Provision of Floral Resources for Biological Control Restoring an Important Ecosystem Service

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ABSTRACT

Modern agriculture has greatly altered and fragmented natural habitats globally. This has led to extensive loss of biodiversity and ecosystem services such as biological control. The provision of key components of biodiversity through ecological engineering can partially restore these ecosystem services. Many natural enemies of agricultural pests are omnivores that feed not only on prey but also on plant material such as nectar and pollen. It is possible to improve biological control through the integration of such alternative food sources into agro-ecosystems. We will here review how provision of flowering plants can increase the fitness and abundance of natural enemies, enhancing their suppression of populations of arthropod pests. We will discuss factors that need to be considered to optimise the likelihood of success for this type of ecological engineering. The plant resources provided should increase the fitness and abundance of the targeted natural enemies, but not benefit pests or higher order carnivores. They should be integrated into the agro-ecosystems in a way that is spatially and temporally favourable for natural enemies as well as practical and cost-effective for producers. We will present practical examples of progress and discuss prospects for the adoption of this more sustainable approach to pest management.

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INTRODUCTION

Ecosystem services are "the conditions and processes through which natural ecosystems, and the species that makes them up, sustain and fulfil human life" (Daily 1997). One such service is biological control (Daily 1997; Landis *et al.* 2007). Costanza *et al.* (1997) estimated the value of ecosystem services to be US$33 trillion/year for the entire biosphere, with biological control alone worth US$417 billion/year. Modern agriculture aims to maximise yield and profitability. The frequently intense disturbance linked with high intensity agricultural practices makes the resulting en-

vironment low in physical and biological resources required by natural enemies of pests (Towners 1972; Powell 1986; Letourneau 1998; Landis *et al*. 2007). The relationship between ecosystem services such as biological control and biological diversity is complex and variable (Cardinale *et al*. 2006; Hector and Bagchi 2007; Hooper *et al*. 2005). One way of reducing the negative effects caused by intense agriculture is through conservation biological control (CBC) in the form of provision of supplementary nectar and pollen resources (Landis *et al*. 2000). These can provide a suitable physical and biological environment within or adjacent to fields for pests' natural enemies, to increase the efficiency of the natural enemies (Olson *et al*. 2005). Here we review the effect of one key component of biological control, that of the provision of floral resource subsidies (Tylianakis *et al*. 2004) for natural enemies. Here we discuss factors that need to be considered to optimise the likelihood of success when providing floral resources for natural enemies.

FLORAL RESOURCES AND NATURAL ENEMIES

Resource subsidies are provided by non-crop plants grown within or around the crop and from which natural enemies can benefit. The pest management purpose of these is to provide the natural enemies with alternative food such as nectar, pollen and alternative prey/hosts as well as shelter or a moderated physical environment for over-wintering or escaping other extreme conditions (Landis *et al*. 2000). An already established natural enemy population at the time of pest colonisation can lead to better biological control (Olson *et al*. 2005).

Many natural enemies are omnivores that consume both plant materials, such as pollen and nectar as well as prey. This omnivory can be divided into two main groups: 1) Life-history omnivory when the arthropod requires plant-provided food at least during part of its life cycle (Polis and Strong 1996) and 2) true omnivory, when the arthropods feed from both plants and prey during the same life stage . True omnivory can be further divided into temporal omnivory, when the otherwise carnivorous diet is supplemented with plant foods during part of the life cycle and permanent omnivory, when the arthropod feeds on prey and plant material in its immature and adult stages (Wäckers and van Rijn 2005). We will focus here on how pollen and nectar can function as dietary supplements for the three different kinds of omnivore described above. Honeydew can also function as a dietary supplement for arthropods but it is nutritionally inferior to nectar for some parasitoids (Wäckers 2005) and is not included it in this review.

### Natural enemies benefiting from floral resources

The level of dependence of natural enemies on non-prey foods varies from true omnivores that are facultative consumers of plant-derived foods to life-history omnivores that are obligatory consumers of plant-derived foods (**Fig. 1**). Facultative consumers complement their diet with non-prey

foods while obligatory consumers require non-prey foods during certain developmental stages (Wäckers 2005). Examples of insect groups showing life-history omnivory are the green lacewings (Chrysopidae) (Stelzl 1991), hoverflies (Syrphidae) (Hickman *et al*. 1995), parasitoid flies (Tachnidae) (Gilbert and Jervis 1998) and parasitoid wasps (Hymenoptera, Parasitica) (Jervis 1998; Lewis *et al*. 1998). Temporal and permanent omnivores include, for example, the temporally omnivorous adult host feeding parasitoids (Hymenoptera, Parasitica) (Gilbert and Jervis 1998; Lewis *et al*. 1998) and the permanently omnivorous ladybirds (Coccinellidae) (Pemberton and Vandenberg 1993) and brown lacewings (Hemerobiidae) (McEwen *et al*. 1993; Stelzl 1991). The developmental stage at which plant provided foods can be utilised and what type – nectar, pollen or both – varies within these three groups. Adult green lacewings and hoverflies require both nectar and pollen (Stelzl 1991) while adult parasitoid flies and wasps use only nectar (Gilbert and Jervis 1998). Ladybirds benefit from nectar and pollen as adults and juveniles (Pemberton and Vandenberg 1993), while parasitoids benefit from nectar only as adults (Wäckers and van Rijn 2005). Active pollen-feeding to supplement the diet is common among predacious arthropods such as hover flies, ladybirds, green lacewings and predatory mites (Phytoseiidae) (Wäckers 2005).

Effects of floral resources on fitness of natural enemies

Dietary floral supplementation can increase longevity, fecundity and other components of ecological 'fitness' and lead to a change in sex ratio (Berndt and Wratten 2005; Landis *et al*. 2000) and in dispersal ability of natural enemies (Wanner *et al*. 2006a). For pro-ovigenic parasitoids, which are born with all or nearly all of their eggs mature (Flanders 1950), floral resources can lead to an increase in fecundity due to prolonged longevity (Gurr *et al*. 2005b) while for synovigenic species, that continuously mature eggs throughout their reproductive life (Flanders 1950), floral resources can increase life-time fecundity due to prolonged longevity and egg-production rate (Gurr *et al*. 2005b). Among Parasitica (Hymenoptera) and Acuelata (Hymenoptera) synovigeny is most common (Jervis *et al*. 2001). The presence of alyssum (*Lobularia maritima* L. Brassicaceae) flowers increased the longevity, fecundity and sex ratio of the parasitoid *Dolichogenidea tasmanica* Cameron (Braconidae) under laboratory conditions (Berndt and Wratten 2005). Maximum longevity for female parasitoids increased seven fold from 2.2 ± 0.17 days to 15.7 ± 2.77 days when alyssum flowers were present. Lifetime fecundity, as estimated by the total number of offspring of each parasitoid reaching the cocoon stage, increased from a mean of 20.2 ± 3.89 cocoons produced without access to flowers to 152.8 ± 24.31 cocoons. The increase was due to the increase in longevity rather than to an increase in the number of offspring per day. The sex ratio of the offspring of parasitoids without alyssum flowers was strongly male biased with a mean sex ratio close to one, while it was around 0.6 when floral resources where present (Berndt and Wratten 2005). Wanner (2006a) showed that nectar from *Anethum graveolens* L. (Apiaceae) and *Origanum vulgare* L. (Lamuaceae) increased the number of flights, distance of single flights and total flight distance for females of the parasitoid *C. glomerata*. This increase in dispersal ability when supplied with the 'right kind' of floral resources could play a key role in biological control of insect pests (Wanner *et al*. 2006a).

Parasitoids and predators lacking floral supplementation exhibit negative changes in qualities, such as increased egg resorption, decreased egg availability, increased rates of diapause and sex ratios favouring males. There can also be changes in flight initiation and timing as well as decisions favouring food foraging rather than host/prey searching efficiency (Jervis 1998; Takasu and Lewis 1995; Wäckers 1994). Consequently, the availability of floral resources is
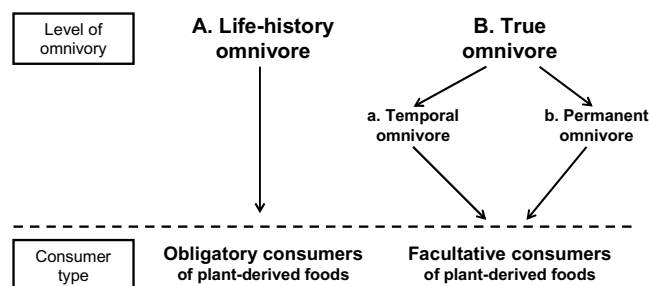
Fig. 1 Consumer type in relation to level of omnivory. (A) Life-history omnivores are obligatory consumers of plant-derived food. **(B)** True omnivores can be divided into temporal omnivores (**a**) and permanent omnivores (**b**). These are both facultative consumers of plant-derived food.

likely to play a key role in the population dynamics of natural enemies, both in predator-prey (van Rijn *et al*. 2002) and parasitoid-host systems (Krivan and Sirot 1997; Wäckers 2003). Earlier parasitoid-host difference-equation models neglected these aspects (Hassell 1978). Kean *et al*. (2003) analysed the possible consequences of this omission. They showed for example that nectar can increase natural enemies' attack rate (a') and its area of discovery (a) (Hassell 1978) leading to greater lifetime search area and more attacks. Resulting in equilibrium prey abundance decreasing towards zero with increasing enemy longevity (Kean *et al*. 2003).

Fewer studies have been done on the effect of supplying pollen alone. However, two studies of predatory mites in this context showed a mean increase of 380% in fecundity. However, such increases have been shown in only two out of seven predatory mite examples (Olson *et al*. 2005), but the potential importance of nitrogen supplied in the form of pollen on natural enemies' fitness is clear.

The relationship between increases in natural enemy abundance and higher parasitism and predation rates

Effects of floral resources can have both negative and positive effects on parasitism and predation rates by natural enemies.

Floral resources can attract more natural enemy species to the targeted area. This increase in biological diversity can be associated with an increase in species' interaction together with aggregation effects of natural enemies in response to prey (Cardinale *et al*. 2006) or host (Dempster 1967) availability. These effects may limit the possible number of co-occurring species. Effects can either be additive, resulting in an increased herbivore suppression rate with an increased number of natural enemy species, or non-additive (Cardinale *et al*. 2006). The latter can lead to 'redundancy' with added specie not markedly contributing to the relationship or coincidental predation (Rosenheim and Harmon 2006) and/or intra-guild predation (IGP) (Snyder and Ives 2001; Finke and Denno 2003; Snyder and Ives 2003;).

Effects of floral resources on omnivore-prey relationships

Factors such as reduced attack rate by natural enemies due to their favouring nectar and/or pollen feeding over predation (Eubanks and Styrsky 2005) or increased herbivore reproductive rate due to herbivore utilisation of the floral resource (van Rijn and Sabelis 2005) can work to counter the positive effect of the supplied dietary supplements, allowing the pest population to escape the control of the predator population (Wäckers and van Rijn 2005). Robinson *et al*. (2007) demonstrated the complex pattern that an omnivore-prey system can show when floral resources are supplied in the laboratory. They investigated how flowers of buckwheat (*Fagopyrum esculentum* Moench Polygonaceae) affected *per capita* predation rate of pea aphids (*Acyrthosiphon pisum* Harris Hemiptera:Aphididae) by adult predatory brown lacewings (*Micromus tasmaniae*) Walker (Neuroptera: Hemerobiidae) and how the longevity and fecundity of the lacewing was affected. Flowers reduced prey consumption. The outcome of the floral supplementation on longevity and fecundity depended on the abundance of the aphid prey. In the absence of aphids, longevity was higher for lacewings supplied with flowers than for those without them. When aphids were abundant, lacewing fecundity was unaffected by flowers. When aphids were less abundant, floral provision decreased the pre-oviposition period and increased the daily oviposition rate. This shows how floral resources can mediate omnivore-prey relationships and how the outcome can, in the context of CBC, either be positive, negative or neutral (Robinson *et al*. 2007).

OPTIMISING THE PROVISION OF FLORAL RESOURCES

We will review here some key points that should be considered to optimise floral provision for biological control. The resource must be of the 'right' kind (Landis *et al*. 1999). The floral attractiveness as well as availability, accessibility and suitability of the nectar and pollen to the natural enemy need to be considered.

Floral attributes which favour natural enemies

Visual aspects of flowers such as shape, colour and contrast with the background can affect their attractiveness to natural enemies. The distance over which flowers can be detected is dependent on the combination of the surface area of the flower that produces achromatic contrast with the background and the visual perception of the insect's compound eye (Ne'-eman and Kevan 2001). The insect movement when approaching a flower enhances the visual perception of the flower (Wehner and Sirnivasan 1989). Many insects are innately attracted to a few colours, in particular yellow, for which the parasitoid, *Cotesia rubecula* Marshall (Hymenoptera: Braconidae) shows a preference when deprived of sugar foods (Wäckers 1994). To the human eye yellow and white are the most common flower colours (Weevers 1952) and pollen is predominately yellow (Lunau 2000). Consequently, only a few innate colour preferences are needed to cover most floral nectar and pollen resources. It is important to determine to which clue the targeted natural enemy species is attracted before choosing floral resources to deploy in CBC programmes. Insects that forage for pollen can, in addition to these clues from the corolla, use signals from the pollen (Wäckers 2005).

The floral odour will depend on the specific blend of emitted volatiles and the rate of emission. The range of floral odours is vast (Knudsen *et al*. 1993) and the floral fragrances are made up by a bouquet of several odours from different chemical classes (Dobson 1994). Parasitoids such as *C. rubecula* (Wäckers 1994), *Cotesia glomerata* L. (Hymenoptera: Braconidae), *Heterospilus prosopidis* Viereck (Hymenoptera: Braconidae), and *Pimpla turionellae* L. (Hymenoptera: Ichneumonidae) (Wäckers 2004) exhibit an innate response to a few common floral volatiles. Wäckers (2004) showed that food-deprived parasitoids responded only to four out of 11 plant volatiles to which they were exposed, supporting this idea. Floral volatiles can also have a repellent effect on parasitoids (Wäckers 2004).

Pollen volatiles work in the same way as other floral volatiles (Wäckers 2005) except that the volatiles may derive from the pollen itself in the form of pollenkitt. Volatiles emitted by pollen are plant-species specific and are chemically distinct from those emitted from other floral parts. Compared with odours such as those from nectar, pollen odours are quantitatively weak and so work only over short distances (Dobson *et al*. 1996).

Floral characteristics

It is important to choose a resource that is available at the most appropriate time for the natural enemy. This is dependent on the targeted agro-ecosystem and what type of subsidy the natural enemies require. The availability of nectar is determined by geographic, seasonal and environmental factors and can vary greatly in time and space depending on the local vegetation and phenology of the plant species (Wäckers 2005). Variation over longer periods, such as seasonal ones, affects the floral abundance to a large extent (Abe and Kamo 2003). For example, in continental areas such as central Europe, distinct seasonal changes make flower abundance highest during the mid-summer period and lowest in early spring and late autumn. Plant species flower abundance during the low flowering periods are high in pollen-rich flowers, compensating for low nectar availability at these times. In contrast, nectar abundance is highest

during early summer when pollen availability is low (Gleim 1985). At a shorter time-scale, the variation in production of pollen and nectar can differ throughout the day. Nectar secretion may follow daily rhythms, being high during the early morning, in the afternoon or at night (Waller *et al*. 1981; Kovacs *et al*. 1995; Kovacs 1996). The peak of daily production often coincides with when the plants' main pollinators are most active (Wäckers 2005) as in the case for milkweeds (*Asclepias* spp. Torr. Apocynaceae) (Bertin and Willson 1980). Similar daily variation occurs in pollen accessibility depending on the period and pattern of the flower opening (Percival 1955). These factors need to be considered when choosing the floral resources and will be discussed in more detail further ahead.

Nectar and pollen accessibility

Accessibility of nectar and pollen varies with floral morphology (Vattala *et al*. 2006). It is important to choose a resource that is accessible to the target natural enemy species, which must be able to reach the resource by either inserting its head into the corolla or by using long mouthparts. The problem of not reaching the resource is not as great for species feeding exclusively on pollen as this is generally more exposed than nectar (Wäckers 2005). Most hymenopteran parasitoids (Gilbert and Jervis 1998) and predators have short mouthparts. This may restrict them to feeding only on flowers with an open, shallow corolla (Wäckers 2005). However, some predators and parasitoids have developed specialised mouthparts termed concealed nectar extraction apparatus. These allow them to reach nectaries of flowers with deep tubular corollae, which would otherwise be inaccessible (Gilbert and Jervis 1998; Jervis 1998). Another method developed by short-tongued arthropods is nectar robbery. These insects chew holes in the corolla, accessing nectar (Baggen *et al*. 1999).

Vattala *et al*. (2006) emphasised the importance of choosing a nectar resource that is accessible to the target natural enemy species. They compared the morphologies of *Microctonus hyperodae* Loan (Hymenoptera: Braconidae) a parasitoid of the Argentine stem weevil, *Listronotus bonariensis* Kuschel (Coleoptera: Curculionidae) and the morphology of seven flower species. They showed that even if in New Zealand abundant flowers such as red clover (*Trifolium pratense* Astred Fabaceae) and white clover (*Trifolium repens* Grassland Kopu Fabaceae) could be beneficial for increasing the longevity and fecundity of *M. hyperodae*, the corolla apertures as well as the corolla depths would prevent the parasitoids from accessing the nectar (Vattala *et al*. 2006).

Nectar and pollen quality

The nutritional value of nectar and pollen may also affect the efficacy of floral resources. The most common sugars in nectar are the disaccharide sucrose and the hexose monosaccharides glucose and fructose (Baker and Baker 1983). Baker and Baker (1983) analysed the sugar ratios of 765 plant species and developed a classification system based on the nectars' sucrose / (glucose + fructose) ratio. Their classification system comprised four classes: hexose-

dominant (<0.1), hexose-rich (0.1-0.499), sucrose-dominant (>0.99) and sucrose-rich (0.5-0.99). Wäckers (2005) concluded that a preference of some insect families for flowers with sucrose or hexose-rich nectar can be seen. Vattala *et al*. (2006) found that the longevity of *M. hyperodae* was significantly increased when buckwheat was supplied compared with phacelia (*Phacelia tanacetifolia* Bentham Boraginaceae), alyssum, coriander (*Coriandrum sativum* L. Apiaceae), white clover, red clover and white mustard (*Sinapis alba* L. Brassicaceae). Buckwheat had the highest sucrose/ (glucose + fructose) ratio and falls into the 'sucrose-dominant' class (Baker and Baker 1983).

In addition to these three main sugars, nectar can contain low concentrations of other carbohydrates such as raffinose, galactose, mannose (Baker and Baker 1983) and rhamnose (Wäckers 2001). Some of these sugars can be deterrent, nutritionally unsuitable or toxic (Barker and Lehner 1976; Wäckers 2001) making sugar mixtures containing otherwise nutritionally favourable nectar sugars unsuitable (Wäckers 2001).

Pollen is generally a good source of nitrogen for insects. Its availability for the insect is generally dependent on the morphological characteristics of the grain with different insect species showing 'preference' for pollen from specific plants. However, some pollen types can be toxic to some insects (Wäckers 2005).

Wratten *et al*. (2003a) developed a hierarchy of eight questions (**Table 1**) that need to be answered to be able to measure the potential success of the application of floral resources when applied in the context of CBC. For the second question '*Does it use pollen and/or nectar?*' it is important to include also the accessibility as well as the quality of the nectar and pollen.

Effects of added floral resources on pest and higher order predators or hyperparaitoids and how to minimize these

The advantage of many natural enemies' being omnivorous in at least some of their life stages is that they are able to feed on alternative food sources, such as nectar and/or pollen, when prey/hosts are scarce. This trait enables them to remain in an area with temporarily low prey/host densities, preventing them from starving or emigrating (Polis and Strong 1996; Olson *et al*. 2005). However, the use of floral resources for omnivorous natural enemies can also have negative effects. These can be either of the second trophic-level, increasing herbivore fitness (Wäckers and van Rijn 2005) or of the fourth, potentially decreasing predator abundance. It is important to ensure the provided floral resources benefit natural enemies but not the pest or enemies of the natural enemies (Baggen *et al*. 1999; Adler and Bronstein 2004; Araj *et al*. 2006) or at least have greater effect on the natural enemies.

Effects on the pest

Baggen *et al*. (1999) showed that flowers from buckwheat and dill benefited the parasitoid *Copidosoma koehleri* Blanchard (Hymenoptera: Encyrtidae) and its host, the potato pest, *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae) increasing its longevity and oviposition period as well as fecundity, mean oviposition rate and number of eggs in the ovaries at death. In contrast, phacelia and nasturtium (*Tropaeolum majus* L. Tropaeolaceae) benefits only the parasitoid.

This is an example of how a plant such as buckwheat, that is extensively used as a floral resource (Gurr *et al*. 2000) can also be beneficial to the pest in particular food webs. As mentioned above however, benefiting the pest may not preclude the deployment of a plant species in biological control if the natural enemies benefits more (Kehrli and Wratten 2007). Modelling may be the most appropriate way of determining the population consequences of such differential effects on 'fitness' (Kean *et al*. 2003).

Table 1 Measures of floral resource success (Derived from Wratten *et al*. 2003a).

- Does the adult parasitoid/agent use floral resources?
- Does it use pollen and/or nectar?
- How compatible is the agent with the use of some pesticides?
- Is the fitness of individual agents improved? (Longevity, fecundity, sex ratio etc.)
- Does the improved fitness apply to males and females?
- Are pest populations reduced as a result of this CBC practice?
- Are pest populations reduced below the economic threshold?
- Does CBC improve farmer profits?

These studies emphasise the importance of choosing a suitable floral resource for each particular food web (Kehrli and Wratten 2007). The difference in response to a floral resource by a herbivore and a parasitoid was clearly demonstrated in a study by Lavandero *et al*. (2006). They used buckwheat as one of five nectar sources, with three different parasitoids and their hosts. These were: *Diadegma semiclausum* Hellen (Hymenoptera: Ichneumonidae) and its host *Plutella xylostella* Linnaeus (Lepidoptera: Hyponomeutidae), *D. tasmanica* and its host *Epiphyas postvittana* Walker (Lepidoptera: Tortricidae) and *C. koehleri* and its host *P. operculella*. For *D. semiclausum*, buckwheat nectar had a large positive effect on the parasitoid's fitness, while it had a small effect on that of the host. The same relative difference could be seen for *D. tasmanica*, while only a medium effect occurred with the fitness of *C. koehleri*. In this case, however, a high positive effect on its host *P. operculella* could be seen (Lavandero *et al*. 2006).

Effects on higher order predators and hyperparasitoids

Araj *et al*. (2006) studied the consequences of making a three or four trophic-level system more complex by adding floral resources. Under laboratory conditions, the effect of a range of plant nectar sources on the longevity of the aphid parasitoid, *Aphidius ervi* Haliday (Hymenoptera: Braconidae) and its hyperparasitoid, *Dendrocerus aphidium* Rondani (Hymenoptera: Megaspilidae) was studied. *A. ervi* and *D. aphidium* were both able to use the resources to mature eggs and increase the longevity, increasing the potential life-time fecundity. Both species are synovigenic so females that live longer should mature more eggs. *D. aphidium* produces fewer than half the number of progeny than does *A. ervi*. However, when *D. aphidium* was provided with buckwheat and water, respectively, *D. aphidium* lived 2.5 and 3 times longer than did *A. ervi* (Araj *et al*. 2006). In terms of community dynamics this suggests that *D. aphidium* with access to nectar, could affect 'top-down' control and cause trophic cascades which may increase aphid populations indirectly (Boenisch *et al*. 1997). Modelling and additional experimentation would be needed to explore this further.

As illustrated above, the effect of supplementation of floral resources on the population dynamics of the species involved is likely to differ according to the food web being investigated. To successfully supply floral resources to enhance biological control, knowledge of the system, including the biology of the herbivore, its enemies and their interactions with the resource subsidy is needed (Lavandero *et al*. 2006).

The fourth question in Wratten *et al*.'s (2003a) table addresses the floral resource-natural enemy fitness relationships. It is important to remember that these questions should not be addresses only for the natural enemy involved, but also for all herbivores, predators, higher order predators as well as parasitoids and hyperparasitoids in the food web.

Timing of floral provision

The correct timing of floral provision is important to avoid or minimise negative effects such as increased parasitism or hyperparasitism rates, or increased herbivory. Due to the complexity of food webs (Tylianakis *et al*. 2007) and the variations in the strength of the linkages between the different species, the synchronisation between the flowering period and when the natural enemies are present and require the resource is important. It is obvious that the phenologies and seasonality of the flowering plant and of the predator or parasitoid should coincide to optimise the outcome of the provision of floral resources (Landis *et al*. 2000; Wäckers 2005). In the work by Jonsson *et al*. (unpublished data), the effect of supplying buckwheat to a four trophic-level system – the lacewing parasitoid, *Anacharis zealandica* Ashmead (Hymenoptera: Figitidae) the predatory lacewing, *M. tasmanae* and the pea aphid – was dependent on aphid numbers. Supplying the lacewing with floral resources when aphid numbers were high had a negative effect on the lacewing population, which was probably due to increased parasitism rate by *A. zealandica*. However, the effect of buckwheat on the lacewing density after the aphid population had declined was positive, probably because lacewings were starving in the absence of buckwheat. This shows how the correct timing of the supplementation of a floral resource is crucial for a successful application to CBC.

Spatial consideration of floral resources

The abundance and diversity of natural enemies are affected by processes acting on the landscape scale. Complex, patchy landscapes with a high proportion of non-crop vegetation often has high densities of natural enemies and low pest pressures (Tscharntke *et al*. 2005). Bianchi *et al*. (2006) summarised the effects of landscape composition on natural enemies from 24 studies. In 74% of the cases, complex landscapes with a high proportion of non-crop vegetation (e.g. forest, hedgerows, field margins, etc.) had higher densities of natural enemies than simpler landscapes dominated by agriculture. Little is known about which particular components of the landscape that are of most importance for biological control. To our knowledge, no studies have been published on how the amount of flowering vegetation at the landscape scale affects biological control.

The effect of local provision of floral resources is likely to be influenced by the composition of the surrounding landscape. Tscharntke *et al*. (2005) suggested that habitat manipulation conducted at the local field scale is most likely to be successful in landscapes with a relative low proportion of non-crop vegetation. In more complex landscapes, local habitat manipulation efforts may be less effective because resources are already abundant in the surrounding landscape.

Natural enemy movement

Organisms with high dispersal and re-colonization ability seem to bee particularly important for biological control in agroecosystems (Tscharntke *et al*. 2005). The individual species dispersal distances will determine the arrangement and overall quantity of resource subsidies required (Wratten *et al*. 2003a, 2003c). A variety of indirect marking techniques can be employed to assess dispersal distances of natural enemies (Lavandero *et al*. 2004). Lavandero *et al*. (2005) used indirect rubidium marking to study how far the diamondback moth parasitoid *D. semiclausum*, moves after floral feeding. It was found that this species can move at least 80 m during a short period. However, parasitism rates were significantly lower only 60 m away from the strip of flowers. Flowers should in this case therefore probably be deployed in patches or rows less than 80 m apart to be most effective. Wanner *et al*. (2006b) used the stable isotope [44]Ca to study dispersal of the parasitoid *Cotesia glomerata* that had been feeding on flowers of dill. This isotope is transferred to the offspring of the wasp and it was therefore possible to assess how floral feeding affected parasitism rates at different distances. The study was conducted in an area 35 m × 35 m large with flowering dill in two diagonally opposing corners. Parasitism rates by females that had feed on the flowers were distributed randomly within the 35 m × 35 m area so dispersal was not limited at this small scale.

Boundaries between fields can affect movement of natural enemies feeding on flowers. In a study by Wratten *et al*. (2003b) the effect of the dispersal of a hoverfly (*Melanostoma fasciatum*) Maquart (Diptera: Syrphidae) across four different field boundary types was tested. The different types of boundaries used were post-and-wire fences, lines of poplars (*Populus* spp.) with gaps, together with dense poplars and a control of no barriers. A strip of phacelia was sown on one side of the boundary. The pollen from the phacelia functioned as a pollen source as well as a marker. Yellow water traps were anchored on each side of the phacelia

strips to provide a trap line on either side of the barrier. The results showed that this hoverfly species could move up to 200m from its pollen source when no barriers were present. Both types of poplar barriers restricted the movement of the hoverfly, while there was no effect of the post-and-wire fence. The implication of this work include that the dispersal rate of a natural enemy can be restricted by field boundaries which however, can also function as refuges for, and a source of beneficial arthropods (Wratten *et al*. 2003b). It emphasises the importance of matching the dispersal capability of the natural enemy with the distance between resource subsidies in relation to habitat heterogeneity.

FURTHER CONSIDERATIONS TO OPTIMISE PROVISION OF FLORAL RESOURCES

To avoid a 'shotgun' approach (Gurr *et al*. 2005b) and successfully integrate flowering plants which provide resource subsidies in agro-ecosystems, further considerations such as practical agronomic factors and grower aspirations must be taken into account alongside the above biological factors. Following such considerations a cost-benefit analysis to assess, case by case, the economic value, if any, of adopting CBC practices should be undertaken (Landis *et al*. 2000; Gurr *et al*. 2005a). The following sections review these agronomic considerations and current grower aims, investigating some of the practicalities of growers' implementing non-crop resources and why adoption of this practice may be hindered.

Agronomic considerations

Several agronomic factors may need to be considered when introducing floral resources to agricultural systems. These include the cost, availability and maintenance of the plant, as well as its weed potential, frost susceptibility and compatibility with the crop and cropping system.

Cost, availability and maintenance of floral resources

The plant species should ideally be readily propagated and available for purchase and the seed or plant purchase cost should not off-set the expected benefits, such as reduced pesticide costs. Similarly, the establishment and maintenance of the non-crop resource must be compatible with grower resources including labour, equipment, technical knowledge, time and land (Landis *et al*. 2000). Ultimately, the amount and spacing of the plants providing the floral resources required must be practical. For instance, any loss of production profit due to the planting of floral resources must be off-set with savings such as enhanced marketing opportunities (Warner 2006b) reduced pesticide costs and labour if the practice is to be acceptable to growers (Gurr *et al*. 2005b).

Weed potential of floral resources

Candidate plants for resource subsidies should be screened for their potential to become weeds. Annual plants, which require sowing each year, are less likely to become weed species, as they do not persist from year to year. For instance, the annual buckwheat is killed by frosts and so is unlikely to become a persistent weed. Perennial plants are more likely to spread beyond their designated areas or harbour invasive weeds (Wratten *et al*. 2003a). However, some plant species with potential to enhance biological control may also suppress weeds. The prostrate growth habit of the European plant *L. maritima* is known to suppress weeds as well as being an abundant source of pollen and nectar (Landis *et al*. 2000; Begum *et al*. 2006).

Frost susceptibility of floral resources

When integrating plant species for floral resources into sites prone to frost, care should be taken to ensure that the added plants do not enhance a crop's susceptibility to frost damage. Where a site is prone to frost, the technical ability and willingness of the grower to mitigate frost damage should be assessed. Mitigation may entail special management of the floral resource such as frequent mowing to maintain low growth thus reducing airflow disruption (Synder and Connell 1993) or increasing the use of frost-fighting techniques such as frost pots, sprinklers, wind machines and helicopters (Evans 2000). Alternatively, well planned selection and spatial arrangement of floral resources will reduce the potential for frost damage. Selection of prostrate or other plants with low growth form will minimise interference of air flow (Begum *et al*. 2006), while sites susceptible to regular frosts could deploy added plants around, rather than within crops.

Compatibility of floral resources with crop and cropping system

Whether a particular cropping system is rotational or permanent and the presence of livestock will affect selection and management of the floral resource. Rotational systems are likely to be suitable for annual floral resources within the cropping area and perennial species around it, while permanent crop can incorporate either annual or perennial floral resources. Where livestock are present, issues of toxicity and palatability of the added plants need to be addressed (Landis *et al*. 2000).

The spatial arrangement of a crop will influence how the floral resource is provided (Wratten *et al*. 2003a). Inter-row cover crops, understorey and ground covers, conservation headlands or 'beetle banks' (MacLeod *et al*. 2004; Thomas *et al*. 1991) are all potential options (Wilkinson and Landis 2005). Also, specific site conditions including soil type, mean rainfall and temperature, exposure and nutrient availability need to be considered when selecting plants to provide resource subsidies.

Floral resource used needs to be compatible with the crop regarding its water and nutrient use as well as the time crops are most susceptible to pest damage. Cover crops have been used in viticulture to de-vigorate grape vines (Wheeler and Pickering 2003). This practice utilises non-crop plant competition in order to manipulate vine growth to achieve quality grape production. Similarly, floral resource provision should take into account any competition between the crop and non-crop and whether such competition is acceptable or can be ameliorated (Landis *et al*. 2000; Zehnder *et al*. 2007).

Planting the floral resource along the edges of the crop is one way in which competition could be minimised (Wilkinson and Landis 2005), although this may reduce the effectiveness of the resource if the required dispersal distance of the natural enemy is too great (Lavandero *et al*. 2004; Scarratt 2005). The selection of plant species with low water requirements can effectively minimise cover crop competition with the crop itself. Grape growers in California are increasingly utilising native drought-tolerant perennial grasses to minimise water competition. These species endure dry periods through dormancy. Deploying these can reduce excessive competition for water between the cover crop and the vines (Blake 2006). Also, water penetration of the soil may be improved because the rooting system of the added plants may improve water infiltration and thereby reduce run-off (Bugg and Van Horn 1998).

Growers' aims

Much modern agriculture relies on intensive mechanization and pesticide use. Consequently natural enemy numbers are often reduced to inefficient levels (Sandhu *et al*. 2007a). Recently, however, growers are becoming interested in diversifying their farming system to enhance natural enemy effects on pests, thus reducing pesticide use and improving agricultural sustainability (Gurr *et al*. 2004; MacLeod *et al*.

2004; Landis and Menalled 2005; Wilkinson and Landis 2005; Warner 2006a; Sandhu *et al*. 2007b).

It could be said it is the growers' goals that define whether floral resource provision has been successful. Gurr *et al*. (2005a) identified four aims of farmers including reducing risk, workload and environmental impact, maximising farm sustainability and alternative income and most importantly, making a profit. Several authors emphasised the obvious point that methods to enhance natural enemies through the provision of floral resource subsidies must be compatible with profitable farming (Wratten *et al*. 2003c; Gurr *et al*. 2005b). This is consistent with the findings of Griliches (1957, 1960) who found economic variables associated with adoption of agricultural technologies often determine the level of adoption.

Research on floral resource subsidies has rarely to date clearly demonstrates whether this aim of reduced variable costs has been achieved at a commercial scale, although some progress has been made recently. However, when understorey plants, which have been used to enhance biological control of arthropods, are mulched and the mulch is placed under the vines, soil microbiological activity can be enhanced to the extent that the life cycle of grey mould, *Botrytis cinerea* (De Bary) Whetzel (Helotiales: Sclerotiniaceae), is disrupted. This leads to lower infection rates of the disease on the grapes at harvest, reducing fungicide inputs (Jacometti *et al*. 2007). This is a good example of multiple ecosystem services being derived from an initially simple biodiversity enhancement.

Adoption by growers: Knowledge transfer between research and practice

The requirement for effective and efficient knowledge transfer between research and practice is paramount. Empirical research in the laboratory and field is certainly needed to ensure that floral resources can be used selectively by the target beneficial species (Gurr *et al*. 2005b) and answer the initial questions posed in (**Table 1**) Wratten *et al*. (2003a). However, findings from this applied type of work need to be applicable and actually at a commercial scale if this CBC practice is to be viewed as successful. Some form of agricultural extension is therefore required.

Agricultural extension is the exchange of knowledge between growers, scientists and extensionists (Laurent 2002). Often poor links between these are cited for knowledge-transfer failures and low grower adoption (Williamson 1998). Addressing this failure is the recent emergence of 'agro-environmental partnerships', 'discovery learning' and 'peoples participation' (Pretty 1995; William-son 1998). These approaches facilitate knowledge transfer through joint grower-researcher projects. Such agro-environmental partnerships are defined by Warner (2006a) as '*an intentional multi-year relationship between at least growers, a grower's organisation and one or more scientists to extend agro-ecological knowledge to protect natural resources through field scale demonstration*.' Landis *et al*. (2007) suggest expanding traditional research partnerships to include stakeholders such as conservation organisations, plant producers and farmers. A key theme to successful knowledge transfer appears to be the participation of growers from an early stage within research to ensure that the research goals are appropriate to the growers that recommendations are practical and that growers are aware of and motivated to adopt new practices.

A current initiative, which demonstrates this theme, is that being produced by Lincoln University, New Zealand. The research group is working with grape growers of the Waipara Valley in North Canterbury to introduce non-native and native plants to vineyards (Waipara_Valley_Winegrowers 2007). This collaboration is an example of agriculture and research working together to enhance adoption of 'sustainable' practices at a commercially-realistic landscape scale. Around forty landowners, predominantly viticulturalists, involved in the development of the benefits that non-

crop resources can provide. This is a collaborative effort to undertake research to identify and measure the contribution native plants provide to the ecological restoration of the area and to its agricultural sustainability, including biological control of pests. As well as growers and university researchers the project is also supported by the district council and by a New Zealand Crown Research Institute (Landcare Research). Due to the 'grass-roots' involvement of this research project, it is hoped that knowledge gained will lead to an even higher adoption rate trough 'social learning' (Warner 2006a).

Other social reasons exist for growers to adopt new technologies such as floral resources. Risk, uncertainty and learning are issues, identified by Marra, Pannell and Ghadim (2003), influence the adoption of new agricultural technologies and practices. Grower adoption may also be affected by future expectations (Rosenberg 1976). The perception of technological advancement and knowledge accrual may in fact slow implementation of floral resource use as growers postpone adoption in anticipation of future improvements of the technology.

Consideration of agronomic practicalities and farmer aims involves case-by-case analysis of agricultural sites. Practicalities of cost, availability and maintenance of the floral resource require attention. The plants' frost and weed potential alongside their compatibility with the crop and cropping system are key factors also to consider. For this reason and other reasons it is not a simple task for growers to avoid a 'shotgun' approach in which indiscriminate use of floral resources in a crop production system occurs. Although more research intensive, a directed case by case approach to floral resource selection should enhance the resources' effectiveness at achieving economically viable pest management within specific agricultural settings. Several publications now exist to help growers select suitable floral resources and should aid selection (Landis *et al*. 2000).

Knowledge-transfer failure has been cited as a reason for low grower adoption generally. However, an increasing number of extension methods such as 'agro-environmental partnerships', 'social learning' and 'discovery learning' (Pretty 1995; Warner 2006a; Williamson 1998) appear to be addressing this failure through enhanced grower participation throughout a research programme. Knowledge transfer is not the only cause of low grower adoption. Social reasons such as risk, uncertainty, learning and future technological expectations (Marra *et al*. 2003; Rosenberg 1976) also appear to play a significant role in determining the adoption of new practices such as CBC, the subject of this review, with all the increasing changes involved in providing food in sustainable way for a fast expanding human population (Tillman 1997). The practices reviewed here will assume a rapidly-increasing importance.

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