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Semiochemical-based alternatives to synthetic toxicant insecticides for pollen beetle management

Alice L. Mauchline¹ · Maxime R. Hervé² · Samantha M. Cook³

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Abstract There is an urgent need to develop sustainable pest management systems to protect arable crops in order to replace the current over-reliance on synthetic insecticides. Semiochemicals are insect- or plant-derived chemicals that are used by organisms as information signals. Integrated pest management tools are currently in development that utilise semiochemicals to manipulate the behaviour of pest insects and their natural enemies to provide effective control of pests within the crop. These innovative tools usually require fewer inputs and can involve multiple elements, therefore reducing the likelihood of resistance developing compared with use of synthetic toxicants. We review here the life cycle of the pollen beetle *Brassicogethes aeneus* (previously known as *Meligethes aeneus*) which is a pest insect of oilseed rape (*Brassica napus*) and describe the current knowledge of any behaviour mediated by semiochemicals in this species. We discuss the behavioural processes where semiochemical-based control approaches may be appropriate and consider how these approaches could be incorporated into an integrated pest management strategy for this important arable crop.

Keywords *Meligethes* · *Brassicogethes aeneus* · Integrated pest management · Oilseed rape · *Brassica napus* · Sustainable agriculture · Push–pull

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✉ Alice L. Mauchline
a.l.mauchline@reading.ac.uk

¹ School of Agriculture, Policy and Development, University of Reading, Reading, Berkshire, UK

² Université Rennes 1, UMR1349 IGEPP, 35000 Rennes, France

³ Biointeractions & Crop Protection Department, Rothamsted Research, Harpenden, Hertfordshire, UK

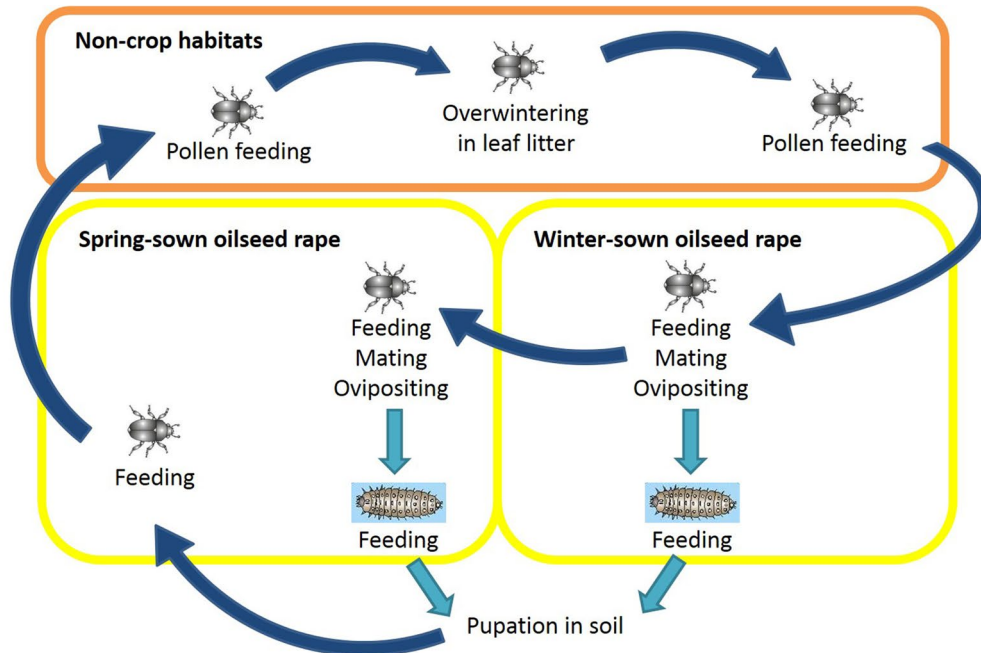
Introduction

The pollen beetle *Brassicogethes aeneus* Fab. (synonym *Meligethes aeneus*) (Coleoptera: Nitidulidae) is a major pest of oilseed rape (OSR) (*Brassica napus* L.) crops (Williams 2010). Of the suite of pests that attack OSR, pollen beetles were found to have the largest negative impact on seed yield (Gagic et al. 2016). They can cause significant feeding damage to the developing flower buds which can result in blind stalks, thereby preventing the growth of pods, leading to large economic losses (Hansen 2004; Zlof 2008). Pyrethroid insecticides have been the main control option for pollen beetles for over 20 years. However, over-reliance on these and overuse of this single control strategy has led to *B. aeneus* populations developing resistance to this class of insecticide (e.g., Hansen 2003; Nauen et al. 2012; Zimmer et al. 2014). Although insecticides with alternative classes of active ingredients are now commercially available (see e.g., HGCA (2012)), alternative ‘ecologically-based’ approaches are needed to increase the sustainability of OSR cropping and to prevent further development of resistance (Cook and Denholm 2008).

Semiochemicals (a term derived from the Greek ‘σημεῖον’ (*semeion*) meaning ‘mark or signal’) (Law and Regnier 1971) are chemicals that mediate interactions between organisms. These can be volatile or non-volatile signals that operate at long or short range (Eigenbrode et al. 2016) to modify the behaviour of the recipient. Plant- and insect-derived semiochemicals can be used for pest control to cause behavioural disruption of the pests themselves and/or their natural enemies (Cook et al. 2007b). These can provide sustainable control alternatives to the use of synthetic toxicant insecticides, however, they take a long time in development and still only make up a small fraction of the pest control market. There are several examples of

semiochemical-based control methods that are currently in commercial usage for pest insect control; reviewed by Cook et al. (2007b) and Eigenbrode et al. (2016). They include insect attractants or stimulants, arrestants, repellents and deterrents. The only commercialised semiochemical-based method for pollen beetle control at the time of writing is a

funnel trap baited with the ‘most potent visual and chemical attractant stimuli for *B. aeneus*’ for mass trapping in the early season. Use of semiochemicals in pest management of *B. aeneus* is therefore currently under-exploited. The most effective deployment of semiochemicals in pest management requires a full understanding of the biology and ecology of



Behavioural process/life stage	Semiochemical cues in pollen beetle behaviour	Potential control options
Emergence from overwintering sites	<i>Unknown</i>	<i>Mass trapping e.g. lure and kill</i>
Food host-plant location (generalist feeding)	Long range cues; general plant volatiles	Attractants as lures for monitoring traps and mass traps, trap cropping,
Food host-plant acceptance (generalist feeding)	Short range cues; e.g. non-volatile plant chemicals, phagostimulants	<i>Antifeedants, repellents, resistant cultivars</i>
Ovipositional host-plant location (specialist on brassicas)	Long range cues; Specific plant volatiles, non-host plant volatiles	Trap cropping, repellents/deterrents, <i>less attractive cultivars, induced plant defence mechanisms</i>
Ovipositional host-plant acceptance (specialist on brassicas)	Short range cues; e.g. <i>Conspecific odour</i> ; epideictic and <i>ovipositional</i> pheromones, plant volatiles	<i>Oviposition deterrents, resistant cultivars</i>
Mate location	<i>Unknown</i>	<i>Mass trapping e.g. lure and kill</i>
Predation by natural enemies	Use of plant host /prey odours by parasitoids	<i>Enhanced biocontrol; induced plant defence</i>
Location of and movement to overwintering sites	<i>Unknown</i>	<i>Mass trapping e.g. lure and kill</i>

Fig. 1 Life cycle of the pollen beetle showing behavioural processes that could be mediated by semiochemicals, along with a table of descriptions of the semiochemical cues and possible control opportunities (italics represent knowledge gaps)

the pest insect (Agelopoulos et al. 1999; Cook et al. 2007b; Norin 2007; Heuskin et al. 2011) as well as an understanding of the scales at which the semiochemicals can be used to provide a holistic control strategy (Eigenbrode et al. 2016).

Pollen beetle life cycle, semiochemical-mediated behaviour and opportunities for control

This review covers the full life cycle of the pollen beetle (see Fig. 1) to provide an overview of the potential for semiochemical-mediated control in both oilseed rape crops and non-crop habitats. The control tools included in this review are either currently in development or are discussed as possible areas for research investment in the future. There are eight life stages or behavioural processes in the life cycle of the pollen beetle that are already known to be (or could be) mediated by semiochemical interactions and therefore offer the potential for control methods. These are (i) emergence from overwintering, (ii) food host-plant location, (iii) food host-plant acceptance, (iv) ovipositional host-plant location, (v) ovipositional host-plant acceptance, (vi) mate location, (vii) predation by natural enemies and (viii) location of and movement to overwintering sites. The current knowledge of the behavioural ecology of the pollen beetle is reviewed here followed by a discussion of potential opportunities for semiochemical-based control methods which exploit or disrupt their natural behaviours.

Emergence from overwintering

Pollen beetles overwinter as adults under the soil surface, in vegetation or leaf litter (Rusch et al. 2012; Gloyna and Thieme 2013). They emerge in early spring when temperatures reach a critical threshold (Fritzsche 1955; Hokkanen 1993; Marczali and Nádas 2006). As pollen beetles emerge from overwintering sites, the ambient temperatures are usually low and the beetles are unlikely to be able to fly long distances; their propensity to fly follows a sigmoidal temperature–response curve between 6 and 23 °C (Ferguson et al. 2015).

Semiachemical control options

It is unknown if semiochemicals are involved in the emergence of pollen beetles in spring, and it seems unlikely. However, there is the potential to trap out large numbers shortly following emergence from hibernation using any semiochemical-baited attractant lures involved in food or mate location processes which occur in spring (see following sections). Baited traps would need to be positioned close to their overwintering sites which could significantly

reduce populations prior to immigration to crops. In order to develop such mass trapping methods (e.g., Foster and Harris 1997; El-Sayed et al. 2006; Witzgall et al. 2010) or ‘lure and kill’ strategies (El-Sayed et al. 2009; Witzgall et al. 2010), more understanding is required about the overwintering sites of pollen beetles and their post-emergence behavioural processes to enable accurate predictions on where the overwintering sites are likely to be (Rusch et al. 2012; Gloyna and Thieme 2013) so that traps can be positioned in areas of high abundance in early spring with the most appropriate attractant semiochemical lure.

Food host-plant location (long range cues)

Following emergence from hibernation, pollen beetles move to find food host-plants. This is the first behavioural process in the pollen beetle life cycle that is known to be strongly influenced by semiochemical cues (reviewed by Williams and Cook 2010). Overwintered adult pollen beetles are generalist feeders on pollen from many different plant families to obtain nutrients for energy (Roulston and Cane 2000) and ovary maturation (Williams and Free 1978; Ouvrard et al. 2016). Pollen beetles locate their food host-plants, which include Brassicas, using a variety of plant semiochemical and visual cues.

Plants have complex biosynthetic pathways that lead to the release of volatile organic compounds, some of which are specifically released following herbivore damage (Turlings and Tumlinson 1992), and insects have evolved to use these volatiles as semiochemical cues in food host-plant location (Dicke and Baldwin 2010). Plant volatiles are a combination of ubiquitous volatiles emitted by all green plants including green leaf volatiles, terpenes and aromatic floral compounds, but some plant species also release species/genus-specific compounds such as the isothiocyanates released by Brassicaceae (Bruce et al. 2005). The response of the pollen beetle to these Brassica-specific cues is reviewed in the later section on ovipositional host-plant location.

Pollen beetles have been found feeding on a wide variety of wild plants (Williams and Free 1978; Mauchline 2003; Ouvrard et al. 2016) and are known to respond positively to whole plant odours from several non-Brassicaceous species including dandelion (*Taraxacum officinale* L.) (Cook 2000), field bean (*Vicia faba* L.) (Cook 2000), rye (*Secale cereale* L.) (Ruther and Thiemann 1997), tomato (*Solanum lycopersicum* L.) (Ruther and Thiemann 1997) and yarrow (*Achillea millefolium* L.) (Ruther and Thiemann 1997). Some of the semiochemicals responsible for this attraction have been identified. *Brassicogethes aeneus* was found to be attracted to general floral compounds such as phenylacetaldehyde and indole in the laboratory (Cook et al. 2007c) and field (Smart and Blight 2000). Their ability to detect and respond to a large number of chemically diverse plant volatiles may be

an adaptation related to its polyphagous nature at this early life stage (Smart and Blight 2000).

Semiochemical control options

Pollen beetles cause the most damage when they feed on oilseed rape crops at the green bud stage. A monitoring trap is available from Oecos made from a yellow sticky card baited with phenylacetaldehyde; a common floral volatile produced naturally by several plant species. This monitoring trap uses the semiochemical lure to allow easier and more accurate measurement of beetle populations at this critical green bud stage and to establish when spray thresholds have been breached in crops.

Food host-plant acceptance (short range/contact cues)

Studies have shown that the volatile profile used by pollen beetles in host-plant location becomes less important after colonisation of a plant as they no longer respond to the same volatiles (Mauchline et al. 2013). At this stage, other chemical stimuli (surface and/or inner tissue semiochemicals) gained from close inspection of the plant become more important. Indeed, Charpentier (1985) found differences between host-plant feeding preferences of pollen beetles and concluded that chemical stimuli were the most important. Hervé et al. (2014) studied these stimuli by comparing six OSR genotypes for pollen beetle feeding preference, and identified possible phagostimulant/deterrent compounds in the bud perianth (the tissue that has to be pierced to access the food source) and in anthers (the tissue containing the food source). It was shown that only the composition of the perianth correlated with feeding damage, suggesting that this tissue is determinant in host-plant acceptance (Hervé et al. 2014). Among ca. 60 sugars, amino acids or secondary metabolites quantified, only five were clearly correlated with feeding damage: sucrose, proline, serine (positively correlated) and two glycosylated flavonols (negatively correlated). The latter are likely not to be biologically relevant for host-plant acceptance by the pollen beetle (Fellenberg and Vogt 2015). However, serine and especially sucrose—a well-known highly stimulant sugar (Chapman 2003)—are good candidates for further behavioural studies. Noticeably, glucosinolates did not seem to exert any major influence on pollen beetle feeding preference (Hervé et al. 2014).

At the interspecific scale, some plants have an attractive volatile profile, such as candytuft (*Iberis amara* L.), but are rejected by pollen beetles at the plant surface (Bartelt et al. 2004), indicating that they produce one or several strong feeding deterrents for pollen beetles. Antifeedants are non-volatile chemicals that prevent or interrupt feeding through contact chemoreception or post-gustatory effects and these

could be exploited for control purposes as reviewed by Cook et al. (2007b).

Semiochemical control options

The influence of semiochemical cues in host-plant acceptance for feeding within the pollen beetle life cycle is less well understood compared with host-plant location, although the important role of non-volatile chemical cues is clear. Further behavioural studies are required to identify all the chemical signals involved. Once identified, there is potential to breed OSR lines that have lower levels of phagostimulants to reduce susceptibility or have altered chemical profiles to deter feeding. Alternatively, effective exogenous antifeedant treatments could be developed such as those based on neem (*Azadirachta indica* A. Juss) extracts that are known to be effective against other herbivorous insects (Smart et al. 1994; Martel et al. 2005).

Ovipositional host-plant location (long range cues)

Finding host-plants

Brassicoglyphus aeneus is a specialist on Brassicas for oviposition (Free and Williams 1978; Williams and Free 1978; Ekblom and Borg 1996); therefore adult beetles use volatiles from OSR plants as cues for locating oviposition sites (by females) and potentially for mate location (by males) resulting in different behaviours on the plant. It is known that the pollen beetle has the ability to locate sources of OSR odour over long distances using upwind anemotaxis (Evans and Allen-Williams 1994; Williams et al. 2007a; Skellern et al. 2017), therefore this section discusses the various control options in development that rely on behavioural disruption during long-range OSR location.

Oilseed rape contains over 30 different glucosinolates (Chen and Andreasson 2001); sulphur-containing compounds that are important in defence against generalist phytophagous insects which are catabolised by myrosinase enzymes when the plant suffers insect attack (Giamoustaris and Mithen 1995; Grubb and Abel 2006). Some of these breakdown products are then released as volatile isothiocyanates which are used as semiochemicals for host location by those insects specialising on Brassicaceae (Hopkins et al. 2009; Ahuja et al. 2010; Bruce 2014) including pollen beetles (Blight et al. 1995; Blight and Smart 1999; Smart and Blight 2000).

Pollen beetles are known to be attracted to both visual (colour) cues (Cook et al. 2013b) and olfactory stimuli associated with their brassicaceous oviposition host-plants (Free and Williams 1978; Blight and Smart 1999; Smart and Blight 2000; Williams and Cook 2010). In laboratory tests, pollen beetles have been found to be attracted to

volatiles from OSR in the bud stage (Evans and Allen-Williams 1994; Cook et al. 2007c; Jönsson and Anderson 2007), at the flowering stage (Evans and Allen-Williams 1994; Cook et al. 2002, 2006b), to floral volatiles from the OSR flower or part of the flower (Charpentier 1985; Byers 1992; Cook et al. 2002), as well as to pollen odour (Cook et al. 2002). The chemical basis for this attraction has been tested in the laboratory using electrophysiological studies and the most active compounds include 2-phenylethyl-, 3-butenyl- and 4-pentenyl- isothiocyanate, phenylacetaldehyde and indole (Cook et al. 2007c). Such attraction has also been demonstrated in the field using baited traps (Smart et al. 1993, 1995; Cook et al. 2013a).

It is important to understand the context in which the semiochemical is detected, as the behavioural response to an odour can be affected by its concentration (Mauchline et al. 2005; Piesik et al. 2013) and by visual cues (Jonsson et al. 2007). A field trapping experiment showed that the magnitude of the effect of an attractant lure on trap catches of pollen beetle was dependent on the nature of the visual cue (Blight and Smart 1999); baited yellow traps caught more beetles than white traps indicating that pollen beetles have wavelength-specific preferences (Döring et al. 2012). Conversely, red and blue petal colours have been shown to reduce attractiveness to OSR flowers by pollen beetles (Cook et al. 2013b) and a recent study has shown that it is feasible to genetically modify *B. napus* by introducing key gene(s) from other species to create a different petal colour (Fu et al. 2017). This approach could lead to lines of red-coloured OSR which could disrupt long-range visual cues for beetles in flight and could be backed up by the use of close-range semiochemical-mediated disruption approaches to provide a second stage of protection. A further consideration is that insect feeding and oviposition damage cause altered emissions of volatile compounds (herbivore-induced plant volatiles) from plants. Piesik et al. (2013) found that feeding by *B. aeneus* suppressed the release of the lilac aldehydes and veratrole volatiles by OSR; whereas oviposition damage induced the release of three other common floral volatiles.

Avoiding non-host-plants

Non-host-plants are those plant species not used by an insect for oviposition or feeding and are recognised and avoided using similar cues as described in the previous section on host finding (Bruce and Pickett 2011). Ruther and Thiemann (1997) studied the olfactory response of pollen beetles to volatiles from host and non-host-plants and concluded that there must be some specific compounds which enable the beetles to distinguish between their host-plants and other plants. They suggested that OSR emits several compounds, such as isothiocyanates, that were missing in the plants used

in their study. However, Bruce et al. (2005) argue that the weight of evidence is that insects identify their host-plants through central processing of olfactory signals following detection of specific ratios of ubiquitous plant volatiles.

Plant-derived repellents applied to crop plants could play a powerful role in pest management (Isman 2006). The behavioural response of pollen beetles to the volatile profile of essential oils from non-host-plants during host location was studied by Mauchline et al. (2005, 2008, 2013). *Lavandula angustifolia* Mill. (lavender) had the greatest repellent effect (Mauchline et al. 2005) and within this complex blend of volatiles, linalool and linalyl acetate were identified as the active compounds (Mauchline et al. 2008). Lavender odour caused a significant reduction in the number of adult pollen beetles in field plots if applied before crop colonisation (Mauchline et al. 2013). However, lavender oil is expensive; therefore, other essential oils have been investigated for similar efficacies (Pavela 2011; Daniel 2014). The highest repellency values were obtained for *Mentha arvensis* L., *Cymbopogon flexuosus* (Steud.) Wats. and *Litsea cubeba* (Lour.) Pers. (Daniel 2014). The commercialisation and application of essential oil-based repellents is limited as the active constituents are very volatile (Pavela 2011) and there are also issues relating to the scarcity of the natural resource, standardisation and registration of the product (Isman 2000). Slow-release solutions and devices are required for field application (Heuskin et al. 2011) and there is currently work underway to formulate lavender essential oil into a slow-release solution for field application as a repellent to pollen beetles.

Semiachemical control options

All of this evidence suggests that manipulation of host/non-host-plant odours can be exploited in IPM strategies to reduce pollen beetle damage in three main ways; decreasing the inherent attractiveness of OSR to pollen beetles, using trap/companion plants and using non-host-plant-derived repellents/deterrents—which can all act either alone or in combination.

- (i) Host-plant location of OSR crops during spring leads to feeding and oviposition and these behaviours cause damage to developing OSR crops, therefore it is extremely important to develop ways to manipulate and control large populations of this pest at this stage. Screening for and/or breeding OSR cultivars with low levels of attractive host-plant volatiles is an extremely promising avenue for further research to combine with other components into an integrated pest management strategy.

Manipulation of the volatile profile of crop plants to reduce attractiveness to pest insects can be achieved through conventional plant breeding or genetic modification, but would probably be most effective if integrated into a two-component system with a second control element (Hervé and Cortesero 2016). The glucosinolate defence system in OSR with their breakdown products and volatile profiles offers great prospects for manipulation to achieve increased pest control (Ahuja et al. 2010). Transgenic OSR has been produced with low myrosinase activity (Borgen et al. 2010) which consequently reduces the production of glucosinolate hydrolysis products (mainly isothiocyanates). Compared to wild-type, these low isothiocyanate releasing seedlings were more preferred in free-choice experiments by generalist aphid species but less preferred by specialist aphid species (Borgen et al. 2012). However, such manipulation of plant volatile emissions can result in physiological costs to the plant (Robert et al. 2013) and it is imperative that any modifications do not impair the plant's natural ability to defend itself against other generalist pests after herbivore attack (Hopkins et al. 2009). Further, genetically modified OSR is unlikely to be accepted in Europe in the near future but the technology is in development and is already accepted in USA/Canada canola.

The main oilseed rape crop can be made relatively less without the need for genetic manipulation. The OSR cultivar 'Starlight' was found to have relatively lower proportions of alkenyl glucosinolates (i.e., those that break down to produce the volatile isothiocyanates such as 2-phenylethyl 3-butenyl- and 4-pentenyl- isothiocyanate to which pollen beetles are most attracted) and higher proportions of indole glucosinolates than conventional cultivars such as 'Canyon' (E Bartlett & G Kiddle, unpubl.). Consequently the volatile profile of 'Starlight' was significantly less preferred in olfactometer tests and less colonised in field tests than conventional varieties (Cook et al. 2006b).

- (ii) Trap cropping is a strategy that utilises attractive semiochemicals, released by plant species or crop cultivars that are more attractive than the main crop, to deter pests from the main crop (Hokkanen 1991; Shelton and Badenes-Perez 2006). In laboratory and field tests, pollen beetles showed a preference for turnip rape (*Brassica rapa* L.) over OSR (*B. napus*) (Büchi 1990; Cook et al. 2004b; Čuljak et al. 2016). The mechanism of action was investigated and found to be semiochemically mediated, at least in part, due to higher release rates of phenylacetaldehyde and indole in turnip rape, particularly in the bud stage, compared to OSR (Cook et al. 2007c). In addition, other close

relatives of oilseed rape such *Brassica nigra* L. (Vero-mann et al. 2012), *B. juncea* (L.) Czern. and *Sinapis alba* L. (Kaasik et al. 2014) have also been shown to be more attractive to *B. aeneus* than *B. napus* plants so could also function as trap crops, however, the mechanism for this increased attraction is currently unknown.

- (iii) Further research into non-host-plant semiochemistry has the potential to develop repellents and deterrents for use IPM strategies for the pollen beetle. However, effective slow-release formulations for field applications are required along with a more detailed understanding of the chemistry in order to develop this strategy. Also, timing is critical. Non-host-plant odour can be used effectively to repel pollen beetles from OSR, however, only if applied before crop infestation, i.e., during immigration flights (Mauchline et al. 2013). Understanding and predicting the triggers for these immigration flights (Mauchline et al. 2017) is crucial to the effective deployment of this element of the pest control strategy and the use of Decision Support Systems could help to optimise timing of such applications (Johnen et al. 2010; Johnen and von Richthofen 2013; Ferguson et al. 2016).

Ovipositional host-plant acceptance (short range cues)

When selecting ovipositional host-plants, pollen beetles have been shown to remain longer on suitable host-plants after landing, whereas they only stay for a short time on less preferred plants such as *Sinapis alba* (Borg and Ekbom 1996; Ekbom and Borg 1996). In their first description of the stereotypical oviposition behaviour of pollen beetles, Borg and Ekbom (1996) concluded that important cues for oviposition are located both on the bud surface and inside the bud. Hervé et al. (2015) went further in the description of this behaviour and of the sensory apparatus born by females' ovipositor, showing that both chemical and physical cues are likely to be used on the bud surface, whereas only physical cues are used inside the bud. These inner cues are probably related to anther shape, size or just presence. Indeed, it was shown in the field that adult females were more abundant on male-fertile (with anthers) OSR plants than on male-sterile plants (with shrivelled anthers containing no pollen) during flowering of a varietal association hybrid crop, and a greater proportion of male-fertile than male-sterile buds were accepted for oviposition (Cook et al. 2004a).

Insect–insect semiochemical communication is also important during oviposition and host-plant acceptance behaviours (Anderson 2003). For example, pheromones such as the oviposition-detering pheromone of another pest of OSR, the cabbage seed weevil (*Ceutorhynchus assimilis* Payk.) are deposited by females following oviposition to

ensure that other conspecific females do not lay their eggs close-by (Ferguson and Williams 1989). Studies by Cook et al. (2006a) and Ruther and Thiemann (1997) found some evidence of a female epideictic (spacing) pheromone in pollen beetles in laboratory trials. In both studies, female beetles were repelled by the odours from a large group of females (200 individuals). This response was not shown in tests involving male beetles. These results suggest that females show epideictic behaviour in response to high densities of other females. It is suspected that several females commonly lay eggs in the same flower bud (Nilsson 1988); however, the presence of an epideictic pheromone could provide a mechanism to prevent intraspecific competition in the larvae. The behavioural response to the pheromone was found to be at least partially due to the odour of the females themselves, rather than due to the volatiles from female-damaged plant material (Ruther and Thiemann 1997; Cook et al. 2006a). However, the effect of this putative epideictic pheromone was not detectable experimentally at the semi-field or field scale (Cook et al. 2006a).

Semiachemical control options

The two semiochemical-based control options at this stage include (i) manipulation of plant cues that mediate ovipositional host-plant acceptance and (ii) pheromone-based oviposition deterrents.

- (i) If the attractive bud surface chemical cues could be identified, there is scope to breed cultivars which have low amounts of these stimulant compounds. However, it is only known at this stage that glucosinolates are not major cues (Hervé et al. 2015). Alternatively, compounds which act as deterrents could be exogenously applied on the plants to reduce or prevent oviposition.
- (ii) While there is some preliminary evidence of pheromone-mediated behaviour in female pollen beetles to prevent too many eggs being laid in one bud, this area needs further investigation to enable control tactics to be developed. Insect pheromones are volatile and so have short-lived effects. Chemical characterisation of the putative epideictic pheromone could lead to the synthesis of artificial compounds in a slow-release formulation that could be sprayed on the crop to act as a repellent.

Mate location

Attractant insect pheromones, such as sex and aggregation pheromones are species-specific semiochemical signals that have been identified and used successfully in many insect

pest management programmes across the world (Baker and Heath 2004; Witzgall et al. 2010). There is currently no scientific evidence of any attractive pheromone in pollen beetles; however, such pheromone research is very well developed for other species, so is briefly reviewed here for completeness. Commonly used semiochemical-based techniques for insect pest control include: the release of synthetic sex pheromones to disrupt and prevent mating, e.g., in codling moths (Witzgall et al. 2008); the use of pheromone lures for monitoring, e.g., in the European corn borer (Laurent and Frérot 2007); and in mass-kill strategies, e.g., for the brinjal fruit and shoot borer (Cork et al. 2003). Aggregation pheromones attract both sexes and have been used in many applications for control and monitoring of insects, such as stored product pests (Trematerra 2012).

Male-produced aggregation pheromones have been identified in other species of Nitidulid beetles (Petroski et al. 1994; Bartelt et al. 2004), but there was no evidence for such a pheromone in pollen beetles in studies by Ruther and Thiemann (1997) and (Cook et al. 2006a).

Semiachemical control options: There is currently insufficient evidence to suggest that investigation into attractive pheromones would lead to the delivery of control tactics for pollen beetles.

Predation by natural enemies

Pollen beetles are predated by both specialist and generalist natural enemies. Generalist predators include Carabid and Staphylinid beetles as well as spiders. Additionally, several species of specialist parasitic wasp attack the larvae of pollen beetles, including *Phradis interstitialis* (Thomson), *Phradis morionellus* (Holmgren) and *Tersilochus heterocerus* (Thomson) which can have a significant impact on pollen beetle control (reviewed by Ulber et al. (2010) and Williams and Cook (2010)). There is evidence that semiochemicals mediate prey location (Williams et al. 2007b; Berger et al. 2015). Exploiting the current knowledge of the semiochemistry of host location by parasitoids could enhance biocontrol of pollen beetles within an IPM system as this has been already been achieved for aphid species in arable cropping systems (Du et al. 1998; Powell and Pickett 2003).

Olfactometer studies found that the three main species of pollen beetle parasitoid were all attracted to volatiles from OSR in the bud stage; however, there was an interesting finding of niche separation between the three competing species as they each displayed preferences for volatiles from insect infestations at different stages of OSR development that corresponded to their preferred host growth stage (Jonsson et al. 2005; Berger et al. 2015). After landing on the host-plant, *T. heterocerus* female parasitoids have also been shown to

Pollen beetle parasitoids are known to use upwind anemotaxis for host-habitat location (Williams et al. 2007b); therefore, volatile semiochemical attractants could be used to attract these natural enemies as an in-field control measure.

New generation pollen beetles leave OSR crops as they cease flowering to feed on pollen of a wide range of later summer-flowering plants in order to accumulate fat reserves; they then migrate to overwintering sites using daylength as the critical cue (Lipa and Hokkanen 1992). Pollen beetles overwinter in leaf litter within wooded areas or field margins and higher numbers of adults were found to be related to local landscape factors such relative altitude, litter thickness, soil

Gloyna and Thieme (2013) investigated overwintering distribution of pollen beetle in different biotypes and found that in suitable biotypes, distribution was highly heterogeneous, even at the small (1 m²) scale, with over 4000 found per m² in some areas (pers. comm.), which suggests aggregation. This could be mediated by pheromones or could indicate very specific selection of suitable biotypes for overwintering. As described in the section on mate location, preliminary work did not find any evidence of an aggregation pheromone (Ruther and Thiemann 1997; Cook et al. 2006a). However, it is probable that the effect of such a pheromone would be life stage specific and that any potential aggregation (or other) pheromone only produced upon arrival at a suitable overwintering site; further research is therefore required to collect and test volatiles from overwintering insects in the field.

This is a research gap clearly worth revisiting. The identification of an aggregation pheromone or other semiochemical cue used in this process at this stage of the beetle's life cycle could open up opportunities for a trapping method which could significantly reduce the overwintering population.

The diagram illustrates the Push-Pull strategy for pest management in oilseed rape. It features two main crop types: Oilseed rape crop (top, green box) and Trap crop (bottom, yellow box).

Oilseed rape crop (Push side):

- A large blue arrow labeled **PUSH** points downwards from the Oilseed rape crop to the Trap crop.
- Text associated with the Push side: Masking of host plant attraction, Repellents and antifeedants, Oviposition deterrents.
- A blue arrow labeled **CONTROL** points left towards the Oilseed rape crop.
- Text associated with the Control side: Attractants for predators and parasitoids.

Trap crop (Pull side):

- A large blue arrow labeled **PULL** points upwards from the Trap crop towards the Oilseed rape crop.
- Text associated with the Pull side: Host plant attractants, Aggregation, sex and oviposition pheromones, Visual attractants.
- A blue arrow labeled **CONTROL** points left towards the Trap crop.
- Text associated with the Control side: Selective control agents (e.g. bioinsecticides).

Prospects for a semiochemical-based IPM strategy for pollen beetles

This review has considered the important behavioural processes in the pollen beetle and the life stages at which they occur, where semiochemically mediated control could be developed as part of an IPM strategy. Individually, the alternative approaches reviewed here are likely to be less effective in terms of pest control compared to the use of an insecticide, however, integrating several of these semiochemical-based approaches into a holistic system could increase their overall efficacy while avoiding the harmful environmental impact of synthetic toxicant insecticides.

In general, most semiochemical-based control methods can be combined; however, it is pertinent to ensure they are not antagonistic to the aims of other IPM tools, e.g., biocontrol methods using natural enemies. The only study to date on pollen beetle control methods to check compatibility looked at the effect of lavender essential oil [a potential repellent (Mauchline et al. 2013)] on the behavioural responses of their two most common parasitoids. Both parasitoid species elicited electrophysiological responses to linalool and linalyl acetate (the compounds stimulating the repellent behaviour to lavender in pollen beetles), but gave no significant behavioural response at the concentrations effective against pollen beetles (Cook et al. 2007a). Therefore, there was no evidence to suggest that lavender-treated plants would negatively affect host location by parasitoids and hence both strategies could be deployed in tandem. However, further tests in field situations are necessary.

There are two holistic pest management approaches currently in development that combine several elements of the control options reviewed here; namely the push–pull system and the potential for a smart, self-protecting crop.

The push–pull system

Push–pull is a formalised pest management strategy that combines attractant and repellent semiochemicals to manipulate pest and natural enemy populations (Miller and Strickler 1984; Pyke et al. 1987; Cook et al. 2007b) (Fig. 2). The pests are deterred from colonising or are ‘pushed’ out of the crop using, for example, repellent crop cultivars and repellent non-host-plant volatiles, plant-derived antifeedants and oviposition-detering pheromones. The pests are simultaneously ‘pulled’ away from the crop into traps/trap crops using attractants such as host-plant volatiles or sex pheromones. A trap crop comprises plants which are designed to be even more attractive to the pest insect than the crop to be harvested (Hokkanen 1991; Shelton and Badenes-Perez 2006), i.e., exploiting host-plant preferences (Cook et al. 2006b). Once the pests have been concentrated on the trap crop, it can be treated if necessary with a selective biopesticide or

synthetic insecticide, thus the area treated is reduced compared to conventional systems where the whole crop area is treated. Pests remaining in the main crop are controlled by natural enemies; their abundance potentially boosted using attractive ‘pull’ signals (Cook et al. 2007b). The components of the system need to be compatible with each other (Smart et al. 1997) and while individually they can be relatively ineffective compared to the use of broad-spectrum insecticides, together they can have an additive or synergistic effect (Campbell and Borden 2009). The combination of relatively weak control elements has the added advantage of not selecting strongly for resistance in the pest species (Pickett et al. 1997; Pickett and Khan 2016).

The push–pull system in development for pollen beetle control incorporates early season monitoring using semiochemical-baited traps (Cook et al. 2013a) followed by using an attractive border trap crop such as turnip rape (*B. rapa*) (Cook et al. 2004b, c; Čuljak et al. 2016) or *B. nigra* (Veromann et al. 2012, 2014) to provide the ‘pull’ element, as they are known to be a preferred host-plant for several OSR pests including the pollen beetle. Ideally, this should be a ‘dead-end’ trap crop (Shelton and Badenes-Perez 2006) such as *Raphanus sativus* (L.) Domin (Veromann et al. 2014). Biological control of the pollen beetles in the trap crop could be enhanced by attracting natural enemies using attractant lures based on host-plant volatiles (Jonsson et al. 2005; Jönsson and Anderson 2007) or volatiles from their host larvae (Straka et al. 2013; Berger et al. 2015), but this concept is still in the early research phase. As the push component, volatiles from lavender essential oil (*Lavandula angustifolia*) were found to be effective in deterring pollen beetles in laboratory bioassays (Mauchline et al. 2005, 2008) and in both semi-field and field trials (Mauchline et al. 2013). Analyses of data from a large-scale field plot experiment in OSR is underway to compare the efficacy of the combination of a repellent lavender spray along with a trap crop to reduce pollen beetle numbers in the main crop. This system is already at the field testing stage, however, slow-release formulations still need to be developed for release of the repellent volatiles; otherwise, this approach is close to practical use IPM system for oilseed rape growers.

Smart, self-protecting crops

A future avenue of research that is currently a bit further away from practical use is the development of oilseed rape plants that are ‘self-protecting’. Attack from herbivores is known to induce natural plant defence systems (Pickett and Poppy 2001; Howe and Jander 2008); therefore, crop plants themselves could act as the source of manipulative semiochemicals, using inducing agents, or natural product plant activators, to ‘switch on’ plant defence prior to attack (Pickett et al. 2006). This alternative approach to genetic

modification uses gene promoter systems that could create a self-protecting crop where primed sentinel crop plants use volatile signals to elicit faster defensive responses from the surrounding plants and natural enemies (Balmer et al. 2015; Conrath et al. 2015; Pickett and Khan 2016; Pickett 2016).

Taken together, these approaches may well deliver the sustainable pest control required to deliver food security without continued reliance on insecticides.

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