

REVIEW

The use of extrafloral nectar in pest management: overcoming context dependence

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Summary

1. Extrafloral nectar (EFN) provides plants with indirect defence against herbivores by attracting predatory insects, predominantly ants. Decades of research have supported the role of EFN as an effective plant defence, dating back to Thomas Belt's description of ants on acacia in 1874.

2. Despite this extensive body of literature, knowledge of the ecological role of EFN has rarely been applied in the field of pest management. We review the existing literature on the use of EFN in agriculture and consider the obstacles that have hindered this transition.

3. Chief among these obstacles is the influence of ecological context on the outcome of EFN-mediated interactions. As such, we consider the options for various agricultural systems in the light of the growth habit of EFN-producing species, focusing first on orchard species and then on herbaceous crops. In each case, we highlight the benefits and difficulties of utilizing EFN as a pest management tool and of measuring its efficacy.

4. *Synthesis and applications.* We argue that it is time for a shift in extrafloral nectar (EFN) research towards applied settings and seek to address the question: How can a context-dependent and often inducible plant trait be utilized as a reliable tool in agricultural pest management? Breeding crops for increased EFN production, and intercropping with EFN-producing plants, can enhance assemblages of beneficial insects in many agricultural settings. Orchard systems, in particular, provide an ecological context in which the attraction of ants can contribute to cost-effective and sustainable pest management programmes over a broad geographic range.

Key-words: agriculture, ants, biological control, extrafloral nectar, nectaries, orchard crops, pest management, plant defence

Introduction

Extrafloral nectaries (EFNs) are nectar-secreting glands located outside of flowers and have been observed on a vast diversity of species, spanning over 93 families and 332 genera (Koptur 1992a; Marazzi, Bronstein & Koptur 2013). These nectaries may serve diverse ecological functions (Baker, Hall & Thorpe 1978; Becerra & Venable 1989; Wagner & Kay 2002; Heil 2011), but they are best known for providing plants with indirect defence against herbivores by attracting predatory insects, predominantly ants (Bentley 1977b; Koptur 1992a; Rosumek *et al.* 2009; Heil 2015).

Extrafloral nectar-producing plants can be divided into two groups based on the nature of their interactions with ants. Myrmecophytes usually provide domatia and food bodies as well as EFN and engage in obligate interactions with ants. *Acacia cornigera* trees in Central America, for example, often succumb to herbivory when resident *Pseudomyrmex ferruginea* ants are experimentally removed (Janzen 1966). A far greater number of plants, however, including all of the cultivated species mentioned in this review, fall into the category of myrmecophiles. Myrmecophiles provide only EFN and engage in facultative interactions with ants. Although their interactions with ants are more varied in their outcomes (Rosumek *et al.* 2009), significant fitness benefits have been reported in many plants (Koptur 1979; Oliveira 1997; Rudgers 2004; Kost & Heil 2005; Leal *et al.* 2006; Koptur *et al.* 2013).

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The production of EFN has often been shown to be induced by insect damage (Koptur 1989; Agrawal & Rutter 1998; Heil *et al.* 2001a). Both the volume of nectar produced by each nectary (Heil *et al.* 2001a) and the number of nectaries (Mondor & Addicott 2003) have been seen to increase in damaged or herbivore infested plants. This plasticity confers several key benefits to plants. Metabolic costs are reduced when EFN production is low, and the variable expression of defensive traits also provides a barrier against the evolution of insect resistance (Heil 2010). In addition to responding to leaf damage, EFN production has been observed to vary with plant age (Boege & Marquis 2005; Kwok & Laird 2012; Quintero, Barton & Boege 2013) and with the age of individual leaves (Heil *et al.* 2000a). Young leaves are nutrient rich (Radhika *et al.* 2008) and are necessarily soft to allow for cell expansion (Yamawo *et al.* 2012). As a result, young leaves are particularly susceptible to herbivory. Optimal defence theory predicts that plant parts that are of particularly high value, or that are highly vulnerable to herbivory, should exhibit heightened defences (McKey 1974). Several plant species have been shown to produce EFN in patterns predictable by optimal defence theory (Heil *et al.* 2004a; Wäckers & Bonifay 2004; Jones & Koptur 2015a). These studies highlight the ability of plants to manipulate the activity of beneficial insects, while minimizing costs.

The mutualism between plants and defensive ants was first described by Thomas Belt (1874) and, since that time, many studies have identified food-for-protection mutualisms between ants and plants (reviewed in Bentley 1977a,b; Koptur 1992a; Rosumek *et al.* 2009). In addition to ants, EFN has often been shown to attract and enhance the performance of other predators (Wang *et al.* 2014; Koptur, Jones & Pena 2015) and parasitoids (Irvin *et al.* 2014; Jamont, Dubois-Pot & Jaloux 2014; Irvin & Hoddle 2015). Our knowledge to date suggests that commercial and subsistence growers could strongly benefit from the use of EFN-producing plants, either as primary crops, or as companion plants to attract natural enemies (Bugg & Dutcher 1989; Heil 2015). Despite this obvious potential, relatively little attention has been paid to the role of EFN in crop plants, and strikingly few studies have taken place in agricultural settings. Here, we review the existing literature in this area, focussing on crop plants with a range of growth habits. We go on to discuss the obstacles that have hindered the transition of EFN research from ecological theory to applied pest management. Finally, we present ideas for overcoming these obstacles and suggest areas for future research.

Extrafloral nectar in orchard crops

Orchard crops represent a promising area for the use of EFN in biological control programmes. The longevity of the plants and the lack of disturbance, relative to other agricultural settings, give orchard habitats the potential to

support and sustain populations of beneficial insects. Intercropping with EFN-producing species that support natural enemies is also possible in orchard settings, with little or no sacrifice to the primary crop. For example, the use of hairy vetch, *Vicia villosa*, as a cool season cover crop has been observed to increase the numbers of predatory lady beetles in pecan orchards (Bugg, Dutcher & McNeil 1991). Other EFN-producing species such as sunflower, *Helianthus annuus*, and cowpea, *Vigna unguiculata*, have shown potential as warm season cover crops for pecan that might enhance biological control while also providing an additional commercial outlet for growers (Bugg & Dutcher 1989).

Many tree species produce EFN, and commercially important species are taxonomically scattered (Table 1). Extrafloral nectaries have been described in rubber (Euphorbiaceae) (Frey-Wyssling 1933), mahogany (Meliaceae) (Lersten & Rugenstein 1982; Peng, Christian & Reilly 2010) and cashew (Anacardiaceae) (Rickson & Rickson 1998), but the best-studied family in this regard is the Rosaceae. Several commonly cultivated species in the family Rosaceae produce EFN in abundance, including cherry, *Prunus avium* (Yee 2008), almond, *Prunus dulcis* (Limburg & Rosenheim 2001), and peach, *Prunus persica* (Mathews, Brown & Bottrell 2007; Mathews, Bottrell & Brown 2009). In almond orchards, for example, EFN has been observed to support the omnivorous lacewing, *Chrysoperla plorabunda* (Limburg & Rosenheim 2001). The presence of EFN enhanced the longevity of first-instar lacewing larvae and allowed them to maintain high levels of searching activity (Limburg & Rosenheim 2001).

Extrafloral nectar in peaches has been studied in greater detail, and several studies indicate the importance of EFN for plant protection in this orchard crop (Mathews 2005; Mathews, Brown & Bottrell 2007; Mathews, Bottrell & Brown 2009, 2011). Mathews, Bottrell & Brown (2009) compared peach trees from a single cultivar (Lovell) with a nectaried and a nectariless phenotype. In the first year following planting, trees with EFNs attracted higher densities of defensive ants and harboured fewer herbivores than trees without EFNs. Trees with EFNs also experienced lower folivory, increased trunk growth and, most significantly, enhanced fruit production. In subsequent years, trees with EFNs produced three times more buds than those without EFNs and supported more diverse arthropod communities (Mathews, Bottrell & Brown 2009). The oriental fruit moth, *Grapholita molesta*, is an important economic pest of peach orchards, and its numbers have been shown to be reduced on peach trees with EFNs (Mathews, Brown & Bottrell 2007; Mathews, Bottrell & Brown 2011). Crucially, *G. molesta* inflicted 90% less damage to fruit on trees with EFNs, indicating that EFN in peach orchards has a protective role for fruit as well as reducing foliar herbivory (Mathews, Brown & Bottrell 2007). These findings clearly indicate the importance of selecting peach cultivars that produce EFN, and

Table 1. Commercially cultivated species bearing extrafloral nectaries

Plant family	Genus	Cultivated species	Citations
Anacardiaceae	<i>Anacardium</i>	<i>Anacardium occidentale</i> (cashew)	Rickson & Rickson (1998)
Aquifoliaceae	<i>Ilex</i>	<i>Ilex paraguariensis</i> (yerba mate)	Junqueira, Diehl & Diehl-Fleig (2001)
Asteraceae	<i>Helianthus</i>	<i>Helianthus annuus</i> (sunflower)	Zimmermann (1932); Bugg & Dutcher (1989); Offenber (2000)
		<i>Helianthus tuberosus</i> (artichoke)	Zimmermann (1932); Offenber (2000)
Bignoniaceae	<i>Crescentia</i>	<i>Crescentia cujete</i> (calabash or bottle gourd)	Elias (1983)
		<i>Parmetiera cereifera</i> (candle tree)	Zimmermann (1932)
Caprifoliaceae	<i>Sambucus</i>	<i>Sambucus nigra</i> (elderberry)	Zimmermann (1932); Fahn (1987); Offenber (2000)
Combretaceae	<i>Terminalia</i>	<i>Terminalia catappa</i> (Indian almond)	Zimmermann (1932); Elias (1983); Tilney & Van Wyk (2004)
Cucurbitaceae	<i>Luffa</i>	<i>Cucurbita pepo</i> (zucchini, pumpkin)	Nepi, Pacini & Willemse (1996); Heil (2015)
		<i>Luffa aegyptica</i> (luffa)	Zimmermann (1932); Elias (1983); Okoli & Onofeghara (1984)
		<i>Telfairia pedata</i> (oyster nut)	Okoli & Onofeghara (1984)
Dioscoreaceae	<i>Dioscorea</i>	<i>Dioscorea esculenta</i> (yam)	Burkill (1960)
Euphorbiaceae	<i>Hevea</i>	<i>Hevea brasiliensis</i> (rubber)	Zimmermann (1932); Frey-Wyssling (1933)
	<i>Manihot</i>	<i>Manihot esculenta</i> (cassava)	Bakker & Klein (1992)
	<i>Ricinus</i>	<i>Ricinus communis</i> (castor)	Zimmermann (1932); van Rijn & Tanigoshi (1999); Offenber (2000)
Fabaceae	<i>Apios</i>	<i>Apios americana</i> (ground nut)	Harvey (2009)
	<i>Phaseolus</i>	<i>Phaseolus lunatus</i> (lima bean)	Heil (2004); Kost & Heil (2005); Balhorn <i>et al.</i> (2007); Radhika <i>et al.</i> (2008); Blue <i>et al.</i> (2015)
	<i>Vicia</i>	<i>Vicia faba</i> (broad bean)	Zimmermann (1932); Jamont, Crepelliere & Jaloux (2013); Lu <i>et al.</i> (2014)
	<i>Vigna</i>	<i>Vigna unguiculata</i> (cow pea)	Pate <i>et al.</i> (1985); Makoi <i>et al.</i> (2010)
Lythraceae	<i>Punica</i>	<i>Punica granatum</i> (pomegranate)	Turner & Lersten (1981)
Malvaceae	<i>Gossypium</i>	<i>Gossypium hirsutum</i> (cotton)	Stapel <i>et al.</i> (1997); Wäckers & Wunderlin (1999); Rudgers (2004); Rudgers & Gardener (2004); Wäckers & Bonifay (2004); Röse, Lewis & Tumlinson (2006); Hagenbucher <i>et al.</i> (2013)
Meliaceae	<i>Swietenia</i>	<i>Swietenia mahagoni</i> (mahogany)	Lersten & Rugenstein (1982)
Oleaceae	<i>Fraxinus</i>	<i>Fraxinus</i> spp. (ash)	Elias (1983)
Orchidaceae	<i>Vanilla</i>	<i>Vanilla planifolia</i> (vanilla orchid)	Bentley (1977a,b)
Passifloraceae	<i>Passiflora</i>	<i>Passiflora incarnate</i> (passion fruit)	Zimmermann (1932); Elias (1983); McLain (1983); Swift, Bryant & Lanza (1994)
Pedaliaceae	<i>Sesamum</i>	<i>Sesamum indicum</i> (sesame)	Zimmermann (1932); Zhu <i>et al.</i> (2013)
Polygonaceae	<i>Fagopyrum</i>	<i>Fagopyrum esculentum</i> (buckwheat)	Irvin <i>et al.</i> (2014); Irvin & Hoddle (2015)
Rosaceae	<i>Prunus</i>	<i>Prunus americana</i> (wild plum)	Zimmermann (1932); Keeler (1979)
		<i>Prunus avium</i> (cherry)	Zimmermann (1932); Brown & Mathews (2007)
		<i>Prunus dulcis</i> (almond)	Limburg & Rosenheim (2001)
		<i>Prunus persica</i> (peach)	Zimmermann (1932); Brown & Mathews (2007); Brown, Mathews & Krawczyk (2010); Mathews (2005); Mathews, Brown & Bottrell (2007); Mathews, Bottrell & Brown (2009, 2011); Spellman, Brown & Mathews (2006)
		<i>Prunus serotina</i> (wild black cherry)	Keeler (1979)

highlight the potential for peach production programmes to embrace biological control and reduce pesticide inputs. As peach is a grafted crop, EFNs could also be a target of stock selection. Peaches may represent a useful companion plant for other orchard crops. Several attempts have been made to utilize EFN-producing peaches to enhance biological control in apples, with varying degrees of success (Spellman, Brown & Mathews 2006; Brown & Mathews 2007; Brown, Mathews & Krawczyk 2010). These studies show how difficult it is to identify the true effects of EFN on biological control, and highlight the need for more comprehensive long-term studies.

Spellman, Brown & Mathews (2006) interplanted peaches with apples, in glasshouse conditions, with a view to enhancing the biological control of spiraea aphids, *Aphis spiraeicola*. Contrary to expectations, aphid control on apples by the predatory beetle, *Harmonia axyridis*, was actually reduced in the presence of peaches. In this case, it seemed that EFN distracted the beetles from their aphid prey. Had the experiment taken place in field conditions, however, EFN may have attracted greater numbers of predators or helped to maintain predator populations during times of prey scarcity (Stapel *et al.* 1997). Extrafloral nectar may also have attracted predators to orchards before pests arrived therefore reducing defensive response time (Mathews 2005). None of these effects, however, could be captured in a short-term glasshouse study.

Brown, Mathews & Krawczyk (2010) used EFN-producing peaches in apple orchards in an attempt to increase parasitism rates of the tufted apple bud moth, *Platynota idaeusalis*. Although the presence of peach trees did increase the number of parasitoids (*Coniozus floridanus*), parasitism rates were not significantly affected. Although control of the tufted apple bud moth was not achieved, damage to apple fruit, from a host of other herbivores, was reduced in the presence of interplanted peaches (Brown, Mathews & Krawczyk 2010). In this study, the collection of data on variables beyond the target species facilitated the discovery of an important and unexpected result. This provides a valuable lesson for future research into the role of EFN in biological control: that the effects of EFN, as with any habitat manipulation, can only be understood in the context of the whole community.

Outside the Rosaceae, one orchard species that has received significant attention in terms of its EFN production is the cashew nut, *Anacardium occidentale*. Cashew trees produce EFN from their leaves, bracts, sepals and from stomata found on the inside curve of developing nuts (Rickson & Rickson 1998). The plant has been described as providing a 'movable feast' for ants (Tilman 1978; Fiala & Maschwitz 1992), shifting their foraging habits, temporally, towards sites most susceptible to herbivory. Interactions between cashew and weaver ants, *Oecophylla* spp, have been the focus of many studies, and the potential to harness these interactions for pest management has been explored over a large geographic range (Peng, Christian & Gibb 1995; Dwomoh *et al.* 2009;

Olotu *et al.* 2013; Peng, Lan & Christian 2014; Anato *et al.* 2015).

The presence of the weaver ant, *Oecophylla smaragdina*, has been correlated with a reduction in key pest species in Australian cashew plantings (Peng, Christian & Gibb 1995). Peng, Lan & Christian (2014) also manipulated weaver ants in cashew plantations in Vietnam. Damage from a range of important economic pests was reduced in the presence of ants, and in the case of mosquito bugs, blue shoot borers and fruit–nut borers, ants provided a level of control equivalent to that achieved through the use of insecticides. Anato *et al.* (2015) studied the effects of weaver ants in cashew plantations in Benin. Not only did the presence of ants increase nut yield, but the benefits of ants were enhanced through the provision of dietary subsidies (30% sucrose solution). Nut yields were highest of all when ants were incorporated into an integrated pest management programme that included spot spraying with insecticides (Anato *et al.* 2015).

The use of ants as agents of biological control in tree crops is by no means a new phenomenon. In Chinese citrus orchards, manipulations of *Oecophylla* ants have been common practice for 1500 years (Huang & Yang 1987; Rickson & Rickson 1998). The crazy ant, *Anoplolepis gracilipes*, has long been manipulated as a cacao pest control agent in Papua New Guinea (Baker 1972) and, in Cameroon, artificial raffia nests are used to transport *Wasmannia auropuncta* to cacao plantations for the control of several pest species (Bruneau De Mire 1969). Enormous potential exists to harness EFN-mediated interactions in a host of orchard crops and reduce or eliminate the use of expensive and environmentally damaging pesticides.

Extrafloral nectar in herbaceous crops

A host of herbaceous crop species from a diverse taxonomy are known to produce EFN. These include several species of huge commercial significance, such as pumpkin (Cucurbitaceae), zucchini (Cucurbitaceae) and yam (Dioscoreaceae), all of which have been little studied in the context of their EFN production (Burkill 1960; Nepi, Pacini & Willemsse 1996; Heil 2015). Several other species have received some attention in this regard, and some have demonstrated the potential to attract beneficial insects. Broad bean, *Vicia faba*, produces EFN from stipular glands, which has been observed to support the cosmopolitan aphid parasitoid, *Diaeretiella rapae* (Jamont, Crepelliere & Jaloux 2013). Cassava, *Manihot esculenta*, produces EFN from its petioles which has been shown to enhance the activity of predatory phytoseiid mites (Bakker & Klein 1992). Passion fruit, *Passiflora incarnata*, bears EFNs on its petioles and bracts, and these nectaries attract ants that discourage insect herbivores. McLain (1983) experimentally removed EFNs from passion fruit vines and found that nectariless plants suffered greater herbivore damage and produced fewer fruits. In passion

fruit, as in many plants, EFN production is inducible by leaf damage (Swift, Bryant & Lanza 1994). This means that plants are able to upregulate ant defence in response to herbivory (Koptur 1989; Agrawal & Rutter 1998).

Although many other commercial crops are known to produce EFN (Table 1), few have been studied in this context. In this section, we focus on two important crop species on which the great majority of attention has focused. These species are cotton, *Gossypium hirsutum* (Malvaceae) (Stapel *et al.* 1997; Wäckers & Wunderlin 1999; Rudgers 2004; Rudgers & Gardener 2004; Wäckers & Bonifay 2004; Röse, Lewis & Tumlinson 2006; Hagenbucher *et al.* 2013), and lima bean, *Phaseolus lunatus* (Fabaceae) (Heil 2004; Kost & Heil 2005; Balhorn *et al.* 2007; Radhika *et al.* 2008; Blue *et al.* 2015).

Cotton (*Gossypium*) represents one of the best-studied plants in terms of the ecology of its EFN and provides some of the best evidence that EFN evolved to attract defensive ants (Wäckers & Bonifay 2004; Hagenbucher *et al.* 2013). Extrafloral nectar is found on all species of *Gossypium* with only two exceptions (Fryxell 1979). The first of these nectariless cotton species, *Gossypium tomentosum*, is endemic to Hawaii (Fryxell 1979), a part of the world with no native ants (Wilson 1996). The second species, *Gossypium gossypioides*, grows at high altitudes where ant activity is greatly limited (Wäckers & Bonifay 2004). In species of cotton that produce EFN, its production has been shown to be inducible by both above- and below-ground herbivory (Wäckers & Bezemer 2003; Wäckers & Bonifay 2004) and appears to be enhanced in the most valuable and vulnerable plant tissues as predicted by optimal defence theory (Wäckers & Bonifay 2004).

In wild cotton, *Gossypium thurberi*, the presence of ants has been shown to reduce herbivory and increase seed production (Rudgers 2003). In addition to ants, assemblages of other beneficial insects have been found to be enhanced on cotton plants with EFNs (Schuster, Lukefahr & Maxwell 1976; Henneberry, Bariola & Kitoc 1977; Adjei-Maafa & Wilson 1983; Adjei-Maafa *et al.* 1983). Stapel *et al.* (1997) and Röse, Lewis & Tumlinson (2006) showed that the presence of EFN increased the efficiency of the parasitoid wasp, *Microplitis croceipes*, on *Gossypium hirsutum*. Other consumers of EFN, such as predatory mites, have also been observed to reduce herbivory in cotton (Agrawal, Karban & Colfer 2000; Hagenbucher *et al.* 2013).

Despite abundant evidence that EFN is an effective plant defence in cotton, relatively few studies have focused on commercially cultivated species, in true agricultural settings. The few studies of this type have revealed a common ecological cost of EFN production. Herbivores, as well as beneficial insects, may utilize EFN as a food source. In agricultural settings, cotton cultivars bearing EFNs have been observed to support larger herbivore populations than cultivars that lack EFNs (Lukefahr & Rhyné 1960; Lukefahr, Martin & Meyer 1965;

Schuster, Lukefahr & Maxwell 1976; Henneberry, Bariola & Kitoc 1977; Adjei-Maafa & Wilson 1983; Scott, Snodgrass & Smith 1988). These findings contrast observations made in more natural settings (Rudgers 2003), but are not entirely surprising. In agricultural ecosystems, land management practices commonly reduce populations of ants and other beneficial insects. Any attempts to utilize EFN in agricultural pest management, therefore, must consider the effects of ecological context.

Perennial legumes have often been used in experimental systems to investigate the ecological role of EFN (e.g. Heil 2004; Choh, Kugimiya & Takabayashi 2006; Jones & Koptur 2015a,b; Koptur, Jones & Pena 2015). These include widely cultivated crop species such as cowpea (black-eyed pea), *Vigna unguiculata* (Pate *et al.* 1985), and lima bean, *Phaseolus lunatus* (Heil 2004; Kost & Heil 2005; Balhorn *et al.* 2007; Radhika *et al.* 2008; Blue *et al.* 2015). In lima bean, several studies support EFN as an effective inducible defence against herbivores (Heil 2004; Kost & Heil 2005; Radhika *et al.* 2008). Kost & Heil (2005) applied artificial nectar to lima bean plants and found that test plants attracted greater numbers of ants, predatory flies and parasitic wasps than untreated controls. Furthermore, treatment plants suffered reduced herbivore damage as a result. Heil (2004) found that EFN production in lima bean could be induced through application of the phytohormone jasmonic acid and that the induction of EFN resulted in lower herbivore damage in natural conditions.

Despite the obvious potential, no attempt has ever been made to harness or manipulate EFN in commercial cotton or lima bean production. This is particularly surprising in lima bean, where manipulation of EFN production has been shown to enhance plant defence (Heil 2004). Below, we explore the factors that have prevented our knowledge of EFN from being applied in agricultural pest management and discuss areas where these obstacles may be overcome.

Obstacles for the use of EFN in agriculture

The role of EFN in plant defence has long been understood and is supported by decades of literature (Heil 2015). Research into the biological control of agricultural pests has been ongoing throughout this time and, yet, startlingly little attention has been paid to the potential role of EFN. A host of factors may have contributed to this phenomenon.

A concern among plant physiologists may have been allocation costs associated with the production of EFN. Is it possible that increased EFN production might result in lower reproductive investment? Reproductive output, after all, is where the interests of most commercial growers lie. Additionally, do trade-offs exist between key plant defence traits? For example, is increased EFN production coupled with a reduction in chemical defences? The inducible nature of EFN itself implies that its production

comes at a tangible metabolic cost (Heil & Baldwin 2002), but existing estimates of these costs are low (O'Dowd 1980). O'Dowd (1980) quantified the costs of EFN and food body production in *Ochroma pyramidale* at around 1% of the investment in leaves. There is no evidence of trade-offs between EFN production and reproductive output; indeed, EFN production has often been observed to increase during flowering and fruit set (Holland, Chamberlain & Horn 2009; Falcão, Dáttilo & Izzo 2014). While trade-offs do exist between plant defensive traits (Koptur 1985; Turner 1995; Heil *et al.* 1999; Heil, Staehelin & McKey 2000b; Dyer *et al.* 2001), the induction of EFN has never been associated with overall defensive cuts. Rudgers & Gardener (2004) looked for trade-offs between resistance traits in wild cotton. Although they found negative correlations between direct plant resistance traits (leaf trichomes and toxic leaf glands), no correlation was found between EFN production and direct defensive traits. Future research should continue to explore potential allocation costs associated with EFN production. Current knowledge, however, suggests that these costs are minimal and should not impede the use of EFN in agriculture.

Despite the well-documented defensive benefits of EFN production, commercial breeders have often deliberately selected for nectariless cultivars, believing the attraction of insects to be detrimental (Beach, Todd & Baker 1985). Breeding strategies have regularly failed to consider top-down control and, in many commercial crop lines, interactions with the third trophic level are impaired compared with their wild relatives (Heil 2015). Commercial cultivars of cotton, for example, produce less EFN (Beach, Todd & Baker 1985) and release seven times less herbivore-induced volatiles than naturalized lines (Loughrin *et al.* 1995). Breeding crops for increased EFN production, and an enhanced capacity to exploit beneficial insects, can contribute to environmentally friendly and sustainable agriculture, a concept explored in detail by Stenberg *et al.* (2015).

The tendency of breeders to ignore the tools of biological control are concerning in themselves, but they also point to a wider problem. Many growers, particularly large enterprises, set their pest control targets at a 100% reduction in infestation. Such targets can only be achieved through the use of pesticides and not through biological pest management programmes that seek to control, not eliminate, pest species. The use of broad-spectrum pesticides, and the harnessing of arthropod communities for pest control, are not strategies that can be easily married. Until growers relinquish their dependence on the former, little progress can be made on the latter.

As the examples above indicate, several of the perceived obstacles for the use of EFN in agriculture exist largely in the minds of breeders, and in the culture of commercial farming. There remain, however, genuine costs of EFN production, and grower concerns about its negative impacts are not entirely without foundation. In the absence of viable ant partners, EFNs are open to

exploitation by a host of other arthropods, many of which may have neutral or negative effects on plant fitness (Koptur 1992a; Heil *et al.* 2004b). Ants, themselves, vary in their defensive qualities. Production of EFN can result in colonization by parasitic ant species which consume nectar but either fail to defend their host plants or actively harm them (Koptur 1992b; Yu & Pierce 1998). Ants that benefit EFN-producing plants must occupy a trophic position whereby they are attracted to EFN, but act predominantly as predators while on the plant. The trophic position and foraging behaviour of ants, however, can vary enormously even within a single species. The degree to which ants act as predators or feed on plant-derived carbohydrates can vary over the life of a colony and can be influenced by ecological conditions (Wilder *et al.* 2011). Even voraciously defensive ants may negatively impact plant fitness by deterring other beneficial insects such as predators (Torres-Hernandez *et al.* 2000; Nahas, Gonzaga & Del-Claro 2012), parasitoids (Koptur & Lawton 1988; Styrsky & Eubanks 2007; Rosumek *et al.* 2009) and pollinators (Ness 2006; Hernández-Cumplido, Benrey & Heil 2010; Assunção, Torezan-Silingardi & Del-Claro 2014).

Among the non-target species subjected to attacks by defensive ants are humans. Many growers are reluctant to encourage the presence of aggressive ants, as their bites and stings represent a potential irritant for farm workers and animals (Risch & Carroll 1982; Offenberg 2015). While the nuisance value of ants can be a significant issue, a number of methods have been adopted to successfully ameliorate this problem. For example, applying fine powders, such as wood ash or cassava flour, to exposed skin has been shown to reduce bites from weaver ants (Van Mele *et al.* 2009). Spraying crops with water can also inactivate ants for short periods and provide a window for harvesting (Offenberg 2015). The dissemination of ecological knowledge, about the benefits of ants, will also increase tolerance among stakeholders.

Ecological costs of EFN production, like those described above, may be a major problem in agricultural ecosystems, which rarely provide stable populations of beneficial insects (Adjei-Mafo & Wilson 1983; Heil 2015). Abiotic factors such as light (Kersch & Fonseca 2005; Jones & Koptur 2015b) or nutrient (Heil *et al.* 2001b) availability are also known to affect EFN production and influence its effectiveness as a plant defence. The outcomes of EFN-mediated interactions, therefore, are greatly influenced by ecological context. This, without doubt, represents the most significant obstacle for the use of EFN in agricultural pest management.

Overcoming context dependence

For any attempt to utilize EFN in agricultural pest management, the chances of success are strongly dependent on ecological context. Improving those chances, therefore, can be achieved in one of two ways. Manipulating the

habitat in favour of beneficial insects or selecting agricultural systems that naturally support diverse arthropod populations.

Most contemporary farming landscapes are characterized by high levels of disturbance, intensive use of pesticides and a reduction in non-crop habitats. These factors bring about a sharp decline in biodiversity and, in turn, the biological control service provided by arthropod natural enemies (Lu *et al.* 2014). The potential to enhance the activity of natural enemies by manipulating the non-crop vegetation on or close to farms has been well-established (Tscharrntke *et al.* 2007; Thomson *et al.* 2010; Simpson *et al.* 2011; Orre-Gordon *et al.* 2013). This form of biological control has been formalized as the 'attract and reward' concept (Simpson *et al.* 2011), and the use of EFN-producing plants for this purpose may be particularly beneficial. In many ecosystems, EFN may be a more important source of sugar than floral nectar, as it is available over longer periods (Heil *et al.* 2004b; Géneau *et al.* 2012), and may contain fewer defensive compounds (Lu *et al.* 2014).

In California vineyards, the glassywinged sharpshooter, *Homalodisca vitripennis*, is a significant pest on grapevines as it vectors the bacterial disease, *Xylella fastidiosa*. Irvin *et al.* (2014) conducted laboratory tests to evaluate the potential of EFN-producing cover crops, to increase parasitization of *H. vitripennis* by the chalcid wasp, *Gonatocerus ashmeadi*. Extrafloral nectar from buckwheat, *Fagopyrum esculentum*, and vetch, *Vicia sativa*, extended the life span of *G. ashmeadi* and enhanced its reproductive fitness. Nectar from buckwheat and vetch also increased the life span of *Anagyrus pseudococci*, a parasitoid of the vine mealybug (Irvin *et al.* 2014).

Several other EFN-producing plants show great potential for supporting natural enemies in agricultural habitats. Géneau *et al.* (2012) tested *Centaurea cyanus* and *Vicia sativa* as companion plants for cabbage. Both plants increased the longevity of the parasitoid wasp, *Microplitis mediator*, and enhanced parasitization rates of the cabbage moth *Mamestra brassicae*. Sesame, *Sesamum indicum*, has also shown potential, in the laboratory, as a nectar plant to enhance biological control in Asian rice systems (Zhu *et al.* 2013). Another focus for future research in this area should be faba bean, *Vicia faba*, which produces nectaries on its stipules well before the emergence of flowers (Lu *et al.* 2014). This early provision of nectar could attract natural enemies very early in the growing season and potentially stunt early season pest population growth.

In addition to providing resources for natural enemies, arthropod assemblages may also be manipulated through the active release of beneficial insects. While established practice in many biological control programmes, active release has never been done specifically with EFN in mind. The potential of ants, the primary consumers of EFN, as biological control agents, however, has received greater attention in recent years (Peng, Christian & Gibb

1995; Peng & Christian 2005; Philpott & Foster 2005; Peng, Christian & Reilly 2010, 2013; Offenberg 2015). Introducing weaver ants, *Oecophylla smaragdina*, to mahogany plantations led to significant reductions in damage by the yellow looper, *Gymnoscelis* sp., and the bush cricket, *Myara yabmanna* (Peng, Christian & Reilly 2013). Providing ants with artificial nesting space has also been shown to enhance predation pressure on pests of coffee, *Coffea arabica* (Philpott & Foster 2005).

Habitat manipulations, like those described above, are an option in the majority of modern agricultural systems, which lack habitat heterogeneity and rely heavily on chemical insecticides. Agricultural practices do exist, however, that actively promote habitat diversity and sustain complex insect assemblages. On the slopes of Mount Kilimanjaro are the Chagga homegardens, a traditional agroforestry system that combines subsistence and commercial farming and makes use of limited space. These multilayered systems are predominantly banana and coffee plantations, with a scattered upper tree layer, but they contain a huge diversity of plants (about 520 vascular plant species including over 400 non-cultivated species) and support a higher diversity of insects than neighbouring habitats (Hemp 2006). A native Cucurbitaceae, *Telphairia pedata*, is an important subsistence crop in these systems (Hemp 2006) and produces EFN from its stipules (Bosa & Mgbeogu 1983). Commercial crop species with EFNs (Casava, *Manihot esculenta*, and black-eyed pea, *Vigna unguiculata*) are also cultivated locally (Hemp 2006; Makoi *et al.* 2010).

Semicultivated ecosystems, such as the Chagga homegardens, may be ideal systems in which to focus future research. Selecting for EFN-producing crop cultivars, introducing defensive ant species, and disseminating local knowledge could be useful tools for harnessing EFN in sustainable biological control programmes with tangible benefits for local people.

Conclusions

Ants, the primary consumers of EFN, have unrivalled potential as agents of biological pest control. Predatory ants tend to have relatively non-specialized diets, making them resilient to periods of prey scarcity (Carroll & Janzen 1973). Sophisticated systems of chemical communication and recruitment make ants highly responsive to spatial variations in prey density, where non-social predators and parasitoids require reproductive time for density response (Risch & Carroll 1982). Because ants store food for their colony, their effectiveness as control agents is not dampened by satiation, and their pugnacious nature means that their deterrence of pests is not limited to prey species. Several studies have observed ants to deter herbivores too large to be captured (Janzen 1966; Bentley 1977a,b). Many ant species are extremely resistant to environmental disturbance. *Solenopsis* species, for example, although unpopular, often thrive in ploughed crop fields

and are known to control a variety of important pests (Summerlin *et al.* 1977; Morrill 1978; Sterling 1978; Risch & Carroll 1982). Perhaps, most importantly, patterns of ant foraging behaviour can be manipulated, through the provision of resources such as EFN, in order to maximize the rate at which they encounter pests (Leston 1973).

We have emphasized that the potential exists to utilize EFN as a resource for crop protection in many agricultural ecosystems. Though we have stressed the importance of ecological context, and the lack of any one-size-fits-all solution, recent reviews have highlighted an overriding trend. In the great majority of cases, ants benefit plants, either a little bit or a lot (Chamberlain & Holland 2009; Rosumek *et al.* 2009). Extrafloral nectar has also shown great potential for enhancing the performance of parasitoids (e.g. Irvin *et al.* 2014; Jamont, Dubois-Pot & Jaloux 2014; Irvin & Hoddle 2015). While the role of EFN in attracting and supporting parasitoids has been well-established (Heil 2015), few studies have demonstrated beneficial effects of parasitoids on plant reproductive fitness. This represents a timely and a potentially fruitful avenue for future research. Also deserving of increased attention is the way that parasitoids use EFN. Do they use it only as a food source, or can it serve as a cue for host location?

In a world of diminishing resources, it is time to work with nature, and shift our focus from simply understanding insect–plant symbioses to harnessing their potential to provide effective and low cost options for pest control. There exists huge potential to utilize EFN-mediated interactions in a range of agricultural settings to maximize crop plant success while minimizing environmental impacts.

Data accessibility

Data have not been archived because this article does not contain data.

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