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Skellern, M. P. and Cook, S. M. 2017. The potential of crop management practices to reduce pollen beetle damage in oilseed rape. *Arthropod-Plant Interactions.*

The publisher's version can be accessed at:

- https://dx.doi.org/10.1007/s11829-017-9571-z

The output can be accessed at: https://repository.rothamsted.ac.uk/item/844zz/the-potential-of-crop-management-practices-to-reduce-pollen-beetle-damage-in-oilseed-rape.

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ORIGINAL PAPER

The potential of crop management practices to reduce pollen beetle damage in oilseed rape

Matthew P. Skellern[1] · Samantha M. Cook[1]

Abstract A major problem associated with agricultural intensification over recent decades has been the development of insecticide resistance in crop pest populations. This has been a particular issue for control of the pollen beetle (*Brassicogethes aeneus* syn. *Meligethes aeneus*), a major pest of oilseed rape throughout Europe. Sustained and often prophylactic use of pyrethroid insecticides has led to the development of insecticide-resistant beetle populations, and alternatively, more environmentally benign integrated pest management strategies are sought for the pest. The population dynamics of pollen beetles and their natural enemies, and the damage caused by the pest, are influenced by processes acting at multiple scales, from the regional or landscape scale down to the local field or within-field scale. In this review, we focus on the within-field scale, and how crop management factors, including tillage, crop plant density, crop nutrition and crop rotations may be optimised and incorporated into integrated pest management strategies for more sustainable and effective control of the pest.

Keywords *Meligethes aeneus* · *Brassicogethes aeneus* · *Brassica napus* · Integrated pest management · Sustainable agriculture · Crop nutrition · Tillage · Insecticide

Introduction

The reliance of modern agriculture on intensive use of agrochemical inputs to maintain crop yields, along with habitat loss and simplification of crop rotations, has resulted in environmental degradation and a loss of biodiversity from arable landscapes (Bianchi et al. 2006; Robinson and Sutherland 2002; Stoate et al. 2001). This has led to a reduction in ecosystem services vital for sustainable food production, including pollination and natural pest control (Bianchi et al. 2006; Vanbergen 2013). Another major problem associated with agricultural intensification over recent decades has been the development of pesticide resistance in pathogen, pest and weed populations, in response to selection pressures arising from sustained pesticide use (Heckel 2012; Busi et al. 2013; Hahn 2014). This, coupled with declining availability of new pesticide active ingredients (due to both decreasing discovery rates and tighter legislation surrounding product approval) (Jensen 2015), represents a real threat to the efficacy of pesticide use, and consequently, to the productivity of pesticide-reliant agricultural systems. Hence, in response to these issues, there is an urgent need to develop more sustainable Integrated Pest Management (IPM) strategies for crop protection.

While the concept of IPM was initially developed by entomologists in response to specific pest-related issues, IPM (as defined within the EU under EU Framework Directive 2009/128/EC) now applies to all aspects of plant protection, and involves eight major principles (Barzman et al. 2015). Primarily, the focus of IPM is on the prevention and suppression of harmful organisms by cultural or non-pesticide means (1). Monitoring (2) followed by threshold-based decision making (3) also play a major role. Where control is necessary, non-chemical methods are prioritised over chemical pesticides (4), but where pesticides are essential to provide adequate control, the least damaging products to the environment, non-target organisms and human health are selected (5). Where pesticides are the only option, their use is kept to a minimum (6) and

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anti-resistance strategies (e.g. combining use of products with differing modes of action) are employed (7). The final principle involves evaluation of the control measures taken (8) (Barzman et al. 2015).

Although IPM strategies may involve consideration of landscape-scale processes (e.g. landscape-scale habitat management to manipulate pest and natural enemy populations; Skellern and Cook in press), appropriate crop management, encompassing factors such as crop rotation, cultivar choice, tillage and fertiliser regime, underpins the implementation of IPM strategies, particularly in terms of the primary principle (1) above. For example, crop rotation (i.e. the spatial and temporal diversification of cropping sequences) has been used for thousands of years as a primary means of suppressing harmful organisms by disrupting life cycle continuity of pests and pathogens associated with different crop species (Bullock 1992; Barzman et al. 2015). European maize-based cropping systems provide an illustration of this; replacement of continuous maize cultivation by incorporation of non-maize crops into the rotation has allowed for the successful management of the Western corn rootworm (*Diabrotica virgifera* subsp. *virgifera*), a pest which requires two maize cultivation cycles to complete egg-to-adult development (Vasileiadis et al. 2011).

In Europe, IPM strategies are urgently needed for control of the pollen beetle *Brassicogethes aeneus* F. (syn. *Meligethes aeneus*) (Coleoptera: Nitidulidae), a key pest of oilseed rape *Brassica napus* L. (OSR), a crop widely grown for cooking oil and biofuel use (EU production 19.8 M tonnes in 2016; Eurostat 2017); in this case, beetle resistance to pyrethroid insecticides, which are often applied prophylactically, has become a major problem (Zimmer et al. 2014; Thieme et al. 2010). Adult beetles emerge in early spring from overwintering habitats in woodlands and grassy areas (Rusch et al. 2012; Blazejewska 1958; Müller 1941), and feed on the flowers of many different plants before seeking OSR crops and other brassicas at the green bud growth stage, for further feeding and oviposition (Free and Williams 1978; Ouvrard et al. 2016). Feeding damage causes OSR flower bud abscission, leading to often extensive yield losses (Zlof 2008) that can approach 80% (Hansen 2004). After eggs are laid in the buds, the developing larvae feed for c. 2 weeks before dropping to the soil to pupate. New generation adults emerge in summer and again feed on pollen from plants of several families before overwintering (Williams 2010; Alford et al. 2003; Ouvrard et al. 2016). The beetles are attacked at the larval stage by a range of parasitoid species, the most abundant and widespread of which in Europe are *Tersilochus heterocerus* Thomson, *Phradis interstitialis* Thomson and *Phradis morionellus* Holmgren (Ulber et al. 2010b); surface-active and plant-climbing natural enemies include ground beetles and spiders (Williams et al. 2010; Frank et al. 2010).

Natural enemy regulation of pollen beetles can be substantial (Buchi 2002; Hokkanen 2008), and the possibility to manipulate both pest and natural enemy populations for beetle control, through local and landscape-scale habitat management, has received significant research interest (e.g. Cook et al. 2007; Schneider et al. 2015; Beduschi et al. 2015; Skellern and Cook in press). At the within-field scale, however, appropriate crop management also provides opportunities to improve beetle control, as crop management factors may affect plant growth and phenology (Valantin-Morison et al. 2007), which in turn influence resource quality. As specific plant quality characteristics, for example relating to bud size or glucosinolate content, are known to play a role in pollen beetle host plant selection (Nilsson 1994; Cook et al. 2006; Valantin-Morison et al. 2007; Hervé et al. 2014a), resource quality-mediated crop management effects are likely to influence pollen beetle abundance and damage in the field. Besides these effects, crop management is also likely to influence insect populations through microclimatic effects, and through variations in plant architecture, which may alter oviposition behaviour and food-seeking efficiency (Valantin-Morison et al. 2007).

Crop management interventions to facilitate improved pollen beetle control are possible at several points within the growing cycle of OSR (summarised in Fig. 1). The crop is usually grown in rotation with cereals, at the crop planning stages, the frequency of its appearance within the rotation and cultivar choice, are important considerations. Winter OSR crops are generally sown between mid-August and mid-September (or early September in more northerly latitudes), with the exact timing of drilling often influenced by the harvesting date of the preceding (usually cereal) crop, while spring crops are drilled in March or April, usually as soon as soil conditions allow (HGCA 2014). Standard plough-based systems (e.g. ploughing followed by a power harrow-drill combination) are frequently used for OSR establishment, but reduced cultivation techniques (tine, disc or subsoiler based), and direct drilling or broadcasting into the stubble of the preceding crop are also common, as farmers look to reduce establishment costs and manage soils more sustainably (Ingram 2010; Jacobsen and Ørum 2009; Townsend et al. 2016). Target plant densities are usually in the range 25–35 plants/m^2 for winter crops (HGCA 2014).

Weed control in winter OSR is achieved through pre- and/or post-emergence herbicides in the autumn, and usually further herbicide applications are necessary in the spring (HGCA 2014). In early summer, just prior to harvest, an herbicide (usually glyphosate) is frequently applied as a desiccant to aid ripening, ease harvesting and control perennial weeds for the following crop. Generally, where plough-based establishment has been used, fewer herbicides are needed (Nilsson et al. 2015). Similarly, a combination of seed treatment, and autumn and spring fungicide applications are
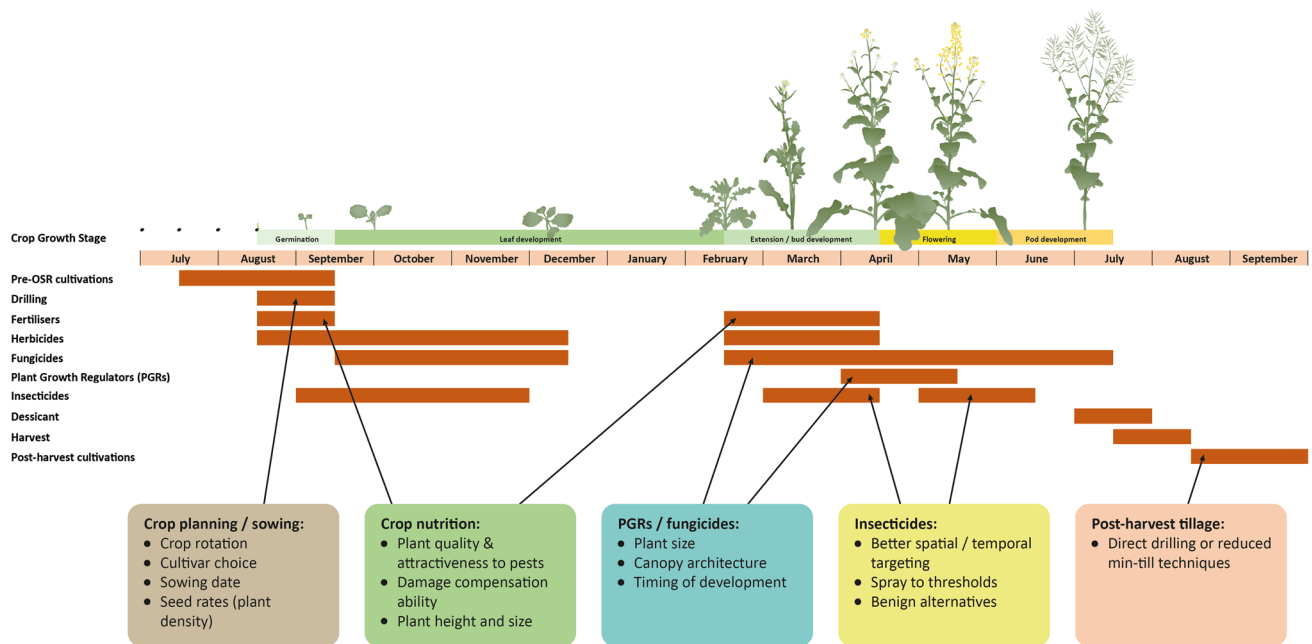
Fig. 1 Oilseed rape crop management practices in relation to crop growth stage and timing and interventions to facilitate improved pollen beetle control

normally required against diseases such as phoma stem canker (blackleg; *Leptosphaeria maculans*), sclerotinia stem rot (*S. sclerotiorum*), light leaf spot (*Pyrenopeziza brassicae*) and verticillium wilt (*V. longisporum*) (HGCA 2014). Plant growth regulators (some of which, including metconazole and tebuconazole, also have fungicidal action) may also be used in the spring to manipulate canopy development and reduce lodging (HGCA 2014).

In addition to base fertiliser applications made to maintain longer term soil phosphate, potassium and magnesium levels, OSR crops typically receive 150–230 kg nitrogen, and 30–60 kg sulphur ha^{-1} (Christen et al. 1999) in order to optimise crop growth and maximise yields. Fertilisers are usually applied in granular or liquid form using either a spinning disc applicator for granules or a crop sprayer fitted with dribble bar-type nozzles for liquids. Applications are usually split between one in the autumn and 2–3 applications in spring, ideally made between the early green and yellow bud growth stages (HGCA 2014). Typical insecticide applications to OSR crops include sprays in the autumn against cabbage stem flea beetles (*Psylliodes chrysocephala*) and the peach-potato aphid (*Myzus persicae*). Further insecticides are used at the green–yellow bud stages against pollen beetles, and during flowering, against seed weevils (*Ceutorhynchus obstrictus*) and pod midge (*Dasineura brassicae*).

While the influence of local and landscape-scale habitat management on pollen beetle abundance, damage and biocontrol are reviewed in another publication (Skellern and Cook in press), in this paper, we review crop management

influences on the pest and its natural enemies, and consider how crop management may be optimised in IPM strategies for sustainable pollen beetle control.

Crop rotation

A trend towards the simplification of crop rotations over the past half-century, to include just a few crop species grown in short succession, is generally considered to have led to increases in pest proliferation and a reduction in the biodiversity of beneficial insects (Rusch et al. 2010). However, for some beneficial insects, particularly carabid beetles, little influence of rotational crop diversity changes has been seen (Holland et al. 1996; Kromp 1999). The cumulative effects of rotation-related decisions made by individual farmers are likely to exert the greatest influence on pollen beetle (and natural enemy) abundance through landscape-scale processes, as differences in the frequency of a particular crop within a rotation lead to corresponding changes in landscape areal crop proportions (Thies et al. 2008; Vinatier et al. 2012, 2013). While over a period of > 3–4 years, the introduction of oilseed rape into landscapes where the crop has not previously been grown has led to proliferation of pollen beetles as a pest (Hokkanen 2000), over the shorter term, temporally (inter-annual) and spatially increasing OSR proportions within the landscape can to lead to dilution effects on pollen beetle abundance (Zaller et al. 2008a, b; Moser et al. 2009; Schneider et al. 2015). This observation

has inspired proposals for crop rotation management at the landscape scale (Beduschi et al. 2015; Schneider et al. 2015) where areas of OSR within an entire region would be progressively increased over a number of years to maintain these dilution effects, before a 'reset' year when little or no OSR would be grown. However, this would require a considerable amount of grower cooperation as the intervention occurs at a scale greater than the farm unit.

Cultivar

There are no commercially available cultivars of oilseed rape currently available that are marketed as resistant or tolerant to any insect pest of the crop. Although breeding for OSR resistance to pollen beetle damage has thus far received little attention, different cultivars vary in their suitability as host plants, and in their tolerance of attack. Hence, potential clearly exists to develop more resistant varieties (for a review, see Hervé and Cortesero 2016). Plant characteristics such as growth stage profile (Kruger and Ulber 2010), glucosinolate content (Cook et al. 2006; Rusch and Valantin-Morison 2013), petal colour and UV reflectance (Cook et al. 2013b), and plant size can all influence infestation and damage, and vary according to cultivar. The optimum pod number for maximum OSR yield is in the region of 6000–8000 pods/m^2 (Berry and Spink 2006). However, significantly more flowers than necessary for optimum pod number are usually produced, and the presence of these 'excess flowers' enables the crop to tolerate some pollen beetle-related flower loss before yields are reduced (Ellis and Berry 2012); excess flower numbers have been shown to vary according to cultivar (Ellis and Berry 2012; Carruthers et al. 2017) and thus are likely to be important determinant of a particular cultivar's tolerance to pollen beetle attack. A recent study showed that, in general, cultivars bred using the cytoplasmic male-sterility (CMS) technique generally had more flowers than hybrids produced by genetic male-sterility (GMS) techniques and open-pollinated varieties (Carruthers et al. 2017). This suggests that CMS cultivars may be more tolerant to pollen beetle, although this has not been tested. Hervé et al. (2014a) identified compounds from the bud perianth, including sucrose, proline and serine that appear to act as key feeding stimulants for pollen beetles; perianth content of these compounds varied among genotypes leading to the suggestion that OSR cultivars with reduced perianth content of these compounds, in particular sucrose, could be selected to reduce damage by the pest. Furthermore, the amount of food eaten by female pollen beetles was positively related to egg numbers and size (Hervé et al. 2014b), suggesting that fewer and/or smaller eggs would also be laid on these cultivars. In another study, fewer eggs were laid on a male-sterile OSR cultivar compared with a male-fertile companion in the varietal association Synergy; larval survival was reduced and developmental time longer on the male-sterile plants (Cook et al. 2004). Manipulation of plant quality to increase larval development time has been suggested as a method to enhance biological control (Hervé et al. 2016); slower larval development on such cultivars would lengthen their window of vulnerability to parasitoid attack.

At present, no comprehensive scheme for rating oilseed rape varieties in terms of their pollen beetle resistance exists, and the current UK spray thresholds err on the side of caution and are based on the least tolerant varieties, i.e. those with few excess flowers (Ellis and Berry 2012). Potential thus clearly exists to provide farmers with information on the pollen beetle resistance characteristics of available varieties, and also reduce pest thresholds further for those with higher resistance. Cultivar choice could be an important factor to maximize the success of trap cropping strategies. Trap crops are plant stands that are grown to attract insects in order to protect target crops from attack (e.g. Hokkanen 1991). Trap cropping strategies targeted against pollen beetles in OSR has been reviewed by Mauchline et al. (2017b) and Skellern & Cook (in press). Late-flowering OSR cultivars could be used to extend the necessary growth stage differential between the main crop and an early-flowering trap crop. There is also potential for development of an OSR cultivar highly attractive to pollen beetles to function as a trap crop. Currently the best performing trap crop is turnip rape (*Brassica rapa*), however if early-flowering cultivars of OSR could be developed possessing the attractive properties of turnip rape, the strategy is more likely to be accepted by farmers.

Sowing date and growth stage profile

Variation in sowing date will influence some pests through alteration of the synchrony between lifecycles and susceptible crop growth stages. For OSR, the difference between winter and spring sowing has the greatest effect, and because the damage-susceptible stages of the crop occur at peak pest abundance, spring sown crops in particular are more susceptible to flea beetle (*Phyllotreta* spp.) and pollen beetle damage (Alford et al. 2003; Dodsall and Stephenson 2005). For the latter, however, as excess flower numbers do not differ between winter and spring crops (Ellis and Berry 2012), it is likely that pollen beetle spillover from large areas of winter crops onto smaller areas of spring crops leads to locally increased pest pressure through beetle concentration effects (except for in more northerly regions where spring crops predominate). For winter crops, an early study found that later sowing dates limited pollen beetle damage (Vasak 1983), and it is possible that this was related to reduced fecundity of older beetles on the less advanced crops. Results from

another study have shown that the fecundity of beetle populations maintained on *Raphanus sativus* late into the season was indeed low (Skellern et al. in prep). By contrast, Rusch et al. (2013b) found that sowing date was not an important predictor of pollen beetle abundance or plant damage, and while earlier sowing can increase root fly damage but decrease cabbage stem flea beetle attack, Valantin-Morison et al. (2007) also found little effect of sowing date on pollen beetle damage.

Pollen beetles often feed on early spring-flowering plants before they move onto oilseed rape (Free and Williams 1978; Ouvrard et al. 2016), and have been observed on the crop at pre-green bud growth stages (Veromann et al. 2012); during most seasons, it seems that the beetles arrive sufficiently early to colonise even the most advanced crops before the susceptible green bud stages are over (Cook et al. 2006; Mauchline et al. 2017a). Relative differences in growth stage, for example between a crop and trap crop or variation within a field, however, are very important in determining infestation levels, because of the beetle's preference for the flowering growth stages (Cook et al. 2007; Mauchline et al. 2017a), which may provide a reliable cue for the availability of buds of the preferred size for oviposition (2–3 mm; Ekbom and Borg 1996), together with food resources (Frearson et al. 2005).

The coincidence between pollen beetle parasitoid emergence and crop development is not precise (Nilsson 1985) and there is some evidence that the parasitoids may be more sensitive to asynchrony therein than their hosts. Larvae present on early flowering winter-sown turnip rape varieties in some seasons may escape parasitisation, probably because the parasitoids do not arrive until after the bud stages are complete (Skellern et al. in prep). It is thus possible that in some seasons, larvae on very early flowering oilseed rape crops may similarly escape parasitisation.

Plant density

Oilseed rape plants have potential to compensate for pollen beetle-related floral bud losses by producing new flower buds carried by either existing or new branches (Tatchell 1983; Nilsson 1994; Williams and Free 1979). Plant density, which can be strongly influenced by crop management through seed rates and sowing date, however, impacts the ability of the crop to compensate for bud losses, with higher planting densities generally leading to more restricted branching as there is less space for compensatory growth (Leach et al. 1999; Momoh and Zhou 2001). Despite this, some studies have shown little or no influence of plant density on pollen beetle abundance or damage (Rusch et al. 2013b; Ferguson et al. 2003), while others have shown negative relationships

(Hurej and Twardowski 2006; Valantin-Morison et al. 2007). It is likely that lower beetle abundance and damage at higher plant densities could occur through dilution effects. Excess flower numbers (defined as the difference between flower and final pod numbers) produced per plant are strongly negatively affected by increasing plant density, meaning that on a per plant basis, beetle susceptibility increases (hence, economic damage thresholds decrease; Ellis and Berry 2012). Although Leach et al. (1999) found fewer branches per plant at high densities, denser crops had more branches per square metre so on a per unit area basis, total excess flower numbers may increase with plant density, explaining why more densely planted crops may suffer less damage. Additionally, Valantin-Morison et al. (2007) observed that root fly (*Delia radicum*), cabbage stem flea beetle (*Psylliodes chrysocephala*) and rape stem weevil (*Ceutorhynchus napi*) damage all decreased with increasing plant density; this too may have been due to dilution effects, but increased competition between plants at higher densities may have reduced resource quality for these insects.

Pollen beetle parasitism rates have been shown to have a positive relationship with plant density (Zaller et al. 2009a), and it is probable that parasitoid searching efficiency is improved where racemes (and hence host larvae) are more closely spaced. Interestingly, Zaller et al. (2009a) also showed that oilseed rape 1000 kernel mass was positively related to pollen beetle parasitism rates, suggesting that the parasitoids may have influenced beetle capacity to cause damage to the growing crop, perhaps through disturbance or interference effects.

Weed management

There has been little, if any, research on the direct effects of weeds on pollen beetle infestation of OSR crops. Similarly, the direct effects of weed management on pollen beetle regulation by natural enemies has been little studied, however, generalist predators such as carabids and spiders may benefit from increased weed cover through provision of shelter and alternative sources of food/prey (Speight and Lawton 1976; Holland et al. 1999; Schmidt et al. 2005; Sunderland and Samu 2000). In particular, omnivorous carabid species that consume weed seeds as well as prey have been shown to be associated with increased weed cover (Kulkarni et al. 2017; Diehl et al. 2012). Potentially, therefore, less intensive weed management regimes may enhance pollen beetle regulation by these natural enemies. However, more work is needed in this area as positive relationships between weed density and generalist predators may not necessarily lead to better pest suppression; alternative weed-associated resources may distract generalist enemies from target pests (Diehl et al. 2012).

To our knowledge, no study has investigated the effect of weed management on pollen beetle specialist parasitoids. However, it is possible that access to weed-derived pollen and nectar could enhance the efficacy of these natural enemies, and that they may benefit from reduced weed management intensity. Floral resource utilisation has been shown to increase parasitoid longevity (Lee et al. 2004; Robinson et al. 2008) and fecundity (Hogg et al. 2011; Baggen and Gurr 1998; Winkler et al. 2006), and the pollen beetle parasitoid *T. heterocerus* is known to acquire nectar while foraging in the field (Rusch et al. 2013a). However, the massive floral resources supplied by the OSR crop itself may mean that the benefits of weed-derived nectar and pollen are marginal, or depend on the phenology of different parasitoid species in relation to that of the crop. For example, *P. interstitialis*, which is active at the OSR bud stages (i.e. before the flowers are open) may benefit more from weed-borne floral resources than *P. morionellus* or *T. heterocerus* which tend to colonise the crop only at the beginning of flowering (Ulber and Nitzsche 2006; Williams 2006). The benefits delivered by weeds to natural enemies of pollen beetles could also be realised through managed companion cropping within-crop (e.g. Howard 2016) or via sown field margins at the field boundry (Baverstock et al. 2014; Skellern & Cook in press), which avoid the negative impact of weeds. However both tactics require further research and development.

Growth regulators

Several compounds, including metconazole and tebuconazole, both of which also have fungicidal action, are used as growth regulators on OSR to manipulate canopy development, root growth and stem extension (HGCA 2014). It seems, however, that no research has been carried out on the influence of these compounds on pest abundance or damage. As plant height can positively influence both pollen beetle and stem weevil *Ceutorhynchus pallidactylus* infestation (Schlinkert et al. 2015, 2016; Ferguson et al. 2003), it is possible that these compounds could be used to manipulate populations of these pests. Additionally, research is needed on the use of these or similar compounds to influence the timing of bud and flowering growth stages, as potential may exist to use growth regulators as an alternative to, or to enhance trap cropping strategies.

Crop nutritional status

Several studies have revealed relationships between crop nutritional status and pollen beetle abundance on OSR. Zaller et al. (2008b) demonstrated a curvilinear relationship between pollen beetle infestation and soil index (a measure used in Austria of the natural yield capacity of soils, on a scale of 0–100, with soils of the highest yield capacity in the country scoring 100, and taking into account soil type, humus content, soil depth, texture, density, structure, lime content, gleying and soil congregation; ÖBG 2001); beetle abundance increased with soil index to average index levels, but then declined at higher values. The authors suggested that at low soil index values, plant quality may have been unsuitable for the pest, but at higher values, the crop may be better able to protect itself from herbivore attack. Indeed, plant glucosinolate content, the breakdown products of which are important for pollen beetle host plant location (Blight and Smart 1999; Cook et al. 2006), has been shown to increase with nutrient supply (Markus et al. 1996), but on higher quality soils, the production of other secondary compounds may enhance plant defences against the pest (Cipollini and Bergelson 2002). Despite these soil quality effects, Zaller et al. (2008b) observed no direct influence of variation in nitrogen fertiliser rates (range 45–143 kg ha^{-1}), perhaps because applications may not have accurately reflected soil nitrogen availability. By contrast, Culjak et al. (2011) found greater pollen beetle abundance on plants treated with lower and higher N rates (of 69 and 115 kg ha^{-1} respectively) than on those treated at medium rates (92 kg ha^{-1}), and Veromann et al. (2013) were also able to demonstrate an influence of nitrogen fertiliser, with increased beetle infestations occurring on both low (60 and 80 kg ha^{-1} N) and high (160 kg ha^{-1}) rate nitrogen-treated plots, compared with zero and medium (100, 120 and 140 kg ha^{-1}) rate treatments. In this case, there was some evidence that differences in infestation rates were mediated through quantitative changes in plant volatile profiles which differed according to nitrogen application rates. In particular, emissions of acetic acid, methyl salicylate and several lipoxygenase pathway volatiles were greater from plants treated at the higher N rates.

It is possible that plant nutrition-mediated differences in visual cues may influence infestation and damage by pollen beetles. Higher nitrogen rates can increase OSR floral spectral reflectance in the UV wavelengths, and in those above 530 nm (Blake et al. 2014); visual stimuli at these wavelengths are known to elicit positive behavioural responses in pollen beetles (Döring et al. 2012; Cook et al. 2013b). Indeed, for the seed weevil, plant nitrogen and sulphur nutrition has been shown to influence attraction to OSR through differences in leaf reflectance characteristics (Blake et al. 2014). As well as altering spectral reflectance characteristics, higher nitrogen rates can lead to increased plant size and height (Grant and Bailey 1993), which can also influence pollen beetle and stem weevil abundance and damage (as discussed above).

In a study investigating both crop management and landscape influences on OSR pest populations and crop damage, Rusch et al. (2013b) reported that crop nitrogen status (as determined by calculation of the nitrogen nutrition index; Lemaire and Meynard 1997) was of little importance in determining pollen beetle infestation, but represented a very important predictor of crop damage; high nitrogen status plants exhibited low proportions of damaged buds. Another study (Valantin-Morison et al. 2007) also showed a similar effect, with reduced proportions of flowers destroyed by pollen beetles on higher nitrogen status soils. In both cases, it is likely that the negative relationship between nitrogen nutrition and pollen beetle damage is related to the greater capacity of higher nutrient status plants to produce defensive secondary compounds (Cipollini and Bergelson 2002) and to compensate for damage, particularly via the production of new racemes (Podlaska et al. 1996).

There is little evidence in the literature of direct crop nutritional status effects on pollen beetle natural enemies; rather, pollen beetle parasitism rates appear to be influenced indirectly through host density-dependence effects (Zaller et al. 2009b; Veromann et al. 2013). Similarly, the activity-density of *Amara similata* (Carabidae) females was found to be negatively correlated with soil index (Haschek et al. 2012), and this is most likely related to prey and/or weed seed abundance; on more productive soils, readily available food resources lead to satiated beetles that are relatively inactive and less likely to be trapped (Lenski 1984).

In general, it seems that the increased capability of high nutrient status crops (particularly with regard to nitrogen) to compensate for pest damage can often offset the effect of greater pollen beetle abundance on these crops, and timing of fertiliser applications to ensure sufficient nutrient availability at the susceptible green to yellow bud growth stages may serve to curb yield losses. Indeed, in dry seasons when nitrogen uptake is limited, it is possible that crops would benefit from foliar nitrogen applications during the damage-susceptible stages.

Insecticide regimes

The insecticides that are routinely used to target pollen beetles and other OSR pests have detrimental effects on natural enemy populations and parasitism rates (Hanson et al. 2015; Nilsson et al. 2015; Jansen and San Martin 2014), meaning that integration of chemical and conservation biological control into IPM strategies is a major challenge (Williams 2004, 2006). These undesirable side effects, however, may be ameliorated in a several ways. Choice of lower toxicity products such as tau-fluvalinate over other pyrethroids (Klukowski 2006) may enhance parasitoid survival. Jansen and San Martin (2014) found that pymetrozine had limited

effects on parasitoid mortality compared with thiacloprid, phosmet, chlorpyriphos-ethyl and tau-fluvalinate. Pymetrozine, tau-fluvalinate and phosmet did not affect the ratio of parasitoids: pollen beetles at the end of the season while thiacloprid and chlorpyriphos-ethyl were found to alter this ratio in the pollen beetles' favour. Reduction of insecticide applications is possible through the use of decision support systems and better use of pest thresholds (Johnen et al. 2010; Ferguson et al. 2016; Junk et al. 2016; Ferguson and Cook 2014). Indeed, in the future, potential for the development of combined thresholds based on multiple pest species, rather than on each pest individually may serve to further reduce insecticide use, as a recent study has shown, counterintuitively, that the interactive effects of high levels of plant damage by seed and stem weevils can lead to increased OSR seed yield, presumably due to plant overcompensation effects (Gagic et al. 2016). Recent research into using more benign natural products, particularly stone meal, Silico-sec (inert silica diatomaceous earth) and liquid manure as alternatives to insecticides have shown promising results in terms of pollen beetle control (Dorn et al. 2014), but further research is needed into effects on non-target insects, timing and frequency of applications and the persistence of formulations. Better targeting of insecticide applications relative to pest incidence and parasitoid phenology also has potential to lower parasitoid mortality. The main activity period of pollen beetle parasitoids extends from the late bud stages to beyond the end of flowering, and consequently, insecticides applied during flowering (typically targeting seed weevils and pod midge) have particularly deleterious effects (Ulber et al. 2010a). Thus, avoidance of insecticide applications during the flowering period and restriction of those targeting pollen beetles to the earlier green bud stages could reduce negative effects on natural pest control. The time of day at which insecticides are applied could also influence the survival of beneficial insects. Ferguson et al. (2013) found that during flowering, the peak flight activity of both pollen beetles and the parasitoid *Phradis interstitialis* was around midday, and few insects were caught before 10:00 am. Further research, however, is needed to determine whether insecticide applications early or late in the day could maintain pollen beetle control yet reduce parasitoid mortality.

Spatial targeting of insecticides only to areas of high pest density is another means by which parasitoid mortality could be reduced. Ferguson et al. (2003) noted that while *P. interstitialis* had a close spatial association with its host, another parasitoid, *Tersilochus heterocerus* was more evenly distributed across the field than the pollen beetle larvae, thus insecticide targeting to only the beetle-dense areas could help to conserve *T. heterocerus* at least. Where a trap crop is used, the application of insecticide to the trap crop before the beetles move on to the main crop also has the potential to improve spatial targeting (Cook et al. 2013a; Čuljak et al.

). It is important to note, however, that where insecticides are used, even if direct effects on beneficial insects are reduced by these strategies, their populations or activity are still likely to be reduced, possibly by sub-lethal effects, or simply through the reduction of available hosts. Unsprayed field margin areas where brassicas are present are therefore likely to be of great importance in maintaining populations of brassica-specialist pollen beetle parasitoids (Skellern et al. in prep).

Tillage

The varying degree of disturbance caused by different pre- and post-OSR soil tillage regimes can differentially impact abundance and survival of pollen beetle parasitoids and generalist predators. In particular, because pollen beetle parasitoids overwinter in the soil of former oilseed rape fields (Nitzsche and Ulber 1998), leaving fallow ground or using reduced-disturbance forms of tillage such as direct drilling in the establishment of the crops following oilseed rape can greatly enhance parasitoid survival compared with plough-based systems. Experiments in Sweden and Finland showed that overwintering survival of parasitoids was around four times higher from fallow or direct drilling treatments, compared with ploughing or disc-based non-inversion techniques (Nilsson 1985; Hokkanen et al. 1988). Ferguson et al. (2007) gave similar results with fallow treatments showing the highest survival rates, followed by non-inversion, and plough-based treatments the lowest. Other studies from Germany have also confirmed the detrimental effects of ploughing on parasitoid survival (Nitzsche and Ulber 1998; Wahmhoff et al. 1999). Hanson et al. (2015), however, detected no difference in parasitoid emergence following ploughing vs disc- or tine-based tillage, but made no comparisons with post-OSR fallow or direct drilling techniques.

There is some evidence that generalist predators, particularly spiders, are influenced by tillage regime with ploughing showing more disruptive effects than lower disturbance methods (House and Stinner 1983; Haskins and Shaddy 1986). However, other studies have shown a beneficial effect of pre-OSR ploughing on *Erigone* and *Oedothorax* (Linyphiidae) populations, but no influence of post-OSR tillage regime (Williams and Ferguson 2008). The same study showed no impact of pre- or post-OSR tillage on carabid numbers or species richness. Many carabid species overwinter in field boundary habitats and migrate into crops in spring and summer and thus may avoid autumn tillage-related injury, but if ploughing is used in the establishment of spring crops, more detrimental effects are seen (Büchs 2003).

Although pollen beetles and their parasitism rates can be indirectly influenced (via growth stage and density-dependence effects) by the tillage treatments used in OSR crop establishment (Williams & Ferguson, 2008), the tillage methods used post-OSR have little effect on the pest, as unlike their parasitoids, the adults overwinter elsewhere and not within-field (Rusch et al. 2012). This implies that the encouragement of low-disturbance tillage methods for the establishment of crops following OSR, in particular direct drilling, presents an opportunity to enhance parasitoid populations without having detrimental effects on generalist predators, and without having positive effects on the pest.

Comparisons of crop management strategies for OSR

An integrated crop management strategy (ICM) for OSR, based on reduced tillage (to enhance parasitoid survival, and to reduce crop establishment-related energy use) and spraying to pest thresholds has been compared with 'standard' agronomic procedures (plough-based tillage and spraying to schedule) as part of an EU project (Nilsson et al. 2015). Standard and ICM procedures were compared at sites in Germany, Poland, Sweden and the UK, in terms of their effects on pests, yields, energy use and crop production costs. Insecticide applications were more than halved where control thresholds were used, and parasitism rates in aggregate across three major pests of OSR (seed and stem weevils, and pollen beetles) were significantly higher in untreated than sprayed plots. While the ICM system generally needed an extra herbicide treatment, because of the need to curb weeds otherwise controlled through ploughing, and yields were slightly lower, total production costs and energy use were also lower for the ICM system, meaning that growing the OSR under ICM would often be economically favourable for farmers, and more environmentally sustainable. These results are encouraging, but potential clearly exists to improve upon the ICM system studied, by integrating more of the crop management practices/aspects discussed above, favouring better control of pollen beetles and other OSR pests.

Conclusions

Crop management has important influences on pollen beetle abundance, the damage caused and on natural enemy populations and activity. It seems that more dense, high nutrient status crops (particularly with regard to nitrogen availability at damage-susceptible growth stages) are the most tolerant of attack and these conditions also facilitate parasitoid activity through density-dependence effects and improved host-seeking efficiency. Choice of cultivar

is also important, but in the absence of a standard pollen beetle resistance rating scheme, farmers have little basis on which to make this decision. Scope exists to adapt the spatial and temporal targeting of insecticides, or to use more benign products to reduce detrimental effects on non-target beneficial insects. The potential to use growth regulators to manipulate pest populations warrants further investigation, and reduced tillage establishment techniques following the OSR crop should be encouraged to enhance parasitoid survival between seasons. Crop rotation can have important effects on pest abundance, but these are mediated mostly at the landscape scale. Indeed, the implications of crop management tactics for pollen beetles and their natural enemies need to be considered alongside landscape-scale processes, as both influence insect abundance and damage. On balance, it seems that landscape-scale processes may be the more important determinant of pollen beetle abundance (Rusch et al. 2013b), while damage is a product of both landscape-scale processes and, through management, the crop's injury-compensation capability (Rusch et al. 2013b; Valantin-Morison et al. 2007).

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