

CONSERVATION BIOLOGICAL CONTROL OF PESTS: MULTI-TROPHIC-LEVEL EFFECTS

Steve D. Wratten¹, Geoff M. Gurr², Doug Landis³, Nicola A. Irvin¹ and Lisa A. Berndt¹
¹Soil, Plant & Ecological Sciences Division, PO Box 84, Lincoln University, Canterbury,
New Zealand (Email: wrattens@lincoln.ac.nz)

² Faculty of Rural Management, The University of Sydney, PO Box 883, Orange, NSW,
Australia 2800

³ Department of Entomology and Center for Integrated Plant Systems, Michigan State University, E. Lansing,
Michigan 49924, USA

ABSTRACT

This paper reviews recent work in conservation biological control by using case studies from Australasia. It explores the ecological and behavioural mechanisms, which may operate when floral resources for natural enemies of pests are added to agroecosystems. Such plants as buckwheat, phacelia and faba (broad bean) provide pollen and/or nectar for beneficial arthropods and this can lead to enhanced rates of predation or parasitism and sometimes to pest suppression. However, there can be negative effects. An example from New Zealand is the enhancement of a parasitoid of the predatory brown lacewing (*Micromus tasmaniensis*) by the provision of buckwheat in apple understoreys. The need for selective 'companion planting' is emphasised so that higher trophic levels are not influenced, leading to negative effects and that populations of the target pest are not enhanced by the presence of the added plant resource.

INTRODUCTION

Conservation biological control (CBC) has, until recently, been the least well-studied sub-discipline of biological control. It has been defined as: the use of "actions that preserve or protect natural enemies" (Ehler 1998). This simple definition encompasses a wide range of empirical and theoretical possibilities, ranging from reducing side effects of pesticides to the provision of floral and over-wintering resources and/or alternative prey/hosts for beneficial arthropods (Cortesero *et al.*, 2000; Gurr *et al.*, 2000; Landis *et al.*, 2000). There has been an apparent recent upsurge in work on CBC, and this has been captured in several recent reviews, such as Barbosa (1998), Pickett and Bugg (1998), Landis *et al.* (2000) and Gurr, Wratten, and Barbosa (2000). However, CBC does have a long pedigree. For example, conservation of ants for the biological control of citrus pests in China dates from ancient times (Samways, 1981) and the transportation of ant colonies from mountains to date groves was practised in "medieval" Arabia (van den Bosch and Messenger, 1973). More recently, but still several decades ago, some pivotal papers pointed the way by providing empirical and intellectual frameworks for current work on CBC. For example, van Emden (1962) placed containers of cut flowers among brassicas and thereby enhanced local densities of parasitic Hymenoptera. Such simple experiments depend on basic knowledge of the food requirements of natural enemies derived from the scholarship of such workers as Schneider (1948), who showed the importance of pollen in the diet of hoverflies (Diptera: Syrphidae). Such studies underpin subsequent experimental work. However, as pointed out by Cortesero *et al.* (2000) and Gurr *et al.* (1998, 2000), adding plant resources to an agroecosystem with the aim of enhancing natural enemy efficacy may, in fact, have a greater role in influencing the biology of the pest through the "resource concentration hypothesis" of Root (1973). This hypothesis describes how adding plant diversity to cropping systems can interfere with pests' host-plant finding. Root's alternative "enemies hypothesis" concerned the way in which plants can provide shelter, alternative prey/hosts and/or pollen and nectar for natural enemies. As pointed out by Landis *et al.* (2000), one of the key challenges of CBC in the future is to understand better than currently the mechanisms behind any enhancement of natural enemy numbers or effectiveness following the provision of plant resources. One of the problems, as well as one of the attractions of CBC is that it appears to be intuitively simple in concept; the idea of "companion planting" is part of many gardeners' vocabulary, but few gardeners or agriculturalists really do understand the ecological basis of what they are trying to achieve when they, for instance, add flowers to a cropping situation. Critics of CBC sometimes call it "chocolate-box ecology", by which they mean that the inherent 'prettiness' of creating floral mixtures among or around crops, and its assumed value in terms of pest suppression, can sometimes be the key motivation, rather than a rigorous experimental or theoretical basis for the selection of the plants in the first place.

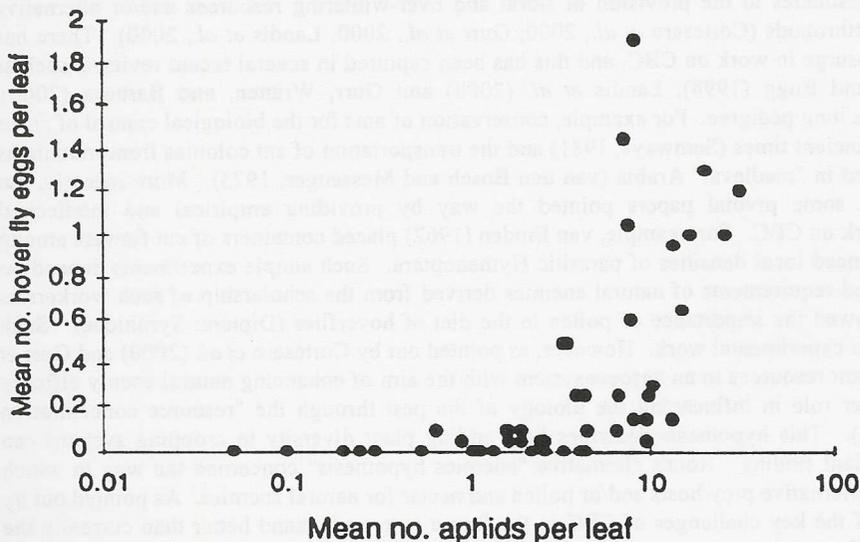
Understanding the mechanisms behind CBC was one of the five key issues identified by Landis *et al.*, (2000) which need to be addressed in future work on this type of biological control. The other four were: a) plant species selection b) scale and spatial arrangement of the plantings c) possible negative aspects of habitat diversity and d) grower acceptance of the value of added biodiversity to cropping systems; the 'risk-averse' attitude of many growers (see Watt *et al.*, 1984) is a key factor in this. This review will concentrate on the need to understand the ecological mechanisms behind the use of "companion plants" by natural enemies and through

that, the management of potential negative effects arising from enhancing plant biodiversity. Some recent case studies from Australasia will be used to illustrate progress on these issues to date.

MECHANISMS INVOLVED IN THE USE OF FLOWERS BY NATURAL ENEMIES

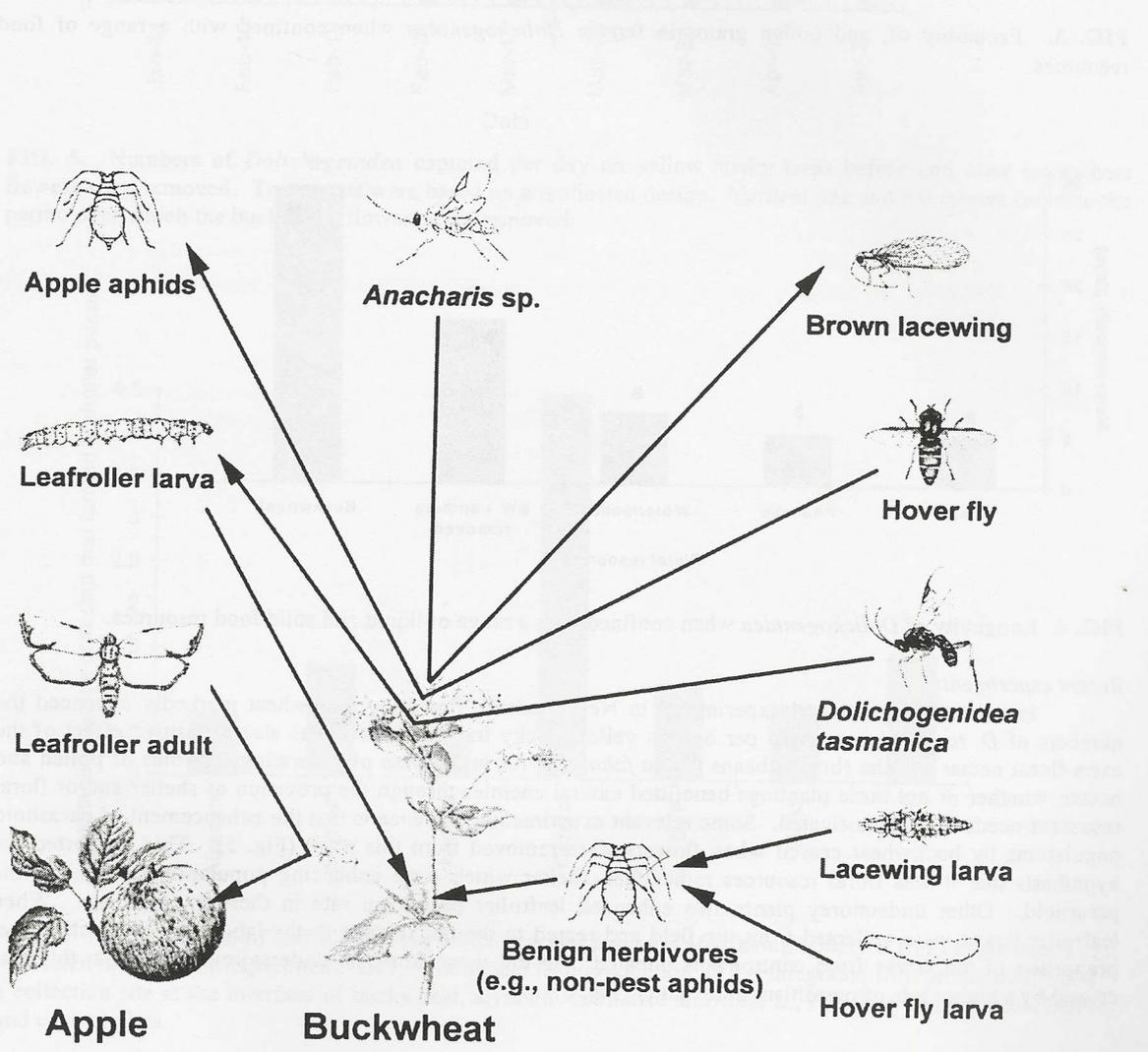
The need for laboratory work

In field experiments in which floral resources are added to an agroecosystem, there is usually a hierarchy of desired effects, the most important of which from an applied point of view is suppression of pest populations below their respective economic thresholds. However, this hierarchy of effects usually begins with the enhancement of predator/parasitoid numbers in the immediate vicinity of the flowers (e.g., Stevens *et al.*, 1998). Data of this type can be obtained by sampling the predator populations by using attractive traps, or sweep-netting or other active sampling techniques, or simply by recording the numbers of natural enemies on flowers in comparison with those in control areas (e.g., Cowgill *et al.*, 1993). Almost invariably, this first step in the hierarchy is achieved (Landis *et al.*, 2000) but the information of most relevance to the grower becomes increasingly difficult to obtain. For instance, step two would most usually be a higher rate of parasitism or predation brought about by the enhanced natural enemy populations. However, the potential mechanisms behind this need careful analysis. For instance, most natural enemies have a prey/host threshold density below which they lay few or no eggs (Barlow and Wratten, 1996 and Fig. 1.). Simply by providing amino acids and protein in the form of pollen, and energy in the form of nectar cannot change that threshold, but, by increasing the proportion of female natural enemies which are gravid or the mean number of fertile eggs per female, higher oviposition rates can be achieved. Other aspects of the natural enemy, which may change when flowers are present include its fitness, including longevity, searching ability etc. Effectively, this type of effect of flowers influences the reproductive numerical response of the predators (*sensu* Solomon, 1949). If the flowers lead to higher numbers of predators arriving in the vicinity of the pest population and/or to their staying there longer, then an enhanced aggregative numerical response (Solomon, 1949) will have been achieved. If prey/host populations are lowered through CBC (step three), then step four, that of addressing whether they are low enough to obviate or reduce the use of pesticides becomes important.



nectar are consumed by the parasitoid is important in the selection of candidate understorey plants. In the agroecosystem described here, buckwheat flowers did not significantly enhance survival of *D. tasmanica* compared with those from which the anthers had been removed, suggesting that in this parasitoid/plant interaction, pollen is not essential for parasitoid longevity (Fig. 3). However, buckwheat flowers did induce a longer survival compared with water and water/pollen treatments (Fig. 4). The likely importance of nectar in this system supports the work of Hagley and Barber (1992), Wäckers and Swaans (1993), Idris and Grafius (1995) and Baggen and Gurr (1998) in other parasitoid/flower systems. Other potential flowering plants for understoreys also enhance the longevity of *D. tasmanica* (Irvin *et al.* 1999) but without the careful separation of pollen and nectar availability, the relative roles of these two resources cannot be deduced. For example, it appears from Fig. 3 that *Dolichogenidea* does consume pollen from *Phacelia*. The small quantities ingested in the other treatments probably indicate ingestion via contaminated nectar.

FIG. 2. Some of the positive and negative ecological interactions, which may follow from the planting of buckwheat in an orchard understorey.



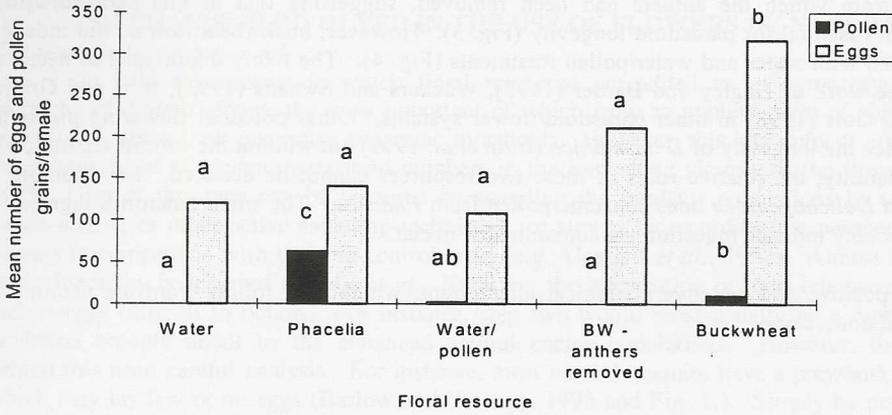


FIG. 3. Fecundity of, and pollen grains in female *Dolichogenidea* when confined with a range of food resources.

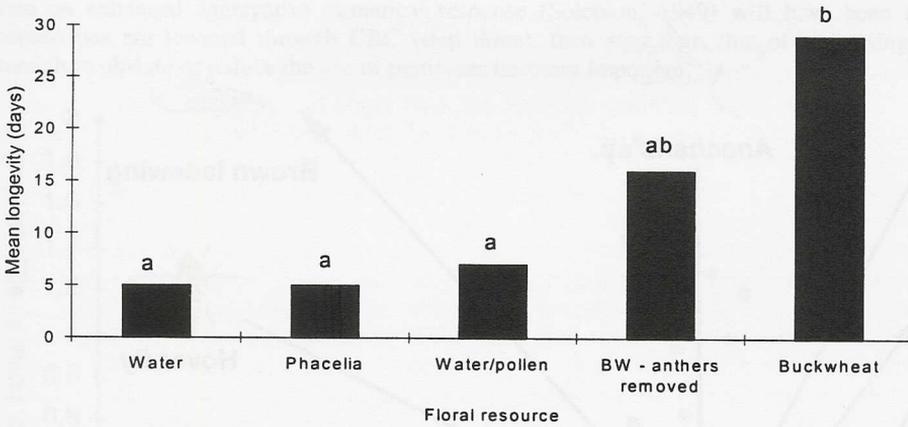


FIG. 4. Longevity of *Dolichogenidea* when confined with a range of liquid and solid food resources.

Recent experiments

In recent apple orchard experiments in New Zealand, flowering buckwheat markedly enhanced the numbers of *D. tasmanica* captured per day on yellow sticky traps and there was also a positive effect of the extra-floral nectar of faba (broad) beans (*Vicia faba* L.). As in the case of separating the roles of pollen and nectar, whether or not these plantings benefitted natural enemies through the provision of shelter and/or floral resources needs to be investigated. Some relevant experimental evidence is that the enhancement of parasitoid populations by buckwheat ceased when flowers were removed from this plant (Fig. 5). This supported the hypothesis that it was floral resources rather than shelter which were enhancing populations/activity of the parasitoid. Other understorey plants also enhanced leafroller parasitism rate in these experiments. When leafroller larvae were collected from the field and reared to the pupal stage in the laboratory, a much higher proportion of the larvae from control pots pupated than did those from the understorey treatments; this was caused by a higher rate of parasitism in the latter (Fig. 6).

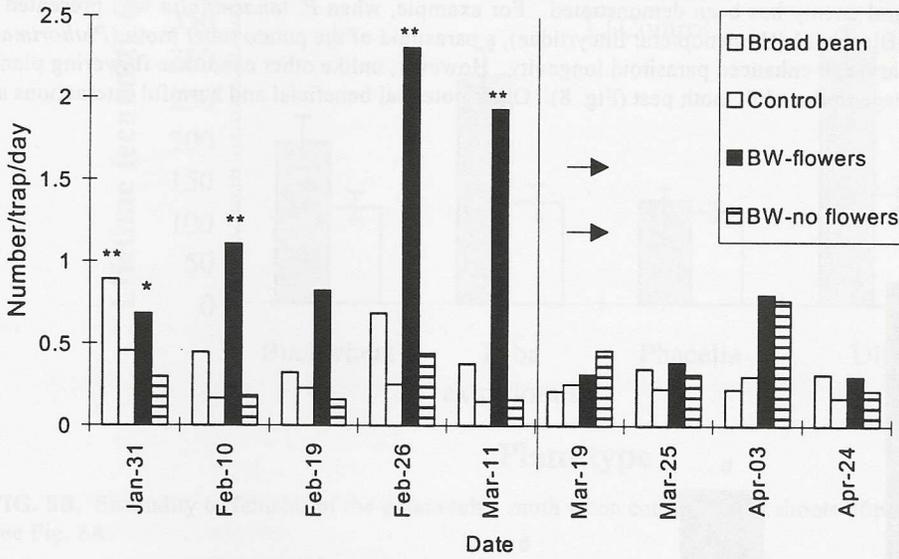


FIG. 5. Numbers of *Dolichogenidea* captured per day on yellow sticky traps before and after buckwheat flowers were removed. Treatments were based on a replicated design. Vertical line and the arrows indicate the period over which the buckwheat flowers were removed.

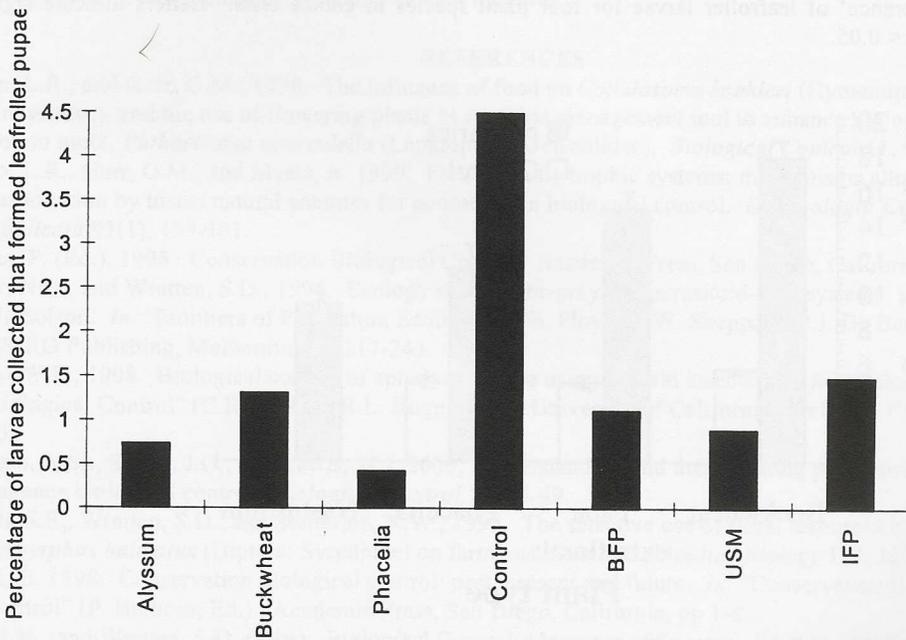


FIG. 6. The proportion of leafroller larvae which reached pupation after being collected from apple leaves in a replicated understorey experiment. BFP = biological fruit production; IFP = integrated fruit production; USM = a collection site at the interface of buckwheat, alyssum, *Lobularia maritima* L., *Phacelia tanacetifolia* (Benth.) and control plots.

Fig. 2 also summarises some of the potentially negative aspects of CBC. Leafrollers are highly polyphagous, feeding on many plant families (Scott, 1984), so adding plants to understoreys could represent an additional food source or overwintering site. In New Zealand, however, recent laboratory food-choice and feeding-rate experiments have shown that *E. postvittana* larvae strongly "prefer" apple leaves compared with buckwheat, clover (*Trifolium* spp.) and faba (broad) bean (Fig. 7). Also, when given no choice, they consumed

much more apple foliage than they did buckwheat, *P. tanacetifolia* and alyssum (*L. maritima*). The latter two plants have been used in other studies to enhance biological control (e.g., Hickman and Wratten, 1996 and Chaney, 1998). In other systems in which CBC has been practised, a clear selectivity of the added floral resources for the natural enemy has been demonstrated. For example, when *P. tanacetifolia* was presented to *Copidosoma koehleri* Blanchard (Hymenoptera: Encyrtidae), a parasitoid of the potato tuber moth (*Phthorimaea operculella* (Zeller)) larvae, it enhanced parasitoid longevity. However, unlike other candidate flowering plants, it conferred no advantage to the adult moth pest (Fig. 8). Other potential beneficial and harmful interactions are summarised in Fig. 2.

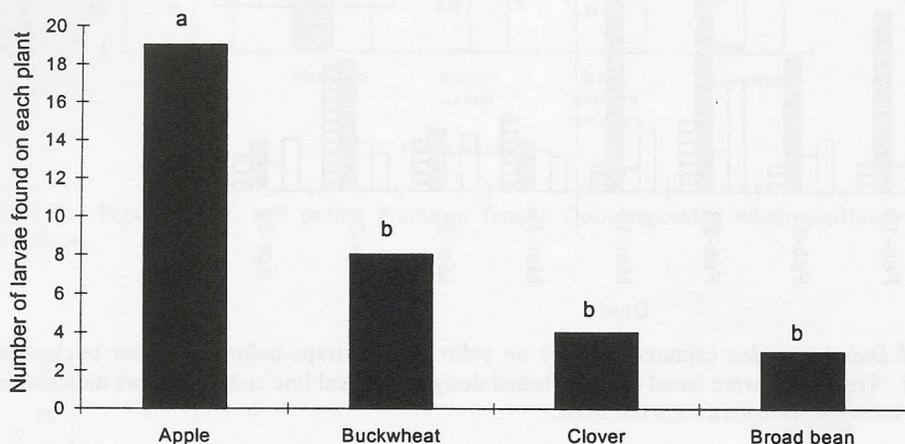


FIG. 7. 'Preference' of leafroller larvae for four plant species in choice tests. Letters indicate significant differences at $P < 0.05$.

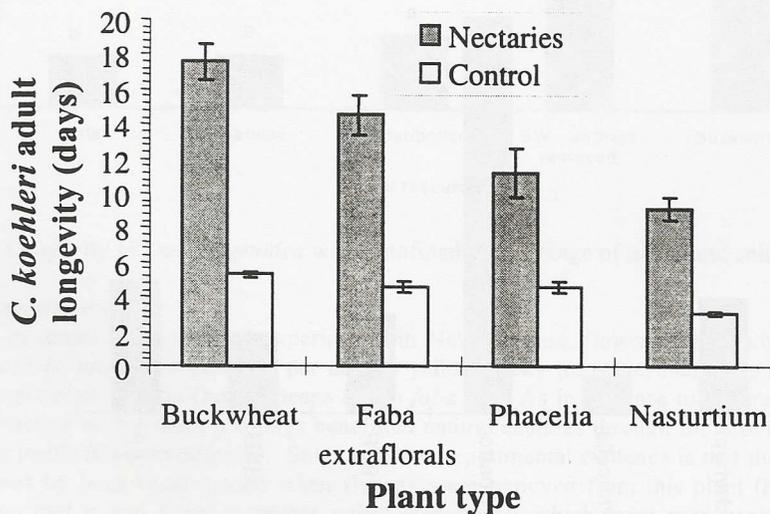


FIG. 8A. Longevity of the parasitoid *Copidosoma koehleri* when confined with plant shoots bearing nectaries in comparison with control shoots without nectaries (from Baggen *et al.*, 1999).

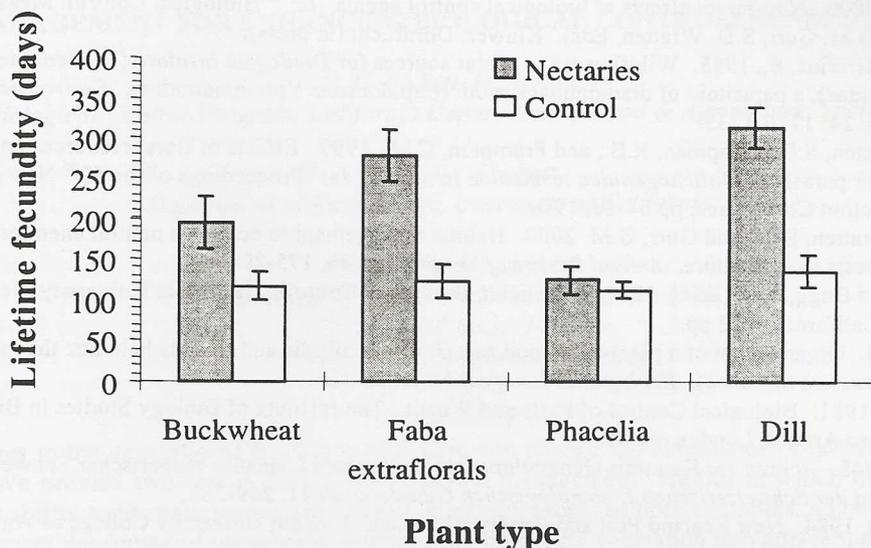


FIG. 8B. Fecundity of females of the potato tuber moth when confined with shoots of plants from four species. See Fig. 8A.

This review has highlighted the potential ecological complexity which may be associated with the apparently simple addition of a flowering plant to an agro-ecosystem. This can have negative, as well as positive effects, and parallels in that way some of the recently-recognised negative aspects of classical biological control (see Howarth, 2000). Understanding this ecological complexity for particular agro-ecosystems will be vital for CBC to achieve the level of adoption by growers, which it deserves.

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