



Review

Overview of *Bruchus rufimanus* Boheman 1833 (Coleoptera: Chrysomelidae): Biology, chemical ecology and semiochemical opportunities in integrated pest management programs

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ABSTRACT

Promoting the cultivation of native legumes, such as faba beans (*Vicia faba* L.) within the European Union is anticipated to contribute to the sustainability of cropping systems and provide food and feed proteins as alternatives to unsustainable imports. However, efficient alternative control methods to pesticides must be implemented to combat key pests that devalue faba bean seeds (namely, *Bruchus rufimanus* Boheman, 1833; Coleoptera: Chrysomelidae). This pest causes significant economic losses in faba bean crops as post-embryonic development (*cf.* seminivorous larvae) occurs inside forming seeds. While there has been extensive research on the biology and chemical ecology of *B. rufimanus*, efficient control methods are lacking. Here, we review this pest species to identify: (i) knowledge gaps on its biology that could enhance management tools; (ii) potential improvements to current semiochemical-based control approaches; and (iii) other method of control based on semiochemicals that could be implemented.

1. Introduction

Vicia faba L. (Fabaceae) (common names: broad bean, field bean, and horse bean) is a leguminous plant that provides multiple ecological services to agricultural systems, and contributes to their sustainability (Köpke and Nemecek, 2010). Jensen et al. (2010) previously listed four benefits of introducing *V. faba* to cropping systems. First, it provides soil with natural green manure by fixing atmospheric nitrogen via root symbiosis (*cf.* *Rhizobium* bacteria located in nodules), significantly enhancing successive crops yields, particularly cereals. Second, this manure input reduces carbon dioxide emissions generated by the manufacture, transport, and spread of synthetic fertilizers (Wani et al., 1994, 1991). Third, *V. faba* diversifies cropping systems, hindering pests and diseases, and promoting biodiversity by providing floral resources that benefit organisms, like pollinators (Abrams et al., 2015; Jensen et al., 2005). Fourth, *V. faba* produces seeds rich in starch and proteins, which are valued in the food and feed market, providing sustainable local alternatives to imports (Duc, 1997; Duc et al., 2010; Köpke and Nemecek, 2010).

Nevertheless, *V. faba* is sensitive to biotic and abiotic threats, which constrain productivity and reduce crop yields (Duc, 1997; Jensen et al.,

2010; Torres et al., 2006). Biotic factors include fungal diseases, like *Ascochyta fabae* Speg., 1898, *Botrytis fabae* Sardiña, 1929, or *Uromyces fabae* (Pers.) de Bary, 1879, and pests, like *Sitona lineatus* (L. 1758) (Coleoptera: Curculionidae), *Bruchus rufimanus* Boheman 1833 (Coleoptera: Chrysomelidae), and *Aphis fabae* Scopoli, 1763 (Hemiptera: Aphididae). All these pests may cause direct yield losses by impacting plant photosynthetic ability, except for *B. rufimanus*, whose larva develops in forming seeds without significantly prejudicing the plant physiology (Roubinet, 2016; Shearman et al., 2005). This pest however quantitatively and qualitatively affects the agricultural products of *V. faba* by (i) reducing the seeds weight due to the endosperm consumption of feeding larvae, (ii) decreasing the seeds nutritional value due to the accumulation of larvae faeces, and (iii) altering the seeds aesthetic quality due to perforations caused by the emergence of adults (Kaniuczak, 2004; Khelfane-Goucem and Medjdoub-Bensaad, 2016). Consequently, seeds are devalued from food and feeding markets that have strict quality standards fixed at respectively max. 3% and 10% of infested seeds (Bruce et al., 2011; Frérot and Leppik, 2016). Germination potential is also lost, and fungal infestation risk increases (Boughdad and Laugé, 1997; Titouhi et al., 2015). The presence of living insects inside seeds also impact access to domestic and international markets

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(Roubinet, 2016). Bachmann et al. (2020) estimated losses of 60 euros/t for faba beans, as damage prevents valuation in food markets, and 176 euros/t, as seed batches cannot be valorized in food and feed markets.

Limited methods exist for controlling *B. rufimanus*, exacerbating seed devaluation. Pyrethroid insecticides are typically sprayed during the flowering and first pod setting stages to target adult pests before oviposition, but the success of this method faces numerous limiting factors. Firstly, active substances approved in the European Union are limited to lambda cyhalothrin, zeta cypermethrin, and deltamethrin, and their uses are either restricted at max. two treatments per crop during the flowering period, either completely banned from “greening measures” foreseen by the Common Agricultural Policy, namely *Environmental Focus Areas*. In addition to these spraying restrictions, *V. faba* dense crop canopy hinders spraying efficiency by preventing a proper penetration into the target plant-parts (i.e., the plant basal nodes, where pods grow and most *B. rufimanus* damage occurs). Also, high temperatures shorten pyrethroid persistence, while it promotes *B. rufimanus* activity (Mansoor et al., 2015; Ward, 2018). As a result, the little amount of active substances, combined with application inefficiency, is likely to promote the onset of resistance mechanisms, as demonstrated for *S. lineatus* (Ward, 2018). These pesticides also negatively impact pollinators through direct contact toxicity and perturbation of foraging behavior, which is exacerbated when combined with fungicides (Sanchez-Bayo and Goka, 2014). It is thus essential to identify efficient and cost effective control methods that enhance the seed quality of native plant proteins, particularly in the context of increasing deficit in vegetable proteins throughout European Union, which is offsetted with unsustainable imports (European Commission, 2018).

Many studies have assessed the development of alternative control method over last decades. These studies highlighted five control levers, namely (i) semiochemicals (Bruce et al., 2011; Frerot et al., 2015; Ward, 1999), (ii) selection of resistant varieties (Carrillo-Perdomo et al., 2019; Seidenglanz and Hun Ady, 2016; Szafirowska, 2012), (iii) vegetal oils (iv) microbial control agents (e.g., entomopathogenic fungi) (Sabbour et al., 2007; Titouhi et al., 2017), and (v) an adaptation of cultural practices (e.g., sowing/harvesting dates, sowing density, and crop association) (Bachmann et al., 2020; Seidenglanz et al., 2011; Szafirowska, 2012; Ward, 2018). To date, management approaches mitigating *B. rufimanus* damage have yet to be implemented in Europe, and some biological aspects of this pest should still be elucidated to develop effective pest management tools, including overwintering behavior, temperature-dependent development, and quantitative economic thresholds. This review presents existing knowledge on *B. rufimanus* biology based on studies conducted across Europe and Mediterranean countries. Emphasis is placed on semiochemical processes regulating *B. rufimanus* interactions at different phenological stages of *V. faba*. Finally, semiochemical-based control methods are reviewed to highlight future research directions to implement efficient integrated pest management (IPM) strategies of *B. rufimanus*.

2. Biology of *Bruchus rufimanus*

2.1. Overview of *B. rufimanus*

Bruchus rufimanus (Fig. 1) (common name: broad bean weevil or bean seed beetle) is a Coleoptera belonging to the Chrysomelidae family, subfamily Bruchinae. This subfamily contains 1700 species, called bruchids or seed beetles. About 30 bruchid species cause major economic damage, of which nine are cosmopolitan, belonging to the genera *Acanthoscelides*, *Bruchus*, *Callosobruchus*, *Caryedon*, and *Zabrotes* (Kingsolver, 2004).

All bruchids are oligophagous or monophagous species (Huignard et al., 2011), with an endophytic ravaging stage corresponding to the post-embryonic development as larvae consume the endosperm inside leguminous seeds (cf. seminivorous larvae). Two ecological groups exist based on female egg-laying behavior and the ability of larvae to develop

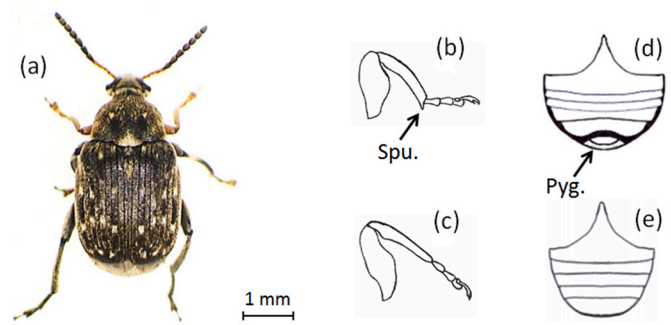


Fig. 1. Morphological illustration of *Bruchus rufimanus* and sexual dimorphism: (a) Adult; (b) Middle leg of males presenting spurs (Spu.); (c) middle leg of females without spurs; (d) Ventral face of males abdomen indented by pygidium (Pyg.); (E) Ventral face of females abdomen without indentation. ©A. Segers.

in dry seeds (Howe and Currie, 1964). The first group includes multi-voltine species that breed and develop in crops and in stored dry seeds, destroying large quantities of stored pulses. The second group includes univoltine species that only develop in crops forming seeds, and do not damage stored pulses.

Bruchus rufimanus is an oligophagous species from the second group. It is a major pest of *Vicia* spp. (Hoffman et al., 1962). It is globally distributed from the temperate to tropical areas in 36 countries, partly due to the trade of infested seeds, and is particularly present in areas where *V. faba* is cultivated as dry seeds (Bahr, 1976; Hoffman et al., 1962; Southgate, 1979; Ward, 2018).

This pest strongly depends on host plant phenology, as adults feed on flowers and larvae feed on forming seeds of host plants along its univoltine life cycle. Kergoat et al. (2007) identified 11 host plants of larvae, including three *Lathyrus* species and eight *Vicia* species. Adults feed on the pollen and nectar of several additional plants, depending on floral resource availability in the environment outside hosts flowering periods (Boughdad, 1994; Medjdoub-Bensaad et al., 2007). Pölitz and Reike (2019) detected the pollen of 12 species in the digestive tube of adults, including *Carduus* sp., *Trifolium repens* L., *Chamaemelum nobile* (L.) All., *Sinapis arvensis* L., *Phacelia tanacetifolia* Benth., *Raphanus sativus* L., *Anethum graveolens* L., *Helianthus annuus* L., *Malva* sp., *Cyanus segetum* Hill, *Calendula officinalis* L., and *Fagopyrum esculentum* Moench.

Fig. 2 presents the life cycle of *B. rufimanus* on faba bean crops. The seasonal population dynamics of this pest are regulated by crop growth and climatic conditions (Ward, 2018). Adults appear when crops flower during spring and summer, with sunshine and warmth (23–26 °C) enhancing feeding, reproduction, and oviposition (Leppik and Frerot, 2014). Embryonic and post-embryonic developments correspond to the fructification period, from when young pods appear to late-summer, when most adults emerge from harvested seeds. The extent of damage (3–100%) varies across years, depending on cultivar, meteorological conditions, and crop location (Boughdad and Laugé, 1997; Roubinet, 2016). Reproductive diapause allows insects to survive winter until trophic resources become available in spring.

2.2. Life cycle

When spring temperatures reach 15 °C (i.e., threshold for adult activity), diapausing adults leave overwintering sites to colonize crops (Hoffman et al., 1962; Medjdoub-Bensaad et al., 2007; Roubinet, 2016). First, males colonize crops at the flower bud stage (Ferot et al., 2015) or vegetative stage, and consume nectar from extrafloral nectaries (Pölitz and Reike, 2019). Once crops flower, females colonize them. Tran and Huignard (1992) and Tran et al. (1993) identified two factors regulating the end of reproductive diapause under laboratory conditions: the increase of the photoperiod to a duration of 16 light

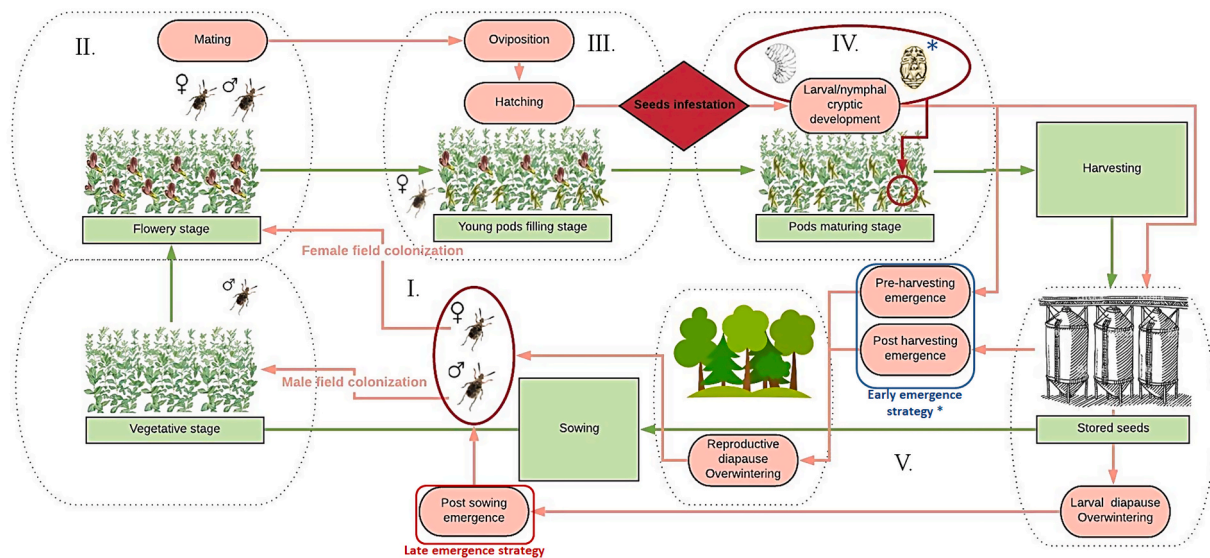


Fig. 2. Illustration of the life cycle of *B. rufimanus* (pink arrows) based on *V. faba* phenology and harvesting practices (green arrows). The univoltine development of *B. rufimanus* is described in five steps: I. Field colonization of males as the crop is still at the vegetative stage, then followed by the females colonization as the crop is at the flowering stage; II. Mating in flowers after feeding which allows the achievement of reproductive diapause; III. Oviposition on young forming pods; IV. Eggs hatching, i.e. seeds infestation by seminovorous larvae during the maturation of the seeds; V. Adult emergence and overwintering in wooded sites in reproductive diapause (cf. early emergence strategy) or larval/nymphal overwintering until the next spring seeding (cf. late emergence strategy). © A. Segers. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

hours that allows males to mature sexually, and the consumption of host plant pollen that is additionally required for females sexual maturation. Adults only become sensitive to these two factors after 6–7 months of diapause (i.e., the obligate period of reduced sexual organ development), and a latency period of 10–15 days is required to terminate diapause (Tran et al., 1993).

Bruchid activity and reproduction is optimal at 20–25 °C (Freret et al., 2015; Roubinet, 2016). Mating spans 2–3 weeks, primarily on faba bean flowers (Boughdad, 1994). After mating, males leave crops when host plants stop flowering. Females remain on fructifying crops to lay eggs on forming pods (Medjdoub-Bensaad et al., 2015; Pölitiz and Reike, 2019).

Oviposition starts when the first pods are produced at the plant basal nodes, and spans around six weeks, corresponding to the fructification period before pods dry (Boughdad, 1994; Medjdoub-Bensaad et al., 2015). Females lay eggs on green pods (Fig. 3), regardless of growth stage; consequently, the first pods are the most ravaged (Medjdoub-Bensaad et al., 2015, 2007). Egg laying lasts 1–2 min, with max. 10 eggs laid/pod, and 100 eggs/female (Boughdad and Laugé, 1997; Huignard

et al., 2011). Eggs are sensitive to rain and low temperature (Roubinet, 2016). Degree-day data are unavailable; however, incubation lasts 1–3 weeks, with most eggs hatching after 10 days (Boughdad, 1994; Pölitiz and Reike, 2019; Roubinet, 2016; Yus-Ramos et al., 2014).

Hatching larvae (Fig. 4) directly bore through the pod walls, and remain in the pericarp for about one week before entering a single forming seed, where they consume the endosperm without damaging the embryo (Pölitiz and Reike, 2019). Two-three larvae may develop inside the same seed (Pfaffenberger, 1977). Survival depends on the composition of food resources, including potential antinutritional factors (e.g., tannins and α -amylase inhibitors), initial egg position at the pod surface, and pod/seed coat physical barriers to larval penetration (Lattanzio et al., 2005; Seidenglanz and Hun Ady, 2016; Tsialtas et al., 2019). Four larval instars occur under different trophic conditions. First larval instars (morphologically recognizable by a prothoracic “H” plate) develop in young forming seeds, with low nitrogen content (0.02 g/100 g). Fourth larval instars occur in nearly dry mature seeds, with 2.88 g/100 g nitrogen content (Boughdad and Laugé, 1997). External factors that influence larval instar development, especially temperature, need

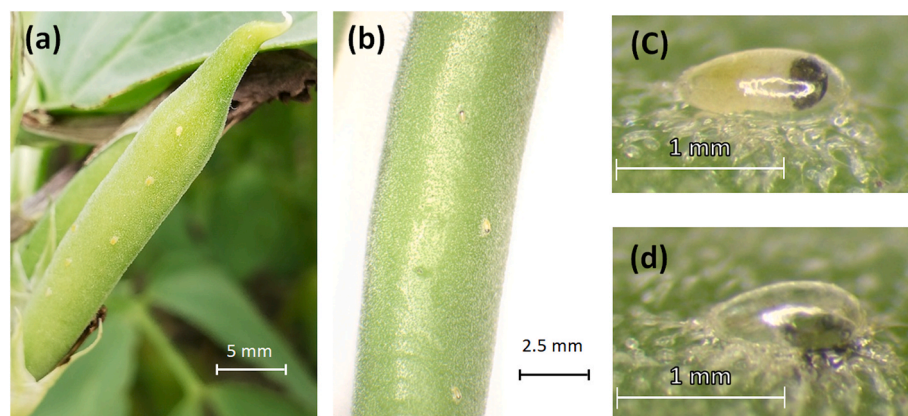


Fig. 3. *Bruchus rufimanus* eggs illustrations: (a) Recently yellow laid eggs on *V. faba* young pod; (b) Eggs about to hatch (white eggs presenting one black point); (c) Egg detail containing “black head” L1 larvae inside; (d) hatched egg presenting a penetration hole on the pod pericarp side. © A. Segers. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

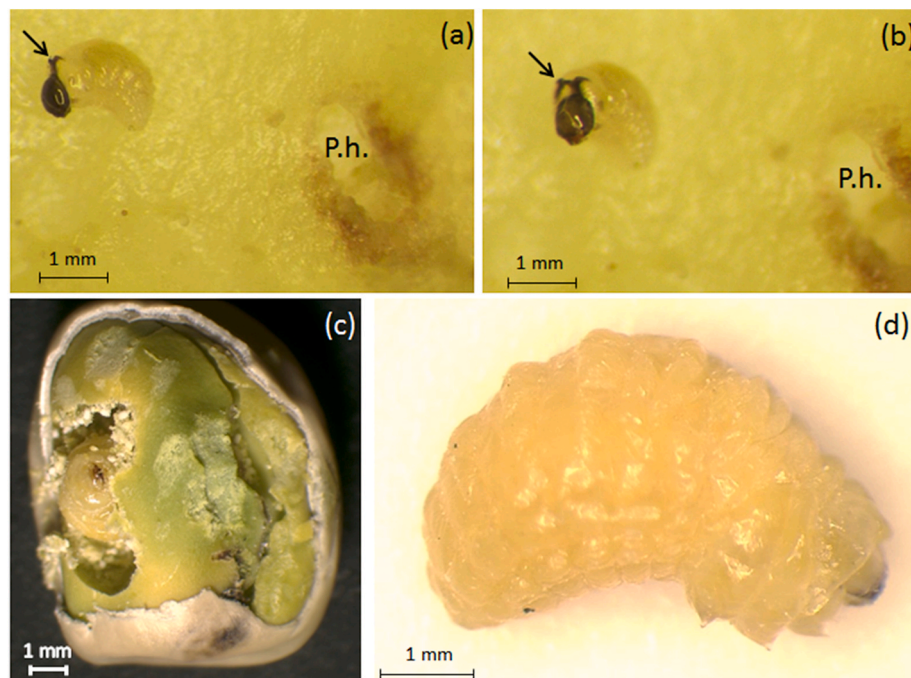


Fig. 4. Illustrations of the first and fourth larva instars of *B. rufimanus*: (a) and (b) First larva instar with prothoracic “H” plate (arrow) and the penetration hole through the pod pericarp (P.h.); (c) Fourth larva instar developing inside seed; (d) Lateral view of fourth larva instar ©A.Segers.

investigation. The mean duration of each larval instar is 23.0, 20.8, 22.5, and 35.6 days, respectively (Boughdad, 1994). Growing larvae position their heads against the grain tegument before nymphosis.

Two developmental strategies, overwintering stages, and sites are possible depending on the time of nymphosis (Huignard et al., 2011; Medjdoub-Bensaad et al., 2007). The “early emergence strategy” involves continuous post-embryonic development of 90–110 days until imagoes emerge in August–September (Boughdad, 1994; Huignard et al., 2011). These adults are in reproductive diapause, actively feeding on flowers available in their environment before decreasing temperatures force them to locate overwintering sites such as the underside of bark, lichen on trees, humus, hedges surrounding crops, and storage facilities (Bruce et al., 2011; Hoffman et al., 1962; Ward, 2018). The “late emergence strategy” involves decelerated larval development, whereby insects overwinter as larvae in seeds, and pupate the following spring when seeds are sown (Medjdoub-Bensaad et al., 2007). Pupation lasts 10–15 days (Boughdad, 1994; Roubinet, 2016). Data describing the external factors of nymph development, especially degree-day, is required.

Consequently, two colonization patterns are possible the next spring. For the latter strategy, adults directly colonize the crop from sown seeds (Boughdad, 1994). Changes to environmental moisture and temperature caused by sowing trigger the onset of larval post-embryonic development of overwintering larvae inside sown seeds (Huignard et al., 2011; Medjdoub-Bensaad et al., 2007). For the former strategy, at 15 °C, insects can fly several kilometers at 8–10 m altitude from overwintering sites to crops (Huignard et al., 2011). Data on overwintering, field colonization, and temperature effects on *B. rufimanus* are required.

Life cycle timing shifts with the latitude and climate at which populations occur. For example, in Morocco, male and female field infestation peaked on March 20 and April 20, 1990–1991, respectively (Boughdad, 1994). In Germany, male and female field infestation peaked on May 22 and June 16, 2018, respectively (Pölitz and Reike, 2019).

3. Chemical ecology of *Bruchus rufimanus*

The life cycle of phytophagous insects imply three essential steps that are (i) locating trophic resources for adult feeding, (ii) locating sexual

partners for reproduction, and (iii) locating adequate spawning substrate for offspring survival (Bernays and Chapman, 1994; Sauvion et al., 2013; Whittaker and Feeny, 1971). Each step is regulated by volatile and non-volatile organic compounds (VOCs and NVOCs) emitted by plants and/or insects, causing chemical signal (i.e., semiochemical) inducing modifications to insects behavior (Law and Regnier, 1971).

Concerning phytophagous insect like *B. rufimanus* that feed, mate, and oviposit on different parts of host plants, three classes of semi-chemicals (or VOCs) regulate the interaction of *B. rufimanus* () with *V. faba* and sexual partners (Bruce et al., 2011; Frerot et al., 2015; Frérot and Leppik, 2016; Ward, 1999) (Table 1). These include: (i) kairomones released by flowers providing food localization signals (Bruce et al., 2011; Ward, 1999), (ii) sexual pheromones emitted by males to locate sexual partners (Bruce et al., 2011), and (iii) kairomones released by *V. faba* pods for oviposition (Ferot et al., 2015; Frérot and Leppik, 2016).

Vicia faba volatiles have different emission rates depending on phenological stage (cf. vegetative, flowering, and fructification). These VOCs are ubiquitous (i.e., emitted by many species). Signal specificity is based on the ratio of the blend, rather than specific compounds (Bruce and Pickett, 2011; Frérot et al., 2017; Leppik and Frérot, 2014). Adding *B. rufimanus* pheromones to *V. faba* volatiles (i.e., chemical signature) synergistically impacts the attractiveness of sexual partners (Bruce et al., 2011; Frerot et al., 2015). Fig. 5 shows the dynamic evolution in chemical signature characterizing the interaction of *B. rufimanus* with *V. faba* during feeding, mating, and ovipositing.

3.1. Kairomones triggering field colonization

Volatile organic compounds emitted by plants are important for host-seeking insects. When adult *B. rufimanus* leave overwintering sites in spring to locate food, flowering faba bean crops trigger field colonization (Fig. 2–I). Semiochemicals governing this attractiveness were identified by Bruce et al. (2011) that collected VOCs from flowering plants and determined nine attractive VOCs: myrcene, (*R*)-limonene, (*E*)-ocimene, (*R*)-linalool, 4-allylanisole (i.e. estragol), cinnamyl alcohol, cinnamaldehyde, α and β -caryophyllene. It was also underlined

Table 1
Semiachemicals (VOCs) regulating *Bruchus rufimanus* feeding, mating and egg-laying behaviors.

Type of semiochemicals	Chemical identification (proportion of the active blend)	Targeted individuals	Laboratory/field efficiency and mode of action	References			
<i>V. faba</i> (var. <i>Sutton dwarf</i>) flower Kairomone	Myrcene (2.7%)	Male - female	Efficient attractiveness both in laboratory and in the field	Ward (1999) Bruce et al. (2011)			
	(R)-limonene (10.4%)						
	(E)-ocimene (1.8%)						
	(R)-linalool (27.5%)						
	4-allylanisole (4.5%)						
	Cinnamyl alcohol (0.6%)						
	Cinnamaldehyde (1.2%)						
	α and β caryophyllene (50.6%)						
	1-undecene				Female	Efficient attractiveness in laboratory but not in the field, attraction synergized by nine floral VOC's	Bruce et al. (2011) Frerot et al. (2015)
	<i>V. faba</i> (var. <i>Espresso</i>) pods kairomone				Cis-3-hexenyl acetate (30.0–40.0%)	Gravid female	Efficient attractiveness both in laboratory and in the field
Limonene (15.0–20.0%)							
Ocimene (15.0–20.0%)							
Linalool (10.0–20.0%)							
α and β caryophyllene (15.0–20.0%)							

in this study that a combination of only three of these components - (R)-linalool (17.7 mg/day), cinnamyl alcohol (0.4 mg/day) and cinnamaldehyde (0.77 mg/day) - were attractive to *B. rufimanus*, and that there is a difference in the attractive response according to sexes, males being more attracted to this scent of flowers than females. Thus, *B. rufimanus* is specifically attracted to *V. faba* flower volatiles, with sex-specific responses corresponding to colonization patterns (*i.e.*, males colonize crops before females).

Frerot et al. (2015) explored how volatile signal evolves with *V. faba* phenological stage. *V. faba* volatile emissions include ~20 ubiquitous components, with emission rates evolving with plant phenology, altering odor profiles. Vegetative stage was demonstrated as being unattractive to *B. rufimanus*, whereas flowering odors are strongly attractive, particularly to males, confirming that insects are attracted to specific scents of host plant flowers.

Insights on the attractiveness of *B. rufimanus* to floral scent according to physiological stage (*i.e.* in reproductive diapause or sexually mature) were recently provided by field monitoring study led by Ward (2018) who followed population dynamic using semiochemical traps baited with three floral volatile blends (from Bruce et al., 2011). They could not significantly catch *B. rufimanus* before crops bloomed, and mean number of catches only increased after blooming finished while insects were present in crops. This suggests that diapausing adults emerging from overwintering sites in spring are attracted by large amount of floral crop scent that strongly competes with synthetic lures. This massive odor emission triggers population movement over great distances to colonize fields. Whether these floral scents attract *B. rufimanus* emerging form seeds in late-summer needs clarifying (*cf.* early emergence strategy).

3.2. Pheromonal communication

After landing on *V. faba*, *B. rufimanus* feed on pollen and nectar to terminate its reproductive diapause, and mate on flowers (Fig. 2 – II). Bruce et al. (2011) investigated which volatiles were involved in the mating behavior by testing the response of mature field-collected adults to volatiles from their mating partner. They found that only one male emitted VOC, 1-undecene, was attractive to female. Subsequent bioassay in laboratory validated this single component VOC as a sexual pheromone. Yet, a field test of traps containing just 1-undecene failed to catch females, but associating it with host plant kairomones was more effective. Thus, host plant kairomones synergistically act with male emitted sexual pheromones in *B. rufimanus* communication. This was later confirmed using flight tunnels, with females being more attracted to combination of male and flowering plants than just flowering plants (Frerot et al., 2015).

A male emission of sexual or aggregation pheromone is common to several Coleoptera species, especially within Curculionidae and Chrysomelidae families (Smyth and Hoffmann, 2003; Witzgall et al., 2010). Such pheromones are therefore difficult to distinguish as they attract both sexes to the same site and induce mating after supposed tactile recognition of sexual partner (Nojima et al., 2007; Qi and Burkholder, 1982; Sauvion et al., 2013; Witzgall et al., 2010). The synergetic effect of host plant kairomones is also frequent concerning Chrysomelidae species. Many examples of male emitted pheromones whose attractiveness was boosted by association with host plant VOCs could be highlighted in the literature (Bartelt et al., 2008, 2006; Cossé et al., 2002; Dickens et al., 2002; Rao et al., 2003). This suggest the collocation of olfactory receptors neurons (ORN(s)) in the same sensillae and an eventual dimorphism in expression of olfactory neurons when male/female are more sensitive to certain chemical signatures (Park et al., 2013; Unelius et al., 2013).

The 1-undecene lack of attractiveness to females during field test is thought to be due to a weak attractive range of this VOC (Bruce et al., 2011). Alternatively, the experimental design might have been unsuitable for detecting all blended components in the pheromone. Single component pheromones being rare (Blomquist et al., 2005); other VOC (s) could probably be blended with 1-undecene and exert a better attraction to females and/or constitute aggregation pheromones. Further investigations are necessary for a better understanding of pheromonal communication.

3.3. Kairomones involved in locating *Vicia faba* pods and oviposition

After mating on flowers, gravid females oviposit on forming pods at the base of *V. faba* (Fig. 2–III). This behavior is also regulated by VOCs, recently identified by Leppik et al. (2016). The authors tested the EAG response of gravid females to host plant odor during the fructification stage, during which green odors mixed with monoterpenes were emitted. Gravid females clearly responded to pod odor. Although no precise data was published, an INRA patent describes the composition of this odor as containing cis-3-hexenyl acetate (30–40%), plus five minor compounds similar to those identified at the flowering stage by Bruce et al. (2011): ocimene (15–20%), linalool (10–20%), α and β caryophyllene (10–20%), and limonene (15–20%) (Frerot and Leppik, 2016).

4. Semiochemical-based control method of *B. rufimanus* in IPM programs

Semiochemicals offer several opportunities for manipulating pest behavior, and could hinder one or more of the three crucial stages preventing the completion of their life cycle (Evensen, 2018). Four semiochemical-based methods have been developed for pest management: (i) monitoring, (ii) mass annihilation (including “mass trapping” and “lure and kill”), (iii) mating disruption, and (iv) push-pull (Smart

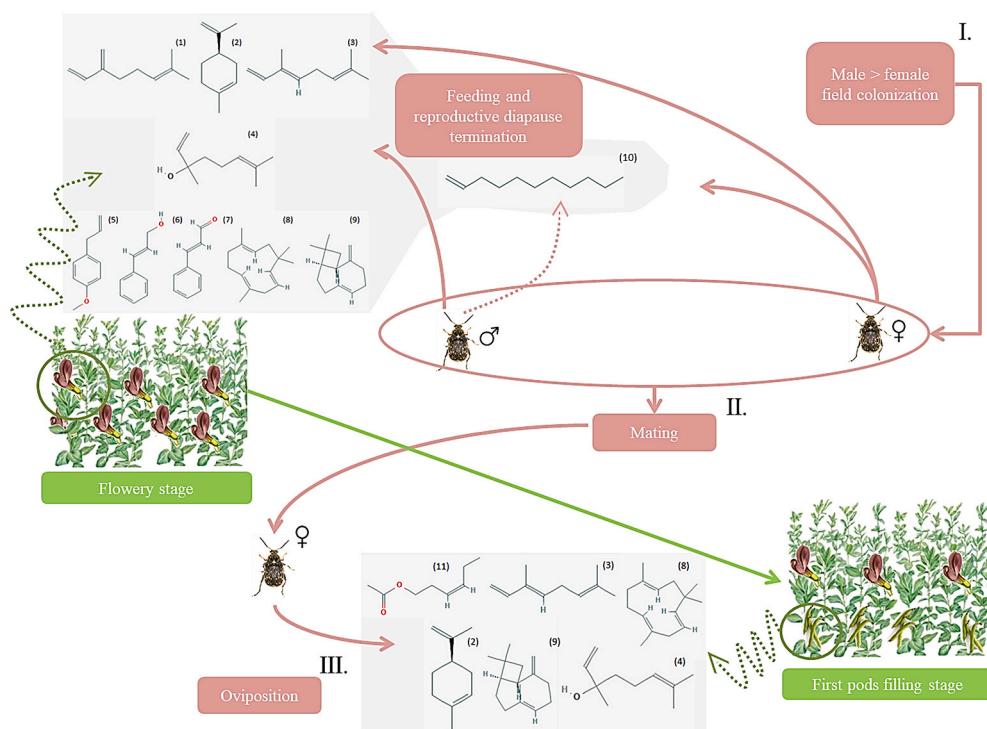


Fig. 5. Detailed chemical process of the three first developing stages of *Bruchus rufimanus* (field colonization, mating and oviposition; pink arrows) according to current knowledge on the evolution of the chemical signature (dotted arrows) related to the host plant phenology (green arrow) - Male and female attractiveness by the VOCs flowers for feeding and mating (Bruce et al., 2011): (1) Myrcene, (2) (*R*)-Limonene, (3) (*E*) Ocimene, (4) (*R*)-linalool, (5) 4-allylanisole, (6) Cinnamaldehyde, (7) Cinnamyl alcohol, (8) β caryophyllene, (9) α -caryophyllene - Female attractiveness by a combination of flowering host plant scent and male sexual pheromones (Bruce et al., 2011): (10) 1 undecene - Gravid female attractiveness by filling pods scent (Frérot and Leppik, 2016): (11) cis-3-hexenyl acetate. ©A. Segers. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

et al., 2014). Based on current knowledge of the chemical ecology of *B. rufimanus*, mating disruption could not be implemented, because it requires efficient sexual pheromones. However, the other methods have potential, with monitoring and mass trapping already being implemented/under implementation.

Monitoring methods based on the use of semiochemical baited traps consists in detecting the presence of pests, and keeping track of population dynamics along crop development in order to determine when to apply pesticides (Witzgall et al., 2010). Integrated pest management typically uses this method of control as this provides a way to rationalize the use of pesticides at the most sensitive times for growers named “economic thresholds” (Smart et al., 2014). In the case of *B. rufimanus* infestations, the determination of economic threshold is currently based on the surveillance of temperatures rather than on the pest population density due to the great influence of this environmental factor on adult mating and ovipositing activities (cf. section 2.2). Economic threshold is defined as two consecutive days of sunny weather manifesting maximum temperatures above 20 °C at the time of first pod setting (Ramsden et al., 2017; Ward and Smart, 2011). When these meteorological conditions are met, semiochemical traps will enable growers to detect and monitor *B. rufimanus* populations to assess whether an intervention or second treatment is necessary depending on the pest persistence.

Practically, the monitoring method consists in displaying semiochemical traps on the edges or inside the crop, and lures them with three components floral attractants elaborated by Bruce et al. (2011). Two trap design are commonly used (i) green ‘cone’ traps (cf. traps for monitoring boll weevil), mounted on 1 m poles; and (ii) green funnel traps with barrier cross which are suspended at the same height as *V. faba* flowers (Dickerson, 2001; Ward, 2018). The monitoring period runs throughout the entire *V. faba* flowering and pod setting period.

However, the efficiency of this method is limited by numerous factors. First of all is the lack of pesticide efficiency and bad side effects on beneficials (cf. introduction). Then, *V. faba* strong floral odors are observed to reduce the lure attractiveness (cf. section 3.2). This

uncompetitive lure issue was therefore put under further observation at the Institute of National Research in Agronomy and Environment (INRAE); which led to the development of two efficient kairomonal attractants: one reproducing a more competitive flower scents (under unavailable patent – license number 20 02150), and the other reproducing the odor of pod scent, as presented at section 3.4 (Frérot and Leppik, 2016). These lures are currently under study for a potential implementation as mass trapping control method.

Mass trapping is a similar method to monitoring, except that it does not relies on pesticides, but it rather aims to catch as many individuals as possible to reduce or eradicate pest population (Smart et al., 2014). Kairomonal attractants developed by INRAE are under investigation by AgriOdor company for mass trapping of *B. rufimanus*. A prototype of pan trap (patent pending), specific to the capture of *B. rufimanus*, was also developed. Mass trapping of Coleoptera species could already be successful proceeded with other pests (Dufour and Frérot, 2008; Faleiro et al., 2003), concerning *B. rufimanus*, pods kairomones have the particular advantage of attracting females offering better chances for avoiding oviposition (Smart et al., 2014). No information concerning the required traps density is currently available and studies are being carried out to develop slow-release devices emitting kairomones up to three weeks (Montagné et al., 2018).

5. Future research areas to control *B. rufimanus*

All the information provided so far concerning the biology and chemical ecology of *B. rufimanus*, as well as semiochemical-based control methods raised four main gaps of knowledge having potential application in IPM strategy: (i) determination of temperature influence on developmental rate and fecundity of *B. rufimanus*, (ii) methodological improvement of pheromonal studies and other pheromonal communication, (iii) implementation of monitoring methods providing quantitative description of population size and movements, and (iv) implementation of other semiochemical-based control methods.

5.1. Influences of temperature on the developmental rate and fecundity of *B. rufimanus*

Temperature dependent development models are often used to anticipate pest activity and seasonality (Lamb, 1992). There is extensive literature emphasizing the influence of temperatures on the developmental rates and fecundity of multivoltine bruchid species (Howe and Currie, 1964; Kistler, 1982; Maharjan et al., 2017; Soares et al., 2015; Wu et al., 2013). But none laboratory study were carried out on univoltine species such as *B. rufimanus*, probably because of economical differences in pest importance, and also due to the difficulty of establishing fairly productive rearing of these insects with complex biology. Only one field study has emphasized the influence of temperature on *B. rufimanus*, and shown that temperature could be a key factor influencing overwintering emergence and oviposition, although data could not statistically prove it (Ward, 2018). Defining temperature thresholds and thermal constants for each development stages of *B. rufimanus* (cf. overwintering and ovipositing adults, eggs incubation and post embryonic development - Fig. 2), could provide a better understanding of interannual fluctuations of damages as well as an accurate determination of the duration of each life cycle stages. This could overall provide growers with useful indications to anticipate the emergence of insects either from overwintering site in spring, or from matures seeds in late summer; and allow them to adopt adequate management measures to hinder pest population. Defining the appropriate time to deploy traps for mass trapping, or proceeding to harvest before the emergence of adults would probably represent a good opportunities minimize short-term damage, and progressively decrease *B. rufimanus* population in the long run, as suggested with *Bruchus pisorum* L. (Mihiretu and Wale, 2013).

5.2. Methodological improvement and other pheromonal communication

Further knowledge on pheromonal communication of *B. rufimanus* is necessary to provide new insights for efficient semiochemical-based control methods. This could be provided on the one hand by adapting experimental odor sampling designs, and on the other hand by investigating whether other type of pheromonal communication such as the oviposition pheromone could have a deterrent effect on egg laying behavior.

Unsuccessful application of sexual pheromone in field trials (cf. section 3.3) suggested that other VOC(s) may be blended with 1-undecene in the pheromone composition, which may therefore constitute an aggregation pheromone. This important issue should be investigated through some improvements in the sampling odor design. Firstly, an increasing pheromone production could increase chances to detect other volatiles. This could be done either by antenectomy, which reduces antennal input of chemical communication and induces a response of increasing pheromonal production, or by application of juvenile pheromone JHIII that stimulates pheromone production as long as JHIII is involved in the biosynthetic pathway of the pheromone production (Dickens et al., 2002; Seybold and Vanderwel, 2003). Secondly, the odor sampling method should be performed with adults feeding on host plant instead of insulating them in a vial. Indeed, most beetles need to consume host plants in order to emit volatiles as host plant feeding contains necessary precursors (Sauvion et al., 2013; Tillman et al., 1999).

“Host marking pheromones” (HMP) or “Oviposition deterring pheromones” (ODP) are semiochemicals regulating or suppressing the egg-laying behavior of insects. Their role is to signal the presence of egg/larva to another conspecific female to avoid supplementary oviposition on the same substrate. This intraspecific regulation of egg density aims to increase fitness of emerging larvae by reducing the risk of competition in a limited food resource, which may lead to cannibalism (Prokopy, 1972; Thiéry, 1991). Several studies have highlighted the deposition of HMP by many species, but none has yet tried to study such pheromonal

communication with *B. rufimanus*, while numerous biological indications support the presence of HMP. Indeed, their heir larvae develop inside limited food resources, i.e. one single seed (Hoffman et al., 1962). High larval density induces a risk of cannibalism where the largest larvae can damage/kill the smallest (Pölitz and Reike, 2019), and the number of eggs laid per green pods in the field rarely exceed 10 (Huignard et al., 2011).

5.3. Standardization of semiochemical-based monitoring methods for quantitative demographical description

Lacks of knowledge concerning seasonal population dynamics and long distance dispersal of *B. rufimanus* are related to the absence of standard monitoring methods. Semiochemical-based monitoring methods taking into account the landscape influence (cf. presence of storage facilities and woods as overwintering sites) offers good opportunity to fillfull this methodological gap and would allow to anticipate areas presenting high risks of infestation for growers.

Establishment of semiochemical monitoring of *B. rufimanus* was already performed by Ward (2018) and could thus be considered as a basis of recommendation for standardization. They displayed floral scented lured traps at the edge of faba bean crops at a height of 0.8–1 m, spaced of about 20 m, and registered catches at least once a week. This method is thought to find potential improvements in the use of more efficient semiochemicals and trap designs for catching *B. rufimanus* (cf. AgriOdor researches), or in technological advances such as connected detection devices providing real time information of pest population to growers, which reduces the logistical burden of monitoring (Bordes, 2017).

Information obtained on spring population densities (number of adults per ha), and on how crops are subsequently damaged (number of damaged seeds per ha) will provide all the necessary data to determine a robust quantitative economic threshold, as well as an eventual decision support model like that developed to manage *Sitodiplosis mosellana* (Gehin, 1857) (Ellis et al., 2009; Gahukar and Reddy, 2018; Ramsden et al., 2017).

5.4. Implementation of other semiochemical control methods: “Lure and kill” and “push-pull”

“Lure and kill”, also called “attract and kill”, “male annihilation”, “bait sprays” or “attracticide”, consists in combining a pesticide/sterilant/pathogenic agent with an attractant in order to kill/sterilize/infect the insect (El-Sayed et al., 2009). Many implementation modalities are possible: lures can be pheromonal and/or kairomonal attractants, while the co-formulation of killing agent (insecticide, sterilant or pathogen) may be arranged in a trap or immediately dropped in the crop (El-Sayed et al., 2009; Smart et al., 2014). To insure a successful implementation, the attractiveness on the insect should not be hampered by the odor of the killing agent (Cayley et al., 1984), and non-chemical killing agents (e.g., entomopathogenic fungi) should be suggested to increase the specificity of the control method and avoid the appearance of resistance mechanism (Roush et al., 1990). Concerning *B. rufimanus*, an interesting implementation of attract and kill strategy would consist in attracting males and females in devices lured with host plant kairomones (cf. section 3) containing entomopathogenic fungi so as to infect insects by contact with conidia. The infected insects could then disseminate the pathogen to other members of their population (Klein and Lacey, 1999). This approach named “autodissemination” was already performed with other insects and is particularly promiscuous for *B. rufimanus* as attractive kairomones are already developed and two efficient pathogenic fungi species were identified, namely *Beauveria bassiana* (Bals.-Criv.) Vuill. 1912 and *Metarhizium anisopliae* (Metschn.) Sorokin 1883 (Sabbour et al., 2007). Proceeding with this method during field colonization of *B. rufimanus* (cf. Fig. 2 I) could furthermore benefit from a natural infection between sexual partners inducing sublethal effects like the inhibition of oviposition, as highlighted with sap beetles (Vega et al.,

1995). Proceeding with this method during the emergence of adults (cf. Fig. 2 V) could also favor the transmission of pathogen between overwintering adults.

“Push Pull” is another implementable semiochemical control method of *B. rufimanus*, consisting in regulating the insect behavior by “pushing” it from protected crops, using repellent or deterrent from associated plants or synthetic compounds, and “pulling” it to the perimeter of the crop where it will develop on other plants. Ideally, the pushing effect also attracts natural enemies such as predators or parasitoids, and pulling plants reduce population with innate defense or with incorporated pesticide (Pickett et al., 2014). In the case of *B. rufimanus*, botanical oils of *Artemisia campestris* L., nigella and mustard were identified as having efficient repellence/oviposition-deterrenting/insecticidal effects on *B. rufimanus* (Sabbour et al., 2007; Titouhi et al., 2017). These could then constitute potential repellent agents, as far as their harmlessness effects against beneficial organisms of faba bean crops, and their stability against oxidation and photo-deterioration can be insured (Ketoh et al., 2005; Smart et al., 1994). Application of these essential oils could be performed on the protected crop using standard flat fan hydraulic nozzle for pushing insects to perimeter trap crops where synthetic kairomones or eventual aggregation pheromones would serve as attractant agents. No information can currently provide input on the concurrent attraction of natural enemies (i.e. predators and parasitoids) as well as on the practices favoring their presence. However, it can be pointed out that two types of parasitoids were identified to date: larvaphagous parasitoids including species from *Braconidae* (Nees, 1811) family such as *Sigalphus pallipes* Nees von Esenbeck, 1816, *S. gibberosus* Szépligeti, 1901, *Triaspis thoracica* (Curtis, 1860), *T. similis* (Szepligeti, 1901), *T. luteipes* (Thomson, 1874) and *Chremylus rubiginosus* (Nees, 1834), and oophagous parasitoids from *Trichogrammatidae* family such as *Uscana semifumipennis* Girault, 1911 (Boughdad, 1994; Pérez-Benavides et al., 2019; Titouhi et al., 2017).

6. Conclusions

Considering the expected increase in *Vicia faba* cultivation throughout Europe (cf. multiple agricultural benefits and promotion by European policies), and the multiple impacts of *Bruchus rufimanus* on seeds, confronted to restricted and low efficiency uses of pesticides, new eco-friendly control strategies must be developed in the coming years. Among the alternatives highlighted to date, this review emphasized on the semiochemical-based methods of control as well as on biological missing information. Indeed, despite the extensive literature describing the biology and ecology of *B. rufimanus*, some key elements are still missing such as the influence of temperature on the pest developmental rate and fecundity, or the seasonal population dynamic and long distances dispersal capacity. Such aspects should now be investigated as they would provide growers with precious tools to proceed with adequate measures to hamper the pest life cycle.

Numerous existing chemical ecology studies provide a comprehensive overview of the semiochemical processes regulating the specific interactions between *B. rufimanus* and *V. faba*. Further studies on pheromonal communication should be undertaken by adapting the sampling odor designs and assessing the presence of HMP, so as to improve both current monitoring and mass trapping control methods. Attract and kill or push-pull methods meet each of the required elements for their implementation, and could constitute promiscuous alternative methods to investigate. All these elements, completed with other control levers, are essential to provide growers with efficient IPM strategies, without resorting to chemical pesticides.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

- Abras, M., Cartryse, C., Froidmont, E., Jamar, D., Rondia, P., Wavreille, J., 2015. Les protéagineux, de la production à la valorisation - La féverole, une légumineuse à graines riches en protéines et en énergie.
- Bachmann, M., Kuhnitzsch, C., Martens, S.D., Steinhöfel, O., Zeyner, A., 2020. Control of bean seed beetle reproduction through cultivar selection and harvesting time. *Agric. Ecosyst. Environ.* 300, 107005. <https://doi.org/10.1016/j.agee.2020.107005>.
- Bahr, I., 1976. On the occurrence of bruchids in imports and leguminous seeds in the interior. *Nachrichtenblatt für den Pflanzenschutz in der DDR* 30, 216–220.
- Bartelt, R.J., Cossé, A.A., Zilkowski, B.W., Weisleder, D., Grode, S.H., Wiedenmann, R.N., Post, S.L., 2006. Dimethylfuran-lactone pheromone from males of *Galerucella calmariensis* and *Galerucella pusilla*. *J. Chem. Ecol.* 32, 693. <https://doi.org/10.1007/s10886-005-9026-3>.
- Bartelt, R.J., Cossé, A.A., Zilkowski, B.W., Wiedenmann, R.N., Raghu, S., 2008. Early-summer pheromone biology of *Galerucella calmariensis* and relationship to dispersal and colonization. *Biol. Contr.* 46, 409–416. <https://doi.org/10.1016/j.biocontrol.2008.05.010>.
- Behavior: the process of host-plant selection. In: Bernays, E.A., Chapman, R.E. (Eds.), 1994. *Host-Plant Selection by Phytophagous Insects*, Contemporary Topics in Entomology. Springer US, Boston, MA, pp. 95–165. https://doi.org/10.1007/978-0-585-30455-7_5.
- Blomquist, G.J., Jurenka, R., Schal, C., Tittiger, C., 2005. *Biochemistry and Molecular Biology of Pheromone Production*.
- Bordes, J.-P., 2017. Numérique et agriculture de précision. *Annales des Mines - Responsabilité et environnement* N° 87, 87–93.
- Boughdad, A., 1994. thèse. Statut de nuisibilité et ecologie des populations de *Bruchus rufimanus* Boheman, 1833 sur *Vicia faba* L. au Maroc, vol. 11. Paris.
- Boughdad, A., Laugé, G., 1997. Life cycle of *Bruchus rufimanus* Boh. (Coleoptera: Bruchidae) on *Vicia faba* var. minor L. (Leguminosae) in Morocco. In: International conference on pests in agriculture, 6–8 January 1997, at le Corum, Montpellier, France, vol. 3, pp. 793–801.
- Bruce, T.J., Martin, J.L., Smart, L.E., Pickett, J.A., 2011. Development of semiochemical attractants for monitoring bean seed beetle, *Bruchus rufimanus*. *Pest Manag. Sci.* 67, 1303–1308. <https://doi.org/10.1002/ps.2186>.
- Bruce, T.J., Pickett, J.A., 2011. Perception of plant volatile blends by herbivorous insects – finding the right mix. *Phytochemistry. Plant-Insect Interactions* 72, 1605–1611. <https://doi.org/10.1016/j.phytochem.2011.04.011>.
- Carrillo-Perdomo, E., Raffiot, B., Ollivier, D., Deulvot, C., Magnin-Robert, J.-B., Tayeh, N., Marget, P., 2019. Identification of novel sources of resistance to seed weevils (*Bruchus spp.*) in a faba bean germplasm collection. *Front. Plant Sci.* 9, 1914. <https://doi.org/10.3389/fpls.2018.01914>.
- Cayley, G.R., Etheridge, P., Griffiths, D.C., Phillips, F.T., Pye, B.J., Scott, G.C., 1984. A review of the performance of electrostatically charged rotary atomisers on different crops. *Ann. Appl. Biol.* 105, 379–386. <https://doi.org/10.1111/j.1744-7348.1984.tb03062.x>.
- Cossé, A.A., Bartelt, R.J., Zilkowski, B.W., 2002. Identification and electrophysiological activity of a novel hydroxy ketone emitted by male cereal leaf beetles. *J. Nat. Prod.* 65, 1156–1160. <https://doi.org/10.1021/np020063q>.
- Dickens, J.C., Oliver, J.E., Hollister, B., Davis, J.C., Klun, J.A., 2002. Breaking a paradigm: male-produced aggregation pheromone for the Colorado potato beetle. *J. Exp. Biol.* 205, 1925–1933.
- Dickerson, W.A., 2001. *Boll Weevil Eradication in the United States through 1999*. Cotton Foundation Publisher.
- Duc, G., 1997. Faba bean (*Vicia faba* L.). Field crops research. *Improvement of Grain Legumes* 53, 99–109. [https://doi.org/10.1016/S0378-4290\(97\)00025-7](https://doi.org/10.1016/S0378-4290(97)00025-7).
- Duc, G., Bao, S., Baum, M., Redden, B., Sadiki, M., Suso, M.J., Vishniakova, M., Zong, X., 2010. Diversity maintenance and use of *Vicia faba* L. genetic resources. *Field Crops Research, Faba Beans in Sustainable Agriculture* 115, 270–278. <https://doi.org/10.1016/j.fcr.2008.10.003>.
- Dufour, B.P., Frérot, B., 2008. Optimization of coffee berry borer, *Hypothenemus hampei* Ferrari (Col., Scolytidae), mass trapping with an attractant mixture. *J. Appl. Entomol.* 132, 591–600. <https://doi.org/10.1111/j.1439-0418.2008.01291.x>.
- Ellis, S.A., Bruce, T.J., Smart, L.E., Martin, J.A., Snape, J., Self, M., 2009. *Integrated Management Strategies for Varieties Tolerant and Susceptible to Wheat Blossom Midge*. HGCA Project Report.
- El-Sayed, A.M., Suckling, D.M., Byers, J.A., Jang, E.B., Wearing, C.H., 2009. Potential of “Lure and Kill” in long-term pest management and eradication of invasive species. *J. Econ. Entomol.* 102, 815–835. <https://doi.org/10.1603/029.102.0301>.
- European Commission, 2018. Report from the Commission to the Council and European Parliament on the Development of Plant Proteins. The European Union.
- Evenden, M.L., 2018. Semiochemical-based management of the pea leaf weevil (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* 111, 154–160. <https://doi.org/10.1093/aesa/say004>.
- Faleiro, J.R., Rangnekar, P.A., Satarkar, V.R., 2003. Age and fecundity of female red palm weevils *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Rhynchophoridae) captured by pheromone traps in coconut plantations of India. *Crop Protect.* 22, 999–1002. [https://doi.org/10.1016/S0261-2194\(03\)00114-5](https://doi.org/10.1016/S0261-2194(03)00114-5).

- Frérot, B., Leppik, E., 2016. Composition attractive pour la bruche de la féverole. FR3035775A1.
- Frérot, B., Leppik, E., Groot, A.T., Unbehend, M., Holopainen, J.K., 2017. Chapter five - chemical signatures in plant-insect interactions. In: Sauvion, N., Thiéry, D., Calatayud, P.-A. (Eds.), *Advances in Botanical Research, Insect-Plant Interactions in a Crop Protection Perspective*. Academic Press, pp. 139–177.
- Frerot, B., Taupin, P., Lefranc, M., 2015. Bruche de la fève sur féverole: des messages chimiques décryptés. *Perspect. Agric.* 60–63.
- Gahukar, R.T., Reddy, G.V.P., 2018. Management of insect pests in the production and storage of minor pulses. *Ann. Entomol. Soc. Am.* 111, 172–183. <https://doi.org/10.1093/aesa/sax077>.
- Hoffman, A., Labeysie, V., Balachowsky, A.S., 1962. Famille des bruchidae. *Entomologie appliquée à l'agriculture* 1, 434–494.
- Howe, R.W., Currie, J.E., 1964. Some laboratory observations on the rates of development, mortality and oviposition of several species of Bruchidae breeding in stored pulses. *Bull. Entomol. Res.* 55, 437–477. <https://doi.org/10.1017/S0007485300049580>.
- Huignard, J., Glietho, I.A., Sembène, M., 2011. L'infestation des cultures puis des stocks de graines par les Coleoptères Bruchinae. Insectes ravageurs des graines de légumineuses: Biologie des Bruchinae et lutte raisonnée en Afrique 33–64.
- Jensen, E.S., Hauggaard-Nielsen, H., Kinane, J., Andersen, M.K., Jørgensen, B., 2005. Intercropping – the practical application of diversity, competition, and facilitation in arable and organic cropping systems. In: Köpke, U., Niggli, U., Neuhoﬀ, D., Lockeretz, W., Willer, H. (Eds.), *Researching Sustainable Systems 2005*. ISOFAR, Bonn, Germany, pp. 22–25.
- Jensen, E.S., Peoples, M.B., Hauggaard-Nielsen, H., 2010. Faba bean in cropping systems. *Field Crops Research. Faba Beans in Sustainable Agriculture* 115, 203–216. <https://doi.org/10.1016/j.fcr.2009.10.008>.
- Kaniuczak, Z., 2004. Seed damage of field bean (*Vicia faba* L. var. Minor Harz.) caused by bean weevils (*Bruchus rufimanus* Boh.) (Coleoptera: bruchidae). *J. Plant Protect. Res.* 125–129.
- Kergoat, G.J., Silvain, J.-F., Delobel, A., Tuda, M., Anton, K.-W., 2007. Defining the limits of taxonomic conservatism in host-plant use for phytophagous insects: Molecular systematics and evolution of host-plant associations in the seed-beetle genus *Bruchus* Linnaeus (Coleoptera: Chrysomelidae: Bruchinae). *Mol. Phylogenet. Evol.* 43, 251–269. <https://doi.org/10.1016/j.ympev.2006.11.026>.
- Ketoh, G.K., Koumaglo, H.K., Glietho, I.A., 2005. Inhibition of *Callosobruchus maculatus* (F.) (Coleoptera: bruchidae) development with essential oil extracted from *Cymbopogon schoenanthus* L. Spreng. (Poaceae), and the wasp *Dinarmus basalis* (Rondani) (Hymenoptera: Pteromalidae). *J. Stored Prod. Res.* 41, 363–371. <https://doi.org/10.1016/j.jspr.2004.02.002>.
- Khelifane-Goucem, K., Medjdoub-Bensaad, F., 2016. Impact of *Bruchus rufimanus* infestation upon broad bean seeds germination. *Adv. Environ. Biol.* 10, 144–152.
- Kingsolver, J.M., 2004. Handbook of the Bruchidae of the United States and Canada (Insecta, Coleoptera).
- Kistler, R.A., 1982. Effects of temperature on six species of seed beetles (Coleoptera: bruchidae): an ecological perspective. *Ann. Entomol. Soc. Am.* 75, 266–271. <https://doi.org/10.1093/aesa/75.3.266>.
- Klein, M.G., Lacey, L.A., 1999. An attractant trap for autodissemination of entomopathogenic fungi into populations of the Japanese beetle *Popillia japonica* (Coleoptera: scarabaeidae). *Biocontrol Sci. Technol.* 9, 151–158. <https://doi.org/10.1080/09583159929730>.
- Köpke, U., Nemecek, T., 2010. Ecological services of faba bean. *Field Crops Research. Faba Beans in Sustainable Agriculture* 115, 217–233. <https://doi.org/10.1016/j.fcr.2009.10.012>.
- Lamb, R.J., 1992. Developmental rate of *Acyrtosiphon pisum* (Homoptera: Aphididae) at low temperatures: implications for estimating rate parameters for insects. *Environ. Entomol.* 21, 10–19. <https://doi.org/10.1093/ee/21.1.10>.
- Lattanzio, V., Terzano, R., Cicco, N., Cardinali, A., Venere, D.D., Linsalata, V., 2005. Seed coat tannins and bruchid resistance in stored cowpea seeds. *J. Sci. Food Agric.* 85, 839–846. <https://doi.org/10.1002/jsfa.2024>.
- Law, J.H., Regnier, F.E., 1971. Pheromones. *Annu. Rev. Biochem.* 40, 533–548.
- Leppik, E., Frérot, B., 2014. Paysage chimique d'une agrobiocénose: un exemple de la féverole et de son ravageur spécialiste *Bruchus rufimanus*. In: Presented at the AFPP – Dixième conférence internationale sur les ravageurs en agriculture Montpellier – 22 et 23 octobre 2014, p. 10.
- Leppik, E., Pinier, C., Frérot, B., 2016. Communication chimique chez le principal ravageur de féverole: *Bruchus rufimanus*. Inra.
- Maharjan, R., Ahn, J., Park, C., Yoon, Y., Jang, Y., Kang, H., Bae, S., 2017. Effects of temperature on development of the azuki bean weevil, *Callosobruchus chinensis* (Coleoptera: bruchidae) on two leguminous seeds. *J. Stored Prod. Res.* 72, 90–99. <https://doi.org/10.1016/j.jspr.2017.04.005>.
- Mansoor, M.M., Afzal, M., Raza, A.B.M., Akram, Z., Waqar, A., Afzal, M.B.S., 2015. Post-exposure temperature influence on the toxicity of conventional and new chemistry insecticides to green lacewing *Chrysoperla carnea* (Stephens) (Neuroptera: chrysopidae). *Saudi J. Biol. Sci.* 22, 317–321. <https://doi.org/10.1016/j.sjbs.2014.10.008>.
- Medjdoub-Bensaad, F., Frah, N., Khelil, M., Huignard, J., 2015. Dynamique des populations de la bruche de la fève, *Bruchus rufimanus* (Coleoptera: Chrysomelidae), durant la période d'activité reproductive et de diapause. *Nature & Technology* 12–21.
- Medjdoub-Bensaad, F., Khelil, M.A., Huignard, J., 2007. Bioecology of broad bean bruchid *Bruchus rufimanus* Boh. (Coleoptera: bruchidae) in a region of Kabylia in Algeria. *Afr. J. Agric. Res.* 2, 412–417.
- Mihiretu, E., Wale, M., 2013. Effect of harvesting and threshing time and grain fumigation of field peas (*Pisum sativum* L.) on pea weevil (*Bruchus pisorum* L.) (Coleoptera: bruchidae) development and damage. *ETH J. Sci. Technol.* 6, 13–24.
- Montagné, Nicolas, Huyghe, Christian, Lannou, Christian, Bardin, Marc, Ris, Nicolas, et al., 2018. Des odeurs pour lutter contre les ravageurs. Les conquêtes de l'INRA pour le biocontrôle 4–9.
- Nojima, S., Shimomura, K., Honda, H., Yamamoto, I., Ohsawa, K., 2007. Contact sex pheromone components of the cowpea weevil, *Callosobruchus maculatus*. *J. Chem. Ecol.* 33, 923–933. <https://doi.org/10.1007/s10886-007-9266-5>.
- Park, K.C., McNeill, M., Unelius, C.R., Oh, H.-W., Suckling, D.M., 2013. Characterization of olfactory receptor neurons for pheromone candidate and plant volatile compounds in the clover root weevil, *Sitona lepidus*. *J. Insect Physiol.* 59, 1222–1234. <https://doi.org/10.1016/j.jinsphys.2013.10.002>.
- Pérez-Benavides, A., Lucía, Hernández-Baz, Fernando, González, Jorge M., Riverón, Alejandro Zaldívar, 2019/07/17. Updated taxonomic checklist of Chalcidoidea (Hymenoptera) associated with Bruchinae (Coleoptera: Chrysomelidae). *Zootaxa* 4638 (3), 301–343. <https://doi.org/10.11646/zootaxa.4638.3.1>. In press.
- Pfaffenberger, G.S., 1977. Comparative descriptions of the final larval instar of *Bruchus brachialis*, *B. rufimanus*, and *B. pisorum* (Coleoptera: bruchidae). *Coleopt. Bull.* 31, 133–142.
- Pickett, J.A., Woodcock, C.M., Midega, C.A.O., Khan, Z.R., 2014. Push-pull farming systems. *Curr. Opin. Biotechnol.* 26, 125–132. <https://doi.org/10.1016/j.copbio.2013.12.006>.
- Pölit, B., Reike, H.-P., 2019. Studies on biology and infestation dynamics of the bean seed beetle (Coleoptera, Bruchidae: *Bruchus rufimanus*) in Saxony. *Gesunde Pflanzen*. <https://doi.org/10.1007/s10343-019-00459-5>.
- Prokopy, R.J., 1972. Evidence for a marking pheromone deterring repeated oviposition in apple maggot flies. *Environ. Entomol.* 1, 326–332. <https://doi.org/10.1093/ee/1.3.326>.
- Qi, Y.-T., Burkholder, W.E., 1982. Sex pheromone biology and behavior of the cowpea weevil *Callosobruchus maculatus* (Coleoptera: bruchidae). *J. Chem. Ecol.* 8, 527–534. <https://doi.org/10.1007/BF00987800>.
- Ramsden, M.W., Kendall, S.L., Ellis, S.A., Berry, P.M., 2017. A review of economic thresholds for invertebrate pests in UK arable crops. *Crop Protect.* 96, 30–43. <https://doi.org/10.1016/j.cropro.2017.01.009>.
- Rao, S., Cossé, A.A., Zilkowski, B.W., Bartelt, R.J., 2003. Aggregation pheromone of the cereal leaf beetle: field evaluation and emission from males in the laboratory. *J. Chem. Ecol.* 29, 2165–2175. <https://doi.org/10.1023/A:1025698821635>.
- Roubinet, E., 2016. Management of the broad bean weevil (*Bruchus rufimanus* Boh. In: *Faba Bean (Vicia faba L.)* (Report). Uppsala.
- Roush, R.T., Hoy, C.W., Ferro, D.N., Tingey, W.M., 1990. Insecticide resistance in the Colorado potato beetle (Coleoptera: Chrysomelidae): influence of crop rotation and insecticide use. *J. Econ. Entomol.* 83, 315–319. <https://doi.org/10.1093/jee/83.2.315>.
- Sabbour, M.M., El-Aziz, A., Sh, E., 2007. Efficiency of some bioinsecticides against broad bean beetle, *Bruchus rufimanus* (Coleoptera: bruchidae). *Res. J. Agric. Biol. Sci.* 3, 67–72.
- Sanchez-Bayo, F., Goka, K., 2014. Pesticide Residues and Bees – a risk Assessment. *PloS One* 9, e94482. <https://doi.org/10.1371/journal.pone.0094482>.
- Sauvion, N., Calatayud, P.-A., Thiéry, D., Marion-Poll, F., 2013. *Interactions Insectes-Plantes*. IRD Quae, Marseille : Versailles.
- Seidenglanz, M., Hun Ady, I., 2016. Effects of faba bean (*Vicia faba*) varieties on the development of *Bruchus rufimanus*. *Czech J. Genet. Plant Breed.* 52, 22–29. <https://doi.org/10.17221/122/2015-CJGPB>.
- Seidenglanz, M., Huňady, I., Poslušná, J., Løes, A.-K., 2011. Influence of intercropping with spring cereals on the occurrence of pea aphids (*Acyrtosiphon pisum* Harris, 1776) and their natural enemies in field pea (*Pisum sativum* L.), 2011 *Plant Protect. Sci.* 47, 25–36. <https://doi.org/10.17221/40/2010-PPS>.
- Seybold, S.J., Vanderwel, D., 2003. 6 - biosynthesis and endocrine regulation of pheromone production in the Coleoptera. In: Blomquist, G., Vogt, R. (Eds.), *Insect Pheromone Biochemistry and Molecular Biology*. Academic Press, San Diego, pp. 137–200. <https://doi.org/10.1016/B978-012107151-6/50008-6>.
- Shearman, V.J., Sylvester-Bradley, R., Scott, R.K., Foulkes, M.J., 2005. Physiological processes associated with wheat yield progress in the UK. *Crop Sci.* 45, 175–185.
- Smart, L.E., Aradottir, G.I., Bruce, T.J.A., 2014. Role of semiochemicals in integrated pest management. In: Abrol, D.P. (Ed.), *Integrated Pest Management*. Academic Press, San Diego, pp. 93–109. <https://doi.org/10.1016/B978-0-12-398529-3.00007-5>.
- Smart, L.E., Blight, M.M., Pickett, J.A., Pye, B.J., 1994. Development of field strategies incorporating semiochemicals for the control of the pea and bean weevil, *Sitona lineatus* L. *Crop Protect.* 13, 127–135. [https://doi.org/10.1016/0261-2194\(94\)90163-5](https://doi.org/10.1016/0261-2194(94)90163-5).
- Smyth, R.R., Hoffmann, M.P., 2003. A male-produced aggregation pheromone facilitating *Acalymma vittatum* [F.] (Coleoptera: Chrysomelidae) early-season host plant colonization. *J. Insect Behav.* 16, 347–359. <https://doi.org/10.1023/A:1024824025210>.
- Soares, M.A., Quintela, E.D., Mascarin, G.M., Arthurs, S.P., 2015. Effect of temperature on the development and feeding behavior of *Acanthoscelides obtectus* (Chrysomelidae: Bruchinae) on dry bean (*Phaseolus vulgaris* L.). *J. Stored Prod. Res.* 61, 90–96. <https://doi.org/10.1016/j.jspr.2014.12.005>.
- Southgate, B.J., 1979. Biology of the bruchidae. *Annu. Rev. Entomol.* 24, 449–473. <https://doi.org/10.1146/annurev.en.24.010179.002313>.
- Szafrowska, A., 2012. The role of cultivars and sowing date in Ccontrol of broad bean weevil (*Bruchus rufimanus* Boh.) in organic cultivation. *Veg. Crops Res. Bull.* 77, 29–36. <https://doi.org/10.2478/v10032-012-0013-2>.

- Thiéry, D., 1991. Les phéromones de ponte: une nouvelle arme contre les insectes? *Courier de la cellule Environnement de l'INRA n°15* 21–24.
- Tillman, J.A., Seybold, S.J., Jurenka, R.A., Blomquist, G.J., 1999. Insect pheromones—an overview of biosynthesis and endocrine regulation. *Insect Biochem. Mol. Biol.* 29, 481–514. [https://doi.org/10.1016/S0965-1748\(99\)00016-8](https://doi.org/10.1016/S0965-1748(99)00016-8).
- Titouhi, F., Amri, M., Jemaa, J.M.B., 2015. Status of coleopteran insects infesting faba bean in Tunisia with emphasis on population dynamics and damage of *Bruchus rufimanus* (Chrysomylidae). *Basic Res. J. Agri. Sci. Rev.* 4, 225–233.
- Titouhi, F., Amri, M., Messaoud, C., Haouel, S., Youssfi, S., Cherif, A., Mediouni Ben Jemaa, J., 2017. Protective effects of three Artemisia essential oils against *Callosobruchus maculatus* and *Bruchus rufimanus* (Coleoptera: Chrysomelidae) and the extended side-effects on their natural enemies. *J. Stored Prod. Res.* 72, 11–20. <https://doi.org/10.1016/j.jspr.2017.02.007>.
- Torres, A.M., Román, B., Avila, C.M., Satovic, Z., Rubiales, D., Sillero, J.C., Cubero, J.I., Moreno, M.T., 2006. Faba bean breeding for resistance against biotic stresses: towards application of marker technology. *Euphytica* 147, 67–80. <https://doi.org/10.1007/s10681-006-4057-6>.
- Tran, B., Darquenne, J., Huignard, J., 1993. Changes in responsiveness to factors inducing diapause termination in *Bruchus rufimanus* (Boh.) (Coleoptera: bruchidae). *J. Insect Physiol.* 39, 769–774. [https://doi.org/10.1016/0022-1910\(93\)90052-S](https://doi.org/10.1016/0022-1910(93)90052-S).
- Tran, B., Huignard, J., 1992. Interactions between photoperiod and food affect the termination of reproductive diapause in *Bruchus rufimanus* (Boh.), (Coleoptera, Bruchidae). *J. Insect Physiol.* 38, 633–642. [https://doi.org/10.1016/0022-1910\(92\)90115-T](https://doi.org/10.1016/0022-1910(92)90115-T).
- Tsialtas, J.T., Irakli, M., Lazaridou, A., 2019. Exit of seed weevil and its parasitoid changed testa color but not phenolic and tannin contents in faba beans. *J. Stored Prod. Res.* 82, 27–30. <https://doi.org/10.1016/j.jspr.2019.03.004>.
- Unelius, C.R., Park, K.-C., McNeill, M., Wee, S.L., Bohman, B., Suckling, D.M., 2013. Identification and electrophysiological studies of (4S,5S)-5-hydroxy-4-methyl-3-heptanone and 4-methyl-3,5-heptanedione in male lucerne weevils. *Naturwissenschaften* 100, 135–143. <https://doi.org/10.1007/s00114-012-1003-4>.
- Vega, F.E., Dowd, P.F., Bartelt, R.J., 1995. Dissemination of Microbial Agents Using an Autoinoculating Device and Several Insect Species as Vectors.
- Wani, S.P., McGill, W.B., Haugen-Kozyra, K.L., Robertson, J.A., Thurston, J.J., 1994. Improved soil quality and barley yields with faba beans, manure, forages and crop rotation on a Gray Luvisol. *Can. J. Soil Sci.* 74, 75–84. <https://doi.org/10.4141/cjss94-010>.
- Wani, S.P., McGill, W.B., Robertson, J.A., 1991. Soil N dynamics and N yield of barley grown on Breton loam using N from biological fixation or fertilizer. *Biol. Fertil. Soils* 12, 10–18. <https://doi.org/10.1007/BF00369382>.
- Ward, R.L., 2018. The Biology and Ecology of *Bruchus rufimanus* (Bean Seed Beetle). Thesis. Newcastle University.
- Ward, R.L., 1999. Monitoring of the bean seed beetle (*Bruchus rufimanus*) in field beans (*Vicia faba*). *Aspect Appl. Biol.* 145–150.
- Ward, R.L., Smart, L., 2011. The effect of temperature on the effectiveness of spray applications to control bean seed beetle (*Bruchus rufimanus*) in field beans (*Vicia faba*). *Aspect Appl. Biol.* 106, 247–254.
- Whittaker, R.H., Feeny, P.P., 1971. Allelochemicals: chemical interactions between species. *Science* 171, 757–770.
- Witzgall, P., Kirsch, P., Cork, A., 2010. Sex pheromones and their impact on pest management. *J. Chem. Ecol.* 36, 80–100. <https://doi.org/10.1007/s10886-009-9737-y>.
- Wu, L.-H., Wang, C.-P., Wu, W.-J., 2013. Effects of temperature and adult nutrition on the development of *Acanthoscelides macrophthalmus*, a natural enemy of an invasive tree, *Leucaena leucocephala*. *Biol. Contr.* 65, 322–329. <https://doi.org/10.1016/j.biocontrol.2013.03.015>.
- Yus-Ramos, R., Ventura, D., Bensusan, K., Coello-García, P., György, Z., Stojanova, A., 2014. Alien seed beetles (Coleoptera: Chrysomelidae: Bruchinae) in Europe. *Zootaxa* 3826, 401–448. <https://doi.org/10.11646/zootaxa.3826.3.1>.