica* survival and supports results obtained in Section 5.1.1. In contrast to the results found in that Section, honey/water did not significantly produce the longest survival. This may have been because the plant material was renewed during the current study, unlike in the previous one, providing a more constant food source.

The 'buckwheat without flowers' treatment reduced parasitoid longevity compared with buckwheat with flowers for both sexes. This supports field work (Section 2.1) and suggests that not only is it the flower that attracts the parasitoid to the plant, but it is also the flower that enhances parasitoid longevity, and not the shelter, aphid honeydew or microclimate, which the plant may also provide.

For male *D. tasmanica*, broad bean also resulted in a greater longevity than did water, indicating that extrafloral nectaries may be an important source of nectar for *D. tasmanica*. This supports other results: Section 5.1.1, Collyer and van Geldermalsen (1975) and Bugg *et al.* (1989). However, for female *D. tasmanica*, broad bean did not result in a significantly higher survival than did water, contradicting previous results. This may have because plant material was replaced in the current experiment and was not in the previous one. This extended the duration of the experiment, which may have helped detect non-suitable or inferior floral resources. Laboratory experiments may, however, underestimate the importance of broad bean compared with that in the field because in the field parasitoids can gain access to floral nectar of the broad bean through holes in the corolla of the flower previously bitten by other insects, such as bees (Newton and Hill, 1983) and ichneumonds (Idris and Grafius, 1997).

The differences in longevity on broad beans between sexes may be attributed to a difference in nutritional requirements between the sexes. Female parasitoids may require greater quantities of different proteins and amino acids for egg maturation and host seeking than males. The quality of extrafloral nectar is different from that of floral nectaries (Baker *et al.*, 1978). Therefore, the quality of the nectar from the broad bean extrafloral nectaries may not be as high as that from buckwheat for sustaining female *D. tasmanica* survival for long periods of time. This may be attributed to the differences in quality between extrafloral nectar and floral nectar as the concentration or composition may differ between the types of nectar (Vansell, 1939). Also, diurnal and seasonal nectar flows may differ between broad bean extrafloral nectaries and buckwheat floral nectaries.

The deep flower structure of broad bean does not, in the laboratory, allow this plant to provide pollen to *D. tasmanica* and in the current study only three *D. tasmanica* cocoons were produced on this treatment. However, as stated on page 114 (Results), only 6.5% of the larvae survived overall. This low overall survival rate may have biased the results; for example, parasitised larvae may be more likely to die than are unparasitised ones. Furthermore, Handel *et al.* (1972) reported that extrafloral nectars tend to be sucrose-rich and are highly attractive to adult Lepidoptera compared with floral nectar. This is probably because lepidopteran adults take up food through narrow tubes so are restricted to less

viscous sugar solutions, such as those of extrafloral nectar (Baker and Baker, 1979). Results suggest that broad bean may not be a favourable understorey plant option for enhancing leafroller biocontrol.

Alyssum did not perform as well as buckwheat in enhancing parasitoid survival. Also, for male *D. tasmanica*, buckwheat gave a greater longevity than did buckwheat/alyssum combined. This would suggest that the addition of alyssum reduced parasitoid survival. Nectar from some plants may contain metabolically harmful substances, such as melezitose (Harborne, 1988), which may depress longevity (Avidov *et al.*, 1970). However, alyssum significantly enhanced parasitoid survival compared with water for both sexes and field work shows a higher parasitism rate in alyssum treatments compared with controls (Section 4.1). Furthermore, Vortis suction sampling of alyssum and control plots resulted in a two-fold increase in *D. tasmanica* abundance in alyssum treatments compared with controls (Section 4.2). This experiment was limited by using cut stems placed in water because they are unlikely to react the same as a flowering stem on an actively growing plant. Removing the stem may have affected the quality of the floral resources and the duration of nectar provision (van Doorn and Woltering, 1991; Brandt and Woodson, 1992; Wernett *et al.*, 1996; see Section 5.1.1.4). The poor performance of alyssum compared with buckwheat may be attributed to a difference in the way the plants react to being cut and placed in water. Alyssum may not perform as well after the stem is severed, cells may become less turgid more quickly and nectar production may cease or it may be reabsorbed.

Over all treatments, of the larvae that survived, 35.2% were parasitised. This is considerably lower than parasitism rates of released larvae in the field and suggests that there may have been a constituent of the diet which deters *D. tasmanica*, or that *D. tasmanica* may require a host plant such as apple leaves to help locate leafroller larvae and stimulate oviposition. Studies show that host plant plays an important role in influencing the behaviour of parasitoids and a parasitoid may not parasitise a preferred host larva on an unfavourable plant species (Laster, 1974; Vinson, 1981). For example, survival of *Apanteles congregatus* Say was affected by high nicotine levels in the host larvae obtained from the host plant (Barbosa *et al.*, 1982). However, see also the comment on this topic on page 116.

Only 6.5% of leafroller larvae survived to produce a pupa or parasitoid cocoon. Allen and Smith (1958) reported that superparasitism is common in the laboratory. Inexperienced parasitoids, such as those which were used in the current study, have lower encounter rates, are less successful in handling their hosts (Samson-Boshuizen *et al.*, 1974) and may superparasitise more readily (Visser *et al.*, 1992). This may have decreased parasitism and the survival of larvae. An experiment was previously conducted to trap live *D. tasmanica* in the field; this attempt was not successful. Low larval survival may also be attributed to low-density larval crowding. This can be defined as the occurrence of more than one larva within the same leafroller web (Danthanarayana *et al.*, 1982) and is possible in the current study because three larvae were placed in each diet tube. Danthanarayana *et al.* (1982) showed that larval crowding, even at low densities, caused an increase in mortality. Furthermore, high mortality in diet tubes may result from desiccation caused by the dry leafroller diet. Tomkins (1984) stated that the foremost climatic factor besides temperature which may affect leafroller development is relative humidity. The Insect Rearing Unit (see previous) successfully rear leafroller in diet tubes using non-absorbent cotton wool to seal them and only one larva per diet tube (A. Barrington, pers. comm). During the current study absorbent cotton wool was used and three larvae were placed in each tube. This may have decreased humidity and increased competition and stress respectively. Clare *et al.* (1987) used airtight containers, 20°C, 50-60% relative humidity and 16:8 L/D photoperiod to rear leafrollers successfully. This indicates that placing diet tubes into airtight containers maintain higher humidity, quality of the leafroller diet and larval survival. However, the high success rate of the culture used by Clare *et al.* (1987) may also be attributed to the leafroller not being exposed to parasitoids compared with the current study.

Although the medians of the cocoon data did not give any significant results, it should be noted that the honey/water treatment did produce a total of 29 parasitoid cocoons. This indicates that pollen is not essential for egg maturation in *D. tasmanica*, although it may be required for maximum fecundity. Results also suggest that honey/water may be sufficient for culturing this parasitoid as it prolongs survival and produces eggs.

Buckwheat and alyssum combined produced the highest total number of parasitoid cocoons (57) indicating that the provision of two pollen and nectar sources may synergistically enhance parasitoid fecundity, possibly by providing a wider range of amino acids and proteins required by the parasitoid. However, buckwheat/alyssum also significantly produced the highest mean number of leafroller pupae. This may be attributed to better survival of the leafroller larvae in this treatment (parasitised or unparasitised) due to their being an additional stem of plant material, which may have increased transpiration and humidity. A humidity experiment was conducted (Section 5.3) to determine differences in humidity between water, water/honey and alyssum. Buckwheat was not available at the time of this experiment. Results showed that there was probably no difference in humidity between treatments. However, alyssum leaves have a small leaf area in comparison with buckwheat. The increase in leaf area in the buckwheat/alyssum treatment compared with alyssum only may have increased transpiration and humidity, influencing larval survival. Furthermore, larger leaves, like buckwheat, tend to have higher temperatures than smaller leaves (Wilmer, 1986).

Emerging *D. tasmanica* from the diet tubes obtained from the 1999 field trials (Section 4.1) were used during this experiment and replicates were set up over time (see Section 5.1.2.2). Replicates five and six had low parasitoid cocoon and pupal numbers. These replicates were set up using parasitoids which emerged from cocoons obtained in the field later in the season. Therefore, these individuals may have been of lower quality or at a different phenological stage than those collected earlier. For example, longevity of *Apanteles medicaginis* varied considerably, depending on the source of adults and the date of emergence (Allen and Smith, 1958). In the current study, low parasitoid quality may have affected the parasitoid's ability to parasitise leafrollers or may have enhanced superparasitism, influencing the number of cocoons produced, and the survival of leafroller larvae, respectively. This may explain the low numbers of cocoons and pupae in the later replicates.

The buckwheat, broad bean and 'buckwheat with flowers' treatments produced a higher number of leafroller pupae compared with water. Again, this may be a result of increased humidity due to the larger leaves of buckwheat and broad bean; however, the 'buckwheat

without flowers' did not produce a higher number of pupae compared with the water-only treatment. Superparasitism increases when parasitoid food resources are scarce (Sirot and Bernstein, 1997). This may explain why the water and 'buckwheat without flowers' treatments produced lower numbers of pupae, because high superparasitism would have decreased larval survival.

The mean female *D. tasmanica* longevity over all treatments in Section 5.1.1 was 14.4 days compared with that in the current study, which was 28.6 days. This may be attributed to renewing plant material in the current study compared with the work in Section 5.1.1 where plant material was not renewed and quality and nectar supply would have deteriorated.

5.1.3 The effect of pollen and nectar on parasitoid fitness

5.1.3.1 Introduction

The previous experiments showed that floral resources are important for parasitoid fitness (Sections 5.1.1 and 5.1.2). However, the question still remains as to the respective importance of pollen and nectar for parasitoid longevity and fecundity. Some parasitoids clearly feed directly on pollen. For example, Hassan (1967) reported several Ichneumonidae adults biting at the anthers of grasses, removing pollen grains. The objective of conservation biological control is to ensure that the occurrence of as many essential predator and parasitoid resources coincide in time and space (Barbosa and Benrey, 1998). Therefore, it would be beneficial to determine the requirement of *D. tasmanica* for nectar and pollen, because an understorey plant can then be chosen that supplies the resources required. The following experiment attempts to separate the role of buckwheat pollen and nectar and investigates their individual effect on parasitoid survival and fecundity.

Despite the fact that phacelia is potentially a good source of nectar (Crane *et al.*, 1984), the flowers have deep corollae which may make the nectar inaccessible to short-tongued parasitoids (Holland *et al.*, 1994). However, some parasitoids may crawl down the corolla to obtain nectar, and the family Braconidae, to which *D. tasmanica* belongs, includes species with elongated mouthparts that are used in the exploitation of flowers that have deep corollae and sugar-rich nectars (Jervis *et al.*, 1996). It is not known whether *D. tasmanica* can access phacelia nectar, therefore an investigation into this is included in the following experiment.

5.1.3.2 Methods

Five replicates of five treatments (water, flowering buckwheat (cv. 'Shinano Natsu'), buckwheat with anthers removed, water/pollen and phacelia (cv. 'Balo')) were set up in a randomised complete block design under a 16:8 L/D photoperiod, at 16.5°C with a 2°C range. The water and plant treatments were set up as described in Section 5.1.1.2. Anthers

and unopened flowers were removed from the buckwheat stems using a pair of 80 mm spring-type micro scissors while the stem was inverted to avoid pollen falling into the nectar, and the surface of the remaining flowers was airbrushed. The cut anthers were placed on a microscope slide and used for the water/pollen treatment. All treatments were topped up with water as necessary and plant material was replaced every nine days. One male and three female newly-emerged adult *D. tasmanica* were placed in each treatment. Parasitoid longevity (measured in days) for the male and one of the female *D. tasmanica* was checked daily on most occasions and when not, every second day. Males were not replaced once dead. After five and ten days, one female parasitoid was removed and placed in alcohol for dissection. The dissection procedure and slide preparation in outline were: the insect was removed from alcohol, placed on a glass slide in alcohol, and the abdomen separated and teased apart with mounted needles. The gut contents were spread over part of the slide, and safranine, gelatine and phenol were added, followed by a coverslip (see Wratten *et al.* (1995) for more details). The number of eggs and pollen grains were counted using 400 x magnification when necessary.

All the parasitoids used to assess longevity died naturally (i.e., they did not escape or drown) and a Kruskal Wallis non-parametric ANOVA was used to compare parasitoid longevity and the number of eggs and pollen grains after five and ten days between treatments. Where the Kruskal-Wallis results indicated significant effects, these were further explored using Mann-Whitney U tests. The Wilcoxon signed rank test was used to compare differences between the sexes over all treatments.

5.1.3.3 Results

Survival

There was a significant effect of floral treatment on male longevity ($U=14.01$, $df=4$, $P<0.01$). In contrast, there was no significant effect of treatment on female longevity ($U=7.57$, $df=4$, $P>0.05$). For male *D. tasmanica*, buckwheat (median=29) resulted in a significantly longer survival than phacelia (5), water (5) and water/pollen (7) ($P<0.05$) (Fig. 5.6). For female *D. tasmanica*, buckwheat (24) resulted in four times the longevity compared with phacelia (5) (Fig. 5.7). The maximum longevity for female *D. tasmanica* was 44 days for buckwheat.

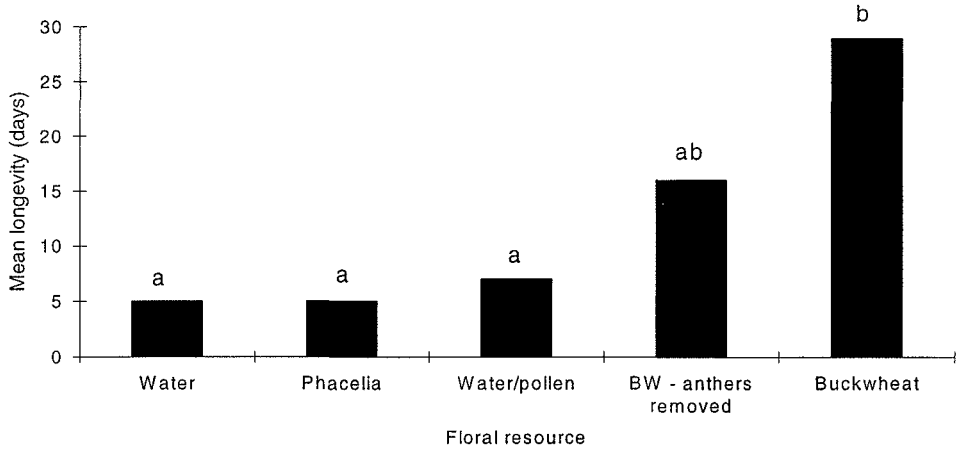


Fig. 5.6 The influence of buckwheat pollen and nectar, and phacelia flowers on the mean longevity (days) of male *D. tasmanica* in the laboratory at 16.5°C (see Fig. 5.1).

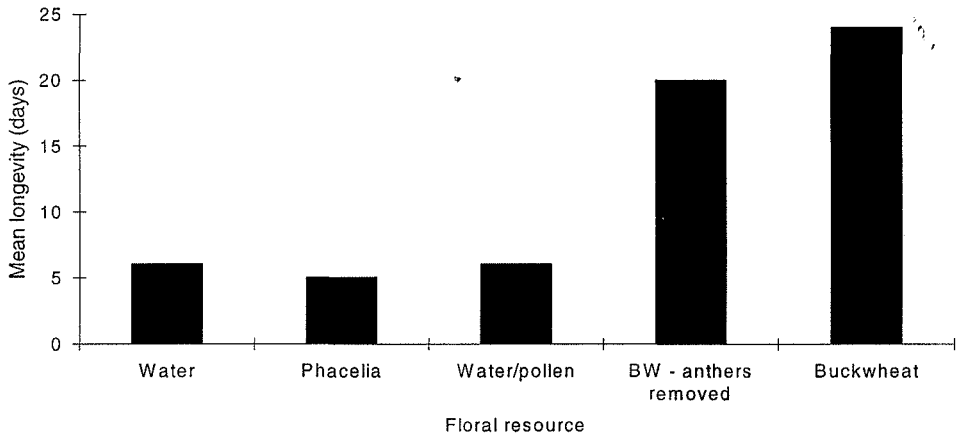


Fig. 5.7 The influence of buckwheat pollen and nectar, and phacelia on the mean longevity (days) of female *D. tasmanica* in the laboratory at 16.5°C (there was no significant difference in female longevity between floral treatments).

Buckwheat did not significantly (P>0.05) enhance parasitoid survival compared with 'buckwheat with anthers removed' treatment for either sex (Figs. 5.6 & 5.7). Although there was a three-fold increase in survival for both sexes, the 'buckwheat with anthers removed' treatment did not significantly increase longevity compared with the water/pollen or water-only treatments (P>0.05) (Figs. 5.6 & 5.7). There was no significant difference in parasitoid survival between the sexes (z=0.245, P>0.05).

Dissection results

There was a significant effect of treatment on the number of pollen grains and eggs in dissected female *D. tasmanica* after five days (pollen: U=14.62, df=4, $P<0.01$; eggs: U=12.77, df=4, $P<0.05$) (Fig. 5.8). However, floral treatment did not significantly influence the number of pollen grains or eggs in dissected female *D. tasmanica* after ten days (pollen: U=7.02, df=3, P>0.05; eggs: U=4.23, df=3, $P>0.05$) (Fig. 5.9).

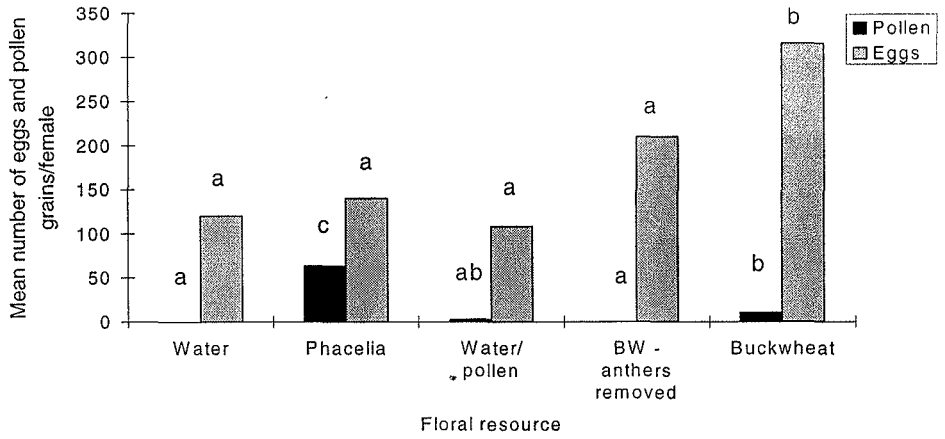


Fig. 5.8 The influence of buckwheat pollen and nectar, and phacelia on the number of eggs and pollen grains in dissected female *D. tasmanica* after five days (see Fig. 5.1).

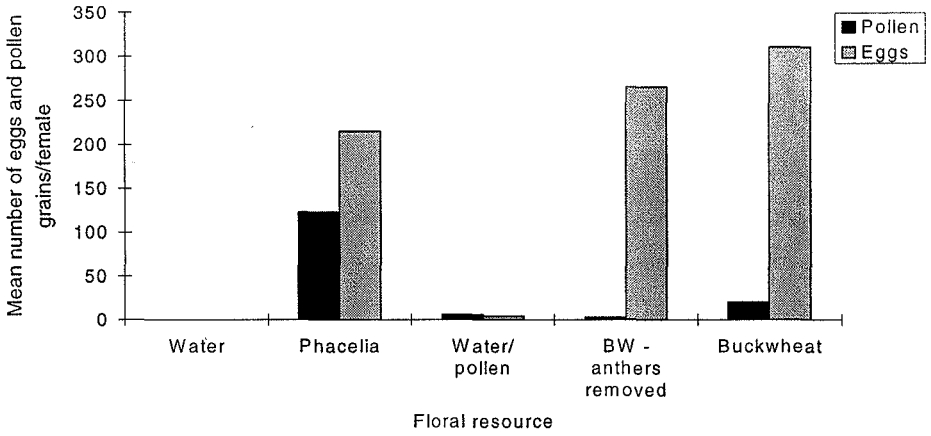


Fig. 5.9 The influence of buckwheat pollen and nectar, and phacelia on the number of eggs and pollen grains in dissected female *D. tasmanica* after ten days (there was no significant difference in the number of pollen grains or eggs between floral treatments).

Dissection after five days showed that buckwheat significantly enhanced fecundity compared with all other treatments ($P<0.05$) (Fig. 5.8). The number of pollen grains found in the gut of parasitoids after five days was significantly higher in the buckwheat treatment compared with the buckwheat with anthers removed ($P<0.05$) and water-only ($P<0.05$) treatments (Fig. 5.8). There were significantly more pollen grains found after five days in the gut of those parasitoids in the phacelia treatment compared with buckwheat ($P<0.05$). However, phacelia did not significantly increase parasitoid fecundity after five days compared with buckwheat ($P<0.05$) (Fig. 5.8). Buckwheat did not significantly increase the number of pollen grains found in the parasitoids' gut after five days compared with the water/pollen treatment ($P>0.05$) (Fig. 5.8). However, the number of pollen grains after five days did not significantly differ between the water/pollen treatment and the water-only treatment ($P>0.05$). Finally, there were more pollen grains found after ten days in the buckwheat treatment compared with the buckwheat with anthers removed treatment (Fig. 5.9).

5.1.3.4 Discussion

The maximum longevity observed for female *D. tasmanica* was 44 days and was similar to the results of Allen and Smith (1958) who recorded a maximum longevity for female *Apanteles medicaginis* of 46 days. For male *D. tasmanica*, buckwheat produced a longer survival compared with water and water/pollen treatments. This reinforces the contention that nectar is essential for parasitoid survival and supports previous Sections (5.1.1 and 5.1.2) and other work (Hagley and Barber, 1992; Wäckers and Swaans, 1993; Idris and Grafius, 1995; Baggen and Gurr, 1998). Buckwheat did not significantly enhance parasitoid survival compared with 'buckwheat with anthers removed' treatment suggesting that pollen is not essential for parasitoid longevity. This supports Hodgson *et al.* (1993) who found an insignificant effect of pollen on longevity of the braconid *Microctonus hyperodae*.

Buckwheat significantly enhanced female longevity and fecundity after five compared with water and there was a similar, although not significant trend after ten days. Many studies demonstrate that a higher percentage parasitism of hosts occur when non-host food is present compared with when it is absent or less available (Chumakova, 1960; Treacy *et al.*,

1987). Therefore, buckwheat sown in orchard understoreys not only has the ability to attract *D. tasmanica* into the orchard but also enhances *D. tasmanica* survival and fecundity, in turn potentially contributing to greater leafroller control.

Survival on phacelia was equivalent to that on water and that phacelia significantly decreased parasitoid longevity compared with buckwheat. This suggests that, unlike some other braconids, *D. tasmanica* does not have elongated mouthparts that are used in the exploitation of flowers that have deep corollae (Jervis *et al.*, 1996) and that it does not crawl down the corolla to obtain nectar. Some small parasitoids crawl down deep corollae to gain access to nectar (Jervis *et al.*, 1993); however, *D. tasmanica* is a relatively large parasitoid (3 mm). Therefore, this plant likely provides only pollen to *D. tasmanica*, whereas buckwheat flowers provide both pollen and nectar. This supports Holland *et al.* (1994) and Section 4.1 which showed that parasitism was not enhanced by planting phacelia in the understorey compared with the control. Also, results in Section 4.2 showed that there were significantly fewer *D. tasmanica* captured by Vortis suction sampling in phacelia plots compared with controls. Parasitoids can learn to recognise a particular nectar odour following feeding experience on that flower (Patt *et al.*, 1999). Results from the current study suggest that there is no nectar reward for *D. tasmanica*, therefore the parasitoid may not visit phacelia plants after an initial encounter, in turn explaining low numbers captured in the field. Hover flies may have a higher pollen requirement than *D. tasmanica*, therefore explaining why phacelia enhances hover fly abundance when sown in field margins (White *et al.*, 1995), yet does not seem to benefit *D. tasmanica*. Results here confirm that phacelia may not be a suitable understorey plant for *D. tasmanica* population enhancement and consequently biological control of leafroller.

Buckwheat resulted in a higher number of pollen grains in the parasitoid's gut compared with 'buckwheat with anthers removed' and water-only treatments, and buckwheat also enhanced fecundity compared with these treatments. This suggests that pollen enhances fecundity and this is similar to results of Schneider-Orelli (1945) and van Emden (1963). However, parasitoids in the phacelia treatment had a higher number of pollen grains in their gut after five days compared with those in the buckwheat treatment, whereas the latter had a higher fecundity. Also, water/pollen did not increase the number of eggs produced

compared with water. Both these results indicate that although pollen may be required for sexual maturation, without nectar, survival is reduced and eggs are reabsorbed. This has been shown by King (1963), Jervis and Kidd (1986; 1992) and Heimpel *et al.* (1997) for other parasitoid species. *D. tasmanica* may have consumed significantly more phacelia pollen than buckwheat because the parasitoids were compensating for a lack of nectar in the phacelia treatment, or the phacelia pollen had a more favourable taste, structure, or availability/productivity, or that the structure of phacelia pollen is such that it clings to the outside of *D. tasmanica*, influencing the dissection results.

The number of pollen grains in the gut of the parasitoids in the water/pollen treatment did not significantly differ from the buckwheat treatment. This suggests that *D. tasmanica* may have specifically ingested pollen that was provided on the slide in the water/pollen treatment. This is similar to the results of Hassan (1967) who reported adult Icheumonidae feeding on pollen grains that had dropped from the anthers of grasses and had lodged at the bases of the flowers. However, the parasitoids in the water/pollen treatment did not have significantly more pollen grains in their gut than in the water-only treatment, which had none. Therefore, the pollen found in the gut of the parasitoids in the water/pollen treatment may have been on the parasitoids' body and therefore could have influenced the dissection or been accidentally ingested during preening. Jervis (1998) concluded that inadvertent consumption of pollen, through feeding on contaminated nectar and honeydew, may be far more common that deliberate pollen consumption.

Parasitoids in the buckwheat treatment had a higher number of pollen grains in their gut after five days compared with 'buckwheat with anthers removed'. However, there was no significant difference in fecundity between these treatments. After ten days, parasitoid quality would have decreased and eggs may have been reabsorbed to compensate for nutritional requirements (King, 1963; Jervis and Kidd, 1986; 1992). Also, some synovigenic parasitoids are able to reabsorb eggs when hosts are absent or scarce. Nutrients from eggs can be used to maintain the female until she can locate hosts for oviposition (Jervis and Kidd, 1986; 1992). There was no significant results from the fecundity and pollen data obtained from dissection after ten days. This is probably due to the lack of

replicates because the water, water/pollen and phacelia treatments had low parasitoid survival and most females did not live long enough to contribute data at ten days.

The mean number of eggs counted in dissected female *D. tasmanica* was 316. This fecundity is similar to that of *Apanteles thompsoni* Lyle the ovaries of who contain an average of 230 eggs (Vance, 1931) and *A. solitarius* (Ratzeburg) who had an average of 402 eggs (Parker, 1935). *Apanteles* is in the subfamily Microgastrinae, the same subfamily as *D. tasmanica*. Other *Apanteles* species have a larger reproductive capacity, such as *A. glomeratus* (L.), gravid females of which have over 2,000 eggs in their ovaries (Clausen, 1940). However, *A. glomeratus* is a gregarious parasitoid which may influence egg production, and the current experiment considered only the number of eggs after five and ten days which may not have been the time at which egg production was at a maximum. Dumbleton (1935) stated that *D. tasmanica* was ready to oviposit a few days after emergence and maximum oviposition may be 3-5 days after emergence (P. Cameron, pers. comm.). Furthermore, newly emerged females were used during the current experiment and they were never exposed to hosts. Morales-Ramos *et al.* (1996) reported that female *Catolaccus grandis* (Burks) (Pteromalidae) with oviposition experience produced four times as many eggs as did inexperienced females.

This experiment was limited by using cut flowers in water instead of actively growing flowering stems because, as discussed earlier (Sections 5.1.1.4 and 5.1.2.4), this may influence nectar quality and the period over which it is produced. Removing anthers may influence quality and duration of the nectar supplied as it was noted that buckwheat flowers tended to close after the anthers were removed. Also, when removing the anthers it was difficult to ensure that no pollen grains became trapped in the nectar. Leius (1960, 1963) observed that this occurred frequently. In the present study, a mean of 2.5 pollen grains was found in the gut of parasitoids in the 'buckwheat with anthers removed' treatment indicating that small quantities of pollen were present in this treatment, which may have underestimated differences between 'with pollen treatments' and those without.
The longevity of parasitoids in the laboratory assays would unlikely be the same as that found in the field. Parasitoids in the field would have a shorter survival time because of the increased energy spent searching for hosts, food and mates, presence of predators, stress

from climatic conditions and fluctuations, death from desiccation, competition with other insects of floral resources, etc.

The average survival of female *D. tasmanica* was 12.2 days compared with an average of 28.6 days for the previous study (Section 5.1.2). This may be attributed to the absence of hosts in the current study which may have reduced *D. tasmanica* survival. Moore and Kfir (1995) and Drost *et al.* (1999) both showed that parasitoid longevity was dependent on the presence or absence of hosts.

5.2 The Effect Of Understorey Plants On Leafroller Larval Development And Adult Fitness

5.2.1 Leafroller preference for buckwheat, broad bean, alyssum and phacelia

5.2.1.1 Introduction

Leafrollers have a wide host range (Chapman, 1973; Spiller and Wise, 1982). LBAM larvae have been recorded feeding on plants belonging to 34 families (Tomkins, 1984). Therefore, sowing plants in the orchard understorey for biological control purposes may also be introducing another favourable host for leafroller, enhancing the leafroller population. For example, blackberry (*Rubus strigolosus* agg.) and *Plantago lanceolata* L. are hosts of leafroller (Tomkins, 1991) and should be avoided in shelter belts and inter-row swards. Poplar (*Populus nigra* L.) is also a host of leafroller and if used in shelter belts can increase leafroller immigration into the orchard (Tomkins *et al.*, 1991). Therefore, two experiments were set up to investigate leafroller larval preference for the understorey plant species used in the 1997 and 1999 field seasons, compared with apple. Coriander was not included in the following trials as foliage was not available in sufficient quantities. Furthermore, it is probably a less favourable understorey plant candidate as it is slow to germinate and does not establish well or compete with weeds.

1. Buckwheat and broad bean

Buckwheat and broad bean have been investigated as possible understorey species in previous field studies (Sections 2.1) and therefore were included in this investigation. Clover was included in the study because it is commonly present in the inter-row sward of apple orchards. Leafroller feeding preference was investigated using two simple choice experiments.

2. Alyssum, phacelia and buckwheat

This experiment extends the previous choice experiment by including the 1999 field season's understorey plants, phacelia, alyssum and buckwheat. It uses leaf area and weight as measurements of leafroller preference to compensate for differences in leaf thickness

and density, and to correct for natural water loss from the leaf. This is particularly important when comparing leaves between species as they are likely to vary in physical characteristics (Walker and Jones, 1989).

5.2.1.2 Methods

1. Buckwheat and broad bean

A) Large containers: Fifteen polythene containers (220 x 120 x 75 mm) were lined with damp tissue paper. One leaf disc (diameter 20 mm) of each of the four plant species was cut out and placed randomly in the four corners of each of the containers. The plant species used were apple (cv. 'Granny Smith'), white clover, buckwheat (cv. 'Shinano Natsu') and broad bean (cv. 'Exhibition Long Pod'). One third instar LBAM larva (Appendix 1) was positioned in the middle of the container and the lid replaced. The containers were labelled and placed under a 16:8 L/D photoperiod at 16.5°C with a 2°C range. After 48 hours the plant on which the larva was found was recorded and the percentage leaf area consumed of each plant species disc was estimated.

B) Petri dishes: Twenty Petri dishes were lined with two sheets of damp filter paper. One leaf disc (diameter 2 cm) of each of the four plant species (see above) was cut out and placed randomly in a square arrangement on the filter paper, 20 mm apart. The plant species used were as above. A third instar LBAM larva (Appendix 1) was positioned in the middle of the square arrangement and the lid replaced. The containers were labelled and placed under a 16:8 L/D photoperiod at 16.5°C with a range of 2°C. After 48 hours the plant on which the larva was found was recorded and the percentage leaf area consumed of each leaf disc was estimated.

Data analysis

The first experiment consisted of larger containers and the second used small Petri dishes thereby reducing the distance between each plant species and increasing the larva's chance of interaction with all four plant species. The resulting trends were similar for both methods so the results from the two experiments were pooled for statistical analysis. Feeding preference was compared between pairs of plant species using McNemars Chi-

square test for correlated categories. Percentage feeding was analysed using Kruskal Wallis non-parametric ANOVAs and significant results were further explored using Mann-Whitney U tests.

2. Alyssum, phacelia and buckwheat

Forty Petri dishes were each lined with two sheets of damp filter paper. A piece of leaf area (approximately 2 cm^2) of each of the four plant species (buckwheat (cv. 'Shinano Natsu'), alyssum (cv. 'Carpet of Snow'), phacelia (cv. 'Balo') and apple (cv. 'Braeburn')) was cut out so that each leaf disc had one cut edge, except for phacelia and alyssum which, due their small size, were cut once at the petiole. The leaf discs were passed through a Licor Model 3100 area meter to record leaf area and the weight of each disc was also recorded for each replicate. A disc of each of the four plant species was placed randomly in a square arrangement on the filter paper. Half the replicates were used as a control to determine natural water, leaf area and weight loss. One, third instar LBAM larva (Appendix 1) was positioned in the middle of each 'treatment' dish and the lid was replaced and labelled. Petri dishes were placed under a 16:8 L/D photoperiod at 16.5°C with a 2°C range and after 48 hours the leaf area and weight of each leaf disc were recorded again. Data were corrected for natural loss in leaf area and weight by removing the average difference in weight loss for each species in the control from the treatment data and were compared between treatments using repeated measures ANOVA. Significant effects were further explored using Fisher's least significant difference test.

5.2.1.3 Results

1. Buckwheat and broad bean

There was a significantly higher number of leafrollers on apple compared with buckwheat, clover and broad bean (buckwheat, X^2=4.48, df=1, P<0.001; clover, X^2=9.78, df=1, P<0.01; broad bean, X^2=11.64, df=1, P<0.001)) (Fig. 5.10). The percentage of leaf disc consumed by the larvae significantly differed between plant species (X^2=9.04, df=3, P<0.05). Of those leafrollers that 'chose' buckwheat over apple, there was significantly more buckwheat (median = 45%) consumed than apple (10%) (P<0.01) (Fig. 5.11). This

trend was also found with clover (35%) and broad bean (50%) although this was not significant (P>0.05) (Fig. 5.11).

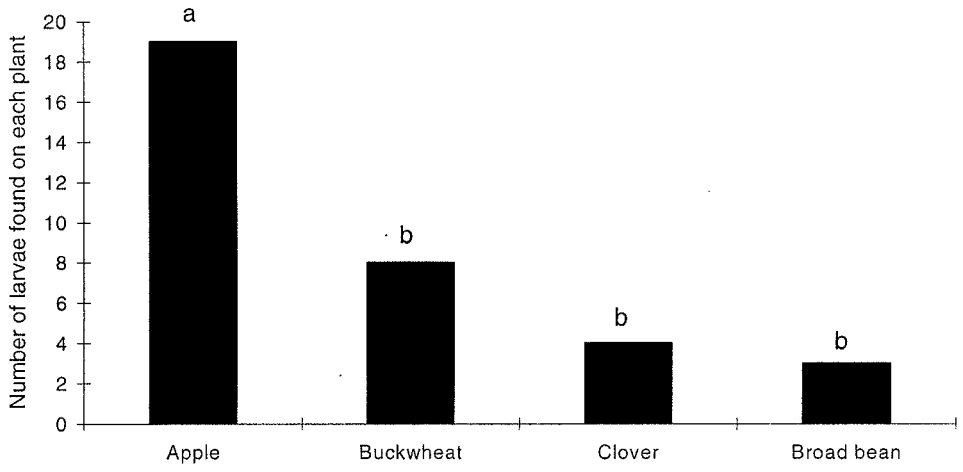


Fig. 5.10 The number of leafroller larvae found on apple, clover, broad bean and buckwheat after 48 hours (see Fig. 5.1).

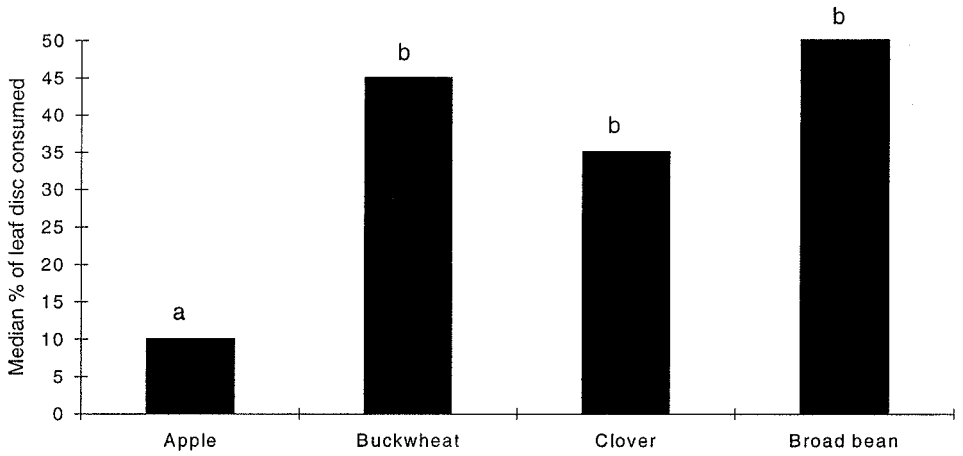


Fig. 5.11 The median percentage of each leaf disc (diameter 20 mm) consumed by leafroller larvae after 48 hours (see Fig. 5.1).

2. Alyssum, phacelia and buckwheat

There was a significant difference in leaf area between treatments in the controls (F=4.358, df=3,57, P<0.01). Phacelia (8 mm^2) lost significantly more leaf area than alyssum (0.6 mm^2), buckwheat (4 mm^2) and apple (1.3 mm^2) (P<0.05). Therefore, leaf area and weight

data were corrected in the treatments for this natural water loss. Corrected data showed that there was no significant difference in leaf area between treatments (F=0.575, df=3,57, P>0.05) (Fig. 5.12); however, there was a highly significant difference in weight between treatments (F=10.64, df=3,57, P<0.001). Leafroller larvae consumed over three-fold more apple than the other three plants (P<0.05) and significantly more phacelia than buckwheat (P<0.01) (Fig. 5.12).

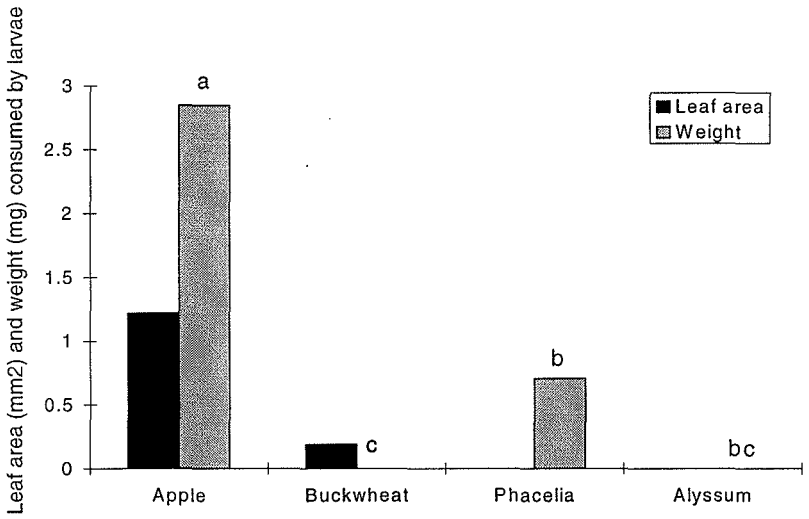


Fig. 5.12 The mean leaf area (mm^2) and weight (mg) of four plant species consumed by leafroller larvae after 48 hours (different letters indicate significant differences in weight consumed between treatments (P<0.05); leaf area consumed did not significantly differ between treatments (P>0.05)).

5.2.1.4 Discussion

LBAM showed a distinct preference for apple over the understorey candidate plants offered because more larvae were found on apple compared with buckwheat and broad bean, and a higher weight of apple was consumed by larvae compared with alyssum, buckwheat and phacelia. This may have been because the understorey plants were of lower nutritional value or contained antifeedants which caused the larvae to stop feeding and move to a more 'preferred' plant species (Russel and Lane, 1993; Schoonhoven *et al.*, 1998). Leafrollers feed on as many as 35 different plant families (Tomkins, 1984), many of which are present

in and around the orchard, in the inter-row sward, weedy areas and shelter belts (Chapman, 1973; Spiller and Wise, 1982). Although poplar, *P. lanceolata* and clover are known hosts of leafroller they are often used in shelter belts or in the inter-row sward (Tomkins, 1991). Given that, in these experiments, a higher number of larvae were found on apple compared with all the treatments, including clover, the understorey plants tested do not appear to be a preferred host of leafroller and they are not likely to contribute in a major way to the leafroller population if sown in the orchard understorey. However, larvae did consume some buckwheat, broad bean and phacelia. This may be a result of the larvae feeding on these species before moving on to a more preferred host, but no-choice laboratory tests would help to confirm whether these plants are suitable hosts of leafroller. This is investigated in Section 5.2.2.

These choice tests were limited because they eliminated numerous variables associated with general plant architecture that might influence larval choice in the field (Stuart and Polavarapu, 1998). For example, leafroller larvae 'prefer' different leaf cluster types and positions in the apple tree canopy (Tomkins, 1984; Suckling and Loriatti, 1996). Also, these experiments used only two apple cultivars ('Granny Smith' in Experiment 1 and 'Braeburn' in Experiment 2). Choice may have varied if a less preferred apple cultivar was used or results may have been more significant if a more favourable cultivar was used.

1. Buckwheat and broad bean

Walker and Jones (1989) surveyed publications regarding leaf consumption and herbivore feeding preference. Fifty-nine percent used only area eaten as the measure of consumption, 10% used biomass removed and 15% measured both parameters for the same data set. The remaining 22% included measurements of feeding duration, first leaf disc consumption and visual estimates of leaf area removed. The current study used the latter parameter, estimating leaf area removed, and the species that the larvae were found feeding on after 48 hours. Of those larvae that fed on buckwheat, there was more than four times the quantity of buckwheat eaten than apple. If only leaf area consumed was taken into account, then it would suggest that the leafroller consumed more buckwheat because it was a more favourable host. However, although the leaf discs of the four species were of equal leaf area, the thickness and density of the leaf may have differed. For example, apple leaves

may be more dense than that of buckwheat, therefore the larvae could consume more of the less dense buckwheat before they reached satiation, underestimating the amount consumed for apple. Measuring the weight of the leaf discs and calculating biomass removed would have corrected for this bias (Walker and Jones, 1989).

The damp filter paper would have minimised water loss from the leaves but the transpiration rate and natural water loss would still have varied between the plant species. Those species which lost more water would have been less turgid and of a lower quality and probably less favourable to the larvae. Therefore, it may be beneficial to repeat the experiment using a weight measurement and correcting for natural water loss from the leaf. This was explored in Experiment 2.

2. Alyssum, phacelia and buckwheat

Phacelia may have lost more leaf area in the controls than did the other plants because the shape of the leaf is strongly dissected and when leaf turgidity decreased, the leaf curled. This would have impeded leaf area measured by the Licor Model 3100 area meter. Also, it was observed that phacelia showed more yellow than did the other treatments over the duration of the experiment. This would have reduced leaf area measured by the Licor Model 3100 because this machine measures shadows, and yellow leaves would transmit more light, compared with green leaves.

Weight was measured to compensate for differing leaf densities between plants; also, treatments were corrected for natural water loss to compensate for the differences between plant species in the rate at which water is lost after cutting. However, this did not take into consideration the length of the cut edge on each plant. For example, due to the finely dissected nature of the phacelia leaves and the small alyssum leaves, they had a smaller cut edge (cut across the petiole) than did the larger leaves of apple and buckwheat (cut along the leaf margin). Attraction of tortricid larvae to host plants is likely to involve olfaction (Sutherland and Hutchins, 1972; Bradley and Suckling, 1995). Therefore, the greater cut surface of the apple treatment compared with the alyssum and phacelia treatments may have emitted more odours and attracted the larvae.

Although the experiment accounted for water loss between species, it did not account for differences in turgidity. For example, leaves from plant species that have a lower solute content will wilt more readily than those with a higher solute content (Grashoff and Verkerke, 1991). Phacelia had a significantly higher leaf area lost in the controls compared with the other plants, which suggests that it is more prone to losing water once cut. This higher water loss would have lowered cell turgidity, making it less favourable to the larvae because larvae prefer turgid, actively growing tissue (Tomkins, 1984).

The weight of leaf tissue consumed by larvae may have been overestimated during this experiment because, as the larvae fed on the leaf disc, they would have increased the area from which water could be lost. The leaf area consumed by the larvae did not significantly differ between treatments, whereas the weight of plant material consumed did. This suggests that because the larvae consumed a higher weight of apple and phacelia but leaf area was not affected, these two plant leaves may be more dense than those species in the other treatments.

5.2.2 Larval development on buckwheat, broad bean, alyssum and phacelia

5.2.2.1 Introduction

Choice tests showed that leafrollers 'prefer' to feed on apple compared with buckwheat, broad bean, phacelia and alyssum (Section 5.2.1). However, some larvae did feed on these species indicating that they still may be suitable as hosts. Although leafrollers can feed on a wide range of hosts, developmental rates are slowed or death can occur when reared on a less favourable host (Barrington *et al.*, 1993; Smirle, 1993). Therefore, two experiments were set up to investigate the developmental rates and survivorship of leafroller larvae when reared solely on the potential understorey plant species. One experiment compared apple with buckwheat and broad bean. Clover was included in the preference test in Section 5.2.1 but was not included in this investigations due to lack of available labour. The second experiment compared apple with phacelia, alyssum and buckwheat.

5.2.2.2 Methods

1. Buckwheat, broad bean and apple

Forty five polythene containers (170 x 120 x 55 mm) were lined with damp tissue paper. Fifteen 150 mm lengths of the top of stems of each of the three plant species were cut and damp cotton wool covered in 'Glad Wrap' was placed over the cut end (Plate 15). The plant species used were apple (cv. 'Braeburn'), buckwheat cv. 'Shinano Natsu') and broad bean (cv. 'Exhibition Long Pod'). One piece of leaf material was placed in each container so each plant species had 15 replicates. Five third instar LBAM larvae (Appendix 1) were placed on the leaf material in each container and the lid replaced. The containers were labelled and placed under a 16:8 L/D photoperiod at 16.5°C with a 2°C range. The leaf material was renewed every seven days and larvae were checked daily on most occasions and when not, every second day. The time to prepupal, pupal and adult stages was recorded. The weight of the pupae was also recorded within two days of the final larval moult. This procedure continued for nine weeks, by which time all unemerged pupae were recorded as dead. Chi-square tests were used to analyse differences between the

proportions of larvae which survived to the respective development stages in each treatment. ANOVA was used to analyse differences in pupal weight between treatments.

Plate 15. Plant stems wrapped in damp cotton wool and 'Glad Wrap'.

2. Alyssum, phacelia and apple

Twenty-one containers (17 x 12 x 5.5 cm) (seven replicates) were lined with damp tissue paper. Foliage from the three treatment plant species (apple (cv. 'Braeburn'), alyssum (cv. 'Carpet of Snow') and phacelia (cv. 'Balo')) were placed in the containers separately so each plant treatment had seven replicates. Enough foliage was placed in each treatment so that food was not a limiting factor. Unlike the previous experiment, stems were not wrapped in damp cotton wool because phacelia stems were too small to wrap individually. Five third instar LBAM larvae (Appendix 1) were placed on the vegetation in each container and the lid replaced. The containers were labelled and placed under a 16:8 L/D photoperiod at 16.5°C with a 2°C range. The plant material was renewed every seven days and larvae were checked daily on most occasions and when not, every second day. The number of days to reach pupal and adult stages was recorded and the weight of the pupae was recorded within two days of the final larval moult. This continued for thirteen weeks,

at which time all unemerged pupae were recorded as dead. ANOVA was used to compare mean weights between treatments and further explored using Fisher's least significant difference test. Chi-square tests were used to detect significant differences in the proportion of larvae which survived to pupae and adults between treatments. A Kruskal-Wallis ANOVA was used to determine the effect of treatments on the time taken to develop to pupal and adult stages. Significant results were further explored using Mann-Whitney U tests.

5.2.2.3 Results

1. Buckwheat, broad bean and apple

There was a significant effect of treatment on the proportion of larvae which survived to prepupal, pupal and adult stages (prepupal, X^2=7.58, df=2, P<0.05, pupal, X^2=12.82, df=2, P<0.01, adult, X^2=23.18, df=2, P<0.001) (Fig. 5.13). Chi-square tests revealed that leafroller survival was significantly higher when they were reared on apple compared with buckwheat and broad bean at prepupal, pupal and adult developmental stages (P<0.05) (Fig. 5.13). There was no significant difference in leafroller pupal weight between the three host plant species (F=0.51, df=2,177, P>0.05) (Fig. 5.13).

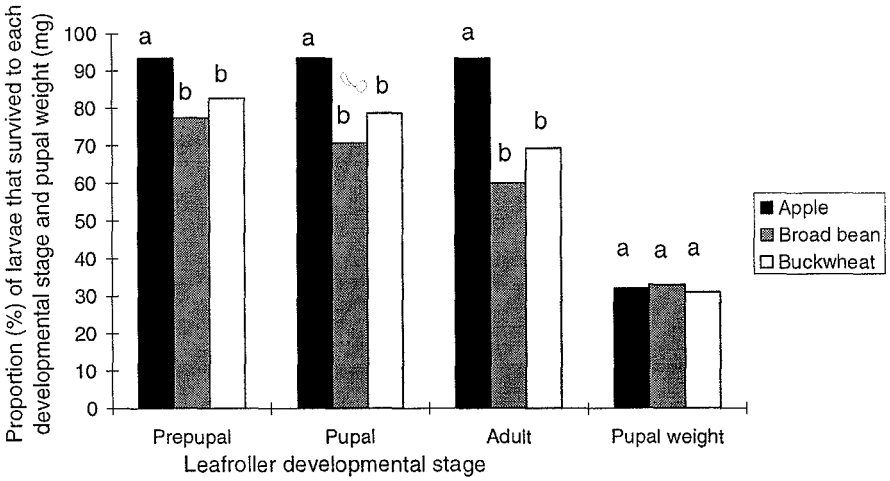


Fig. 5.13 The proportion of leafroller larvae that survived to each developmental stage, and pupal weight when reared on apple, buckwheat and broad bean (see Fig. 5.1).

2. Alyssum, phacelia and apple

There was a highly significant effect of treatment on the proportion of larvae that survived to the pupal and adult stage, respectively (pupa: X^2= 21.34, df=2, P<0.001; adult: X^2= 38.19, df=2, P<0.001). The proportion of larvae reaching the pupal and adult stage was significantly higher when reared on apple compared with phacelia and alyssum (P<0.01) (Fig. 5.14). There was an overall significant difference in leafroller pupal weight between the three host plant species (F=9.594, df=2,44, P<0.001). Least significant difference tests revealed that larvae reared on alyssum produced a significantly smaller pupae than those on apple and phacelia (P<0.01). There was no significant difference in pupal weight between apple and phacelia (P>0.05) (Fig. 5.14).

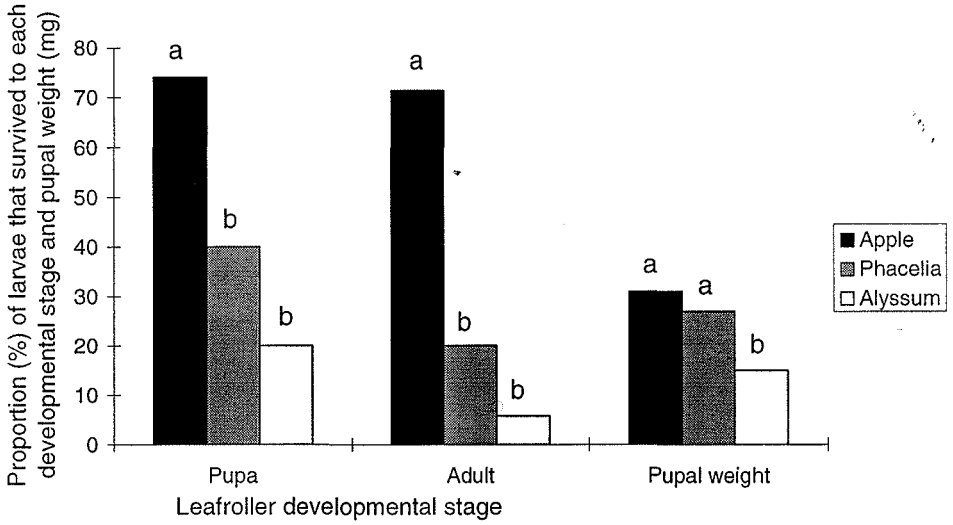


Fig. 5.14 The proportion of leafroller larvae that survived to each developmental stage, and pupal weight when reared on apple, phacelia and alyssum (see Fig. 5.1).

Time to reach the pupal stage was significantly different between the three treatments (X^2=9.68, df=2, P<0.01) (Fig. 5.15). Larvae reared on alyssum took significantly longer to develop into pupae than those on phacelia (P<0.01). Larvae reared on apple also took a shorter time to reach the pupal stage than on alyssum; however, this was not significant (P>0.05) (Fig. 5.15). There was no significant difference in the time to reach adult stage between treatments (X^2=1.50, df=2, P>0.05) (Fig. 5.15).

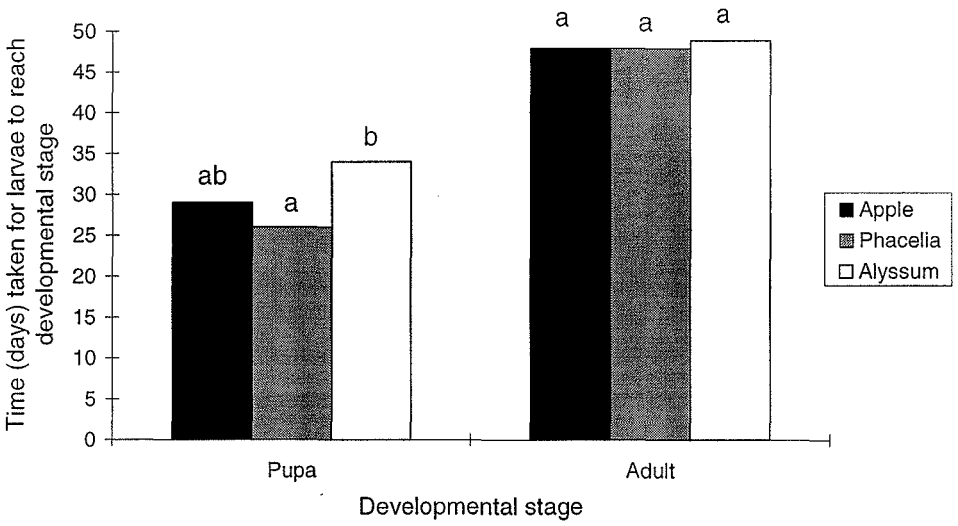


Fig. 5.15 Time taken to develop to pupal and adult stages when reared on apple, phacelia and alyssum (see Fig. 5.1).

5.2.2.4 Discussion

Sixty percent of larvae survived to the adult stage when reared on broad bean. Although this was significantly lower than for those reared on apple, Geier and Briese (1981) showed that LBAM larvae develop rapidly on broad bean. In conjunction with the inability of this plant to provide sufficient floral nectar and pollen to *D. tasmanica* (Sections 5.1.1 and 5.1.2), this plant is probably not a suitable candidate for understorey management in orchards. In contrast, buckwheat shows potential for attracting *D. tasmanica* and enhancing both longevity and fecundity (Sections 5.1.1, 5.1.2 and 5.1.3) and it produced a significantly lower leafroller larval survival rate than apple in the current study. However, 70% of larvae still survived to adult stage when reared on this species, suggesting that buckwheat may be a potential host of leafroller. It's important to choose a plant candidate which will not enhance leafroller populations as some cover crops have been shown to enhance pest populations. For example, Mass *et al.* (1998) showed that the presence of the European corn borer, *Ostrinia nubilalis* Hubner, in strawberries was associated with a cover crop of millet (*Setaria italica* Beauv.), and insect pests were more abundant in crimson clover, *Trifolium incarnatum* L., when it was used as a cover crop in cotton fields

(Stapel *et al.*, 1998). However, 265 host species are known in New Zealand for leafroller (Thomas, 1989) and the host range of LBAM encompasses 34 different plant families (Tomkins, 1984), many of which are present in and around the orchard, in the inter-row sward and in weedy areas and shelter belts (Chapman, 1973; Spiller and Wise, 1982). For example, although poplar and *P. lanceolata* are known hosts of leafrollers, they are often used in shelter belts or as a herb ley mix in the inter-row sward, respectively (Tomkins, 1984; Tomkins *et al.*, 1991), and leafroller larvae have been reported to feed on 13 species of weeds present in the apple orchard (Danthanarayana, 1983). Therefore, given the extreme abundance of preferred leafroller hosts in the orchard, buckwheat is not likely to contribute to the leafroller population. Also, if adult leafrollers do oviposit on buckwheat or the other understorey plants, then it is likely that these egg batches will be smaller than those laid on apple because batches that are laid on preferred hosts are larger than those laid on a less suitable host (Tomkins, 1984). Furthermore, larval survival to the adult stage would be reduced compared with apple; pupal weight would also be reduced and hence fecundity of the resulting female would be lower, and development time to reach adulthood would be increased. If developmental stages are prolonged, then the leafroller larvae will be available to natural enemies, or to die from unfavourable temperatures or desiccation, for longer periods of time (Feeny, 1976; Clancy and Price, 1987; Damman, 1987). Neonate larvae which accidentally blow into the understorey should not produce adults which are more likely to oviposit on the understorey plants because Tomkins (1984) showed that the majority of egg batches were laid on apple even though leafroller were reared on blackberry.

There was no significant difference in the weight of pupae from larvae reared on apple, broad bean and buckwheat. This may have been because male and female pupae were not separated in the analysis, which would have increased the variability of these data, making it more difficult to detect differences between treatments.

Leafroller survival on alyssum and phacelia was below 20%, strongly suggesting that these plants are not favourable hosts. Therefore, using these plants as understorey plant options for leafroller biological control should not contribute to an increase in the leafroller population. Alyssum shows good characteristics for an understorey management option in

apple orchards because it is not preferred by leafroller (Section 5.2.1) and when they are forced to feed on it, high mortality (94.3%) and low pupal weight (15 mg) results. Similar results have been found by Tomkins (1984) who found that pupal weight of larvae reared on the apple 'Red Delicious' was 1.3 times heavier than when reared on poplar. The high mortality of larvae reared on alyssum may be due to the plant not providing the nutrients required for leafrollers to develop or to the presence of antifeedants which caused larvae to stop feeding and starve (Russel and Lane, 1993). The low pupal weight of larvae reared on alyssum suggests that this is not a favourable host of leafrollers because individuals which disperse are smaller and are produced on sub-optimal hosts (Danthanarayana, 1976). Gu and Danthanarayana (1990) found significant correlations between fecundity and total body weight, therefore, leafrollers reared on alyssum should also have low fecundity. Fecundity is associated with the quality and quantity of larval food resources (Danthanarayana, 1975a,b) so because food was provided in access, alyssum is not a high quality host for leafroller.

Rearing leafrollers on alyssum (5.7%) and phacelia (20%) led to a lower survival to the adult stage than did buckwheat (69.33%) and broad bean (60%). The higher survival on the latter plants (Experiment 1) may be due to the stems' being wrapped in damp cotton wool and 'Glad Wrap' to prevent water loss and wilting. Although the alyssum and phacelia treatments (Experiment 2) were placed in an airtight container on damp tissue paper they may have been of a lesser quality, producing a lower larval survival. The proportion of larvae surviving on apple in Experiment 1 (93.3%) was higher than those reared on apple in Experiment 2 (74%), which supports this theory. However, pupal weights for apple were comparable between studies (Experiment 1 = 33 mg, Experiment 2 = 31 mg).

The plant material used in these studies would have differed from that in a field situation because it was not actively growing. Even though the ends of the plant stems were wrapped in damp cotton wool for Experiment one, cell turgidity would still have been reduced. Therefore, the survival values represented here probably underestimate the performance of leafrollers on these plants grown in the field. Also, the plant species may have differed in their ability to take up water or in the quantities of cytokinins and auxins which are known to influence leaf yellowing and stem quality (van Doorne and Woltering, 1991).

The apple leaves used during these experiments were from mature apple foliage, whereas faster LBAM larval development occurs on young rather than mature apple foliage (Dumbleton, 1939; Geier and Briese, 1980). Therefore, using mature leaves may have influenced the results because young foliage may have further decreased larval development time on apple, therefore making the differences between treatments more marked. Also, only one cultivar of apple ('Braeburn') was used during these no-choice tests which may have influenced the significance of the results. For example, larvae reared on 'Red Delicious' took 1.2 days longer than those feeding on 'Granny Smith' and the pupae were 1.1 times heavier (Tomkins, 1984). Furthermore, larvae reared on the less favourable plants would be less likely to endure low-density larval crowding because less larvae were present as mortality was higher than on favourable hosts. Larvae reared at low larval densities have a shorter larval period (Danthanarayana *et al.*, 1982); therefore, this would have underestimated the negative effects of unfavourable hosts.

These laboratory studies were limited because only one leafroller species, LBAM was used, whereas there are three important species of leafroller in Canterbury. LBAM was selected because it is the most common leafroller in Canterbury, there is some evidence that *D. tasmanica* prefers LBAM (Wearing *et al.*, 1991), and because of the ease at which it can be obtained (from Insect Rearing Unit (see previous)). However, it may be beneficial to repeat the choice and no choice laboratory studies on the understorey plants with the greatest potential, using the other leafroller species. Also, there are many other pests of apple, for example, spider mites, that the understorey plants may enhance or shelter. Investigations into the influence of understorey plants on the complete apple pest complex are required.

5.2.3 Effect of floral resources on adult leafroller fitness

5.2.3.1 Introduction

Previous field and laboratory studies have shown that floral resources enhance parasitoid abundance, longevity, fecundity and leafroller parasitism (Sections 2.1, 3.1, 4.1, 5.1.1, 5.1.2 and 5.1.3). However, some adult Lepidoptera also feed on floral nectar (Kevan and Baker, 1984), so lepidopteran pests may make use of nectar from food plants intended for natural enemies (Baggen and Gurr, 1998). Increased crop damage by lepidopterans has been associated with the availability of adult food (Burleigh, 1972). For example, greater numbers of *Pieris rapae* and *Plutella xylostella* in plots of *Brassica oleracea* L. have been associated with the presence of nectar-producing plants (Zhao *et al.*, 1992). In contrast, the longevity of *Copidosoma keohleri*, an important parasitoid of potato moth, was significantly increased on borage flowers compared with borage without flowers, but no such benefit occurred to the pest (Baggen and Gurr, 1998). Therefore, it may be possible to select an understorey management option which selectively benefits *D. tasmanica* and not the leafroller adult.

Gu and Danthanarayana (1990) showed that longevity of LBAM increased when fed on honey/water compared with water, but fecundity was not affected. However, this experiment did not consider the effect of floral resources on egg fertility and the quality and nutritional value of honey/water solution compared with that of floral nectar. The following experiment extends this research by investigating the influence of floral resources on leafroller adult longevity, fecundity and fertility and by using alyssum as a source of floral nectar.

5.2.3.2 Methods

Seven replicates of four treatments (water, 50:50 honey/water solution, flowering alyssum (cv. 'Carpet of Snow') and no food/water) were set up in a randomised block design under a 16:8 L/D photoperiod, at 16.5°C with a 2°C range (Plate 16). The water and honey/water treatments were contained in a 40 mm vial filled and sealed with a cotton wool plug. Alyssum treatments consisted of a 50 mm length of flowering stem placed in a 40 mm

water-filled vial and sealed with a cotton wool plug. All treatments were topped up with water or honey/water solution as necessary and plant material was replaced every six days. Vials were covered with a cylindrical acetate sheet with netting glued on one end (Plate 16). Positioned inside these acetate sheets was another, scored with lines 1 cm apart. This surface enhances leafroller oviposition (King, 1972).

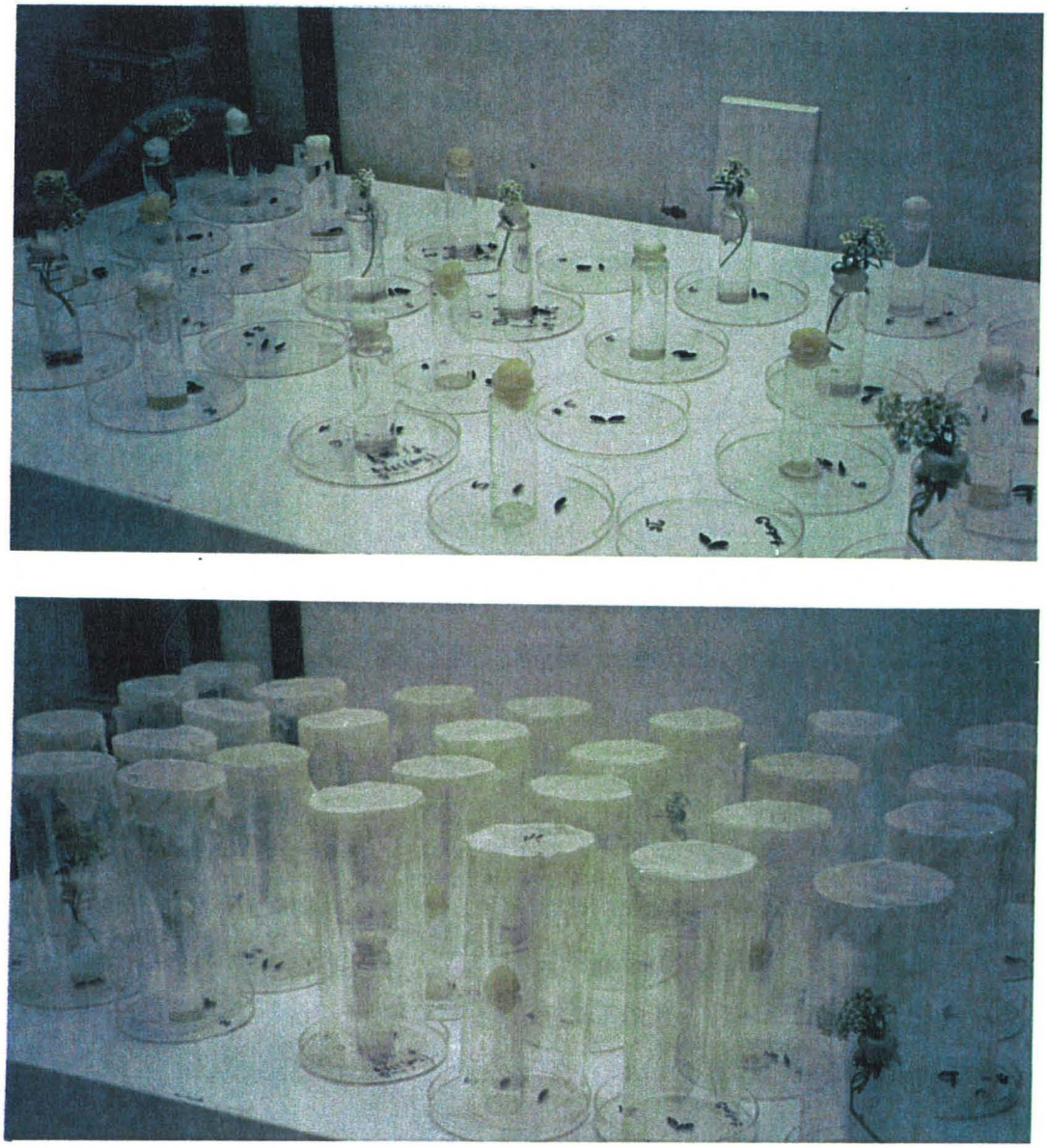


Plate 16. Top: Experimental layout of no food, water, honey/water and alyssum treatments with a pair of leafroller pupae in each treatment. Bottom: Cylindrical acetate sheets covering treatments.

A pair of LBAM pupae (Appendix 1), due to emerge within three days, was placed in each treatment. The number of days until death of each sex was recorded. Males were not replaced. The acetate sheets inside the cylindrical cages were replaced every three days and the number of leafroller eggs laid on these and any other surfaces were counted for each treatment under a binocular microscope. Eggs from the acetate sheets (not from any other surface) were incubated at 20°C with a 2°C range and the percentage of eggs which hatched were counted as a measure of fertility.

Survival curves were compared between treatments using a log rank test and Kaplan Meier estimates of mean survival were calculated (Kaplan and Meier, 1958). Total numbers of eggs and the number of fertile eggs were compared between treatments using ANOVA and significant effects were further explored using Fisher's least significant difference test. Those females which died of unnatural causes, such as drowning, or which escaped, were not included in the egg production analysis.

5.2.3.3 Results

Survival

There was a significant effect of treatment on adult female leafroller longevity (X^2=21.73, df=3, P<0.001). An alyssum diet led to a significantly longer survival than water and no food (P<0.05) (Fig. 5.16). Honey/water produced a significantly greater longevity than water and no food (P<0.05) (Fig. 5.16).

There was an overall significant effect of treatment on longevity for male leafroller adults (X^2=19.48, df=3, P<0.001). Water significantly reduced male survival compared with alyssum, honey/water and no food (P<0.01) (Fig. 5.16). No food produced a significantly greater longevity than honey/water (P<0.01) (Fig. 5.16). There was no significant (X^2=0.429, df=1, P>0.05) gender effect on longevity over all treatments (mean male longevity: 13.4 days; female: 15.3).

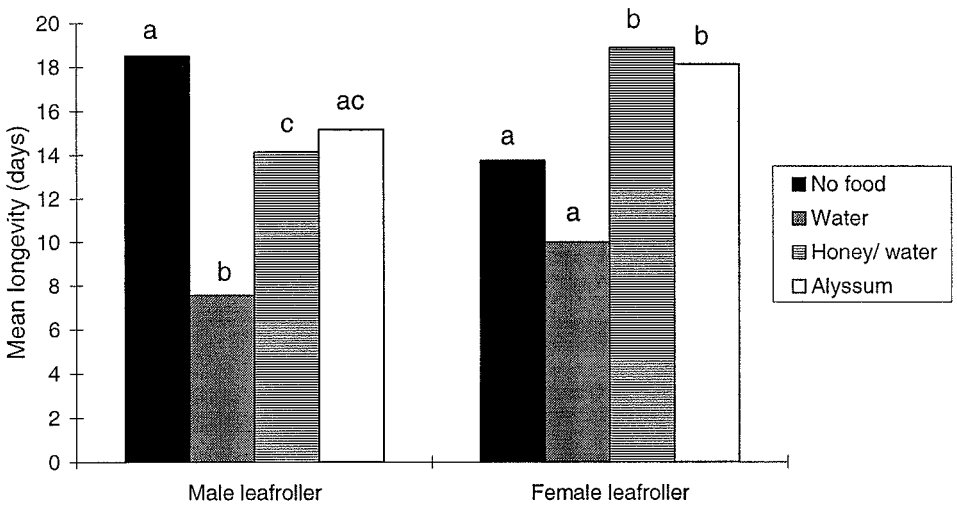


Fig. 5.16 Mean longevity (days) of male and female adult leafrollers provided with different food sources in the laboratory at 16.5°C (different letters indicate significant differences between treatments within sex).

Fecundity and fertility

There was a highly significantly effect of floral treatment on the total number of eggs produced (F=21.91, df=3,14, $P<0.001$). Alyssum produced a significantly higher total number of eggs per female than did honey/water, water and no food ($P<0.05$) (Fig. 5.17). Honey/water did not significantly ($P>0.05$) increase the total number of eggs compared with no food but it led to a significantly ($P<0.05$) lower number of eggs than did a water diet (Fig. 5.17). The number of fertile eggs laid significantly differed between floral treatments (F=6.52, df=3,13, $P<0.01$). Alyssum led to a significantly ($P<0.01$) larger number of fertile eggs than did no food and honey/water but did not significantly ($P>0.05$) enhance the number of fertile eggs produced compared with water (Fig. 5.17).

5.2.3.4 Discussion

Survival

For female leafroller adults, results were similar to those of Gu and Danthanarayana (1990) in that honey/water enhanced adult longevity compared with no food. The early mortality of female adults not given food or water is probably due to dehydration rather than

exhaustion of their metabolic resources (Gu and Danthanarayana, 1990). Also, honey/water solution may have enhanced female longevity due to increasing humidity, although the humidity experiment in Section 5.3 suggests that humidity did not differ between water, honey/water and alyssum treatments.

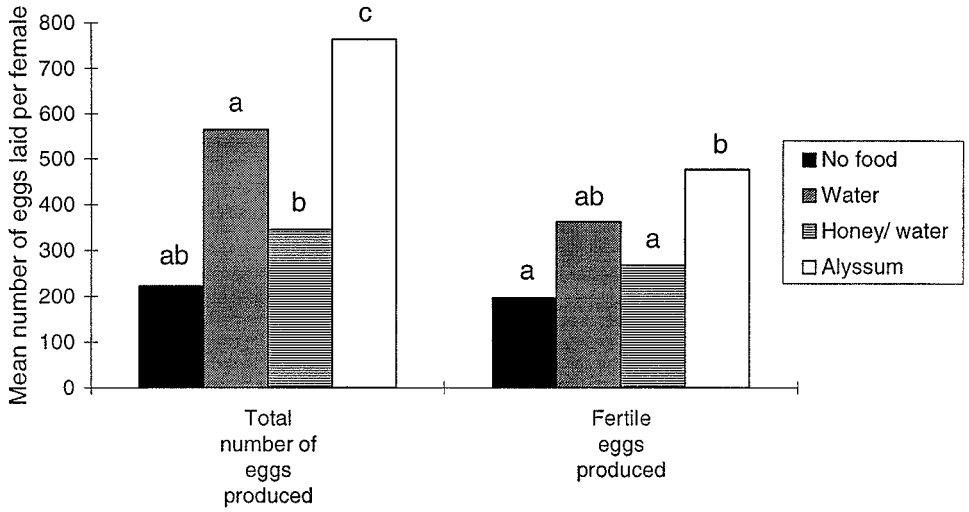


Fig. 5.17 The mean number of total and fertile eggs produced by female leafrollers provided with different food sources in the laboratory at 16.5°C (see Fig. 5.1).

Honey/water increased longevity of both sexes compared with water, also supporting the results of Gu and Danthanarayana (1990). However, for males, longevity was decreased compared with no food, which contrasts with results obtained by Gu and Danthanarayana (1990). This may suggest that the honey/water ratio used in this experiment may have been too viscous to for males to imbibe. Lepidoptera take up food through narrow tubes, therefore they are restricted to less viscous sugar solutions (Baker and Baker, 1979). The width of this tube may differ between male and female LBAM. The ratio used in the work of Gu and Danthanarayana (1990) was 30%, whereas in the current study it was 50%, as this was also used for the parasitoid floral laboratory tests (Sections 5.1). Furthermore, male leafrollers may not feed on floral resources or they may not require as many nutrients compared with females as the former do not produce eggs. This may cause males to survive longer in the absence of floral resources. For example, Alm *et al.* (1990) showed that

females of *P. rapae* consumed more sugar-amino acid nectar than sugar-only nectar, whereas males did not discriminate between the two nectars.

For female moths, alyssum enhanced longevity compared with no food and water, suggesting that this lepidopteran can access the nectar of alyssum. However, for male leafrollers, alyssum did not enhance survival, compared with no food. This also supports the above theory that male leafrollers are more resilient when given no food, but it also may indicate that the mouth parts of male leafrollers may differ from those of females and do not allow them to access floral nectar. Floral nectar from plants that rely on small insects for pollination have hexose-rich sugar ratios and are unattractive to most lepidopterans (Baker and Baker, 1979), whereas extrafloral nectar, such as that in broad bean, tends to be sucrose-rich (Handel *et al.*, 1972) and highly attractive to adult Lepidoptera.

Fecundity and fertility

Female adults were able to lay eggs when given no water or floral resources. This supports results of Gu and Danthanarayana (1990) who showed that because LBAM is able to lay fertile eggs without the ingestion of food or water, it is an 'autonomous' insect species, using their definition.

Not only did alyssum enhance female leafroller survival compared with water and no food but it enhanced total egg production compared with all other treatments. However, the number of fertile eggs did not significantly differ between alyssum and water. This suggests that even though survival is increased and the number of eggs laid is increased, overall fertility is not increased. This may be because eggs laid later in the life of female leafroller are less fertile (Howell, 1981). Although the production of fertile eggs following alyssum feeding is equivalent to that of water, they are produced over a longer period of time because survival is enhanced, allowing the moth a greater potential for dispersal.

Although honey/water enhanced female survival compared with water, it led to a lower total number of eggs and fertile eggs than did water. This is similar to results obtained by Gu and Danthanarayana (1990). In the current study, however, honey/water solution did not

significantly enhance the total number of eggs or the number of fertile eggs compared with no food. These results suggest that the honey/water solution may have been too viscous for the female leafroller adults to imbibe and influence egg production. Furthermore, a high proportion of males are incapable of mating (Geier *et al.*, 1969), therefore because only one male was provided per treatment in the current study, some females may not have been mated. This may explain the high variability of the fecundity data.

It may be beneficial to repeat this experiment, including broad bean and buckwheat as treatments to determine the effect of extrafloral nectar on adult leafroller fitness and whether buckwheat is less beneficial to this pest. Additional leafroller species could also be included in conjunction with other apple pests that use floral resources.

5.3 Influence Of Floral Treatments On Humidity

5.3.1 Introduction

Results from the laboratory experiments investigating the effects of floral resources on *D. tasmanica* and adult leafroller suggest that floral resources enhance parasitoid and leafroller adult longevity. Female *Apanteles medicaginis*' survival was increased from 18.4 to 28.2 days when humidity was increased from 30 to 55%, indicating that humidity is an important factor in parasitoid longevity (Allen and Smith, 1958). Also, high humidity is important for the survival of *Microctonus hyperodae* (Hodgson *et al.*, 1993) and the foremost climatic factor besides temperature which may affect leafroller development is relative humidity (Tomkins, 1984). Humidity was not measured during the studies in this chapter. The honey/water treatment may have caused the atmosphere to be at saturation, and the plant material in the floral treatments would have transpired, which may have increased humidity. Therefore it is not known whether the increase in parasitoid and leafroller longevity, shown in some treatments, was affected by an increase in humidity. The following experiment investigates the influence of water, honey/water and alyssum on relative humidity.

5.3.2 Methods

Three 'Tiny Tag' humidity loggers were placed into a cylindrical acetate sheet with netting glued to one end. These were the same cages used in the previous parasitoid and adult leafroller laboratory trials. A vial of water containing 50 mm of flowering alyssum, sealed with a cotton wool plug was placed under the acetate sheet. After two hours, graphs were produced from the loggers to determine that they were within a few percent humidity of each other. After this was confirmed, three replicates of three treatments (water, 50:50 honey/water solution, and flowering alyssum (cv. 'Carpet of Snow')) were set up in a randomised block design under a 16:8 L/D photoperiod, at 16.5°C with a 2°C range. The water and honey/water treatments were contained in a 40 mm vial filled and sealed with a cotton wool plug. The alyssum treatment consisted of 50 mm of flowering stem placed in a 40 mm water-filled vial, sealed with a cotton wool plug. A humidity logger was randomly placed in each treatment of the first replicate and left for two hours. The loggers were

removed and placed randomly into the treatments of the second replicates and left for two hours. Finally this was repeated for the third replicate. Humidity, measured at five-minute intervals, was down-loaded into a computer from the humidity loggers and an average was calculated for each treatment and replicate over a two hour period.

5.3.3 Results

There was only a 5 % difference in humidity over all treatments (Table 5.1) indicating that there was not a major humidity difference between treatments. There was also only a 5% difference in humidity over all humidity meters and humidity increased from 56.7-79.5% with replicate/time (Table 5.1).

Table 5.1 The influence of water, honey/water and alyssum treatments, of replicate and humidity meter on relative humidity.

Treatment	Humidity	Replicate/time	Humidity	Humidity meter	Humidity
Water	63.5%	1	56.7%	1	66.2%
Honey/water	64.5%	2	60.3%	2	62.5%
Alyssum	68.4%	3	79.5%	3	67.8%

5.3.4 Discussion

The results suggest that treatment did not influence the humidity within the cylindrical acetate sheet cages (see Plates 14 & 16) and that the increase in parasitoid and adult leafroller longevity in some floral treatments in the experiments discussed in this chapter were not because of differences in humidity between treatments. However, this experiment investigated only alyssum, whereas buckwheat and broad bean have a larger leaf and surface area from which to transpire. Also, leaves from different plant species may differ in the density of stomata. It may be beneficial to repeat this experiment using buckwheat and a combination of flowering stems to determine whether an increase in leaf area increases transpiration and humidity. Humidity increased through time because the cylinder tubes were almost sealed.

6. BEHAVIOUR OF PARASITISED AND UNPARASITISED LEAFROLLER LARVAE IN THE LABORATORY

6.1 INTRODUCTION

Parasitism rates of up to 100% occur when leafroller larvae are released to estimate parasitism rate, whereas naturally-occurring parasitism is approximately 20-30% (Collyer and van Geldermalsen, 1975; Green, 1984; Suckling *et al.*, 1996a). Releasing leafrollers on to branches in the field produces high densities of larvae. High parasitism rates may be due to the parasitoid ovipositing in all larvae once a patch is found. Bias towards either parasitised or unparasitised hosts when using sampling methods to estimate percentage parasitism is a common problem (van Driesche, 1993). High parasitism rates obtained in the field may be attributed to the parasitoid influencing the behaviour of the leafroller larva once it is parasitised. For example, codling moth larvae parasitised by *Ascogaster quadrientata* Wesmael are only one-fourth to one-third the normal size (Clausen, 1940) and *Pseudaletia unipuncta* (Haworth) larvae parasitised by *Apanteles militaris* (Walsh) eat less than half as much as do unparasitised larvae (Tower, 1916). Behavioural modifications often are the result of mechanical damage or chemical interference by the parasitoid with the host's physiology (Helluy and Holmes, 1990; Holmes and Zohar, 1990; Hurd, 1990). These changes in larval behaviour may influence larval dispersal or survival, or make them more prone to predation. Larvae parasitised by *D. tasmanica* may be less mobile, disperse less readily or be less prone to dropping to the ground to pupate, compared with unparasitised larvae. Therefore, the larvae which are collected from the field to measure parasitism rate may be more likely be parasitised, because the unparasitised larvae have dispersed. It is important to determine the influence of *D. tasmanica* parasitism on leafroller larval dispersal and behaviour as this has important implications for the analysis of future experiments using these techniques. The following two experiments investigate the dispersal of parasitised and unparasitised larvae in the laboratory to provide some understanding of why the released leafroller larval technique used in the field produces what appears to be high parasitism rates.

6.2 METHODS

6.2.1 Recovery of parasitised and unparasitised larvae in the laboratory

On March 26, 1999 seven potted crab apple trees (*Malus* ex 'Crimson Rod') (700-800 mm high) were placed in each of two Perspex culture boxes (550 x 510 x 510 mm) and 180 hatching LBAM eggs (Appendix 1) were released into each box. Thirteen male and thirteen female newly-emerged *D. tasmanica* were placed into one culture box and after four days, the trees were removed from the culture boxes and placed 1 m apart on a bench in a randomised complete block design (refer Fig. 6.1). Parasitoids were obtained from emerging parasitoids collected from released larvae in the field (Section 4.1). A sticky polybutene-based insect trap adhesive was brushed on to the bench between the trees to stop larvae moving between treatments. The insectary building (Lincoln University) was not heated but continuous lighting was provided to maintain adequate growth and plant quality. Trees were watered every second day and after three weeks the leaves from each tree were removed and taken into the laboratory. The larvae were removed and placed into individual diet tubes, sealed with cotton wool and incubated at 16.5°C with a range of 2°C. The proportion of parasitised larvae was calculated and the median number of larvae recovered was compared between parasitised and unparasitised larval treatments using a Mann-Whitney U test.

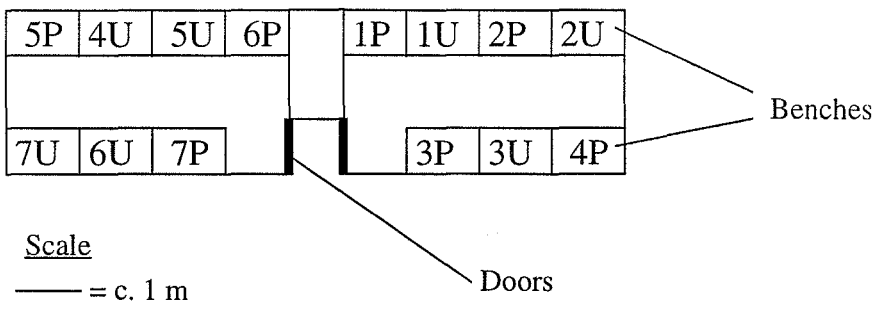


Fig. 6.1 Experimental set up of parasitised and unparasitised larvae on potted crab apple trees placed on benches in the laboratory (number = replicate, U = unparasitised, P = parasitised).

6.2.2 Ability of leafroller larvae to disperse via dropping from a thread

First instar LBAM were placed on leafroller diet (Appendix 1) and exposed to five male and five female newly-emerged *D. tasmanica* for 48 hours. Parasitoids were obtained as in the previous experiment and supplied with 50:50 honey/water solution. Some larvae were left on diet and not exposed to parasitoids. An arena was constructed using a Petri dish as a base with a glass microscope cover slip suspended on top of an 11 cm glass rod (Plate 17). A green card (refer Appendix 3 for spectral reflectance) was placed underneath the Petri dish as it has been shown that neonate leafroller larvae are attracted to this colour and readily spin down on a silk thread towards it (Harris *et al.*, 1995). Five or ten larvae that were presumed to be parasitised were placed onto the cover slip arena at one time and the time taken for them to drop from the cover slip via a silk thread was recorded. As the larvae dropped from the arena they were removed by placing a fine paint brush to the silk thread approximately 2-4 cm above the larva and transferring them into individual diet tubes. These were labelled with a number corresponding to the time taken to drop from the arena. After ten minutes, the experiment was stopped and a time of 600 seconds was recorded for the remaining larvae. This was repeated, alternating between parasitised and unparasitised larvae, until four replicates of five larvae and three replicates of ten larvae had been conducted. Each larva was tested only once. Diet tubes were maintained at 16.5°C with a range of 2°C for incubation to determine whether the larvae in the parasitised treatment were in fact parasitised.

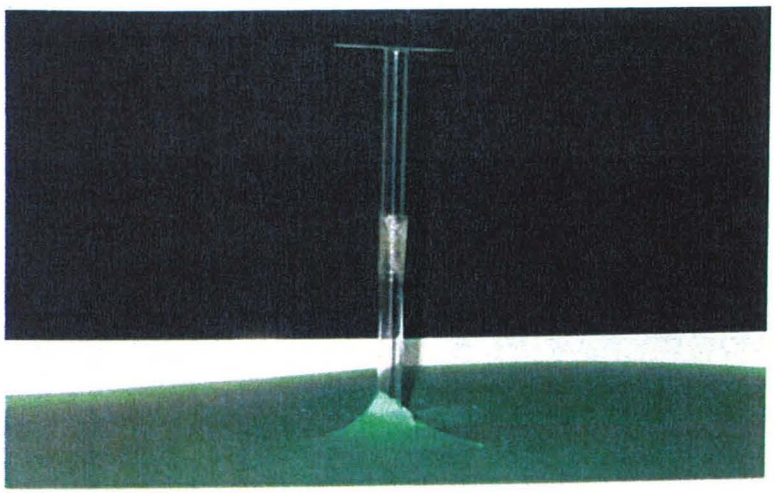


Plate 17. Experimental arena (11 cm high).

The median, minimum and time to the fifth larva dropping were calculated and compared between parasitised and unparasitised larval treatments using the non-parametric Mann-Whitney U test. These statistical parameters were also compared between the number of larvae per replicate (five or ten) using the same test to determine whether placing more larvae on the arena influenced the rate at which they dispersed.

6.3 RESULTS

6.3.1 Recovery of parasitised and unparasitised larvae in the laboratory

The proportion of larvae parasitised in the parasitised and unparasitised larval treatments was 50% and 0% respectively. Although the total number of larvae recovered was almost twice as high for parasitised (total=70, median=5) larvae compared with unparasitised (38,1), the median number of larvae recovered did not significantly differ between treatments (U=35.5, 1, $P>0.05$). The proportions of larvae that died after collection in the parasitised and unparasitised larval treatments were 14.3% and 2.7% respectively.

6.3.2 Ability of leafroller larvae to disperse via dropping from a thread

The median and minimum time taken for larvae to drop from the arena was significantly longer for parasitised larvae (median=582 seconds, minimum=140 seconds) compared with unparasitised larvae (255, 45) (median: U=4.5, 1, $P<0.05$; minimum: U=5.0, 1, $P<0.05$) (Fig. 6.2). There was a no significant difference in time to fifth larva dropping between parasitised (fifth=600) and unparasitised (405) larvae (fifth: U=13.0, 1, $P>0.05$) (Fig. 6.2). Using five larvae compared with ten larvae per replicate significantly increased the time taken for the fifth larva to drop (U=41.0, 1, $P<0.05$) (Fig. 6.2). The larvae in the diet tubes did not survive to allow a percentage parasitism rate to be calculated.

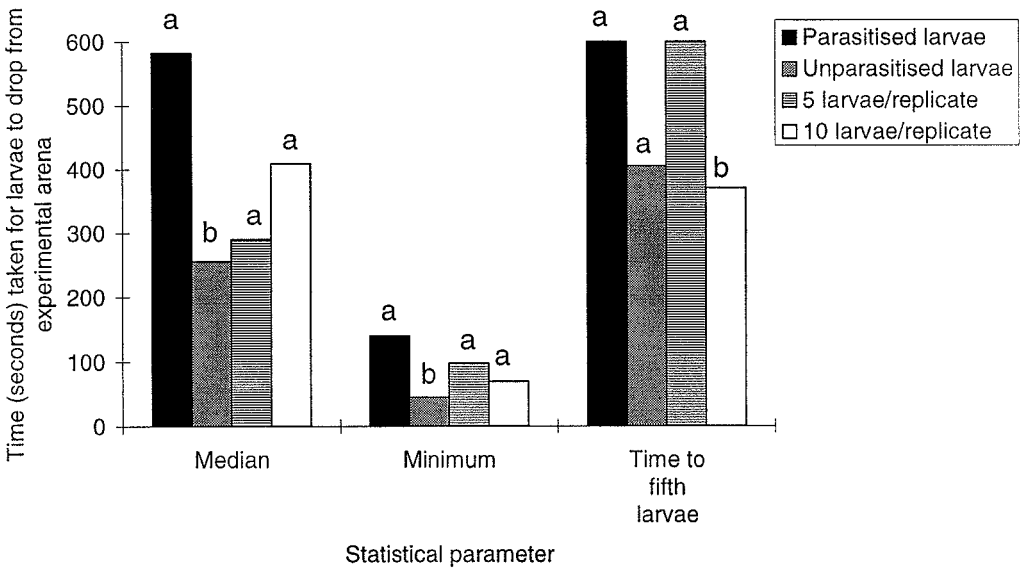


Fig. 6.2 The effect of parasitism by *D. tasmanica* and the number of larvae used per replicate on the time taken for larvae to drop by a thread from the experimental arena (mean time to fifth larvae = time taken for fifth larvae in each replicate to drop; different letters indicate significant differences between treatments ($P<0.05$)).

6.4 DISCUSSION

6.4.1 Recovery of parasitised and unparasitised larvae in the laboratory

Results showed that increasing the proportion of larvae parasitised from 0-50% increases the total number of larvae recovered after three weeks by almost two-fold. This may suggest that parasitised larvae are less mobile and do not disperse as readily as unparasitised larvae. Also, in some species, parasitised larvae feed less than unparasitised larvae (Chapman, 1973; Nealis *et al.*, 1990; Yang *et al.*, 1994). If this occurs with LBAM then it may allow parasitised larvae to remain in their webbed shelters for a longer period before finding a new feeding site.

If the above results were confirmed statistically in further work (for example, with a higher number of replicates) then they may explain the un-naturally high parasitism rates of

released larvae in the field. Leafroller larvae disperse by spinning a thread down to the lower canopy or the ground cover, or they and the thread may become airborne and disperse great distances (Chapman, 1973). Also, male larvae frequently leave their webbed shelters and prepare a site for pupation, usually on the lower portion of the tree (MacLellan, 1973). Therefore, most of the larvae that are released on to a branch in the field to estimate parasitism rate between treatments will disperse from the release branch. If parasitism by *D. tasmanica* influences the behaviour of the larvae so that they are less mobile, then a large proportion of those larvae collected will be parasitised, hence giving higher parasitism rates and making it difficult to detect differences between treatments.

Once *D. tasmanica* finds the release branch with high leafroller densities, it may parasitise all larvae within that patch. However, in the current study, the thirteen newly-emerged female *D. tasmanica* which were left in a culture box with 180 leafroller larvae and honey/water solution for four days, produced only 50% parasitism. Dumbleton (1935) reported that *D. tasmanica* is ready to oviposit a few days after emergence and in Section 5.1.3 an average of 120 eggs was dissected from *D. tasmanica* fed water after five days. However, during the current experiment, potted crab apple trees, un-naturally high host densities, honey/water solution and un-naturally high *D. tasmanica* abundance in a confined area of the culture box were used. This was a very artificial situation and may have influenced the ability of the females to locate their hosts due to high quantities of host chemical cues within a confined area and competition between females.

Although the results here may support those from in the field, field parasitism rates are higher than those presented here, suggesting that the effect of parasitism in reducing larval mobility is enhanced in the field. This might be attributed to the presence of predators in the field. Spiders and earwigs are important predators of LBAM larvae, and birds, chysopids and predatory mites also feed on them (Danthanarayana, 1983). If parasitised larvae feed less than unparasitised larvae, then they would remain in their webbed shelters for a longer period of time before moving to a new feeding site. This may make them less prone to predation because they are protected by their web shelter. Also, the characteristic movements of leafroller larvae make them vulnerable to predation by spiders which rely almost solely on movement of their prey for detection (MacLellan, 1973). Therefore, if

larvae parasitised by *D. tasmanica* are less mobile, they may be less likely to be detected by predators. However, in contrast, parasitism of *Synaxis cervinaria (*Packard) increased bird predation by changing the normal larval resting behaviour (Valenti *et al.*, 1997).

Neonate leafroller larvae disperse by spinning down on a silk thread that can be carried by the wind or walking (Geier and Briese, 1980). The current study was conducted in a building to reduce wind currents, so larvae could disperse only by dropping to the ground and walking. Limiting the air currents in the building and using the sticky polybutene-based insect trap adhesive prevented larvae from commuting between treatments. However, the absence of wind currents in the laboratory would have reduced larval dispersal compared with the field, also explaining the higher parasitism rates in the field compared with the current study. Furthermore, the larvae were left on the tree for 4-6 weeks during the field experiments carried out in Sections 2.1 and 3.1, whereas in the current laboratory experiment, larvae were collected and placed into diet tubes after three weeks. Third instar larvae leave their feeding sites in search of new ones (Tomkins, 1984) so early larval collection may have reduced dispersal compared with field work because larvae would not have yet reached the third instar.

A higher proportion of larvae died after collection in the parasitised (14.3%) treatment compared with the unparasitised (2.7%). This may have been because these larvae were superparasitised or because parasitised larvae are less resilient (because their immune system is countering the effects of the parasite (Poulin, 1994)) to drier conditions in the diet tubes.

Eighty-six percent of the larvae in the parasitised treatment survived in the diet tubes to produce parasitoid cocoons or leafroller pupae. In contrast, 6.5% of the larvae exposed to parasitoids in diet tubes during the fecundity experiment in Section 5.1.2 survived. This may be because larvae in the current study had three weeks on the apple tree before being transferred to the diet tubes, therefore avoiding desiccation at these early vulnerable instars. Also, the diet would not have dried out in the current study until the late instars which would have increased survival.

Of the larvae that survived to produce a parasitoid cocoon or leafroller pupa, 58.3% were parasitised in the current study compared with 35.3% in the experiment in Section 5.1.2. Larvae in the current study were exposed to parasitoids on the leaves of the plant, whereas in the fecundity experiment (Section 5.1.2), larvae were on leafroller diet within the tubes. This may suggest that *D. tasmanica* requires plant odours to locate the larvae and stimulate oviposition and that the diet lacks these essential chemical cues. Host plant plays an important role in influencing the behaviour of parasitoids and a parasitoid may not parasitise a preferred host larva on an unfavourable plant species (Laster, 1974; Vinson, 1981).

6.4.2 Ability of leafroller larvae to disperse via dropping from a thread

The low collection rate of parasitised larvae compared with unparasitised ones, as suggested in the previous experiment and in the field, may be due to a reduced ability to spin a silk thread for dispersal. This may be because the developing parasitoid larva consumes tissue or organs required by the leafroller larva for silk production. A reduction in a parasitised leafroller larva's crawling speed may be attributed to the parasitoid larva consuming muscles required by the leafroller larva for mobility. In fact, some nematodes or cestode larvae cause muscle damage to their hosts, coincidentally affecting their behaviour (Poulin, 1994).

Because of the artefacts associated with laboratory exposure of larvae to parasitoids, and the use of sleeving techniques in the field, it may be more realistic to sample natural populations of leafroller larvae in understorey plant treatments to get a better estimation of the influence and potential of understorey management on parasitism and leafroller populations. This was explored in Section 4.3.

7. SUMMARY AND DISCUSSION

Leafrollers have a high pest status in apple production mainly because of the zero tolerance for their presence in export markets and the high requirement for blemish-free fruit (Lo *et al.*, 1997; Walker *et al.*, 1997). Their management is the main consideration determining the number of insecticide applications in commercial orchards; export apple growers had applied in the past, between three and eleven post-bloom organophosphate applications per season (Wearing *et al.*, 1991). This intensive insecticide use has led to leafroller resistance (Suckling *et al.*, 1984; Wearing, 1995; Lo *et al.*, 1997). Furthermore, consumers are increasingly questioning the negative effects of pesticides and are demanding lower pesticide residues on fruit, or pesticide-free fruit (Wilson-Salt, 1993). Recently, one of the specifications being applied by some British supermarkets is that exporters must produce agricultural products under 'environmentally friendly' practices (Batchelor, 1996). It is very important for the New Zealand apple industry to meet these criteria because 25% of New Zealand apple exports are to the United Kingdom (Anon., 1998a). Also, the range of pesticides available is diminishing, pesticide registration costs are rising, and permissible spray residue levels continue to be reduced (Wearing *et al.*, 1993; Anon., 1999). Therefore, the pipfruit industry has moved towards a more sustainable management approach, called integrated fruit production (IFP). This programme requires growers to use monitoring procedures and action thresholds to determine when pesticide application is essential and strongly favours the use of insect growth regulators (IGR) and the reduction of the use of broad-spectrum insecticides (Batchelor *et al.*, 1997). The introduction of IGRs has allowed an opportunity for utilising natural enemies such as *D. tasmanica*, for the biological control of leafrollers.

This study has investigated understorey management in Canterbury, New Zealand apple orchards for the enhancement of *D. tasmanica* for leafroller biological control. The first objective of this research was to determine the influence of understorey plants on the abundance of *D. tasmanica* and leafroller parasitism, and to investigate the mechanisms behind this influence. This is discussed in Section 7.1. The second objective was to determine the most suitable understorey plant in terms of its ability to enhance parasitoid

abundance, leafroller parasitism, parasitoid longevity, parasitoid fecundity and its ability to not benefit leafroller. This is discussed in Section 7.3. During the course of the study it became apparent that the method for calculating leafroller parasitism rate was an important consideration for future investigations involving parasitism of leafroller and is discussed in Section 7.2. Finally, Section 7.4 discusses how orchard understorey management for the enhancement of natural enemies can be incorporated into an IFP programme.

7.1 The Influence Of Flowering Plants In The Understorey On Parasitoid Abundance, Parasitism Rate And Parasitoid Fitness

Results from three consecutive field seasons showed that buckwheat, coriander, alyssum, and to a lesser extend broad bean, enhanced parasitoid abundance and leafroller parasitism. The mechanisms behind the effects of understorey plants have largely been unexplored. Parasitoids may have been attracted to the flowering strips due to the presence of aphid honeydew as some parasitoids use this as a source of sugar (Idris and Grafius, 1995; Landis and Marino, 1997), resulting in an increase in longevity (Hagley and Barber, 1992). Alternatively, they may have been attracted by the shelter the plant provides or the higher humidity within the plant strip resulting from the transpiring foliage. Microclimate is an important abiotic factor for parasitic Hymenoptera (Lewis, 1965; van Emden, 1965a; 1965b; Townes, 1972). However, after manipulating the 'buckwheat with and without flowers' treatments in Section 2.1, it was evident that it was the flowers of the buckwheat that 'attracted' the parasitoid to the plant and not the shelter, aphids or microclimate that the plant may also have provided.

Section 5.1.2 confirmed in the laboratory that it was the flowers of buckwheat which influenced parasitoid longevity because the 'buckwheat with flowers' treatment significantly enhanced parasitoid longevity compared with water, whereas there was no significant difference between 'buckwheat without flowers' and water. Results from Section 4.1 suggested that the understorey plants had no influence on the female:male ratio of *D. tasmanica*. This may indicate that, like most Hymenoptera and most *Apanteles* spp. (Allen and Smith, 1958), *D. tasmanica* has arrhenotokous reproduction in that haploid eggs develop into males if not fertilised, and into females if fertilised. Therefore, the sex ratio of

progeny from *D. tasmanica* may be more strongly determined by whether the females are mated, than by food supply.

Section 4.4 investigated the movement of *D. tasmanica* to the buckwheat plots and into the apple canopy. The data suggested that *D. tasmanica* may have flown upwind from the apple canopy to the buckwheat strip, whereas in the controls, parasitoids followed wind direction. This would indicate that the nectar source did influence the movement of *D. tasmanica* and that buckwheat strips attracted parasitoids from surrounding areas where floral resources are low. In support of this suggestion, Altieri and Whitcomb (1979), Altieri and Letourneau (1982) and Jervis *et al.* (1996) indicated that providing flowering plants increases immigration of parasitoids and decreases the numbers lost through emigration.

Another mechanism behind the enhanced parasitism rates seen in the field was the ability of floral resources to enhance parasitoid longevity and fecundity (Section 5.1). Since fecundity was increased with the provision of floral resources (Section 5.1.3), it is likely that *D. tasmanica* is a synovigenic parasitoid. Increasing longevity would increase the potential for *D. tasmanica* to produce more eggs; increasing fecundity would increase the biological control potential of *D. tasmanica* because a high fecundity is considered necessary for parasitoids to be able to reproduce more rapidly than the pest's population and to respond to changes in the abundance of the pest (Sweetman, 1958; Waage and Hassell, 1982; Waage, 1990; Ehler, 1995). There is a significant positive relationship between the outcome of biocontrol and parasitoid fecundity for Lepidoptera (Lane *et al.*, 1999).

Sowing flowering plants in the understorey may interfere with parasitoid host finding mechanisms by masking chemical cues used to locate hosts (Sheehan, 1986; Andow, 1991) leading to a reduction in parasitism (Smith, 1976; Andow and Risch, 1987). Alternatively, if *D. tasmanica* searches for hosts randomly then adding flowering plants in the understorey may cause this parasitoid to spend more time searching on vegetation which does not harbour hosts, in turn leading to a reduction in host encounters (Costello and Altieri, 1995). Therefore, it would be useful to determine whether *D. tasmanica* locates hosts randomly or whether chemical cues are involved.

Other mechanisms behind flowering plants contributing to leafroller biocontrol may include improving parasitoid searching ability (Wäckers *et al.*, 1996), decreasing generation time (Rogers, 1985), increasing parasitoids quality so they are less prone to hyperparasitism, increasing mating efficiency, and improving handling time and oviposition success. Further research is required to explore these mechanisms, so that flowering plants can be selected that maximise the potential of *D. tasmanica* to suppress or delay population increases of leafrollers in the apple orchard.

7.2 Recommended Methods For Future Studies Of Conservation Biological Control

The movement of *D. tasmanica* from a buckwheat plot along a row and into adjacent rows was investigated in Section 3.2. Higher numbers of *D. tasmanica* were captured in the middle, edge and 1 m from the plot compared with 10 m away from it. This suggests that small experimental plots with buffer zones of 10 m may be adequate in future work, to minimise the parasitoids' commuting between plots.

During this study the question rose of what would be the best method of releasing larvae in the field and calculating parasitism rate, so two sleeve types (closed-ended and open-ended) and three methods of calculating parasitism rate were compared. The calculations were:

1. Collection of larvae and parasitoid cocoons after 4-6 weeks and calculating parasitism rate as: (no. cocoons / total number of cocoons + larvae) x 100.
2. Collection of cocoons after 4-6 weeks and counting the number of webbed shelters as a measure of initial establishment rate. Parasitism rate was calculated as: (no. cocoons / number of webbed shelters) x 100.
3. Collection of larvae after two and four weeks placing them into individual diet tubes for further development. Parasitism rate was calculated as: (no. of cocoons / the number of larvae collected) x 100.

Using closed-ended sleeves for leafroller release increased the number of cocoons recovered from the release site compared with open-ended sleeves because neonate

leafroller larvae disperse by spinning a silk thread and dropping to the lower canopy or the ground cover, or becoming airborne and dispersing great distances (Chapman, 1973). Closed-ended sleeves surround the larvae during emergence so they cannot disperse. This may increase larval establishment, therefore increasing the number of cocoons recovered.

The first method of calculating parasitism rate produced rates up to 100%. In fact, a high proportion of the leafroller larvae that were parasitised had 100% parasitism, making it difficult to detect differences between treatments and indicating that once *D. tasmanica* finds a branch of high leafroller densities it may parasitise all hosts within that patch. Counting the number of webbed shelters to calculate parasitism rate produced rates of 20-30% which are comparable with natural parasitism cited by Collyer and van Geldermalsen (1975), Green (1984) and Suckling *et al.* (1996a). However, numbers of cocoons collected were too low to detect significant trends between buckwheat and control treatments. Collecting larvae after two weeks and placing them into diet tubes for further development proved the most optimal way to calculate parasitism rate for comparison between treatments, because it recovered over three-fold more larvae from the release sites than collection after four weeks. This may be because the larvae were collected before the third instar, which is when larvae leave their feeding sites in search of new ones (Tomkins, 1984). However, this technique still produced very high parasitism rates of up to 78.2%. Chapter 6 showed that parasitised larvae were less mobile than unparasitised larvae, and hypothesised that the very high parasitism rates obtained from releasing larvae in the field are attributed to the parasitoid larva influencing the behaviour of the leafroller larva so that parasitised larvae are less likely to disperse, and have a lower predation rate compared with unparasitised larvae. Bias towards either parasitised or unparasitised hosts when using sampling methods to estimate percentage parasitism is a common problem (van Driesche, 1983). Furthermore, the methods used in the current study did not take into consideration other forms of parasitoid-induced mortality such as host-feeding. It is not known whether *D. tasmanica* host-feeds so further research into this aspect is required, in conjunction with investigating the influence of parasitism on the behaviour of leafroller larvae, to design an adequate method for estimating parasitism of leafrollers by *D. tasmanica*.

Future studies using leafroller release techniques to estimate parasitism rates should be aware of the possible selectivity towards parasitised larvae from releasing larvae at large densities because they may over-estimate *D. tasmanica* parasitism rate and the potential of this parasitoid to control leafroller. Also, high parasitism rates in all treatments makes it difficult to detect differences between them. It may be more practical to collect larvae from natural populations of leafroller on all trees within a treatment. Placing them into individual diet tubes and calculating the percentage parasitised may be a better estimation of the influence and potential of understorey management on parasitism and leafroller populations.

7.3 Choosing The Most Suitable Understorey Plant Species

During this study coriander, broad bean, phacelia, buckwheat and alyssum were investigated for their potential as understorey plants for the enhancement of *D. tasmanica*. There are several criteria that are important to consider when evaluating prospective cover crops. Not only is it essential to enhance parasitoid abundance, longevity, fecundity and also be of no benefit to leafrollers but it is also important to consider competitive ability of the plants, cost and availability of seed, stand persistence or self-seeding capabilities (Bugg *et al.*, 1996), early flowering (Bowie *et al.*, 1995; Wratten and van Emden, 1995), agronomic suitability (Gaffney and van der Grinten, 1991) and its ability to survive with little maintenance (Matthews-Gehringer *et al.*, 1994).

Coriander enhanced leafroller parasitism three-fold in the field compared with controls but failed to enhance the longevity of either sex of *D. tasmanica* in the laboratory, compared with water-only. Increasing survival of *D. tasmanica* would increase the potential to produce more eggs over time and enable more leafrollers to be parasitised. Therefore, coriander may not be the optimum understorey plant because although it may attract *D. tasmanica* into the crop, it would not maximise leafroller control because it failed to enhance parasitoid survival and fecundity. Furthermore, coriander does not show good agronomic characteristics for incorporation into the IFP programme because it does not establish well and is a poor competitor with weeds. It also has a longer sowing-to-

flowering time than does buckwheat, which may make this plant less useful for early summer enhancement of natural enemy populations (Bowie *et al.*, 1995).

Extrafloral nectaries are easily accessible to parasitoids (Butler *et al.*, 1972; Yokoyama, 1978; Adjei-Maafo and Wilson, 1983) and because the extrafloral nectar sites are both predictable and detectable, parasitoids are able to search for food more efficiently (Stapel *et al.*, 1997). *D. tasmanica* has been seen feeding on the extrafloral nectaries of *Acacia longifolia* and *A. leprosa* (Collyer and van Geldermalsen, 1975) so broad beans may provide an alternative nectar source in the field for this parasitoid. In fact, in the present study broad beans significantly enhanced parasitoid abundance three-fold and significantly increased parasitism from 0-75% compared with the controls. With the caveat that this effect was significant on only one date in that experiment, it does give some support to the work of Altieri and Schmidt (1985) who documented a reduction in codling moth damage due to the presence of *V. faba*. However, in the current study, laboratory trials showed that broad bean enhanced the longevity of male *D. tasmanica* but failed to enhance female longevity, and female *D. tasmanica* foraging on broad bean produced a total of only three parasitoid cocoons. However, interpretation of this result needs to be made with caution, as overall survival of leafroller larvae (parasitised and unparasitised) was only 6.5% in this experiment. Results presented here suggest that this plant does not provide pollen to short-tongued parasitoids and its extrafloral nectar fails to meet the nutritional requirements of female *D. tasmanica*.

D. tasmanica abundance in the broad bean treatment was significantly lower than that in the buckwheat treatment, suggesting that sugar concentration or nutrient composition differs between floral and extrafloral nectar (Vansell, 1939). Handel *et al.* (1972) also reported that extrafloral nectars tend to be sucrose-rich and are highly attractive to adult Lepidoptera compared with floral nectar. Furthermore, in most cotton species, extrafloral nectar secretion is limited to the period of new growth and the secretion ceases as the leaves mature (Stapel *et al.*, 1997). This could explain the results from Section 2.1 which showed a decrease in *D. tasmanica* abundance in the broad bean treatments over time, as the plants matured. Overall, results showed that broad bean is not the most suitable understorey plant for *D. tasmanica* enhancement.

Phacelia was the most reliable species of the plants tested by Bowie *et al.* (1995), in terms of resistance to low temperatures and frosts and studies have shown it has good biological control potential (Telenga, 1958; Chumakova, 1960; Hickman and Wratten, 1996). However, laboratory experiments in the current study showed that survival of *D. tasmanica* on phacelia was equivalent to that on water and significantly lower than on buckwheat. These results suggest that *D. tasmanica* does not crawl down the corolla of phacelia to exploit nectar or have elongated mouthparts that are used to feed on flowers that have deep corollae. Therefore, phacelia is unlikely to provide nectar to *D. tasmanica*, but only pollen. Section 5.1.2 showed that nectar was essential for the survival of *D. tasmanica* and that pollen was not required by *D. tasmanica* for egg production, although it may be necessary for maximum fecundity. Parasitoids can learn to recognise a particular nectar odour after feeding on that flower (Patt *et al.*, 1999) so if there is no nectar reward from phacelia flowers, then *D. tasmanica* may not revisit these plants after an initial encounter. This would explain why phacelia did not significantly enhance parasitism rate in the field compared with controls, and why numbers captured by suction sampling were significantly lower in phacelia treatments compared with alyssum, buckwheat and control plots. These results confirm that phacelia is not a suitable understorey plant for *D. tasmanica* enhancement in orchards.

Buckwheat shows good agronomic performance for incorporation into integrated pest management programmes. It germinates easily, has a short sowing to flowering time, and in Canterbury, New Zealand, if sown in August, it flowers from November for up to three months (Bowie *et al.*, 1995). Its seed is also inexpensive and readily available (Wratten *et al.*, 1995). For example, the cost of buckwheat seed from Prebble Seeds Ltd, Christchurch, New Zealand was $1/kg in 1999. Not only did buckwheat enhance numbers of *D. tasmanica* seven-fold, but it also increased predacious lacewing abundance three-fold, and enhanced the number of aphidophagous hover flies captured on yellow sticky traps seven-fold, compared with the controls (Section 2.1).

Leafroller parasitism by *D. tasmanica* was enhanced from sowing buckwheat in the understorey from 0% to 86% compared with the controls on one release date. Similarly,

under-sowing orchards in Russia with buckwheat has enhanced populations of *Trichogramma* spp. (Zandstra and Motooka, 1978). The shallow flower structure of buckwheat provides both nectar and pollen to natural enemies, explaining why it also enhanced *D. tasmanica* longevity and increased fecundity in the laboratory compared with water-only. Furthermore, buckwheat was not preferred by leafroller larvae over apple (Section 5.2), and did not enhance numbers of *A. zealandica*, a parasitoid of lacewings, compared with controls. This contrasts, Stephens *et al.* (1998). In conclusion, buckwheat showed characteristics that are highly favourable for an annual understorey plant for conservation biological control in orchards.

Alyssum showed favourable attributes as a perennial plant which may be attractive to orchard growers. The seeds are inexpensive and available in New Zealand as it is often used as an ornamental or bedding plant in household gardens. For example, the cost of seed from Egmont Seed Co., Canterbury, New Zealand, in 1999 was $0.75/g with approximately 2,500 seeds/gram. However, further research is required to investigate the ability of alyssum to survive the Canterbury winter, leaf fall and tractor movement as wheel marks and leaf fall may kill some cover crops (Harrington, 1995).

Alyssum increased parasitism rate compared with controls, and over two-fold more *D. tasmanica* were suction sampled in these plots compared with controls. This was similar to the data of Grossman and Quarles (1990) who showed that parasitism of green pea aphids by the wasp *D. rapae* was enhanced by interplanting alyssum within lettuce fields. Alyssum had the additional benefits of harbouring significantly fewer aphids than buckwheat and control plots, and *A. zealandica* abundance was three times lower in alyssum plots compared with controls. It also enhanced longevity of both sexes of *D. tasmanica* compared with water, and showed the most favourable characteristics in terms of being of no benefit to leafroller. This is because it was not preferred by leafroller larvae over apple and when they were forced to feed on it, there was high mortality (94.3%) and low pupal weight (15 mg). Furthermore, alyssum did not enhance the number of fertile eggs produced by adult leafrollers compared with water-only.

In New Zealand, apple orchards are usually grassed-down permanently with a mixed grass-legume understorey vegetation (Goh and Malakouti, 1992; Goh *et al.*, 1995). Results here suggest that buckwheat and alyssum were the greatest potential as understorey plants in apple orchards for *D. tasmanica* enhancement. However, sowing a mixed herb ley in the inter-row sward and placing straw in the tree line may be an alternative method to enhance parasitism rate (Section 4.1). If rows are mown alternately then long growth can be maintained to provide flowering plants in the orchard. However, further research is required into the effect of mixed herb ley and straw mulch on all aspects of crop production because although studies show that straw mulch reduces temperature extremes (Hartley and Rahman, 1994; Hartley *et al.*, 1996) and increases potassium and nitrogen availability, there may be some disadvantages. For instance, an increase in potassium and nitrogen status can correspond to a lower uptake of calcium and an increased incidence of calcium related storage disorders (Ferguson and Watkins, 1989).

The current study has indicated that providing three flowering species did not further enhance parasitism rate compared with alyssum and buckwheat alone (Section 4.1). However, parasitism rates of up to 77.5% were already occurring in the buckwheat and alyssum treatments. Section 5.1.1 suggested that providing *D. tasmanica* with both coriander and buckwheat synergistically enhanced longevity of male *D. tasmanica*, possibly by providing a wider range of amino acids and proteins. Providing female parasitoids with both buckwheat and alyssum produced the highest number of parasitoid cocoons, suggesting that fecundity may also be enhanced (Section 5.1.2). This indicates that there is potential for further enhancing parasitoid activity against leafrollers by providing two flowering plant species in the understorey. This may decrease competition for floral resources between insects and provide a seasonal sequence of foods to natural enemies. Research is required to determine which plant species best complement each other in terms of time and duration of flowering, maximum nectar production times and duration of anther opening. If the activity period of *D. tasmanica* were determined, then this could also be matched with plant nectar flows.

7.4 Incorporating Buckwheat And Alyssum Into IFP Programmes

Leafrollers have three generations per year in Canterbury (Penman, 1984); however, the last generation is the main concern for apple growers because at this time fruit harvest occurs, so the leafrollers may cause major quality and quarantine problems. Therefore, it would be essential for *D. tasmanica* to synchronise well with the phenology of leafrollers if effective control was to be achieved. Results from this study have shown that *D. tasmanica* trap catches remained stable throughout the season, suggesting the potential of *D. tasmanica* as a biocontrol agent throughout the summer.

Although *D. tasmanica* accounts for approximately 20% parasitism of LBAM in Australia, Danthanarayana (1983) reported that parasitism of LBAM by *D. tasmanica* in Victoria, Australia was an insignificant mortality factor. However, the parasitoid complex in this Australian study differs markedly from that in New Zealand (Collyer and van Geldermalsen, 1975) where leafroller parasitism rates by *D. tasmanica* of 30-46% have been recorded (Collyer and van Geldermalsen, 1975; Early, 1984; Tomkins, 1984). Therefore, the leafroller parasitoid complex in New Zealand may have more potential for controlling leafroller populations. Using selective IGRs in IFP programmes in conjunction with conservation biological control may further increase this potential, because the distance between parasitoid hosts and food resources is minimised, hence increasing parasitism, and decreasing superparasitism and mortality (Leeper *et al.*, 1974; Sirot and Bernstein, 1997).

Field trials suggested that the percentage of leafroller larvae which pupated were three-fold and six-fold lower in the buckwheat and alyssum treatments, respectively, compared with the controls (Section 4.1). Also, damage from leafrollers and number of leafroller larvae were 20.3% and 29.3% lower, respectively, in these flowering treatments compared with the controls (Section 4.3). These results, despite the lack of significance, indicate that increasing leafroller parasitism rate from understorey management in orchards will translate into an increase in pest control, decreasing the abundance of leafroller larvae and a reducing damage to apple foliage.

Buckwheat not only enhanced parasitoid abundance but also increased the number of lacewings and hover flies. These beneficial insects are also important predators in the orchard. *M. tasmaniae* is a general insect and mite predator (Leathwick, 1989) so increasing its abundance may contribute to mite control and enhance the biological control of other orchard pests. The larvae of some New Zealand hover flies feed on aphids and early-instar lepidopterans (Valentine, 1967a; Miller, 1971; Ashby and Pottinger, 1974) so incorporating flowering strips into orchards may enhance hover fly populations for woolly apple aphid and leafroller biocontrol. In fact, Asante (1997) suggested that predators such as Syrphidae may contribute effectively to the management of woolly apple aphid if they could be conserved and augmented in apple orchards. Furthermore, Valentine *et al.* (1996) concluded that it is likely that spider mites, woolly apple aphids and San Jóse scale may be better controlled under IFP programmes that use selective pesticides such as tebufenozide. Therefore the introduction of selective IGRs and the provision of flowering plants in the understorey into IFP programmes may not only enhance natural enemies of leafrollers but also lead to greater control of many other orchard pests by aiding the recovery of their natural enemies. Examples are: *A. mali* for woolly apple aphid control, *Aspidiotiphagus citrinus* (*Encarsia citrina* (Crawford)), *Neophyllobius* spp. for oystershell scale control and predatory mites for control of spider mites. Furthermore, spiders are natural enemies of aphids, mites and lepidopteran pests (Mansour *et al.*, 1980; Klein, 1988) and they can limit prey populations (White, 1978). Not only do they consume these pests but web-forming spiders can kill as many as 50 times the number of prey they actually consume (Kajak, 1978). Wyss *et al.* (1995) showed that weed strips can enhance spider populations in orchards, therefore conservation biological control may also have the potential to enhance these important natural enemies of orchard pests.

It is important to determine how far *D. tasmanica* can move between host-containing and food-containing areas, and to determine whether it would be better to grow a cover crop within the crop, every second row, or bordering the crop. Section 3.3 showed that *D. tasmanica* travels into rows adjacent to buckwheat plots and Powell (1986), Lővei *et al.* (1993a) and Long *et al.* (1998) have found that parasitoids commute between nectar sources and the crop. Therefore, it is possible that *D. tasmanica* will travel into the apple canopy after feeding on the flowering strip. However, rich floral patches may act as a 'sink'

for ovipositing females, in turn negatively affecting integrated pest management programmes. For example, MacLeod (1999) found that providing additional resources slowed the rate of dispersal of *Episyrphus balteatus* by over three times compared with the control. Therefore, it would be beneficial to conduct some mark/release/recapture work to help track the scale of movement of *D. tasmanica* from the flowering strips to the apple canopy. Parasitoids can be monitored by marking them with paints (Driessen and Hemerick, 1992), fluorescent dusts (Messing *et al.*, 1993; 1994; Corbett and Rosenheim, 1996), biomarkers (Lővei *et al.*, 1993a; Holland e*t al.*, 1994), and rare and radioactive elements (Corbett *et al.*, 1996; Hopper and Woolson, 1991).

A high proportion of the leafroller larvae that were parasitised in Section 2.1 had 100% parasitism. This may suggest that once *D. tasmanica* finds the release branch with high leafroller densities, it may parasitise all larvae within that patch. Further research is required into the importance of density-dependent searching by *D. tasmanica*, as this may answer a fundamental biological question regarding whether this parasitoid would be suitable as a biological control agent for leafroller biological control. It would be essential for *D. tasmanica* to operate under very low larval densities due to the low thresholds required for export (Wratten *et al.*, 1998). When hosts are scarce, parasitoids have to search more extensively so there is a greater energy requirement. Therefore, providing floral resources in the vicinity of crops may increase the ability of *D. tasmanica* to reduce low leafroller populations. However, research needs to determine whether conservation biological control can enhance leafroller parasitism to an extent that reduces leafroller populations to below economic thresholds for local and export apple markets.

Some cover crops have been shown to enhance pest populations (Mass *et al.*, 1998; Stapel *et al.*, 1998). However, there is a high level of immigration of leafrollers into orchards; males can disperse 600 m and females 275 m (Suckling *et al.*, 1994). Also, 265 host species are known in New Zealand for leafrollers (Thomas, 1989) and the host range of LBAM encompasses 34 different plant families (Tomkins, 1984), many of which are present in and around the orchard (Chapman, 1973; Spiller and Wise, 1982). Therefore, given the high level of immigration of adults and the extreme abundance of preferred leafroller hosts in the orchard, buckwheat and alyssum are not likely to contribute

significantly to the leafroller population. These plants were less favourable hosts than apple so if adult leafroller do choose to oviposit on the understorey plants, then it is likely that these egg batches will be smaller (Tomkins, 1984), developmental stages would be prolonged (Section 5.2.2), survival to adult stage and pupal weight would be reduced (Section 5.2.2), and the fecundity of the resulting female reduced (Gu and Danthanarayana, 1990).

The longevity of *Copidosoma koehleri*, an important parasitoid of potato moth, was significantly increased on borage flowers compared with borage without flowers, but no such benefit occurred to the pest (Baggen and Gurr, 1998). In the current study alyssum did not enhance the fertility of female leafroller adults compared with water but increased longevity compared with water. This suggests that female adult leafrollers may be able to access the nectar of alyssum and, although the production of fertile eggs on alyssum is equivalent to that of water, they are produced over a longer period of time because survival is enhanced, allowing the moth a greater potential for dispersal. It may be beneficial to conduct research into understorey plants that are more selective towards parasitoids due to taste, which is determined by amino acid concentration (Baker *et al.*, 1978), or flower morphology, as leafroller adults are larger than parasitoids so are less likely to access some flower structures.

Tomkins (1984) found that although *D. tasmanica* parasitised up to 45.4% of leafroller larvae in an unsprayed orchard, it failed to prevent damage to fruit. This is probably because this parasitoid fails to stop attacked larvae from feeding. Mills (1994) found that the later the host-stage killed by a parasitoid, the lower the rate of success in biological control of Lepidoptera. For this reason, an egg parasitoid like *Trichogramma* may fit more neatly into a leafroller biological control programme because no larva develops so no damage is caused by the pest. If *Trichogramma* is present in Canterbury it is likely that sowing flowering plants in orchards will enhance its abundance and longevity because it is known that adult *Trichogramma* spp. feed on nectar (Andow and Risch, 1987; Wellinga and Wysoki, 1989; Knutson, 1998). However, results from this study (Appendix 4) showed that *Trichogramma* was not present in Canterbury, supporting the conclusions of Thomas and Burnip (1993). This may be attributed to most leafroller species over-wintering in the

larval stage, depriving *Trichogramma* of the host egg to diapause in. It is not known whether alternative egg hosts are available for over-wintering *Trichogramma* in Canterbury, so further research is required into the presence of *Trichogramma* in New Zealand.

If *Trichogramma* spp. are not present in Canterbury then inundative releases may offer a solution to reducing leafroller larvae emergence in apple orchards as they have demonstrated promising levels of control in Australian vineyards (Anon., 1997a; Bailey, 1997; Glenn and Hoffmann, 1997). Providing flowering plants in the orchard understorey has potential to maximise longevity and fecundity, decrease emigration of *Trichogramma* and maximise the return of investment, while also aiding larval parasitism by *D. tasmanica*. Investigations into this aspect are under way in New South Wales (Gurr *et al.*, 1998).

7.4.1 Benefits and disadvantages of sowing plants in orchard understoreys

Aside from the enhancement of natural enemies, there can be many other benefits from sowing plants in orchard understoreys. Cover crops can reduce nutrient leaching and improve soil fertility or nutrient availability (Christensen, 1971; Lanini *et al.*, 1989; Hirschfelt *et al.*, 1993), promote soil life (Lüftenegger and Foissner, 1989), prevent soil erosion (Miller *et al.*, 1989; Gaffney and van der Grinten, 1991; Louw and Bennie, 1991), improve soil structure (Grimes and Goldhamer, 1989; Gaffney and van der Grinten, 1991), replenish organic matter (Schonbeck *et al.*, 1991), manage soil moisture (Haynes, 1980; Blake, 1991), increase earthworm populations (Daly, 1993b) modify microclimate (Miller *et al.*, 1989) and suppress weeds (Aldrich, 1984). Cover crops may also reduce the amount of sunlight reflecting into the crop which can decrease sunburn damage to fruit, and mite infestations (Miller *et al.*, 1989).

Studies have shown that buckwheat can effectively suppress weeds (Schonbeck *et al.*, 1991; DeHaan *et al.*, 1994) possibly due to its rapid growth, heavy canopy and allelopathic effect after it's tilled into the soil (Schonbeck, 1988). Allelopathy is the release of compounds that inhibit germination and early growth of other plants (Aldrich, 1984). Alyssum is slower to establish than buckwheat but its spreading growth habit may result in

an ability to suppress weeds once established. Further research is required to determine the competitive ability of alyssum and to investigate the influence of buckwheat and alyssum on soil quality and erosion.

Not all effects from sowing plants in orchard understoreys may be advantageous. Apple trees are poor competitors for water and nutrients (Bould *et al.*, 1972; Atkinson and White, 1980; Haynes, 1981) and water stress caused by competition with understorey plants can lead to significant losses of fruit size, yield (Assaf *et al.*, 1982; Marsh and Daly, 1993) and storage ability of the fruit (Marsh *et al.*, 1996). Cover crops may enhance frost risk in the orchard by reducing the wind speed and decreasing temperatures (because vegetation absorbs less radiation during the day than bare soil). They may also impede trafficability and access for harvesting, pruning and other management practices (Bugg *et al.*, 1996). However, due to its low growth habit, it is unlikely that alyssum would impede trafficability and management practices could be imposed to reduce these effects for buckwheat (see Section 7.4.3).

Sowing plants in the understorey may increase humidity from plant transpiration and limit air movement, therefore leading to an increase in diseases which favour humid environments, such as blackspot (*Venturia inaequalis* Cke. Wint.) (Tate *et al.*, 1996). Buckwheat is more likely to impede air movement compared with alyssum because it grows up to 70 cm (Bowie *et al.*, 1995) into the lower canopy of the tree. If buckwheat shelters orchard pests, such as spider mites, they could easily migrate to the apple tree. Therefore, additional research is required to address the overall effect of buckwheat and alyssum on crop production and orchard management. For example, one such study showed that sowing buckwheat in zucchini crops significantly reduced aphid numbers, delayed the onset of the aphid transmitted virus PRSV-W, decreased whitefly abundance, reduced silverleaf severity, increased mean fresh and dry biomass of zucchini plants and increased the proportion of marketable fruit (Hooks *et al.*, 1998). However, similar research is required to investigate the influence of buckwheat and alyssum on apple production, via effects on tree yield, fruit quality, frost risk, disease incidence, soil quality, weeds and other pest complexes.

7.4.2 Perennial versus an annual understorey option

Using buckwheat as a living mulch reduces leaching of nutrients, reduces soil erosion, suppresses weeds and improves soil quality (Lanini *et al.*, 1989). Therefore, using a perennial understorey species such as alyssum may further enhance these favourable attributes as it is present all year round. Buckwheat is an annual plant and therefore may require re-sowing every year, although further research is required to determine whether buckwheat is self-perpetuating as this may help reduce any expense associated with re-sowing every year. Furthermore, alyssum flowers for most of the year, whereas buckwheat flowers for up to three months (Bowie *et al.*, 1995). However, buckwheat has an added advantage of an annual life cycle so it would be less likely to prevent leaf breakdown in winter, which could increase blackspot incidence (Daly, 1993a). It also cannot act as an over-wintering site for pests such as leafrollers (Thomas and Burnip, 1993). Research is required into the influence of alyssum on winter leaf matter breakdown and into whether buckwheat and alyssum harbour and over-winter other apple pests, such as spider mites.

7.4.3 Agronomy

Results presented in Section 3.3 showed that there was no difference in parasitoid abundance between the edge and 1 m from the plot, and the adjacent row. This indicates that buckwheat may fit neatly into an IFP programme as growers may be able to sow flowering plants in every second or third row of the orchard and still enhance leafroller biocontrol while minimising the adverse effects of a cover crop. Although Section 4.3 did not find more leafroller damage or larvae around the perimeter of the blocks, it is well known that there is often an edge effect where LBAM eggs are found in higher numbers along the ends of rows or in sheltered locations (Clancy, 1997). Therefore, it may be beneficial to sow flowering plants around the perimeters of the orchard because they are often not sprayed with insecticide, so can act as a refuge for natural enemies. They could then move into surrounding trees where leafroller populations are most prevalent. This technique may also reduce the likelihood of buckwheat impeding traffic access. Alternatively, understorey plants could also be sown in areas where trees have died or been removed, or on land around the orchard that is not in use.

A sowing rate of 100 kg/ha for buckwheat and 20 kg/ha for alyssum (seed coated) was used during the field trials in this study to guarantee plant establishment and data. However, it may not be necessary to sow these species at such high densities. Buckwheat seeds germinate quickly, which makes them good competitors with weeds, whereas alyssum is establish but has a spreading growth habit so, once established, it should prevent weed growth. Further research is required to determine optimal sowing rates which allow good establishment at minimal cost. It may also be possible to develop selective herbicides for alyssum to aid initial establishment.

7.4.4 Phenology and timing

D. tasmanica is most abundant during the second and third generations of LBAM, although it has been present early enough to attack first generation larvae in some seasons (Collyer and van Geldermalsen, 1975). Therefore, it may be beneficial to sow annual cover crops to coincide flowering with early leafroller populations that occur from early December. This may also enhance populations of natural enemies of woolly apple aphid, which would be beneficial because if its natural enemies are not present by late December then they cannot be relied on for aphid control during the season (L. Haughey, pers. comm.). Buckwheat plants sown in Canterbury orchards in August would flower from November for up to three months and plants would reach a height of only 80 mm (Bowie *et al.*, 1995). This would reduce problems associated with growth into the lower apple canopy. It would be optimal to sow another half-row of buckwheat in November to extend the flowering period to March. This would produce plants 550 mm high, whereas delaying sowing until December would increase plant height to 700 mm (Bowie *et al.*, 1995), possibly causing problems in the lower canopy. If buckwheat and alyssum were flowering from November to March, it may reduce the number of tebufenozide and lufenron (Match®) applications applied under the IFP programme for pipfruit during this period. Removing the top two thirds of the buckwheat plants 3-4 weeks after sowing will also extend the period of flowering by encouraging lateral shoots.

Suckling *et al.* (1996a) reported that where an IFP programme includes a post-bloom organophosphate insecticide, a single application will severely reduce or eliminate natural enemies, possible resulting in an increase of non-lepidopteran pests. An organophosphate application (azinphos-methyl) is one of the three harvest clean-up options for apple

growers under the IFP programme. Although this is not compulsory, it is estimated that approximately 50% of apple growers supplying the USA market will comply (B. Mackie, pers. comm.). However, this is late in the season and so should not interfere with populations of natural enemies and therefore pest control during the growing season. Further research is required on the effect of pre-harvest organophosphate applications on over wintering populations of natural enemies as this application may reduce numbers available for the following season.

Although there may be no direct effects of the selective IGRs and *Bt* spray on parasitoids, there is an indirect effect of removing potential hosts or killing the host before the parasitoid emerges. However, if parasitised larvae feed less than unparasitised ones then they may be more likely to survive exposure to sprays such as *Bt* because they are less likely to consume a lethal dose (Nealis and van Frankenhuyzen, 1990). In IFP programmes pheromone traps can be used to guide spraying and reduce spray applications by identifying periods of low adult activity when spraying is not necessary (Suckling *et al.*, 1990b). Furthermore, the cooler climate of Canterbury causes leafroller generations to be more distinct than in northern New Zealand (Tomkins, 1984) so fewer sprays are necessary because stage-specific sprays, such as IGRs can be timed more accurately. This may suggest a greater potential of conservation biological control for natural enemy enhancement in the Canterbury region.

7.5 Organic Apple Production

So far, understorey management using floral resources for the enhancement of natural enemies has been discussed in light of IFP; however, this technique would also have potential in organic apple production. The organic produce market is one of the most rapidly growing in the western world (Manhire, 1993) and each year export organic apple premiums have been more than 100% (Anon., 1999). Organic apple growers face problems from secondary pests such as apple leafcurling midge which increases dramatically after a full spray programme is suddenly stopped (van Epenhuijsen and Carpenter, 1990). There are not many options for pest control available in organic apple production and there is a

high reliance on natural enemy populations. Therefore, conservation biological control may be an important tool for enhancing their populations and effects on pests.

7.6 Concluding Remarks

Buckwheat and alyssum clearly enhance the populations of *D. tasmanica* and possibly other natural enemies such as lacewings and hover flies. These plants can also increase leafroller parasitism, prolong parasitoid survival and enhance fecundity. This study indicates that sowing these plants in the understorey will contribute to leafroller biological control and could lead to a decrease in insecticide applications in IFP programmes and enhance pest control in organic production. Although information is still required on the effects of understorey plants on all aspects of crop production, such as soil fertility and quality, fruit production, pest and disease complexes, and on the ability of this technique to reduce leafroller populations below economic thresholds, the cost of seed to manipulate the orchard environment is very low and the potential of the approaches outlined here is very high. Therefore, understorey management using floral resources may be an added advantage for pest control if incorporated into IFP programmes and organic apple production.

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APPENDIX 1

Source of LBAM eggs, larvae and pupae, and of leafroller diet and diet tubes

Anne Barrington

The Insect Rearing Unit

Insect Science Group

HortResearch

Mt. Albert

Auckland

New Zealand

Abbreviations used throughout this thesis

LUHRA = Lincoln University Horticultural Research Area

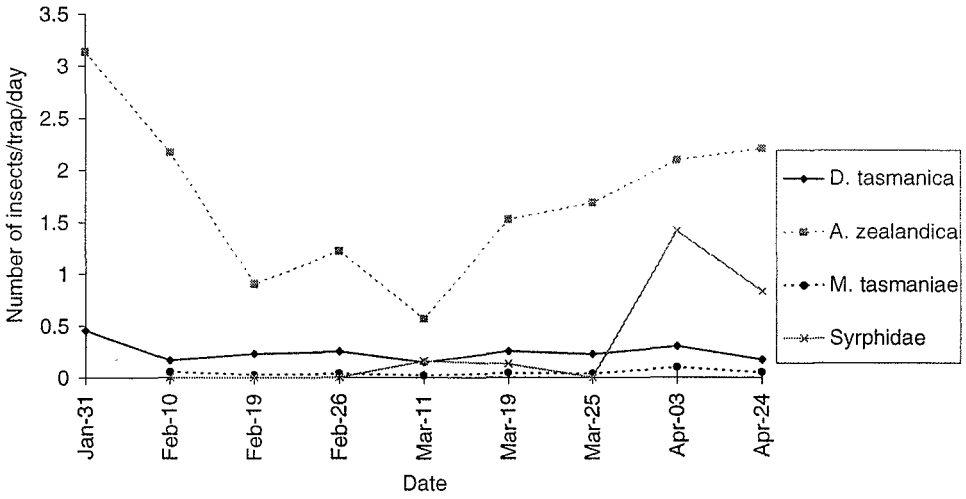
LBAM = Lightbrown apple moth (*Epiphyas postvittana*)

IGR = Insect growth regulator

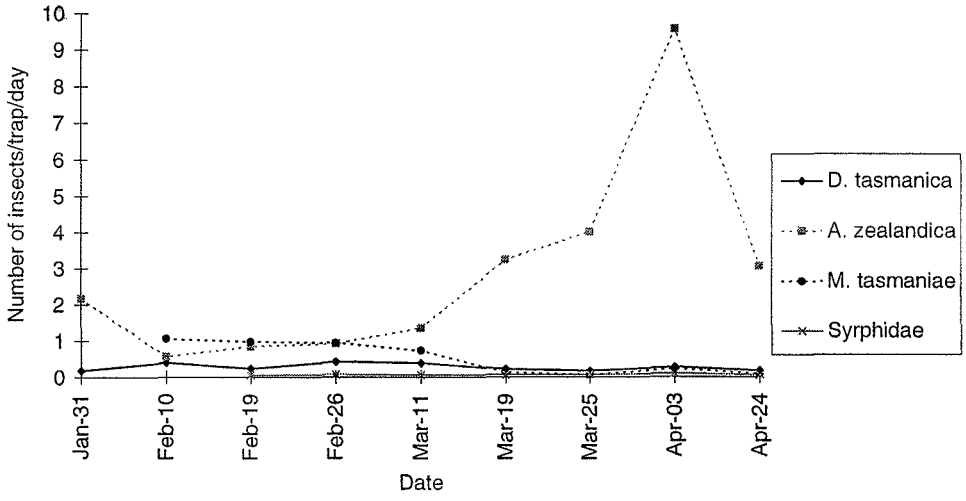
Bt = *Bacillus thuringiensis*

IFP = Integrated fruit production

APPENDIX 2

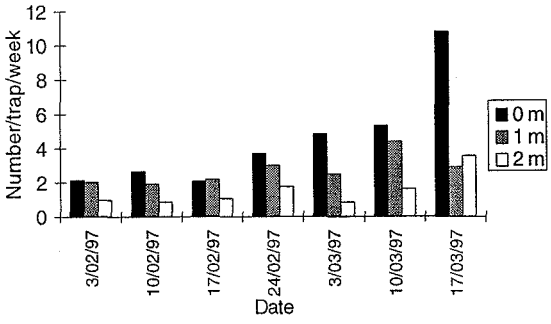


A) Small control plots

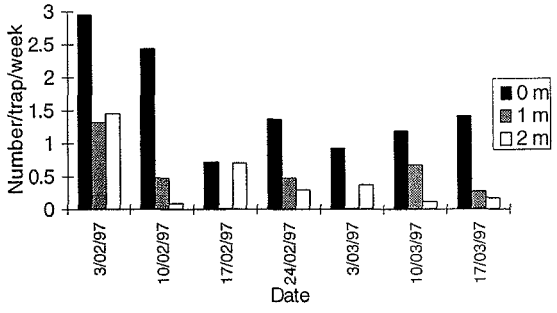


B) Large control plots

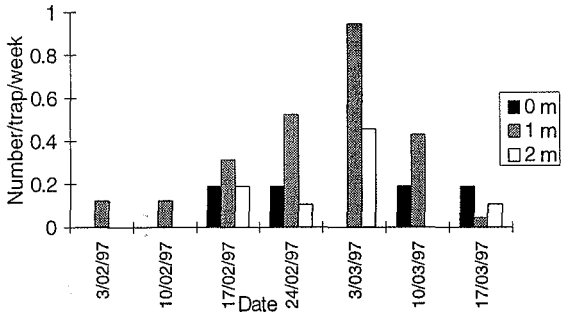
Fig. 1 The abundance of insect groups captured from January 13 to April 24, 1997 in small and large control plots.



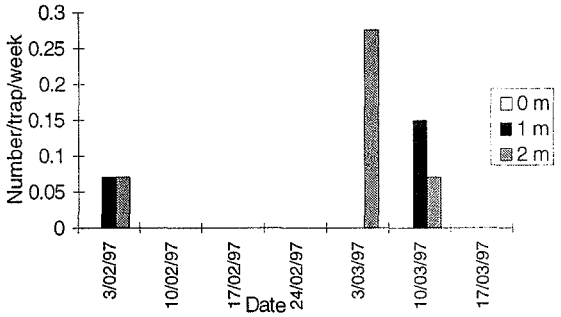
a) *Anacharis zealandica*



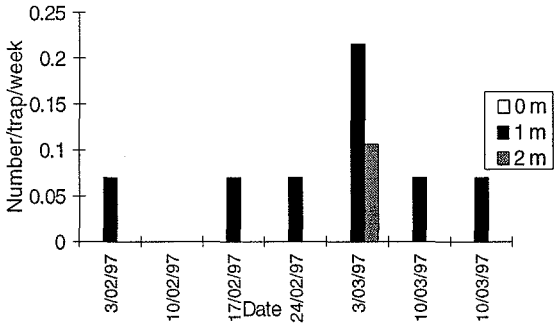
b) *Micromus tasmaniae*



c) *Melanstoma fasciatum*

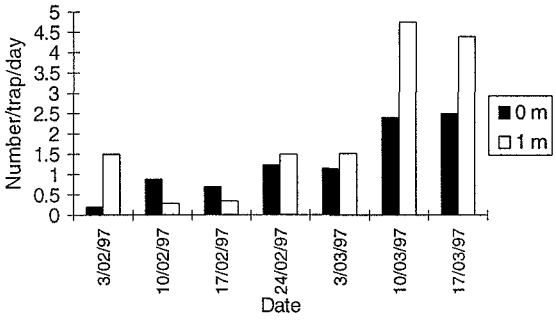


d) *Melangyna novaezelandiae*

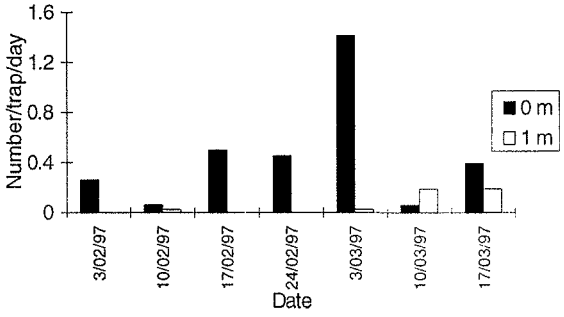


e) *Eristalis tenax*

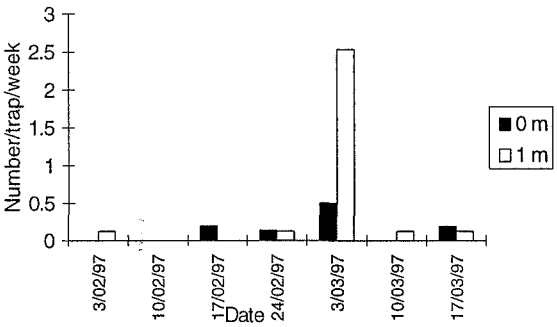
Fig. 2 The abundance of insect groups captured on three heights of yellow sticky traps from February 3 to March 17, 1997 (there were no significant differences between heights at any date).



a) *Anacharis zealandica*



b) *Micromus tasmaniae*



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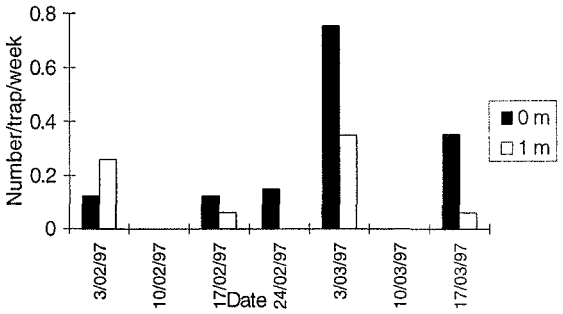
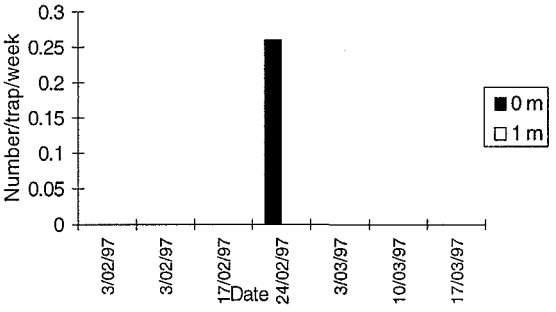
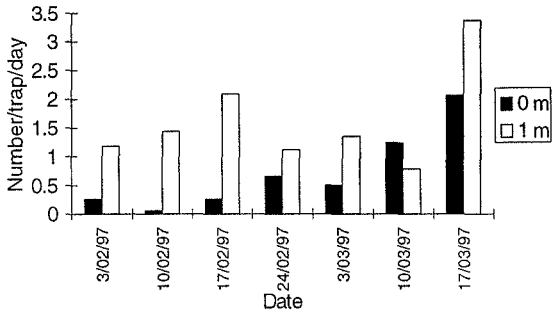


d) *Melangyna novaezelandiae*

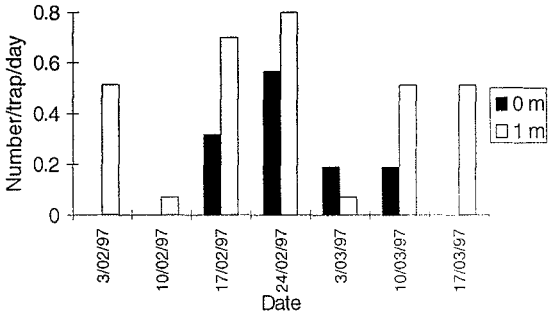


e) *Eristalis tenax*

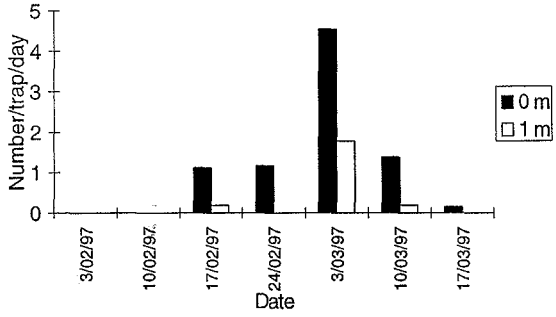
Fig. 3 The abundance of insect groups captured on two heights of yellow sticky-water traps from February 3 to March 17, 1997 (see Fig. 2).



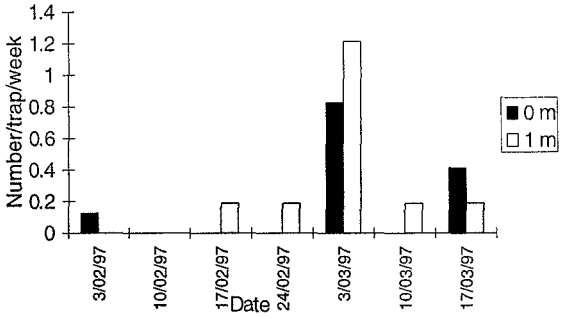
a) *Anacharis zealandica*



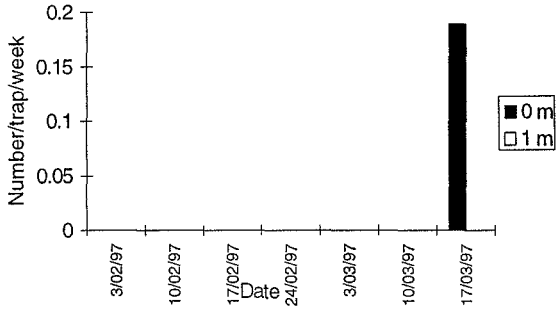
b) *Micromus tasmaniae*



c) *Melanstoma fasciatum*



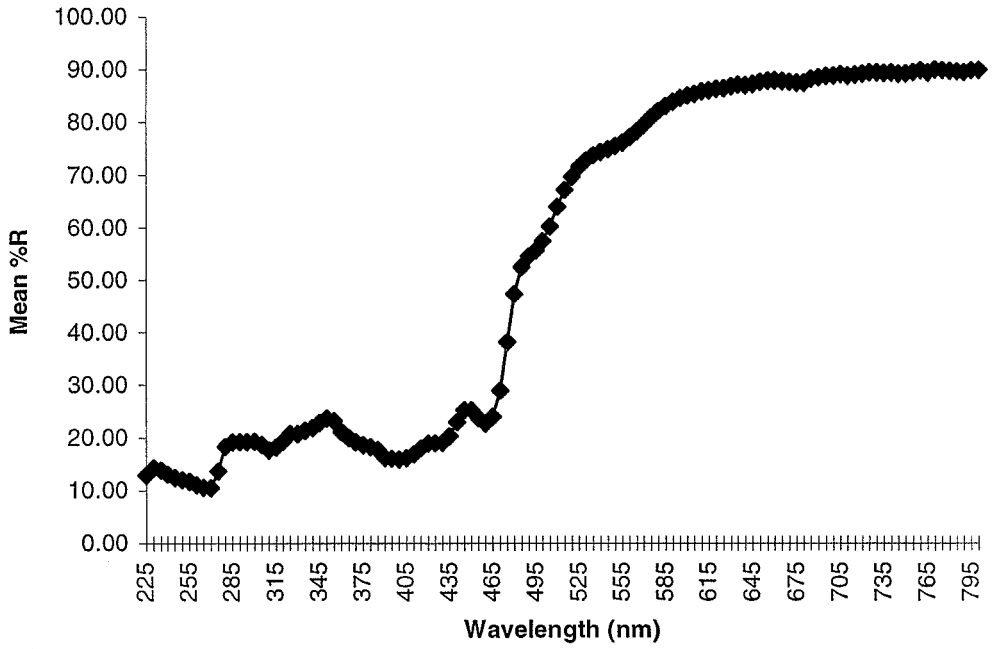
d) *Melangyna novaezelandiae*



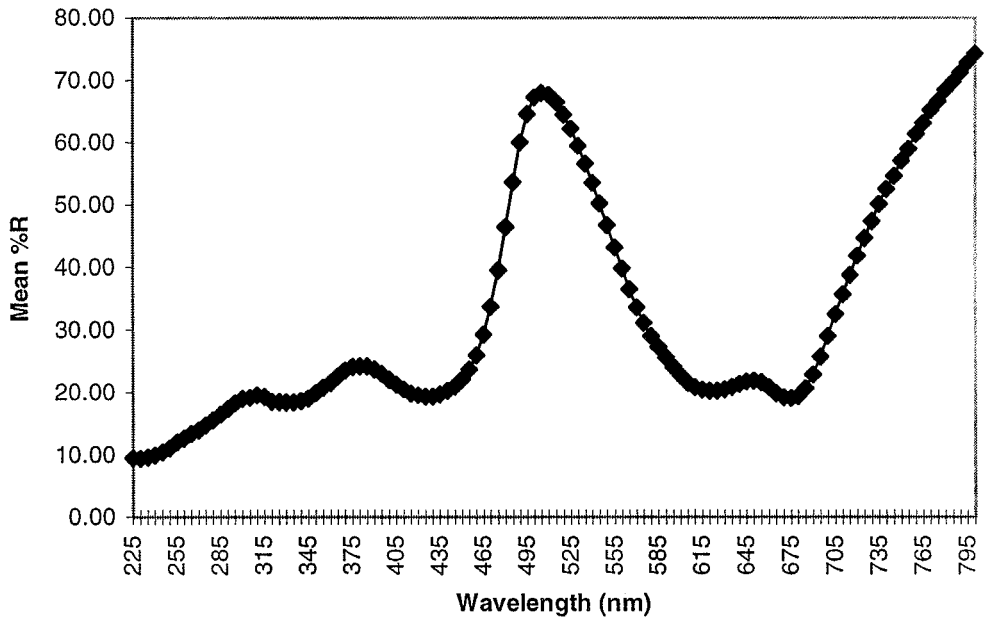
e) *Eristalis tenax*

Fig. 4 The abundance of insect groups captured on two heights of yellow water traps from February 3 to March 17, 1997 (see Fig. 2).

APPENDIX 3



A) Spectral reflectance of yellow sticky traps used throughout this study.



B) Spectral reflectance of green card placed below experimental arena in experiment 6.2.2.

APPENDIX 4

Egg Baiting For Trichogramma

Introduction

One disadvantage of using larval parasitoids, such as *D. tasmanica*, to control leafroller is that they attack the pest but do not prevent the larvae from continuing to feed on the crop. In contrast, egg parasitoids, such as *Trichogramma* spp., attack the egg stage, so no larva develops and no damage is caused by the pest. Tomkins (1984) found that although *D. tasmanica* parasitised up to 45.4% of leafroller larvae at an unsprayed orchard site, it failed to prevent damage to fruit. This is probably because this parasitoid fails to stop attacked larvae from feeding, although parasitised larvae may feed less, as occurs in *P. xylostella*, which is parasitised by *Diadegma semiclausum* Hellén (Yang *et al.*, 1994). Mills (1994) found that the later the host-stage killed by a parasitoid, the lower the rate of success in biological control of Lepidoptera. For this reason, an egg parasitoid like *Trichogramma* may be more useful in a leafroller biological control programme. The following experiment was conducted to investigate whether *Trichogramma* was present in large numbers in Canterbury, New Zealand and to determine whether further studies involving this parasitoid should be considered.

Methods

Two pairs of newly-emerged LBAM adults (Appendix 1) were fed honey/water solution and placed into a closed-ended nylon material sleeve (600 x 200 mm). This sleeve was placed over an apple (cv. 'Braeburn') branch and the end tied with a piece of string. After 24 hours the sleeve was removed and the branch labelled. This was replicated eight times on different trees. Egg batches laid by the pairs were examined every two days for 'blackening'. After one week the leaves containing the egg batches were removed and taken into the laboratory. They were placed in Petri dishes lined with damp tissue paper to keep the leaves turgid and checked every few days for the presence of *Trichogramma*. This

was repeated every two weeks from January to March. The intention was to record the number of blackened eggs and emerged *Trichogramma* adults.

Results and discussion

No blackened eggs occurred or *Trichogramma* adults emerged from the egg batches collected from the field. This suggests that *Trichogramma* was not present in the Canterbury orchard in which this study was done, so further studies involving *Trichogramma* were not conducted. This supports Thomas and Burnip (1993) who examined many leafroller egg batches in South Canterbury, New Zealand and found none to be parasitised. Although a trichogrammatid egg parasitoid was recorded from the eggs of *Graphania mutans* (Walker) on one or two occasions each season, they concluded that *Trichogramma* egg parasitoids are not present. *Trichogramma* may not be present in Canterbury because most leafroller species such as LBAM over-winter in the larval stage and deprive *Trichogramma* of the host egg in which to diapause. Huber and Hassan (1991) reported that in most cases, a very small number of egg parasitoids are able to over-winter on alternative hosts, but these are usually not sufficient to control the pest and require a number of generations to build up the population to an effective level. It is not known whether alternative egg hosts are available for over-wintering *Trichogramma* in Canterbury.

Results here contradict Valentine (1967b) and Thomas (1965) who found that this parasitoid does occur in Canterbury. It is unlikely that the eggs in the current study were not the correct age for *Trichogramma* because this parasitoid prefers and parasitises eggs between 1-3 days old (Berti and Marcano, 1991; Miura and Kobayashi, 1998; Pratissoli and de Oliverira, 1999). So the difference between studies may be due to differences in weather conditions between years or the baiting method used in the current study for *Trichogramma* collection. For example, a high proportion of males are incapable of mating (Geier *et al.*, 1969) so the females in the sleeves may not have been mated, causing production of infertile eggs. Studies show that some *Trichogramma* species prefer to oviposit in fertile versus infertile host eggs (Zhang and Cossentine, 1995), and that a higher proportion of *Trichogramma* hatches from fertile compared with infertile eggs (Cossentine

et al., 1996). In contrast, Sengonça and Schade (1991) found that sterilised *Eupoecilia ambiguella* Hb. eggs were equally suitable for parasitisation by *T. semblidis* (Auriv.).

If *Trichogramma* is present in Canterbury it is likely that sowing flowering plants in orchards will enhance their abundance and longevity because adult *Trichogramma* spp. feed on nectar (Andow and Risch, 1987; Wellinga and Wysoki, 1989; Knutson, 1998) and feeding has been shown to increase longevity (Hohmann *et al.*, 1989), flight propensity (Forsse *et al.*, 1992), and parasitising ability (Somchoudhury and Dutt, 1988) of some *Trichogramma* species. Furthermore, sowing phacelia and the umbellifer *Eryngium* sp. in apple orchards has been associated with an increase in *Trichogramma* wasp activity (Telenga, 1958). This may be because *Trichogramma* spp. are very small and can crawl down the corollae of phacelia to exploit nectar.

In Australia, control of LBAM in vineyards has been developed using *T. carverae* Carver and promising levels of control have been reported (Anon, 1997a; Bailey, 1997; Glenn and Hoffmann, 1997). Therefore, if *Trichogramma* spp. are not present in Canterbury then inundative releases may offer a solution to reducing leafroller larvae emergence in apple orchards. However, the cost of release is approximately Aust.$85/ha and two such releases are usually required per season (Glenn and Hoffmann, 1997). This is significantly more than costs of control based on chemical insecticides or *Bt* applications (Glenn and Hoffmann, 1997). Providing flowering plants in the orchard understorey could maximise the efficiency of these releases by decreasing emigration of *Trichogramma* and increasing longevity and fecundity, while also aiding parasitism of larvae by *D. tasmanica*.