

Chemical and visual ecology of the Symphyta

Quentin Guignard¹  | Bernard Slippers²  | Jeremy Allison^{1,3} 

¹Department of Zoology and Entomology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa

²Department of Biochemistry, Genetics and Microbiology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa

³Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, Ontario, Canada

Correspondence

Quentin Guignard, Department of Zoology and Entomology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria 0002, South Africa.
Email: quentin.guignard@fabi.up.ac.za

Abstract

1. The Symphyta is the most basal sub-order of the Hymenoptera and includes the woodwasps, horntails and sawflies, many of which are pests. Adults are generally short-lived and as a result males and females experience strong selection to rapidly find a mate and females to find oviposition sites. Mate-searching typically relies on visual and olfactory stimuli such as sexually dimorphic morphology (i.e., body parts used in signalling) and pheromones.
2. Here we review the available literature on the chemical and visual ecology of the Symphyta with potential for use in survey and detection programmes. Stimuli reviewed include but are not limited to sex pheromones, larval defensive compounds, plant kairomones and colour preferences.
3. Sex pheromones are known for 19 species of Symphyta and show shared evolutionary patterns in chemistry, production site and ecological role.
4. In general, sex pheromones in the Symphyta are female-produced, oxidized cuticular hydrocarbons and yellow traps capture more individuals than other colours, although exceptions do exist. More work is needed to expand on these and identify new patterns in the visual and chemical ecology of the Symphyta.

KEYWORDS

colour vision, Hymenoptera, insect control, pheromone

INTRODUCTION

The Hymenoptera started to diversify ~280 million years ago during the Permian period. More than 115,000 extant species of Hymenoptera (e.g., bees, ants, wasps, sawflies) have been described, but it has been estimated that as many as a million species remain undescribed (Sharkey et al., 2017). Two suborders are recognized (Peters et al., 2017). The Symphyta is an older paraphyletic group that contains the primitive Hymenoptera (woodwasps, horntails and sawflies). The younger suborder, the Apocrita (e.g., ants, bees, wasps), is monophyletic. Although the Symphyta is not a monophyletic group, we use it in this review to refer to non-Apocrita Hymenoptera.

The Symphyta contains ca. 8855 species in 817 genera, 7 superfamilies and 14 families (Sharkey et al., 2017; Taeger et al., 2010, 2018). Phylogenetic studies split the Symphyta into three major

groups that differ in larval feeding habit. The suspected ancestral group, the Eusymphyta (superfamily: Tenthredinoidea, Xyeloidea and Pamphiloidea) are ectophytophagous and monophyletic. The second group, the endophytophagous Symphyta (superfamily: Cephoidae, Xiphidrioidae, Siricoidea) are paraphyletic. The third group includes the superfamily of Orussoidea which are larval parasitoids and are monophyletic.

Similar to many other insects, the Symphyta are important components of food webs. Larvae actively contribute to the carbon chain by decomposing plant material. Larvae usually feed on plant tissues (e.g., nectar, pollen, leaves, sap, fruit juice) although some species feed on fungal and insect tissues (Jervis & Vilhelmsen, 2000). Adults can be important pollinators (Asenbaum et al., 2021; Barbir et al., 2019). Several species from the family Tenthredinidae have potential for use as biological control agents against invasive plants (Smith, 1993). For

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Agricultural and Forest Entomology* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society.

example, the Tenthredinidae *Nematus oligospilus* was identified as a potential biological control agent for *Salix* spp. in Australia (Caron et al., 2011, 2014). Another Tenthredinidae, *Lophyrotoma zonalis*, was found to be a potential biological control agent for the paperbark tree in Florida (Burrows & Balciunas, 1997), and *Heteroperryia hubrichi* (Pergidae) as a potential biological agent of the Brazilian peppertree (Cuda et al., 2005).

Some species of Symphyta can be important pests of cultivated plants including roses (Özbek & Çalmaşur, 2005), fruit trees (Boevé et al., 1996; Ibrahim et al., 2019), rapeseed-mustard (Patel et al., 2017), stem crops (Wallace & McNeal, 1966), plum trees (Kárpáti et al., 2021) and pine trees (Slippers et al., 2011). Some pest species of Symphyta can have significant economic impact. For example, the wheat stem sawfly *Cephus cinctus* can cause more than 30% crop loss with an associated cost of \$350 million in the Great Plains of North America (Beres et al., 2011). The potential losses associated with the establishment of the invasive woodwasp *Sirex noctilio* in Eastern Canada on pine trees were estimated to range from \$86 to \$254 million per year (Yemshanov et al., 2009). In Finland, the large pine sawfly *Diprion pini* was found to reduce growth of pine trees up to 94% and kill up to 30% of trees after an outbreak with an estimated cost of \$310/ha in 1 year (Lyytikäinen-Saarenmaa & Tomppo, 2002). Between 1997 and 2010 at Mt. Hinokiboromary (Japan), ~18% of beech trees were killed by the nematine sawfly *Fagineura crenativora* (Koshiji et al., 2012 in Watanabe et al., 2018). Two years of severe attack by the pine sawfly *Neodiprion sertifer* caused a 33% volume loss in mature pine trees (Austarå et al., 1987). In Sweden, larvae of the European birch sawfly *Arge pullata* are toxic and can be ingested by pets and cattle (Anderbrant & Broad, 2019).

With the exception of Antarctica, Symphyta are found on every continent on earth. They occupy diverse environments, from arid to tropical forests, wherever their host plants are present. New discoveries of symphytan pests outside their native range have often been reported (Blank et al., 2010; Kirichenko et al., 2019; Looney et al., 2016; Macek & Sipek, 2015; Park et al., 2019) suggesting that as a group they have a high invasion potential. The rate of introduction of invasive pests and pathogens is expected to increase with climate change and globalization (Bradshaw et al., 2016; Chakraborty & Newton, 2011; Huang et al., 2011; Qin et al., 2019; Sharma et al., 2017; Yan et al., 2017; Ziska et al., 2011) suggesting that incursions by Symphyta may become more common.

Globally there has been an increase in the need for survey and detection tools against insect pests, including the Symphyta. Understanding and managing the spread of invasive species is more important than ever and relies on efficient detection tools. Survey and detection tools facilitate determination of which pests are present, population levels and associated damage. They also facilitate the evaluation of the impact of intervention treatments. However, the development and implementation of efficient survey and detection tools require a good understanding of the biology of the targeted insect pest.

Adult Symphyta usually live for a few days up to a few weeks (Smith, 1993) and thus experience selection to rapidly locate mates

and host plants. Adults generally rely on vision and olfaction to locate these resources. As a result, these stimuli alone or in combination can be replicated on traps to significantly increase insect capture (Domingue et al., 2013; Hawkes et al., 2017; Raguso & Willis, 2005; Shrestha et al., 2019; Silk et al., 2019; Vuts et al., 2012). Research on the visual and chemical ecology of the Symphyta offers opportunities to develop survey and detection tools. This review synthesizes the literature on and the chemical and visual ecology of the Symphyta with an emphasis on stimuli with potential applications for survey and detection.

VISUAL AND CHEMICAL BASIS FOR MATE LOCATION IN SYMPHYTA

The morphology and behaviour of the Symphyta suggest that vision and olfaction play an important role in its biology. The majority of Symphyta possess antennae, two compound eyes and three ocelli. Most adult Symphyta are diurnal (Naumann, 1997) and diurnal species typically rely, at least partially, on visual stimuli to locate mates and hosts.

In some insects, mate location is mediated by sexually dimorphic traits. Sexual dimorphism in the Symphyta includes differences in eye (e.g., Abiinae), mandible (e.g., Cimbicidae) and hind leg (e.g., Siricidae, Cimbicidae) size, antennal morphology (e.g., Diprionidae), body colouration and pheromone production (Cooperband et al., 2012; Crook et al., 2008; Hallberg, 1979; Vilhelmsen, 2019). Martínez et al. (2014) placed sticky mesh at various heights in pine canopies in Argentina and observed that females flew higher when males were present than when males were absent. Field trials comparing traps baited with males to traps without males suggest that female *S. noctilio* use visual stimuli to locate males (Allison et al., 2019). Cumulatively, the available morphological and behavioural evidence suggests that Symphyta use visual stimuli to locate mates and hosts.

Transcriptome studies reflect the importance of olfaction in the Symphyta. A total of 72 odorant receptor genes were found in the *C. cinctus* genome (a smaller number than all species of Apocrita with known numbers of odorant receptors) (Robertson et al., 2018), and 28 odorant receptors were identified in the antennal transcriptome (Gress et al., 2013). A phylogenetic analysis of these odorant receptors revealed homology with other apocritan (*Apis mellifera* and *Nasonia vitripennis*) odorant receptors, but some lineages conserved in the Symphyta have been lost in the Apocrita (Ferguson et al., 2021; Robertson et al., 2018). Antennal structures in the Symphyta also suggest an important role for long- and short-range communication. Lower Cretaceous Symphyta fossils already showed large male antenna supposedly used in long-distance mate finding (Krogmann et al., 2013). Studies of *S. noctilio* antennae show that ~80% of sensilla on the antennae were contact pheromone receptors (Crook et al., 2008). The sensillar structure and/or the morphology of the antenna can be sexually dimorphic (Hallberg, 1979; Schmidt et al., 2006). For example, differences in the antennal ultrastructure of male and female *Acantholyda posticalis* (Pamphilidae) strongly suggest

the presence of a long-range sex pheromone (Yuan et al., 2013). Transcriptomic, morphological and physiological data show that Symphyta can use their antenna and other body parts [*S. noctilio* can detect host volatiles with their ovipositor (Hayes et al., 2015)] to detect volatile organic compounds.

Cuticular hydrocarbon (CHC) production in the Symphyta is also sexually dimorphic. The primary role of CHCs in communication of solitary hymenoptera is to mediate mate, species and sex recognition. The complexity of CHC profiles in the Symphyta is similar to the rest of the Hymenoptera, including social species (Kather & Martin, 2015). Long chains of alkenes in *C. cinctus* [(Z)-9-pentacosene and (Z)-9-heptacosene] and *S. noctilio* [(Z)-7-heptacosene, (Z)-7-nonacosene and (Z)-9-nonacosene], or alkadienes in *Pikonema alaskensis* [(Z,Z)-9,19-alkadiene] and *A. erythrocephala* [(Z,Z)-1,9,15-pentacosatriene] were only found on females and were shown to elicit a copulatory response or to excite males (Bartelt et al., 1982, 2002; Böröczky et al., 2009). Experimental evidence suggests that female *L. analis* (Pergidae) with their CHCs removed are not attractive to males but become attractive when their CHCs are reapplied (Schmidt et al., 2006). Similarly, body washes of virgin females in two *Cephalcia* species were more attractive to males than male extracts (Borden et al., 1978; Nemer et al., 2007).

PHEROMONES IN SYMPHYTA

We mapped known sex pheromones of Symphyta onto a recent phylogeny representing the relationships of the families in this order (Peters et al., 2017) to look for possible evolutionary patterns (Figure 1). Volatile pheromones from 19 species within 6 families of Symphyta are known from the literature; 12 species of Diprionidae and in 1 to 2 species from the 5 other families (2 Pamphiliidae, 1 Nematinae, 1 Tenthredininae, 1 Siricidae and 2 Cephidae). All the pheromones described were released by females, except for the putative male pheromone of the woodwasp *S. noctilio*. The chemical structure found in most Symphyta pheromones includes an oxygen functional group (mostly aldehyde, alcohol, ketone or ester) followed by a long alkene, alkane or branched-alkane chain. The different compounds found within and between species mostly differ in their functional groups and carbon chain lengths. This chemical structure is found in several families and may be ancestral in the Symphyta.

In the Symphyta, volatile pheromones have been most extensively studied in the family Diprionidae (Genus: *Diprion*, *Neodiprion*, *Macrodicprion*, *Microdiprion* and *Gilpinia*). In brief, sex pheromones in this family are released by females and usually follow a similar structural motif. The sex pheromone precursor in the Diprionidae is typically a chain of 3,7-methylalkane-2-ol 11–16 carbons long (Anderbrant et al., 2011, 2021; Bång et al., 2011; Bergström et al., 1995, 1998; Hedenström et al., 2006, 2009; Jewett et al., 1976; Olaifa et al., 1987, 1988; Östrand et al., 2003; Tai et al., 1998, 2002; Wassgren et al., 1992, 2000). Some species possess an additional methyl group at various positions on the 3-methylalkane-2-ol precursor (Bergström et al., 1998; Wassgren et al., 2000). The pheromone

precursor is stored in the female and is esterified into an acetate and/or a propionate during release (Anderbrant, 1999). Pheromone precursors are typically present in higher titres than the pheromone making them easier to identify.

The pheromone production pathway appears to be well conserved in the Diprionidae. In addition to known pheromones, field trials with different possible esterified isomers were attractive to several species of Diprionidae (Anderbrant et al., 1997; Guo-fa et al., 1997; Kikukawa et al., 1982; Kraemer et al., 1983, 1984; Olaifa et al., 1984; Zhang et al., 2005). Although these structures have not been confirmed as pheromones, their activity in field trials and similarity to known pheromones of other species of Diprionidae suggest that they are pheromones. To date, pheromones and/or pheromone precursors of 12 Diprionidae species have been identified and field trials have identified putative pheromones in an additional 8 species (see Table S1, Supporting Information). For these compounds, additional work is required to confirm production and release of the pheromone and/or precursors. Usually, one isomer elicits larger antennal responses and/or captures more males in field trials (Anderbrant et al., 2005; Hedenström et al., 2006, 2009; Kraemer et al., 1984). The response of Diprionidae to additional isomers can vary with dose (Anderbrant et al., 2021), ratios (Olaifa et al., 1988) and among populations (Anderbrant et al., 2000). Details of the precursor chemistry, antennal activity and field trial responses to the different isomers in the Diprionidae have been reviewed by Anderbrant (1993, 1999).

The chemistry of volatile pheromones identified in the rest of the Symphyta is similar among distant families. Volatile pheromones in the Symphyta generally include a long chain of alkene with an oxygen-containing functional group [Pamphiliidae (Baker et al., 1983; Staples et al., 2009), Nematinae (Bartelt et al., 1983; Bartelt & Jones, 1983), Tenthredininae (Hall et al., 2017), Cephidae (Bartelt et al., 2002; Cossé et al., 2002), Siricidae (Cooperband et al., 2012; Faal et al., 2022; Guignard et al., 2020)]. Within species, pheromone components usually have similar functional groups but different alkene chain lengths. Functional groups include alcohols (Siricidae and Nematinae), aldehydes (Pamphiliidae, Nematinae), esters (Tenthredininae) and acetoxyl (Cephidae). The sex pheromone of the web-spinning larch sawfly (Pamphiliidae) differs from the rest of Symphyta as it is the only one with two functional groups (amino and ketone) branched on a cyclohexatriene (Baker et al., 1983). This pheromone induced abdomen flexing and short flights in males but no upwind flight. There is a need to study more families to get a broader understanding of the evolution of pheromone chemistry in the Symphyta.

Two primary sites of sex pheromone production have been reported in the Symphyta. In the Pamphiliidae (Staples et al., 2009), Nematinae (Bartelt et al., 1983), Siricidae (Faal et al., 2022) and Cephidae (Bartelt et al., 2002) female-specific CHCs are oxidized into smaller and more volatile sex pheromones. Extracts of the female abdomen of the cedar web-spinning sawfly *C. tannourinensis* and the pine sawfly *N. sertifer* had much higher titres of sex pheromone than extracts of the head and thorax (Nemer et al., 2007; Wassgren et al., 1992). The putative sex-aggregation pheromone released by

male *S. noctilio* is the only pheromone in the Symphyta known to be stored in a specific body part (the hind legs) (Guignard et al., 2020). Pheromones for the rest of the Symphyta were not found to be stored

in a specific gland and are all released by females. The chemistry of pheromones from different release sources does not strongly differ in the Symphyta.

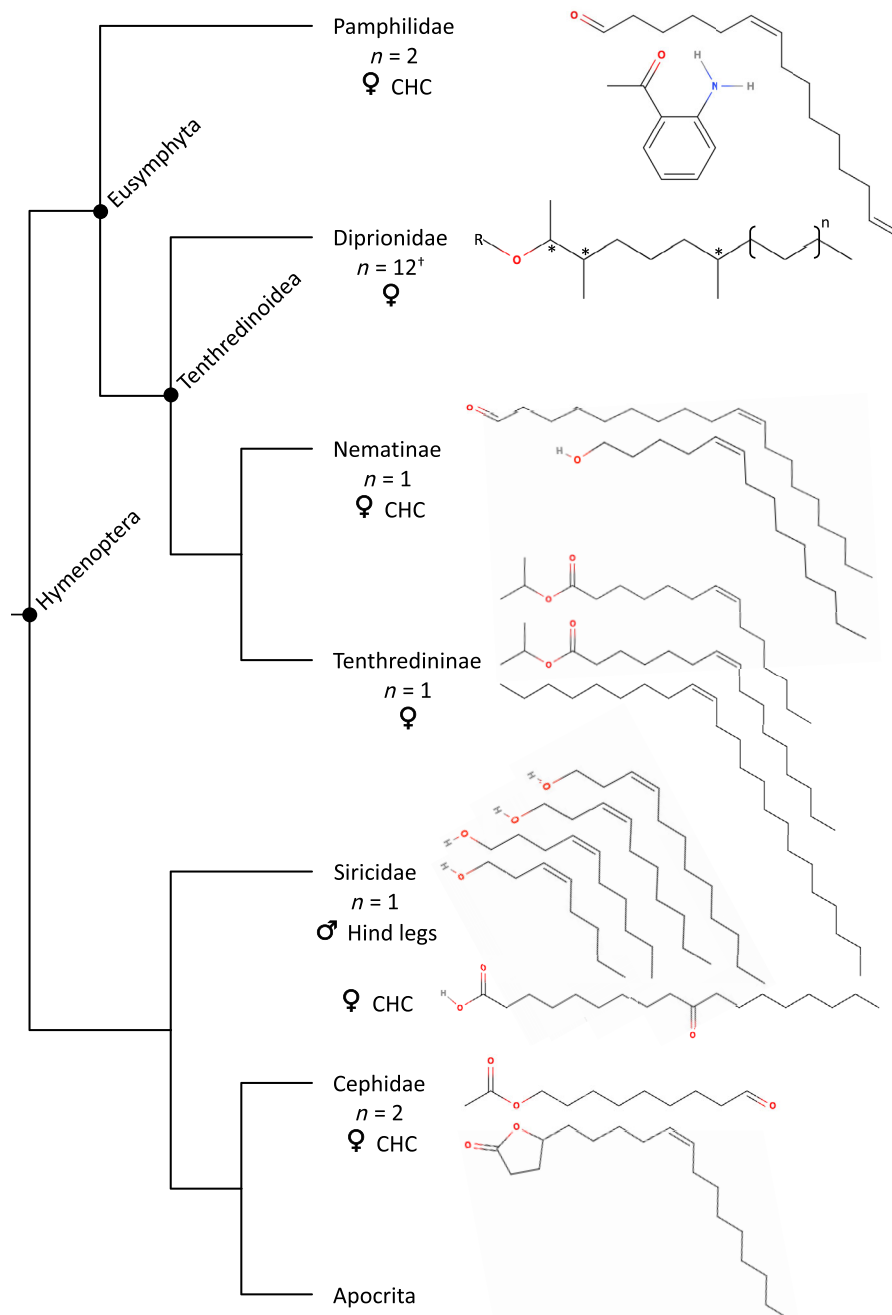


FIGURE 1 Phylogenetic tree of non-Apocrita hymenopteran families (left, adapted from Peters et al., 2017) and their corresponding pheromone structures (right). The number of species where the pheromone was available from literature was indicated by N. In Diprionidae, three structures are possible: R=H for the alcohol precursor, R=COCH₃ for the acetate or R=COCH₂CH₃ for the propionate. Only the acetate or propionate is active in the field. *Indicates asymmetric centres. †Pheromones in Diprionidae were identified in 12 species but attractive isomers were tested in 20 species (see text). The length of carbon chain (n) after the 7th carbon can vary for a total of 11–16 and can include an extra methyl group (e.g., *Macrodiprion nemoralis*, *Microdiprion pallipes* or *D. nipponica*). Pamphiliidae: (Baker et al., 1983; Staples et al., 2009), Nematinae (Bartelt et al., 1983; Bartelt & Jones, 1983), Tenthredininae (Hall et al., 2017), Cephidae (Bartelt et al., 2002; Cossé et al., 2002), Siricidae (Cooperband et al., 2012; Guignard et al., 2020), Diprionidae; see Table S1, Supporting Information

Pheromone-based tactics have potential for use in the field to manage populations of Symphyta. For example, strong mating disruption of the pine sawfly *N. sertifer* was observed in plantations where the percentage of male cocoons (this species is parthenogenetic and unmated females only produce male progeny) increased from 3% to 46% in forests treated with sex pheromones (Martini et al., 2002). In the field, traps baited with the respective synthetic female sex pheromones of *Cephalcia lariciphila* (Baker et al., 1983), *A. erythrocephala* (Staples et al., 2009), *Janus integer* (James et al., 2003), *P. alaskensis* (Bartelt et al., 1983), *Nematus olfaciens* (Hall et al., 2017) and *C. cinctus* (Cossé et al., 2002) captured more males than unbaited controls. In *N. olfaciens*, the addition of the (Z)-9-tricosene CHC present in both male and female to a blend of two volatile pheromones extracted from virgin females significantly increase the number of catches compared with blends without the CHC (Hall et al., 2017). Although the potential for use in the field to monitor these species has been demonstrated, management programmes that include the use of these pheromones have not yet been developed. In *S. noctilio*, both the male and female pheromones were attractive in lab bioassays, but have not been shown to be attractive in the field (Cooperband et al., 2012; Faal et al., 2022; Hurley et al., 2015) suggesting they may have limited utility for survey and detection of this pest of plantation pines.

The chemical ecology of the Symphyta includes larval compounds. Tenthredinidae larvae release a great diversity of volatile compounds from their ventral gland thought to be defensive compounds (Boevé et al., 1992, 2000; Duffield et al., 1990; Jonsson et al., 1988). 1,6-Germacradien-5-ol released from larvae of the diprionidae *N. sertifer* likely possess an antimicrobial function (Bergström et al., 1994). These larval compounds have not been shown to be attractants and for that reason are not considered further in this review. However, unidentified larval compounds such as trail pheromones (Flowers & Costa, 2003; Vincent et al., 2019) could be useful for future pest control programmes.

VISION IN SYMPHYTA

Very little is known about the visual ecology of the Symphyta. Humans typically perceive colour by comparing the information received from the red, green and blue photoreceptors ($\lambda_{\max} = 564, 534$ and 420 nm, respectively). The three photoreceptors found in most Apocrita are the ultraviolet, blue and green sensitive photoreceptors, but their respective sensitivity can vary among species (van der Kooi et al., 2021). Peitsch et al. (1992) used intracellular electroretinograms to demonstrate that between two and four photoreceptors are present in several species of Symphyta. The ultraviolet, blue and green photoreceptors were found in *Tenthredo campestris* (Tenthredinidae) ($\lambda_{\max} = 328, 464$ and 540 nm, respectively), which also possesses an extra red photoreceptor ($\lambda_{\max} = 596$ nm) (Peitsch et al., 1992). The green and red photoreceptors were found in two other species of Symphyta, *T. scrophulariae* ($\lambda_{\max} = 532$ and 592 nm, respectively) and *Xiphydria cameus* (Xiphydriidae) ($\lambda_{\max} = 556$ and 604 nm, respectively). Finally, the only photoreceptor found in

Urocerus gigas (Siricidae) was the green photoreceptor ($\lambda_{\max} = 542$ nm). The ultraviolet and blue photoreceptors are assumed to be present in all species, but were not found during intracellular recordings of *T. scrophulariae*, *X. cameus* and *U. gigas* (Briscoe & Chittka, 2001). A more recent study showed that *S. noctilio* has lost the blue photoreceptor and its associated opsin gene (Guignard et al., 2021). Males and females of this woodwasp express both the ultraviolet ($\lambda_{\max} = 364$ nm) and green photoreceptors ($\lambda_{\max} = 527$ nm), but the red photoreceptor found in other Symphyta seems to have been lost in the Siricidae and in the Apocrita (Guignard et al., 2022).

Colour preference in the field has been tested in a total of 16 species belonging to 4 families (13 Tenthredinidae, 1 Cephidae, 1 Diprionidae and 1 Argidae) of Symphyta (Anderbrant et al., 1989; Barker et al., 1997; Digweed et al., 1997; Holuša & Drápela, 2006; Song et al., 2015; Taniwaki, 2013). Not all the colours were tested for each species, but yellow was preferred to the other colours tested in 12 out of 15 species (Figure 2). In the genus *Dolerus*, results from five different coloured traps were more variable (Barker et al., 1997). The colours non-ultraviolet reflective white (410–700 nm) and yellow (550–770 nm) captured similar numbers of *Dolerus puncticollis*. Black traps (reflecting <2% of reflective light) were preferred to *D. haematodes*, whereas *D. picipes* and *D. nigratus* had no preferences for any of the five colours tested. Finally, *N. sertifer* was more attracted to white traps compared with other colours tested (reflectance was not measured), but yellow traps were not tested (Anderbrant et al., 1989). Koch et al. (2015) reported that yellow traps are particularly attractive to *Athalia* species and *Xenapates similis*. In the same study, the authors reported that white and blue attract different species of Symphyta than yellow and observed that a 'brighter' yellow was more attractive for some species (the authors did not define what brighter means in this context).

The basis for the observed general attraction towards yellow in the Symphyta remains unclear. Colour patterns in Symphyta mostly include orange, yellow or red; green or blue are rarely expressed. Colour patterns can be sexually dimorphic. The frequent occurrence of yellow and colour of close wavelength might partially explain a general attraction of Symphyta to yellow to facilitate mate location. Alternatively, some species of Symphyta are pollinators and feed on pollen or on other insects (Smith, 1993). Hymenopteran pollinators can also be attracted to yellow flowers as they can be a source of food (Papiorek et al., 2016; Reverté et al., 2016). In addition, many herbivorous insects might be attracted to yellow because yellow could be perceived as a super-normal foliage stimulus of a greater intensity than green (Prokopy & Owens, 1983; van der Kooi et al., 2021).

COMMON PATTERNS, KNOWLEDGE GAPS AND FUTURE PROSPECTS

Some patterns in the use of pheromones are beginning to emerge in the Symphyta. Pheromones of different families of Symphyta, feeding on different hosts, released by different sexes, with different sites of

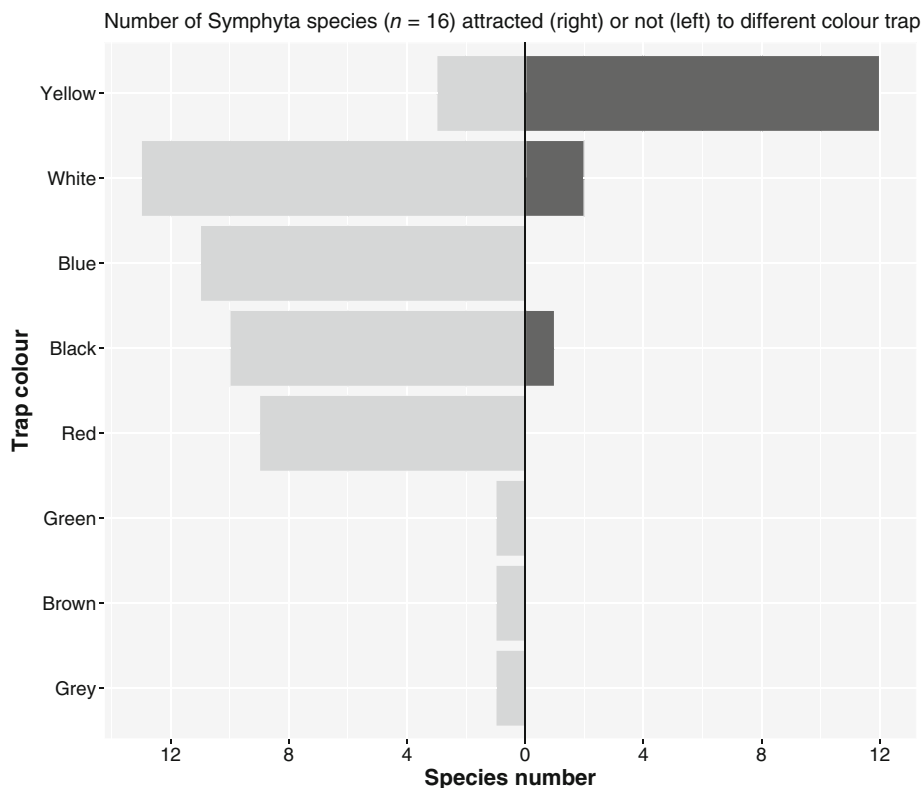


FIGURE 2 Total number of non-Apocrita hymenopteran species ($n = 16$) attracted (right, dark grey) or not attracted (left, light grey) to different colour traps. Colours were considered as attractive when it caught more insects compared with other colours tested. Colours were labelled as non-attractive when significantly less insects were caught as it was not possible to distinguish between nonresponsive or repelled insects in the literature due to the experimental design.

biosynthesis, generally possess a common chemistry: a long alkene (alkane in Diprionidae) chain with oxygen-containing functional group on one end. The (*Z*)-isomer is the common configuration for all double bonds found in Symphyta pheromones. The similar ecology, diet, genes and pathways involved to produce pheromone likely share a common evolutionary origin before the divergence of Symphyta.

The identification of the correct isomer is critical to optimizing the sensitivity of surveillance programmes. Recent re-investigation of *D. similis* reported different pheromone isomers and effects on trap capture than previously reported (Anderbrant et al., 2021). Similarly, more attractive sex pheromone homologues were identified in *D. nipponica* (Tai et al., 1998, 2002) and in *M. pallipes* (Bergström et al., 1998; Östrand et al., 2003) after re-investigation. Anderbrant et al. (2021) suggested that some of the Diprionidae pheromones identified in the 1970s and 1980s could have been misidentified due to poor replication and contaminated mixtures of stereoisomers. Coupled gas-chromatography with electroantennographic detection and/or mass-spectrometry has become more affordable and machines more sensitive. These improved technologies combined with separation methodologies to quickly identify the pheromone precursor isomers (Bång et al., 2012) should facilitate the re-investigation of potentially misidentified pheromones.

The site of pheromone biosynthesis and storage has received limited attention to date. Sex pheromones in Symphyta (except Diprionidae) are thought to be oxidized CHCs and could be ancestral

in the Hymenoptera. The impact of factors such as light, humidity or temperature on CHC oxidation is unknown in the Symphyta but can be significant in other insects (Hatano et al., 2020). This information could accelerate future research on where and how to find pheromones in the Symphyta. In addition, knowledge of the biosynthetic pathways involved could decrease the cost of production of synthetic pheromone for large scale integrated pest management programmes.

The performance of a synthetic pheromone in the field could be negatively affected by multiple factors. For example, temperature, light and humidity could all alter the chemical composition of a pheromone blend (Nielsen et al., 2019; Zhu et al., 2015). For these reasons, care must be taken to guarantee that the chemistry of the synthetic pheromone blend does not degrade over time. For example, extensive studies with *N. sertifer* show that both isomerism and chemical composition have a strong influence on the performance of pheromone-baited traps. Field experiments using shorter analogues of the main pheromone were not as successful as those baited with the original pheromone (Anderbrant et al., 2010). Field trials also demonstrated geographic variation in the response of male *N. sertifer* to isomers of pheromone components with synergistic, antagonistic or no effects observed in different populations (Anderbrant et al., 2000, 2010). New materials available for use as dispensers can provide better protection of pheromone components from abiotic factors, in addition to more stable release rates.

In some cases, the performance of pheromone lures can be improved when they are coupled with other stimuli such as kairomones or visual attractants. For example, in some species of woodborers, traps baited with synthetic pheromone lures alone capture few individuals but high numbers are captured when pheromone is coupled with host volatiles (Allison et al., 2012; Silk et al., 2007; Teale et al., 2011). Artificial lights are used to control and manage populations of some pest insects (Kim et al., 2019) and provide basic ecological information, often missing for species of Symphyta. The performance of semiochemical-baited traps could be enhanced with the addition of visual stimuli such as artificial lights. In cases where artificial lights cannot be implemented, odourless paint (to avoid any negative interactions between the paint and semiochemical lures) may improve trap captures.

The biology of some Symphyta suggests that attractive stimuli other than pheromones may have more potential to trap insects and could be easier to use in the field. For example, both male and female *S. noctilio* fly to the top of the canopy after they emerge from host trees. There, males form leks which may be mediated by the putative sex-aggregation pheromone (Cooperband et al., 2012; Guignard et al., 2020) and mate with females. Traps placed at the bottom of trees and baited with this putative pheromone are not attractive in the field (Hurley et al., 2015; Sarvary et al., 2015). It is possible that at this height the activity of the male pheromone is reduced as only females searching for an oviposition site fly at this height. Mated *S. noctilio* females were shown to be more attracted to the volatiles emitted by their symbiotic fungus than a closely related fungus (Sarvary et al., 2016). The symbiotic fungus in *S. noctilio* degrades the wood into nutrients ingested by larvae (Thompson et al., 2013). It is possible that females coming down from the canopy might choose trees already infected by the fungus indicating a suitable environment for their brood. In this context, traps baited with a fungal kairomone and coupled with ultraviolet lights [shown to attract females (Sarvary et al., 2015)] may have more application for *S. noctilio* management than traps baited with the putative male pheromone deployed at the base of host trees. Traps baited with these visual and olfactory stimuli may capture mate- (ultraviolet light) and host- (fungal kairomone) searching females.

The chemical and visual ecology of Symphyta does not feature prominently in the management of Symphyta. Silviculture (Dodds et al., 2014), selection for resistant plants (Beres et al., 2011), entomopathogenic nematodes (Narayanan & Gopalakrishnan, 2003; Nježić & Ehlers, 2020; Portman et al., 2016; Slippers et al., 2012) and fungi (Fätu et al., 2021), parasitoids (Fischbein & Corley, 2015; Portman et al., 2018) and nucleopolyhedrovirus (Lucarotti et al., 2007) are effective methods alone or in combination to control Symphyta pests. In some Symphyta insecticides are ineffective due to the larvae being protected inside the host plant [e.g., *C. cinctus* (Portman et al., 2018)].

Symphyta are often host specific and several studies have identified kairomones such as plant volatiles (Crook et al., 2012; Piesik et al., 2008) that can be used to monitor and capture these pests. Specific host volatiles can also influence Symphyta oviposition behaviour.

For example, *C. cinctus* lays more eggs in the susceptible hollow wheat due to less mechanical resistance, which also release the (Z)-3-hexenyl acetate in higher quantities than the more solid and resistant cultivar (Piesik et al., 2008; Weaver et al., 2009). At shorter range, contact kairomones (Barker et al., 2006; Braccini et al., 2015; Fernández et al., 2019) and host physiology (Madden, 1974; Mumm & Hilker, 2006) are important factors to trigger oviposition. Recently, it was shown that exposure of host trees to sawfly pheromones induces host plant defences (Bittner et al., 2019). Mechanisms underlying these responses remain unknown but offer potential for incorporation into sawfly management programmes.

A single electroretinogram study (Peitsch et al., 1992) of four species demonstrated that some Symphyta possess an extra photoreceptor sensitive to red light. This photoreceptor seems to be lost in the rest of the Hymenoptera (Guignard et al., 2021; Peitsch et al., 1992). The role of the extra red photoreceptor is unknown, but it could allow Symphyta to respond to light not visible to other Hymenoptera. Investigating if the wavelengths that activate this photoreceptor (~600–700 nm) are attractive to Symphyta could improve selectivity and efficiency of traps. Narrow-band LED and paint could also be used to determine the most attractive colour, if any. In addition, the loss of blue photoreceptor and associated gene in *S. noctilio* demonstrates that Symphyta possess from two to four photoreceptors in a few closely related families (Guignard et al., 2021). As a result, the Symphyta offer a unique opportunity to study the ecological mechanisms (e.g., feeding habits) underlying the rapid gain and loss of visual opsins and associated photoreceptors.

The Symphyta are difficult to rear in the laboratory and thus the availability of insects is dependent on labour-intensive laboratory rearing or field-collected material and as a result is usually limited. Laboratory colonies do not exist for many of the most damaging species (e.g., *S. noctilio*) and researchers have to collect infested material from the field and store it until insects emerge. Typically, insects are available for a short time window and research cannot be conducted continuously throughout the year. Ultimately, the unreliable supply of insects limits the number of experiments that can be conducted during the year and influences the number of replicates for each experiment. By contrast, continuous rearing of *C. cinctus* is possible, although it takes ca. 7 months to rear one generation (Macedo et al., 2005). In most cases, the rearing of Symphyta is difficult due to their sensitivity to abiotic conditions (e.g., temperature, photoperiod, humidity) (Knerer, 1984). As a result, a model Symphyta which would facilitate detailed experimental work and improve the fundamental knowledge of Symphyta, does not exist at the moment.

CONCLUSION

Understanding the modalities and stimuli that mediate host and mate location in the Symphyta has immense potential to inform the development of management tactics. In many Symphyta, pheromones are present and mediate mate-searching. Pheromone baited lures remain one of the most specific and sensitive methods to monitor population

levels and subsequently prevent outbreaks together with other control methods. Technological advances have the potential to facilitate the development of management tactics for forest insects, including the Symphyta (Slippers et al., 2020). More Symphyta genomes are available, which facilitates the development of new technology such as reverse chemical ecology (Li et al., 2021) or CRISPR-Cas9 (Pickett, 2014). Accurate identification of Diprionidae pheromone isomers and an increase in compound purity can increase the number of insects caught in 'attract and kill' programmes. The visual ecology of Symphyta has received little attention from a genetic to a behavioural level. The effect of factors such as achromatic visual contrast with the background or polychromatic stimuli is largely unknown and could be attractive at long and short ranges. Finally, developing rearing protocols for Symphyta could greatly accelerate research done on this group of insects.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Quentin Guignard  <https://orcid.org/0000-0002-9566-4365>

Bernard Slippers  <https://orcid.org/0000-0003-1491-3858>

Jeremy Allison  <https://orcid.org/0000-0002-0765-3149>

REFERENCES

- Allison, J.D., McKenney, J.L., Millar, J.G., McElfresh, J.S., Mitchell, R.F. & Hanks, L.M. (2012) Response of the woodborers, *Monochamus carolinensis* and *Monochamus titillator* (Coleoptera: Cerambycidae) to known cerambycid pheromones in the presence and absence of the host plant volatile α -pinene. *Environmental Entomology*, 41(6), 1587–1596. <https://doi.org/10.1603/EN12185>
- Allison, J.D., Slippers, B., Bouwer, M. & Hurley, B.P. (2019) Simulated leks increase the capture of female *Sirex noctilio* in the absence of host volatiles. *International Journal of Pest Management*, 67(1), 58–64. <https://doi.org/10.1080/09670874.2019.1695074>
- Anderbrant, O. (1993) Pheromone biology of sawflies. In: *Sawfly life history adaptations to woody plants*, Vol. 119. San Diego, CA: Academic Press Inc, p. 154.
- Anderbrant, O. (1999) Sawflies and seed wasps. In: *Pheromones of non-lepidopteran insects associated with agricultural plants*. Wallingford: CABI Publishing, pp. 99–226.
- Anderbrant, O., Bengtsson, M., Löfqvist, J. & Baeckström, P. (1992) Field response of the pine sawfly *Neodiprion sertifer* to controlled release of diprionyl acetate, diprionyl propionate and trans-perillenal. *Journal of Chemical Ecology*, 18(10), 1707–1725. <https://doi.org/10.1007/BF02751097>
- Anderbrant, O. & Broad, G.R. (2019) The European birch sawfly, *Arge pullata* (Hymenoptera: Argidae), in Sweden, and the first national record of its parasitoid *Scolobates testaceus* (Hymenoptera: Ichneumonidae). *Entomologisk Tidskrift*, 140, 59–64.
- Anderbrant, O., Hansson, B.S., Hallberg, E., Geri, C., Varama, M., Hedenström, E. et al. (1995) Electrophysiological and morphological characteristics of pheromone receptors in male pine sawflies, *Diprion pini* (Hymenoptera: Diprionidae), and behavioural response to some compounds. *Journal of Insect Physiology*, 41(5), 395–401. [https://doi.org/10.1016/0022-1910\(94\)00126-2](https://doi.org/10.1016/0022-1910(94)00126-2)
- Anderbrant, O., Löfqvist, J., Hedenström, E., Bång, J., Tai, A. & Högberg, H.-E. (2010) Field response of male pine sawflies, *Neodiprion sertifer* (Diprionidae), to sex pheromone analogs in Japan and Sweden. *Journal of Chemical Ecology*, 36(9), 969–977. <https://doi.org/10.1007/s10886-010-9834-y>
- Anderbrant, O., Löfqvist, J., Högberg, H.-E., Hedenström, E., Baldassari, N., Baronio, P. et al. (2000) Geographic variation in the field response of male European pine sawflies, *Neodiprion sertifer*, to different pheromone stereoisomers and esters. *Entomologia Experimentalis et Applicata*, 95(3), 229–239. <https://doi.org/10.1046/j.1570-7458.2000.00662.x>
- Anderbrant, O., Löfqvist, J., Jönsson, J. & Marling, E. (1989) Effects of pheromone trap type, position and colour on the catch of the pine sawfly *Neodiprion sertifer* (Geoff.) (Hym., Diprionidae). *Journal of Applied Entomology*, 107(1–5), 365–369. <https://doi.org/10.1111/j.1439-0418.1989.tb00270.x>
- Anderbrant, O., Lyons, D.B., Bång, J., Hedenström, E. & Högberg, H.-E. (2011) Sex pheromone of the introduced pine sawfly, *Diprion similis* (Diprionidae), revisited: No activity of earlier reported synergists. Available at: <http://urn.kb.se/resolve?urn=urn:nbn:se:miun:diva-14659>
- Anderbrant, O., Lyons, D.B., Bång, J., Hedenström, E. & Högberg, H.-E. (2021) Sex pheromone of the introduced pine sawfly, *Diprion similis*, revisited to define a useful monitoring lure: deviating chiral composition and behavioural responses compared to earlier reports. *Insects*, 12(10), 886. <https://doi.org/10.3390/insects12100886>
- Anderbrant, O., Östrand, F., Bergström, G., Wassgren, A.-B., Auger-Rozenberg, M.-A., Geri, C. et al. (2005) Release of sex pheromone and its precursors in the pine sawfly *Diprion pini* (Hym., Diprionidae). *Chemoecology*, 15(3), 147–151. <https://doi.org/10.1007/s00049-005-0306-8>
- Anderbrant, O., Zhang, Q.-H. & Chu, D. (1997) Diprionyl esters attractive to males of the dailing pine sawfly *Neodiprion dailingensis* Xiao et Zhou (Hym., Diprionidae) in north-eastern China. *Journal of Applied Entomology*, 121(1–5), 281–283. <https://doi.org/10.1111/j.1439-0418.1997.tb01406.x>
- Asenbaum, J., Schäffler, I., Etl, F., Dötterl, S., Schönenberger, J. & Chartier, M. (2021) Comparative pollination ecology of five European *Euphorbia* species. *International Journal of Plant Sciences*, 182(9), 763–777. <https://doi.org/10.1086/715759>
- Austarå, Ø., Orlund, A., Svendsrud, A. & Veidahl, A. (1987) Growth loss and economic consequences following two years defoliation of *Pinus sylvestris* by the pine sawfly *Neodiprion sertifer* in West-Norway. *Scandinavian Journal of Forest Research*, 2(1–4), 111–119. <https://doi.org/10.1080/02827588709382450>
- Baker, R., Longhurst, C., Selwood, D. & Billany, D. (1983) Ortho-aminoacetophenone: a component of the sex pheromone system of the web-spinning larch sawfly, *Cephalcia lariciphila*. *Experientia*, 39(9), 993–994. <https://doi.org/10.1007/BF01989767>
- Bång, J., Hedenström, E. & Anderbrant, O. (2012) Stereoisomeric separation of derivatized 2-alkanols using gas chromatography-mass spectrometry: sex pheromone precursors found in pine sawfly species. *Analytical Letters*, 45(9), 1016–1027. <https://doi.org/10.1080/00032719.2012.670789>
- Bång, J., Hedenström, E. & Sjödin, K. (2011) Purification, stereoisomeric analysis and quantification of sex pheromone precursors in female whole body extracts from pine sawfly species. *Journal of Chemical Ecology*, 37(1), 125–133. <https://doi.org/10.1007/s10886-010-9886-z>
- Barbir, J., Aguado Martín, L.O. & Rodríguez Lloveras, X. (2019) Impact of climate change on sawfly (suborder: Symphyta) pollinators in Andalusia region, Spain. In: *Handbook of climate change and biodiversity*.

- Cham: Springer International Publishing, pp. 93–111. https://doi.org/10.1007/978-3-319-98681-4_6
- Barker, A.M., Molotsane, R., Müller, C., Schaffner, U. & Städler, E. (2006) Chemosensory and behavioural responses of the turnip sawfly, *Athalia rosae*, to glucosinolates and isothiocyanates. *Chemoecology*, 16(4), 209–218. <https://doi.org/10.1007/s00049-006-0349-5>
- Barker, A.M., Sanbrooke, K.J. & Aebischer, N.J. (1997) The water trap colour preferences of farmland sawflies. *Entomologia Experimentalis et Applicata*, 85(1), 83–86. <https://doi.org/10.1046/j.1570-7458.1997.00236.x>
- Bartelt, R.J., Cossé, A.A., Petroski, R.J. & Weaver, D.K. (2002) Cuticular hydrocarbons and novel alkenediol diacetates from wheat stem sawfly (*Cephus cinctus*): natural oxidation to pheromone components. *Journal of Chemical Ecology*, 28(2), 385–405. <https://doi.org/10.1023/A:1017994410538>
- Bartelt, R.J. & Jones, R.L. (1983) (Z)-10-Nonadecenal: a pheromonally active air oxidation product of (Z,Z)-9,19 dienes in yellowheaded spruce sawfly. *Journal of Chemical Ecology*, 9(9), 1333–1341. <https://doi.org/10.1007/BF00994802>
- Bartelt, R.J., Jones, R.L. & Krick, T.P. (1983) (Z)-5-Tetradecen-1-ol: a secondary pheromone of the yellowheaded spruce sawfly, and its relationship to (Z)-10-nonadecenal. *Journal of Chemical Ecology*, 9(9), 1343–1352. <https://doi.org/10.1007/BF00994803>
- Bartelt, R.J., Jones, R.L. & Kulman, H.M. (1982) Hydrocarbon components of the yellowheaded spruce sawfly sex pheromone. *Journal of Chemical Ecology*, 8(1), 95–114. <https://doi.org/10.1007/BF00984008>
- Beres, B.L., Dossall, L.M., Weaver, D.K., Cárcamo, H.A. & Spaner, D.M. (2011) Biology and integrated management of wheat stem sawfly and the need for continuing research. *The Canadian Entomologist*, 143(2), 105–125. <https://doi.org/10.4039/n10-056>
- Bergström, G., Wassgren, A.-B., Anderbrant, O., Fägerhag, J., Edlund, H., Hedenström, E. et al. (1995) Sex pheromone of the pine sawfly *Diprion pini* (Hymenoptera: Diprionidae): chemical identification, synthesis and biological activity. *Experientia*, 51(4), 370–380. <https://doi.org/10.1007/BF01928898>
- Bergström, G., Wassgren, A.-B., Anderbrant, O., Ochieng, S.A., Östrand, F., Hansson, B.S. et al. (1998) The sex pheromone of the pine sawfly *Microdiprion pallipes* (Hymenoptera: Diprionidae). *Naturwissenschaften*, 85, 244–248. <https://doi.org/10.1007/s001140050492>
- Bergström, G., Wassgren, A.-B., Birgersson, G., Springborg, J., Wang, D.-N., Paulsen, G.B. et al. (1994) 1,6-Germacradien-5-ol identified in the larval discharge of the pine sawfly *Neodiprion sertifer*. *Acta Chemica Scandinavica*, 48, 187–188. <https://doi.org/10.3891/acta.chem.scand.48-0187>
- Bittner, N., Hundacker, J., Achotegui-Castells, A., Anderbrant, O. & Hilker, M. (2019) Defense of scots pine against sawfly eggs (*Diprion pini*) is primed by exposure to sawfly sex pheromones. *Proceedings of the National Academy of Sciences*, 116(49), 24668–24675. <https://doi.org/10.1073/pnas.1910991116>
- Blank, S.M., Hara, H., Mikulas, J., Csoka, G., Ciornei, C., Constantineanu, R. et al. (2010) *Aproceros leucopoda* (Hymenoptera: Argidae): an east Asian pest of elms (*Ulmus* spp.) invading Europe. *European Journal of Entomology*, 107(3), 357–367. <https://doi.org/10.14411/eje.2010.045>
- Boevé, J.-L., Dettner, K., Francke, W., Meyer, H. & Pasteels, J.M. (1992) The secretion of the ventral glands in *Nematus* sawfly larvae. *Biochemical Systematics and Ecology*, 20(2), 107–111. [https://doi.org/10.1016/0305-1978\(92\)90097-W](https://doi.org/10.1016/0305-1978(92)90097-W)
- Boevé, J.-L., Heilporn, S., Dettner, K. & Francke, W. (2000) The secretion of the ventral glands in *Cladius*, *Priophorus* and *Trichiocampus* sawfly larvae. *Biochemical Systematics and Ecology*, 28(9), 857–864. [https://doi.org/10.1016/S0305-1978\(00\)00008-9](https://doi.org/10.1016/S0305-1978(00)00008-9)
- Boevé, J.-L., Lengwiler, U., Tollsten, L., Dorn, S. & Turlings, T.C.J. (1996) Volatiles emitted by apple fruitlets infested by larvae of the European apple sawfly. *Phytochemistry*, 42(2), 373–381. [https://doi.org/10.1016/0031-9422\(95\)00948-5](https://doi.org/10.1016/0031-9422(95)00948-5)
- Borden, J.H., Billany, D.J., Bradshaw, J.W.S., Edwards, M., Baker, R. & Evans, D.A. (1978) Pheromone response and sexual behaviour of *Cephalcia lariciphila* Wachtl (Hymenoptera: Pamphiliidae). *Ecological Entomology*, 3(1), 13–23. <https://doi.org/10.1111/j.1365-2311.1978.tb00899.x>
- Böröczky, K., Crook, D.J., Jones, T.H., Kenny, J.C., Zylstra, K.E., Mastro, V. C. et al. (2009) Monoalkenes as contact sex pheromone components of the woodwasp *Sirex noctilio*. *Journal of Chemical Ecology*, 35(10), 1202–1211. <https://doi.org/10.1007/s10886-009-9693-6>
- Braccini, C.L., Vega, A.S., Coll Aráoz, M.V., Teal, P.E., Cerrillo, T., Zavala, J. A. et al. (2015) Both volatiles and cuticular plant compounds determine oviposition of the willow sawfly *Nematus oligospilus* on leaves of *Salix* spp. (Salicaceae). *Journal of Chemical Ecology*, 41(11), 985–996. <https://doi.org/10.1007/s10886-015-0637-z>
- Bradshaw, C.J.A., Leroy, B., Bellard, C., Roiz, D., Albert, C., Fournier, A. et al. (2016) Massive yet grossly underestimated global costs of invasive insects. *Nature Communications*, 7(1), 12986. <https://doi.org/10.1038/ncomms12986>
- Briscoe, A.D. & Chittka, L. (2001) The evolution of color vision in insects. *Annual Review of Entomology*, 46(1), 471–510. <https://doi.org/10.1146/annurev.ento.46.1.471>
- Burrows, D.W. & Balciunas, J.K. (1997) Biology, distribution and host-range of the sawfly, *Lophyrotoma zonalis* (Hym. Pergidae), a potential biological control agent for the paperbark tree, *Melaleuca quinquenervia*. *Entomophaga*, 42(3), 299–313. <https://doi.org/10.1007/BF02769822>
- Caron, V., Ede, F., Sunnucks, P. & O'Dowd, D.J. (2014) Distribution and rapid range expansion of the introduced willow sawfly *Nematus oligospilus* Förster (Hymenoptera: Tenthredinidae) in Australasia. *Austral Entomology*, 53(2), 175–182. <https://doi.org/10.1111/aen.12067>
- Caron, V., Moslih, F., Ede, F.J. & O'Dowd, D.J. (2011) An accidental biological control agent? Host specificity of the willow sawfly *Nematus oligospilus* (Hymenoptera: Tenthredinidae) in Australia. *Australian Journal of Entomology*, 50(3), 290–295. <https://doi.org/10.1111/j.1440-6055.2011.00816.x>
- Chakraborty, S. & Newton, A.C. (2011) Climate change, plant diseases and food security: an overview. *Plant Pathology*, 60(1), 2–14. <https://doi.org/10.1111/j.1365-3059.2010.02411.x>
- Cooperband, M.F., Böröczky, K., Hartness, A., Jones, T.H., Zylstra, K.E., Tumlinson, J.H. et al. (2012) Male-produced pheromone in the European woodwasp, *Sirex noctilio*. *Journal of Chemical Ecology*, 38(1), 52–62. <https://doi.org/10.1007/s10886-012-0060-7>
- Cossé, A.A., Bartelt, R.J., Weaver, D.K. & Zilkowski, B.W. (2002) Pheromone components of the wheat stem sawfly: identification, electrophysiology, and field bioassay. *Journal of Chemical Ecology*, 28(2), 407–423. <https://doi.org/10.1023/A:1017946527376>
- Crook, D.J., Böröczky, K., Zylstra, K.E., Mastro, V.C. & Tumlinson, J.H. (2012) The chemical ecology of *Sirex noctilio*. In: Slippers, B., de Groot, P. & Wingfield, M.J. (Eds.) *The siren woodwasp and its fungal symbiont: research and management of a worldwide invasive pest*. Dordrecht: Springer Netherlands, pp. 149–158. https://doi.org/10.1007/978-94-007-1960-6_11
- Crook, D.J., Kerr, L.M. & Mastro, V.C. (2008) Sensilla on the antennal flagellum of *Sirex noctilio* (Hymenoptera: Siricidae). *Annals of the Entomological Society of America*, 101(6), 1094–1102. <https://doi.org/10.1603/0013-8746-101.6.1094>
- Cuda, J.P., Medal, J.C., Vitorino, M.D. & Habeck, D.H. (2005) Supplementary host specificity testing of the sawfly *Heteroperlyria hubrichi*, a candidate for classical biological control of Brazilian peppertree, *Schinus terebinthifolius*, in the USA. *BioControl*, 50(1), 195–201. <https://doi.org/10.1007/s10526-004-0459-3>
- Digweed, S.C., Spence, J.R. & Langor, D.W. (1997) Exotic birch-leafmining sawflies (Hymenoptera: Tenthredinidae) in Alberta: distributions, seasonal activities, and the potential for competition. *The Canadian Entomologist*, 129(2), 319–333. <https://doi.org/10.4039/Ent129319-2>

- Dodds, K.J., Cooke, R.R. & Hanavan, R.P. (2014) The effects of silvicultural treatment on *Sirex noctilio* attacks and tree health in northeastern United States. *Forests*, 5(11), 2810–2824. <https://doi.org/10.3390/f5112810>
- Domingue, M.J., Imrei, Z., Lelito, J.P., Muskovits, J., Janik, G., Csóka, G. et al. (2013) Trapping of European buprestid beetles in oak forests using visual and olfactory cues. *Entomologia Experimentalis et Applicata*, 148(2), 116–129. <https://doi.org/10.1111/eea.12083>
- Duffield, R.M., Shafagati, A., Riddick, E.W., Bowen, S. & Wheeler, J.W. (1990) Mandelonitrile in larval secretion of mountain ash sawfly, *Pristiphora geniculata* (Hymenoptera: Tenthredinidae). *Journal of Chemical Ecology*, 16(4), 1103–1110. <https://doi.org/10.1007/BF01021014>
- Faal, H., Silk, P.J., LeClair, G. & Teale, S.A. (2022) Biologically active cuticular compounds of female *Sirex noctilio*. *Entomologia Experimentalis et Applicata*, 170, 327–338. <https://doi.org/10.1111/eea.13150>
- Fătu, A.-C., Cardaş, G., Constantin, C. & Andrei, A.-M. (2021) Experimental field application of *Beauveria bassiana* (Bals.) Vuill. for control of the invasive sawfly *Aproceros leucopoda* Takeuki, 1939 (Hymenoptera: Argidae) in Romania. *Acta Zoologica Bulgarica*, 72, 661–666.
- Ferguson, S.T., Ray, A. & Zwiebel, L.J. (2021) Olfactory genomics of eusociality within the Hymenoptera. In: *Insect pheromone biochemistry and molecular biology*, 2nd edition. London: Academic Press, pp. 507–546. <https://doi.org/10.1016/B978-0-12-819628-1.00016-X>
- Fernández, P.C., Braccini, C.L., Dávila, C., Barrozo, R.B., Aróz, M.V.C., Cerrillo, T. et al. (2019) The use of leaf surface contact cues during oviposition explains field preferences in the willow sawfly *Nematus oligospilus*. *Scientific Reports*, 9(1), 4946. <https://doi.org/10.1038/s41598-019-41318-7>
- Fischbein, D. & Corley, J.C. (2015) Classical biological control of an invasive forest pest: a world perspective of the management of *Sirex noctilio* using the parasitoid *Ibalia leucospoides* (Hymenoptera: Ibalidae). *Bulletin of Entomological Research*, 105(1), 1–12. <https://doi.org/10.1017/S0007485314000418>
- Flowers, R.W. & Costa, J.T. (2003) Larval communication and group foraging dynamics in the red-headed pine sawfly, *Neodiprion lecontei* (Fitch) (Hymenoptera: Symphyta: Diprionidae). *Annals of the Entomological Society of America*, 96(3), 336–343. [https://doi.org/10.1603/0013-8746\(2003\)096\[0336:LCAGFD\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2003)096[0336:LCAGFD]2.0.CO;2)
- Gress, J.C., Robertson, H.M., Weaver, D.K., Dlakić, M. & Wanner, K.W. (2013) Odorant receptors of a primitive hymenopteran pest, the wheat stem sawfly. *Insect Molecular Biology*, 22(6), 659–667. <https://doi.org/10.1111/imb.12053>
- Guignard, Q., Allison, J.D. & Slippers, B. (2022) The evolution of insect visual opsin genes with specific consideration of the influence of ocelli and life history traits. *BMC Ecology and Evolution*, 22(1), 2. <https://doi.org/10.1186/s12862-022-01960-8>
- Guignard, Q., Bouwer, M., Slippers, B. & Allison, J. (2020) Biology of a putative male aggregation-sex pheromone in *Sirex noctilio* (Hymenoptera: Siricidae). *PLoS One*, 15(12), e0244943. <https://doi.org/10.1371/journal.pone.0244943>
- Guignard, Q., Spaethe, J., Slippers, B., Strube-Bloss, M. & Allison, J.D. (2021) Evidence for UV-green dichromacy in the basal hymenopteran *Sirex noctilio* (Siricidae). *Scientific Reports*, 11(1), 15601. <https://doi.org/10.1038/s41598-021-95107-2>
- Guo-fa, C.H.E.N., Qing-he, Z., Zhang-Yuan, L.I., Zhe-wang, M., Li-zhong, W. & Anderbrant, O. (1997) A preliminary study on the sex pheromone of *Diprion jingyuanensis* Xiao et Zhang. *Chinese Journal of Biological Control*, 13(2), 61.
- Hall, D., Farman, D., Douglas, P., Cross, J., Fountain, M. & Shaw, B. (2017) Components of the sex pheromone of blackcurrant sawfly, *Nematus olfaciens* (Hymenoptera: Tenthredinidae): novel isopropyl esters and the role of hydrocarbons. *Pheromones and Other Semiochemicals in Integrated Production*, 126, 34–39.
- Hallberg, E. (1979) The fine structure of the antennal sensilla of the pine saw fly *Neodiprion sertifer* (Insecta: Hymenoptera). *Protoplasma*, 101(1), 111–126. <https://doi.org/10.1007/BF01293440>
- Hatano, E., Wada-Katsumata, A. & Schal, C. (2020) Environmental decomposition of olefinic cuticular hydrocarbons of *Periplaneta americana* generates a volatile pheromone that guides social behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 287(1921), 20192466. <https://doi.org/10.1098/rspb.2019.2466>
- Hawkes, F.M., Dabiré, R.K., Sawadogo, S.P., Torr, S.J. & Gibson, G. (2017) Exploiting Anopheles responses to thermal, odour and visual stimuli to improve surveillance and control of malaria. *Scientific Reports*, 7(1), 17283. <https://doi.org/10.1038/s41598-017-17632-3>
- Hayes, R.A., Griffiths, M.W. & Nahrung, H.F. (2015) Electrophysiological activity of the *Sirex noctilio* ovipositor: you know the drill? *Journal of Asia-Pacific Entomology*, 18(2), 165–168. <https://doi.org/10.1016/j.aspen.2015.01.003>
- Hedenström, E., Edlund, H., Wassgren, A.-B., Bergström, G., Anderbrant, O., Östrand, F. et al. (2006) Sex pheromone of the pine sawfly, *Gilpinia pallida*: chemical identification, synthesis, and biological activity. *Journal of Chemical Ecology*, 32(11), 2525–2541. <https://doi.org/10.1007/s10886-006-9161-5>
- Hedenström, E., Edlund, H., Wassgren, A.-B., Bergström, G., Anderbrant, O., Östrand, F. et al. (2009) The sex pheromones of two pine sawfly species, *Gilpinia frutetorum* and *Gilpinia socia*: chemical identification, synthesis and biological activity. *Zeitschrift Für Naturforschung C*, 64(9–10), 733–742. <https://doi.org/10.1515/znc-2009-9-1020>
- Holuša, J. & Drápela, K. (2006) Yellow sticky boards: a possible way of monitoring little spruce sawfly (*Pristiphora abietina*) (Hymenoptera: Tenthredinidae). *Journal of Forest Science*, 52(1), 13–21. <https://doi.org/10.17221/4482-JFS>
- Huang, D., Haack, R.A. & Zhang, R. (2011) Does global warming increase establishment rates of invasive alien species? A centennial time series analysis. *PLoS One*, 6(9), e24733. <https://doi.org/10.1371/journal.pone.0024733>
- Hurley, B.P., Garnas, J. & Cooperband, M.F. (2015) Assessing trap and lure effectiveness for the monitoring of *Sirex noctilio*: trap and lure effectiveness for *S. noctilio*. *Agricultural and Forest Entomology*, 17(1), 64–70. <https://doi.org/10.1111/afe.12081>
- Ibrahim, M.A.I., Antary, T.M.A. & Kaakeh, N.A. (2019) Evaluation of the susceptibility of four different cultivars for cherry slug *Caliroa cerasion* (Hymenoptera: Tenthredinidae). *Fresenius Environmental Bulletin*, 28(11), 7.
- James, D.G., Petroski, R.J., Cossé, A.A., Zilkowski, B.W. & Bartelt, R.J. (2003) Bioactivity, synthesis, and chirality of the sex pheromone of currant stem girdler, *Janus integer*. *Journal of Chemical Ecology*, 29(10), 2189–2199. <https://doi.org/10.1023/A:1026210111334>
- Jervis, M. & Vilhelmsen, L. (2000) Mouthpart evolution in adults of the basal, ‘symphytan’, hymenopteran lineages. *Biological Journal of the Linnean Society*, 70(1), 121–146. <https://doi.org/10.1111/j.1095-8312.2000.tb00204.x>
- Jewett, D.M., Matsumura, F. & Coppel, H.C. (1976) Sex pheromone specificity in the pine sawflies: interchange of acid moieties in an ester. *Science*, 192(4234), 51–53.
- Jonsson, S., Bergström, G., Lanne, B.S. & Stensdotter, U. (1988) Defensive odor emission from larvae of two sawfly species, *Pristiphora erichsonii* and *P. wesmaeli*. *Journal of Chemical Ecology*, 14(2), 713–721. <https://doi.org/10.1007/BF01013918>
- Kárpáti, Z., Bognár, C., Voigt, E., Tóth, M. & Molnár, B.P. (2021) Monitoring of three Hoplocampa sawfly species in plum orchards. *Acta Phytotaxonomica et Entomologica Hungarica*, 56(2), 143–152. <https://doi.org/10.1556/038.2021.00128>
- Kather, R. & Martin, S.J. (2015) Evolution of cuticular hydrocarbons in the Hymenoptera: a meta-analysis. *Journal of Chemical Ecology*, 41(10), 871–883. <https://doi.org/10.1007/s10886-015-0631-5>
- Kikukawa, T., Matsumura, F., Kraemer, M., Coppel, H.C. & Tai, A. (1982) Field attractiveness of chirally defined synthetic attractants to males of *Diprion similis* and *Gilpinia frutetorum*. *Journal of Chemical Ecology*, 8(1), 301–314. <https://doi.org/10.1007/BF00984025>

- Kikukawa, T., Matsumura, F., Olaifa, J., Kraemer, M., Coppel, H.C. & Tai, A. (1983) Field evaluation of chiral isomers of the sex pheromone of the European pine sawfly, *Neodiprion sertifer*. *Journal of Chemical Ecology*, 9(6), 673–693. <https://doi.org/10.1007/BF00988775>
- Kim, K., Huang, Q. & Lei, C. (2019) Advances in insect phototaxis and application to pest management: a review. *Pest Management Science*, 75(12), 3135–3143. <https://doi.org/10.1002/ps.5536>
- Kirichenko, N., Augustin, S. & Kenis, M. (2019) Invasive leafminers on woody plants: a global review of pathways, impact, and management. *Journal of Pest Science*, 92(1), 93–106. <https://doi.org/10.1007/s10340-018-1009-6>
- Knerer, G. (1984) Diprionid sawflies: biological topics and rearing techniques (Hymenoptera: Symphyta). *Bulletin of the Entomological Society of America*, 30(3), 53–57. <https://doi.org/10.1093/besa/30.3.53>
- Koch, F., Goergen, G.E. & van Noort, S. (2015) The sawflies of Namibia and western South Africa (Symphyta, Hymenoptera). *Abc Taxa*, 15, i–viii, 262 pp.
- Koshiji, M., Taniwaki, T., Aihara, K. & Yamane, M. (2012) Severe damages on beech trees (*Fagus crenata*) caused by the outbreaks of a sawfly (*Fagineura crenativora*) in Mt. Hinokiboramaru (in Japanese). *Bulletin of the Kanagawa Prefecture Natural Environment Conservation Center*, 9, 95–104.
- Kraemer, M., Coppel, H.C., Matsumura, F., Kikukawa, T. & Mori, K. (1979) Field responses of the white pine sawfly, *Neodiprion pinetum*, to optical isomers of sawfly sex pheromones 12. *Environmental Entomology*, 8(3), 519–520. <https://doi.org/10.1093/ee/8.3.519>
- Kraemer, M.E., Coppel, H.C., Kikukawa, T., Matsumura, F., Thomas, H.A., Thompson, L.C. et al. (1983) Field and electroantennogram responses to sex pheromone optical isomers by four fall-flying sawfly species (Hymenoptera: Diprionidae, Neodiprion). *Environmental Entomology*, 12(5), 1592–1596. <https://doi.org/10.1093/ee/12.5.1592>
- Kraemer, M.E., Coppel, H.C., Matsumura, F., Kikukawa, T. & Benoit, P. (1984) Field and electroantennogram responses to sex pheromone optical isomers by monophagous jack pine sawflies (Hymenoptera: Diprionidae). *Journal of Chemical Ecology*, 10(7), 983–995. <https://doi.org/10.1007/BF00987507>
- Krogmann, L., Engel, M.S., Bechly, G. & Nel, A. (2013) Lower cretaceous origin of long-distance mate finding behaviour in Hymenoptera (Insecta). *Journal of Systematic Palaeontology*, 11(1), 83–89. <https://doi.org/10.1080/14772019.2012.693954>
- Li, Y.-N., Hao, E.-H., Li, H., Yuan, X.-H., Lu, P.-F. & Qjiao, H.-L. (2021) Computational interaction analysis of *Sirex noctilio* odorant-binding protein (SnocOBP7) combined with female sex pheromones and symbiotic fungal volatiles. *Agronomy*, 11(12), 2461. <https://doi.org/10.3390/agronomy11122461>
- Looney, C., Smith, D.R., Collman, S.J., Langor, D.W. & Peterson, M.A. (2016) Sawflies (Hymenoptera, Symphyta) newly recorded from Washington state. *Journal of Hymenoptera Research*, 49, 129–160.
- Lucarotti, C.J., Morin, B., Graham, R.I. & Lapointe, R. (2007) Production, application, and field performance of Abietiv™, the balsam fir sawfly nucleopolyhedrovirus. *Virologica Sinica*, 22(2), 163–172. <https://doi.org/10.1007/s12250-007-0018-z>
- Lyytikäinen-Saarenmaa, P. & Tomppo, E. (2002) Impact of sawfly defoliation on growth of scots pine *Pinus sylvestris* (Pinaceae) and associated economic losses. *Bulletin of Entomological Research*, 92(2), 137–140. <https://doi.org/10.1079/BER2002154>
- Macedo, T.B., Macedo, P.A., Peterson, R.K.D., Weaver, D.K. & Morrill, W.L. (2005) Rearing the wheat stem sawfly on an artificial diet. *The Canadian Entomologist*, 137(4), 497–500. <https://doi.org/10.4039/n04-100>
- Macek, J. & Sipek, P. (2015) Azalea sawfly *Nematus lipovskyi* (Hymenoptera: Tenthredinidae), a new invasive species in Europe. *European Journal of Entomology*, 112(1), 180–186. <https://doi.org/10.14411/eje.2015.018>
- Madden, J. (1974) Oviposition behaviour of the woodwasp, *Sirex Noctilio* F. *Australian Journal of Zoology*, 22(3), 341–351.
- Martínez, A.S., Villacide, J., Ajó, A.A.F., Martinson, S.J. & Corley, J.C. (2014) *Sirex noctilio* flight behavior: toward improving current monitoring techniques. *Entomologia Experimentalis et Applicata*, 152(2), 135–140. <https://doi.org/10.1111/eea.12205>
- Martini, A., Baldassari, N., Baronio, P., Anderbrant, O., Hedenström, E., Högberg, H.-E. et al. (2002) Mating disruption of the pine sawfly *Neodiprion sertifer* (Hymenoptera: Diprionidae) in isolated pine stands. *Agricultural and Forest Entomology*, 4(3), 195–201. <https://doi.org/10.1046/j.1461-9563.2002.00143.x>
- Mumm, R. & Hilker, M. (2006) Direct and indirect chemical defence of pine against folivorous insects. *Trends in Plant Science*, 11(7), 351–358. <https://doi.org/10.1016/j.tplants.2006.05.007>
- Narayanan, K. & Gopalakrishnan, C. (2003) Evaluation of entomopathogenic nematode, *Steinernema feltiae* against field population of mustard sawfly, *Athalia lugens proxima* (Klug) on radish. *Indian Journal of Experimental Biology*, 41(4), 376–378.
- Naumann, I.D. (1997) A remarkable, new Australian sawfly with brachypterous, nocturnal or crepuscular females (Hymenoptera: Symphyta: Pergidae). *Journal of Natural History*, 31(9), 1335–1346. <https://doi.org/10.1080/00222939700770751>
- Nemer, N., Kawar, N.S., Kfoury, L. & Frerot, B. (2007) Evidence of sexual attraction by pheromone in the cedar web-spinning sawfly. *The Canadian Entomologist*, 139(5), 713–721. <https://doi.org/10.4039/n06-042>
- Nielsen, M.-C., Sansom, C.E., Larsen, L., Worner, S.P., Rostás, M., Chapman, R.B. et al. (2019) Volatile compounds as insect lures: factors affecting release from passive dispenser systems. *New Zealand Journal of Crop and Horticultural Science*, 47(3), 208–223. <https://doi.org/10.1080/01140671.2019.1604554>
- Nježić, B. & Ehlers, R.-U. (2020) Entomopathogenic nematodes control plum sawflies (*Hoplocampa minuta* and *H. flava*). *Journal of Applied Entomology*, 144(6), 491–499. <https://doi.org/10.1111/jen.12755>
- Olaifa, J.I., Kikukawa, T., Matsumura, F. & Coppel, H.C. (1984) Response of male jack pine sawfly, *Neodiprion pratti banksianae* (Hymenoptera: Diprionidae), to mixtures of optical isomers of the sex pheromone, 3, 7-dimethylpentadecan-2-ol. *Environmental Entomology*, 13(5), 1274–1277. <https://doi.org/10.1093/ee/13.5.1274>
- Olaifa, J.I., Matsumura, F. & Coppel, H.C. (1987) Field response and gas-liquid chromatograph separation of optically active synthetic and natural pheromones in two sympatric diprionid sawflies, *Neodiprion nanulus nanulus* and *Neodiprion sertifer* (Hymenoptera: Diprionidae). *Journal of Chemical Ecology*, 13(6), 1395–1408. <https://doi.org/10.1007/BF01012286>
- Olaifa, J.I., Matsumura, F., Kikukawa, T. & Coppel, H.C. (1988) Pheromone-dependent species recognition mechanisms between *Neodiprion pinetum* and *Diprion similis* on white pine. *Journal of Chemical Ecology*, 14(4), 1131–1144. <https://doi.org/10.1007/BF01019341>
- Östrand, F., Anderbrant, O., Wassgren, A.-B., Bergström, G., Hedenström, E., Högberg, H.-E. et al. (2003) Stereoisomeric composition of the sex pheromone of the pine sawfly *Microdiprion pallipes* (Hym., Diprionidae). *Chemoecology*, 13(3), 155–162. <https://doi.org/10.1007/s00049-003-0244-2>
- Özbek, H. & Çalmaşur, O. (2005) A review of insects and mites associated with roses in Turkey. *Acta Horticulturae*, 690, 167–174. <https://doi.org/10.17660/ActaHortic.2005.690.25>
- Papiorek, S., Junker, R.R., Alves-dos-Santos, I., Melo, G.a.R., Amaral-Neto, L.P., Sazima, M. et al. (2016) Bees, birds and yellow flowers: pollinator-dependent convergent evolution of UV patterns. *Plant Biology*, 18(1), 46–55. <https://doi.org/10.1111/plb.12322>
- Park, B., Nguyen, N.H., Lee, J.-W. & Hong, K.-J. (2019) A new sawfly pest, *Monocelicampa pruni* Wei (Hymenoptera, Tenthredinidae) attacking fruitlets of Japanese plum in South Korea. *Korean Journal of Applied Entomology*, 58(4), 329–333. <https://doi.org/10.5656/KSAE.2019.11.0.038>

- Patel, S., Yadav, S.K. & Singh, C.P. (2017) Foraging behavior of mustard sawfly, *Athalia lugensproxima* Klug on rapeseed-mustard. *Journal of Experimental Zoology*, 21, 379–381.
- Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D.F. & Menzel, R. (1992) The spectral input systems of hymenopteran insects and their receptor-based colour vision. *Journal of Comparative Physiology A*, 170(1), 23–40. <https://doi.org/10.1007/BF00190398>
- Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K. et al. (2017) Evolutionary history of the Hymenoptera. *Current Biology*, 27(7), 1013–1018. <https://doi.org/10.1016/j.cub.2017.01.027>
- Pickett, J.A. (2014) Chemical ecology in the post genomics era. *Journal of Chemical Ecology*, 40(4), 319. <https://doi.org/10.1007/s10886-014-0418-0>
- Piesik, D., Weaver, D.K., Runyon, J.B., Buteler, M., Peck, G.E. & Morrill, W. L. (2008) Behavioural responses of wheat stem sawflies to wheat volatiles. *Agricultural and Forest Entomology*, 10(3), 245–253. <https://doi.org/10.1111/j.1461-9563.2008.00380.x>
- Portman, S.L., Jaronski, S.T., Weaver, D.K. & Reddy, G.V.P. (2018) Advancing biological control of the wheat stem sawfly: new strategies in a 100-yr struggle to manage a costly pest in the northern Great Plains. *Annals of the Entomological Society of America*, 111(3), 85–91. <https://doi.org/10.1093/aesa/say002>
- Portman, S.L., Krishnankutty, S.M. & Reddy, G.V.P. (2016) Entomopathogenic nematodes combined with adjuvants presents a new potential biological control method for managing the wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae). *PLoS One*, 11(12), e0169022. <https://doi.org/10.1371/journal.pone.0169022>
- Prokopy, R.J. & Owens, E.D. (1983) Visual detection of plants by herbivorous insects. *Annual Review of Entomology*, 28(1), 337–364. <https://doi.org/10.1146/annurev.en.28.010183.002005>
- Qin, Y., Wang, C., Zhao, Z., Pan, X. & Li, Z. (2019) Climate change impacts on the global potential geographical distribution of the agricultural invasive pest, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae). *Climatic Change*, 155(2), 145–156. <https://doi.org/10.1007/s10584-019-02460-3>
- Raguso, R.A. & Willis, M.A. (2005) Synergy between visual and olfactory cues in nectar feeding by wild hawkmoths, *Manduca sexta*. *Animal Behaviour*, 69(2), 407–418. <https://doi.org/10.1016/j.anbehav.2004.04.015>
- Reverté, S., Retana, J., Gómez, J.M. & Bosch, J. (2016) Pollinators show flower colour preferences but flowers with similar colours do not attract similar pollinators. *Annals of Botany*, 118(2), 249–257. <https://doi.org/10.1093/aob/mcw103>
- Robertson, H.M., Waterhouse, R.M., Walden, K.K.O., Ruzzante, L., Reijnders, M.J.M.F., Coates, B.S. et al. (2018) Genome sequence of the wheat stem sawfly, *Cephus cinctus*, representing an early-branching lineage of the Hymenoptera, illuminates evolution of hymenopteran chemoreceptors. *Genome Biology and Evolution*, 10(11), 2997–3011. <https://doi.org/10.1093/gbe/evy232>
- Sarvary, M.A., Cooperband, M.F. & Hajek, A.E. (2015) The importance of olfactory and visual cues in developing better monitoring tools for *Sirex noctilio* (Hymenoptera: Siricidae): developing monitoring tools for *S. noctilio*. *Agricultural and Forest Entomology*, 17(1), 29–35. <https://doi.org/10.1111/afe.12077>
- Sarvary, M.A., Hajek, A.E., Böröczky, K., Raguso, R.A. & Cooperband, M.F. (2016) Investigating the effects of symbiotic fungi on the flight behaviour of *Sirex noctilio* (Hymenoptera: Siricidae). *The Canadian Entomologist*, 148(5), 543–551. <https://doi.org/10.4039/tce.2016.10>
- Schmidt, S., Walter, G.H., Grigg, J. & Moore, C.J. (2006) Sexual communication and host plant associations of Australian pergid sawflies (Hymenoptera: Symphyta: Pergidae). In: *Recent sawfly research: synthesis and prospects*. Keltern: Goecke & Evers, pp. 173–193.
- Sharkey, C.R., Fujimoto, M.S., Lord, N.P., Shin, S., McKenna, D.D., Suvorov, A. et al. (2017) Overcoming the loss of blue sensitivity through opsin duplication in the largest animal group, beetles. *Scientific Reports*, 7(1), 1–10. <https://doi.org/10.1038/s41598-017-00061-7>
- Sharma, S., Kooner, R. & Arora, R. (2017) Insect pests and crop losses. In: Arora, R. & Sandhu, S. (Eds.) *Breeding insect resistant crops for sustainable agriculture*. Singapore: Springer, pp. 45–66. https://doi.org/10.1007/978-981-10-6056-4_2
- Shrestha, M., Garcia, J.E., Chua, J.H.J., Howard, S.R., Tscheulin, T., Dorin, A. et al. (2019) Fluorescent pan traps affect the capture rate of insect orders in different ways. *Insects*, 10(2), 40. <https://doi.org/10.3390/insects10020040>
- Silk, P., Mayo, P., Ryall, K. & Roscoe, L. (2019) Semiochemical and communication ecology of the emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae). *Insects*, 10(10), 323. <https://doi.org/10.3390/insects10100323>
- Silk, P.J., Sweeney, J., Wu, J., Price, J., Gutowski, J.M. & Kettela, E.G. (2007) Evidence for a male-produced pheromone in *Tetropium fuscum* (F.) and *Tetropium cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). *Naturwissenschaften*, 94(8), 697–701. <https://doi.org/10.1007/s00114-007-0244-0>
- Slippers, B., de Groot, P. & Wingfield, M.J. (2011) *The Sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest*. Dordrecht: Springer Science & Business Media.
- Slippers, B., Hurley, B.P. & Allison, J.D. (2020) Harnessing the potential of precision pest management in plantation forests. *Southern Forests: A Journal of Forest Science*, 82(3), 197–201. <https://doi.org/10.2989/20702620.2020.1813651>
- Slippers, B., Hurley, B.P., Mlonjeni, X.O., de Groot, P. & Wingfield, M.J. (2012) Factors affecting the efficacy of *Deladenus siricidicola* in biological control systems. In: Slippers, B., de Groot, P. & Wingfield, M.J. (Eds.) *The sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest*. Dordrecht: Springer Netherlands, pp. 119–133. https://doi.org/10.1007/978-94-007-1960-6_9
- Smith, D.R. (1993) Systematics, life history, and distribution of sawflies. In: *Systematics, life history, and distribution of sawflies*. San Diego, CA: Academic Press, pp. 3–32.
- Song, J.H., Yang, Y.T., Yang, C.J., Choi, B.R. & Jwa, C.S. (2015) Responses of *Phyllotreta striolata* and *Athalia rosae ruficornis* to colored-sticky traps and aggregation pheromone and seasonal fluctuations in radish fields on Jeju Island. *Korean Journal of Applied Entomology*, 54(4), 289–294. <https://doi.org/10.5656/KSAE.2015.08.0.039>
- Staples, J.K., Bartelt, R.J., Cossé, A.A. & Whitman, D.W. (2009) Sex pheromone of the pine false webworm *Acantholyda erythrocephala*. *Journal of Chemical Ecology*, 35(12), 1448–1460. <https://doi.org/10.1007/s10886-009-9736-z>
- Taeger, A., Blank, S.M. & Liston, A.D. (2010) World catalog of Symphyta (Hymenoptera). *Zootaxa*, 2580(1), 1–1064. <https://doi.org/10.11646/zootaxa.2580.1.1>
- Taeger, A., Liston, A.D., Prous, M., Groll, E.K., Gehroldt, T. & Blank, S.M. (2018) *ECatSym - electronic world catalog of Symphyta (Insecta, Hymenoptera). Program version 5.0 (19 Dec 2018), data version 40 (23 Sep 2018)*. Müncheberg: Senckenberg Deutsches Entomologisches Institut (SDEI). Available at: <https://sdei.de/ecatsym/> [Accessed 10th February 2022].
- Tai, A., Higashiura, Y., Kakizaki, M., Naito, T., Tanaka, K., Fujita, M. et al. (1998) Field and electroantennogram responses of the pine sawfly, *Diprion nipponica*, to chiral synthetic pheromone candidates. *Bioscience, Biotechnology, and Biochemistry*, 62(3), 607–608. <https://doi.org/10.1271/bbb.62.607>
- Tai, A., Morimoto, N., Yoshikawa, M., Uehara, K., Sugimura, T. & Kdcukawa, T. (1990) Preparation of stereochemically pure sex pheromone components of the pine sawfly (*Neodiprion sertifer*) and field tests of the synthetic compounds. *Agricultural and Biological Chemistry*, 54(7), 1753–1762. <https://doi.org/10.1271/bbb1961.54.1753>
- Tai, A., Syouno, E., Tanaka, K., Fujita, M., Sugimura, T., Higashiura, Y. et al. (2002) Regio- and stereochemical study of sex pheromone of pine

- sawfly; *Diprion nipponica*. *Bulletin of the Chemical Society of Japan*, 75(1), 111–121. <https://doi.org/10.1246/bcsj.75.111>
- Taniwaki, T. (2013) Effect of color on the efficiency of flight interception traps for sampling adults of the beech sawfly, *Fagineura crenativora*. *Japanese Journal of Entomology (New Series)*, 16(3), 159–165. <https://doi.org/10.20848/kontyu.16.3.159>
- Teale, S.A., Wickham, J.D., Zhang, F., Su, J., Chen, Y., Xiao, W. et al. (2011) A male-produced aggregation pheromone of *Monochamus alternatus* (Coleoptera: Cerambycidae), a major vector of pine wood nematode. *Journal of Economic Entomology*, 104(5), 1592–1598. <https://doi.org/10.1603/EC11076>
- Thompson, B.M., Grebenok, R.J., Behmer, S.T. & Gruner, D.S. (2013) Microbial symbionts shape the sterol profile of the xylem-feeding woodwasp, *Sirex noctilio*. *Journal of Chemical Ecology*, 39(1), 129–139. <https://doi.org/10.1007/s10886-012-0222-7>
- van der Kooij, C.J., Stavenga, D.G., Arikawa, K., Belušič, G. & Kelber, A. (2021) Evolution of insect color vision: from spectral sensitivity to visual ecology. *Annual Review of Entomology*, 66(1), 435–461. <https://doi.org/10.1146/annurev-ento-061720-071644>
- Vilhelmsen, L. (2019) Giant sawflies and their kin: morphological phylogeny of Cimbicidae (Hymenoptera): phylogeny of giant sawflies (Cimbicidae). *Systematic Entomology*, 44(1), 103–127. <https://doi.org/10.1111/syen.12314>
- Vincent, C., Babendreier, D., Świergiel, W., Helsen, H. & Blommers, L.H.M. (2019) A review of the apple sawfly, *Hoplocampa testudinea* (Hymenoptera tenthredinidae). *Bulletin of Insectology*, 72(1), 35–54.
- Vuts, J., Kaydan, M.B., Yarımbatman, A. & Tóth, M. (2012) Field catches of *Oxythyrea cinctella* using visual and olfactory cues. *Physiological Entomology*, 37(1), 92–96. <https://doi.org/10.1111/j.1365-3032.2011.00820.x>
- Wallace, L.E. & McNeal, F.H. (1966) *Stem sawflies of economic importance in grain crops in the United States* (Technical Bulletin No. 171355). United States Department of Agriculture, Economic Research Service. Available at: <https://econpapers.repec.org/paper/agsuetsb/171355.htm>
- Wassgren, A.B., Anderbrant, O., Löfqvist, J., Hansson, B.S., Bergström, G., Hedenström, E. et al. (1992) Pheromone related compounds in pupal and adult female pine sawflies, *Neodiprion sertifer*, of different age and in different parts of the body. *Journal of Insect Physiology*, 38(11), 885–893.
- Wassgren, A.-B., Bergström, G., Sierpinski, A., Anderbrant, O., Högberg, H.-E. & Hedenström, E. (2000) Sex pheromone of the pine sawfly *Macrodiprion nemoralis* (Hymenoptera: Diprionidae): identification of (2S,3R,7R,9S)-3,7,9-trimethyl-2-tridecanol as the precursor for the active pheromone acetate. *Naturwissenschaften*, 87(1), 24–29. <https://doi.org/10.1007/s001140050003>
- Watanabe, K., Taniwaki, T. & Kasparyan, D.R. (2018) Revision of the tryphonine parasitoids (Hymenoptera: Ichneumonidae) of a beech sawfly, *Fagineura crenativora* Vikberg & Zinovjev (Hymenoptera: Tenthredinidae: Nematinae). *Entomological Science*, 21(4), 433–446. <https://doi.org/10.1111/ens.12327>
- Weaver, D.K., Buteler, M., Hofland, M.L., Runyon, J.B., Nansen, C., Talbert, L.E. et al. (2009) Cultivar preferences of ovipositing wheat stem sawflies as influenced by the amount of volatile attractant. *Journal of Economic Entomology*, 102(3), 1009–1017. <https://doi.org/10.1603/029.102.0320>
- Yan, Y., Wang, Y.-C., Feng, C.-C., Wan, P.-H.M. & Chang, K.T.-T. (2017) Potential distributional changes of invasive crop pest species associated with global climate change. *Applied Geography*, 82, 83–92. <https://doi.org/10.1016/j.apgeog.2017.03.011>
- Yemshanov, D., McKenney, D.W., de Groot, P., Haugen, D., Sidders, D. & Joss, B. (2009) A bioeconomic approach to assess the impact of an alien invasive insect on timber supply and harvesting: a case study with *Sirex noctilio* in eastern Canada. *Canadian Journal of Forest Research*, 39(1), 154–168. <https://doi.org/10.1139/X08-164>
- Yuan, X., Zhang, S., Zhang, Z., Kong, X., Wang, H., Shen, G. et al. (2013) Antennal morphology and sensilla ultrastructure of the web-spinning sawfly *Acantholyda posticalis* Matsumura (Hymenoptera: Pamphiliidae). *Micron*, 50, 20–28. <https://doi.org/10.1016/j.micron.2013.04.001>
- Zhang, Z., Wang, H., Chen, G., Anderbrant, O., Zhang, Y., Zhou, S. et al. (2005) Sex pheromone for monitoring flight periods and population densities of the pine sawfly, *Diprion jingyuanensis* Xiao et Zhang (Hym., Diprionidae). *Journal of Applied Entomology*, 129(7), 368–374. <https://doi.org/10.1111/j.1439-0418.2005.00983.x>
- Zhu, H., Thistle, H.W., Ranger, C.M., Zhou, H. & Strom, B.L. (2015) Measurement of semiochemical release rates with a dedicated environmental control system. *Biosystems Engineering*, 129, 277–287. <https://doi.org/10.1016/j.biosystemseng.2014.11.003>
- Ziska, L.H., Blumenthal, D.M., Runion, G.B., Hunt, E.R. & Diaz-Soltero, H. (2011) Invasive species and climate change: an agronomic perspective. *Climatic Change*, 105(1), 13–42. <https://doi.org/10.1007/s10584-010-9879-5>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Table S1 References list of alcohol precursor identification and pheromone-based field trial for 21 species of Diprionidae.

How to cite this article: Guignard, Q., Slippers, B. & Allison, J. (2022) Chemical and visual ecology of the Symphyta. *Agricultural and Forest Entomology*, 24(4), 453–465. Available from: <https://doi.org/10.1111/afe.12510>