PLANT-RESISTANCE TO INSECT HERBIVORES AND SEMIOCHEMICALS:

IMPLICATIONS FOR FIELD PEA PEST MANAGEMENT

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Introductory Paper at the Faculty of Landscape Architecture,
Horticulture and Crop Production Science 2014:1
Swedish University of Agricultural Sciences
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Summary

Field pea is one of the important pulse crops which play a key role in human and animal nutrition as well as soil fertility in cropping systems. Insect pests are among the main biotic production constraints causing a considerable amount of losses worldwide. Like any other pulse crops, insect management of field pea pests mainly depends on the use of chemical insecticides. For sustainable and environmentally friendly pest management methods, it is crucial to understand plant-insect interactions such as how the plant defends against insect herbivore attack in ecological context. IPM strategy for field pea insect pests offers a sustainable and environmentally friendly pest management options. In this introductory paper, I have presented plant volatiles and mechanisms of host plant resistance, and their potential as a component of development of IPM strategy for major insect herbivores of field pea.

Contents

1. Introduction

Field pea, *Pisum sativum* is a cool-season legume crop that belongs to the family Fabaceae. The importance of field pea is not only due to its high protein content (Khan and Croser, 2004), but also the vital role it plays in cropping system where it contributes for soil fertility due to its nitrogen fixing ability and thereby improves crop productivity (French, 2004; Messiaen et al., 2006). Furthermore, it is an important source of protein for animal feed (Khan and Croser, 2004). During the period from 1990 – 2011, field pea has been grown in about 100 countries of the world (FAO STAT, 2011). Based on recent report of FAO, the major producing countries of field pea are Canada followed by Russian Federation, India, France and Australia (FAO STAT, 2011). Ethiopia was ranked eighth for this period. According to the Central Statistical Agency of Ethiopia (CSA, 2011), during 2009/10 a total of 2,570,314.09 quintal of field pea was produced on 226,533 ha of land.

Due to their nutritional value, mainly through high protein content, grain legumes are subjected to damage inflicted both by field and storage pest insects (Sharma et al., 2010). Like any other pulse crops, field pea is attractive to various insect pests. Among these pea weevil, *Bruchus pisorum*, is one of the main biotic production constraints worldwide. Pest management methods of field pea insect pests are mainly depending on the use of chemical insecticides (Horne and Bailey, 1991; Clement et al., 2002). Nevertheless, wide use of synthetic insecticides for the control of major pests has also resulted in more pest problem due to upset of balance between insect and natural enemies, insecticide resistance development, and effect on non target beneficial organisms (Thomas and Waage, 1996). Such adverse effects of dependence on chemical insecticides prompted for an increased interest in the development of integrated pest management (IPM) program, which is sustainable and environmentally friendly pest management method. IPM uses different pest management tactics such as cultural practices, host plant resistance, semiochemicals, biological control, etc in a compatible manner with due consideration of the ecology (Dent, 2000; Bajwa and Kogan, 2004).

Host plant resistance and semiochemicals play a vital role as a component of development of IPM program for field pea insect pests. Semiochemical is defined as “signaling compounds mediating interactions between organisms” (Bruce et al., 2005). Semiochemicals can be used in mass trapping, mating disruption, detection and monitoring of insect pests (Agelopoulos et al., 1999; Bruce et al., 2005; Schoonhoven et al., 2005; Witzgall, et al., 2010). In addition, semiochemicals can be used in push-pull system as a sustainable pest management strategy (Pickett et al., 2006; Cook, et al., 2007). In general, semiochemicals and host plant resistance can play a significant role as a component of IPM of field pea insect pests with the combination of other pest management methods such as cultural practices and phytosanitory measures.

2. Plant volatiles

It is well known that all plants emit volatile organic compounds (VOCs) into the air. Such VOCs play a significant ecological role, which mediate interactions of plants to other organisms (Dudareva et al., 2006). A review by Knudsen et al. (2006) described 1719 chemical compounds of floral scent from plant species belonging to 90 families. Although all plants are releasing VOCs, the amount released increased significantly after herbivory or wounding of the plant (Schoonhoven et al., 2005; Opitz et al., 2008). Major classes of plant volatiles include terpenoids, phenylpropanoids/ benzenoids, fatty acid and amino acid derivatives (Dudareva et al., 2006). Plant volatiles can also be grouped into two major groups viz. green leaf volatiles, which is formed by oxidation of lipids (e.g. 6-carbon alcohol and aldehyde), and taxon-characteristics volatiles which are emitted by specific plant species such as Isothiocyanates of Brassicaceae family (Bernays and Chapman, 1994; Schoonhoven et al., 2005).

2.1. Role of plant volatiles

Plants produce VOCs either constitutively or induced after damage caused by insect herbivores. Such VOCs have an immense role in plant-insect as well as tritrophic interactions (Kessler and Baldwin, 2001; Schoonhoven et al., 2005; Dudareva et al., 2006). Various reports indicate the role of VOCs in defense of plants against herbivores either as a direct defense that negatively affect the herbivores or indirect defense through attraction of natural enemies (predators and parasitoids) of insect herbivores (Pare and Tumlinson, 1999; Dicke and van Loon, 2000; Kessler and Baldwin, 2001; Mithöfer and Boland, 2012). In many plants there is a change in composition of VOCs emission after damage inflicted by herbivores (Dicke and van Loon, 2000). Recent findings of Zakir et al (2013) shows herbivore induced plant volatiles not only defend host plant from insect herbivores, but also provide resistance of neighboring plants as confirmed by reduction in oviposition on neighboring plants. Although plant volatile plays a role to defend plants from insect attack, insect herbivores also exploit volatiles emitted by plants in order to locate their host plants for feeding and oviposition (Bruce et al., 2005; Schoonhoven et al., 2005). Various studies confirmed the importance of plant volatiles in host location by herbivores (e.g. Visser, 1986; Schoonhoven et al., 2005).

2.2. Intra species variation in profiles of plant volatiles

Qualitative and quantitative variations in profile of volatiles are observed not only in different plant species, but also different cultivars/varieties of the same plant species (Schoonhoven et al., 2005), which might have a relation with the level of resistance of the cultivar against insect herbivores. Such variation in volatile profile among different cultivars and its significance in plant resistance against insect herbivores has been reported in various crops. For example, in *Capsicum* spp. cultivars against *Aphis gossypii* (Costa et al., 2011); mango fruit to west Indian fruit fly, *Anastrepha oblique* (Malo et al., 2012); wheat against sawfly, *Cephus cinctus* Norton (Weaver et al., 2009); tomato to *Tuta absoluta* (Profit et al., 2011); barley to aphid (Ninkovic and Åhman, 2009); Brassica genotypes to the root flies, *Delia radicum* and *D. floralis* (Baur et al., 1996). It is important to note that herbivore induced plant volatiles can be lost during crop breeding program targeting with particular traits such as yield and quality (Tamiru et al., 2011), hence it is imperative to consider both induced and constitutively produced volatiles of resistant and susceptible verities in breeding program (e.g. Ninkovic and Åhman, 2009; Åhman et al., 2010).

3. Plant-resistance to insect herbivores

Insect herbivorous depend on host plants for feeding, oviposition and shelter. On the other hand, infested plants respond in various ways to attack caused by insect herbivore which may be ranging from plant morphological traits to chemical compounds (Kessler and Baldwin, 2002). Plant resistance to arthropods is defined as “the sum of the constitutive, genetically inherited qualities that result in a plant of one cultivar or species being less damaged than a susceptible plant lacking these qualities” (Smith, 2005).

3.1. Resistance categories

There are three types of plant-resistance categories, viz. antibiosis, antixenosis and tolerance (Fig. 1).

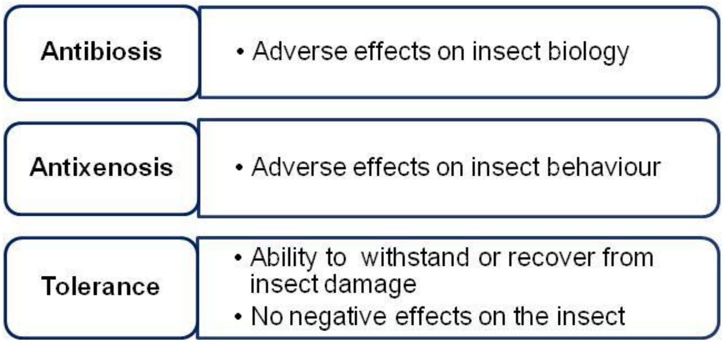

Figure 1. The antibiosis, antixenosis, and tolerance categories of plant resistance to insects (Modified from Smith, 2005).

Antibiosis

Antibiosis is a category of plant resistance which adversely affects the physiology of an insect such as its survival, development and fecundity (Kogan, 1994; Smith, 2005; Smith et al., 2012). Adverse effects of antibiosis on insect attacking a resistant plant may range from a mild effect to death. Some of the main effects observed due to antibiosis resistance on insect include larval mortality, disturbance on life cycle, reduction in fecundity and fertility of the insect (Kogan, 1994). Plant morphological traits and chemical factors are involved in antibiosis resistance of host plant against insect herbivores (Sadasivam and Thayumanavan, 2003; Smith et al., 2012).

Antixenosis

Antixenosis refers to the category of plant resistance where the plant is not preferred as a suitable host by the insect herbivore due to its morphological traits or chemical compounds that repel or deter the insect or minimizes the chance of infestation (Smith, 2005; Sadasivam and Thayumanavan, 2003; Smith et al., 2012). A plant with antixenotic resistance mainly affects the behavior of the insect (Dent, 2000; Smith, 2005; Smith et al., 2012).

Tolerance

Plant tolerance is a category of resistance where the infested plant shows the ability to withstand or recover from insect pest damage without adverse effect on insect herbivore (Dent, 2000; Smith et al., 2012). Plant tolerance measure response of a plant to a given level of damage caused by insect herbivore, and it doesn’t reflect amount of damage caused by the insect (Farrell, 1977).

3.2. Evaluating antibiosis and antixenosis categories of plant resistance

There are overwhelming numbers of scientific papers dealing with host plant resistance for various insect herbivores (e.g. review of Smith et al., 2012). The three categories of resistance are described for various crops against their pest insects. Usually different cultivars/genotypes of a particular plant species or crop are evaluated for resistance against its insect pest. Such studies can be conducted in the laboratory and/or field condition. However, different experimental procedures are followed to evaluate antixenosis and antibiosis resistance. For example, antixenosis resistance is evaluated either in choice or no-choice situation test, while antibiosis resistance is tested under no-choice test (Dent, 2000).

Parameters considered while evaluating test plants for antibiosis resistance against a particular pest insect is mainly the biology of insect, such as insect development, reproduction, survival and mortality, and plant damage score. On the other hand, antixenosis resistance is expressed in terms of oviposition and number of emigrating insect in a given test cultivars (Dent, 2000). As an example, table 1 depicts categories of resistance for some of major insect pests of field pea. Usually more than one category of resistance has been identified in field pea against those major insect pests. For example, a combination of antixenosis, antibiosis and tolerance category of resistance was reported in field pea plant against pea aphid, *Acyrthosiphon pisum* (Ali et al., 2005). A combination of antibiosis and antixenosis resistance in wild pea, *Pisum fulvum* accessions was found for resistance to pea weevil (Hardie and Clement, 2001).

Table 1. Categories of host plant resistance in field pea insect pests (Modified from Clement et al., 1994).

Insect	Categories of genetic resistance		
	Antixenosis	Antibiosis	Tolerance
Acyrthosiphon pisum	+	+	+
Bruchus pisorum	+	+	
Sitona lineatus		+	+
Chromatomyia horticola	+	+	

3.3. Mechanisms of plant resistance to insect herbivores

In order to overcome damage inflicted by insect herbivores, plants evolved various resistance mechanisms (Schoonhoven et al., 2005). Plant resistance is induced either after herbivory or constitutively expressed, where both resistant traits are mainly genetically controlled (Kogan, 1994, Schoonhoven et al., 2005). Constitutive resistance refers to the inherent resistance ability of host plant which occurs regardless of herbivory or abiotic factors, which negatively affect insect herbivore attacking the plant. On the other hand, induced resistance is a mechanism of host plant resistance in response to attack caused by insect herbivores, diseases or abiotic factors (Schoonhoven et al., 2005; Smith, 2005). Insect herbivory can induce change in plant chemistry such as induction of secondary metabolites (Schoonhoven et al., 2005). Constitutive and induced resistance can be either direct or indirect resistance.

3.3.1. Direct resistance

Plants have developed both morphological traits and secondary metabolites as direct defense strategies to resist insect herbivores attack. Both plant structural traits and secondary metabolites play a role in direct resistance of plant against insect herbivores (Kessler and Baldwin, 2002; Schoonhoven et al., 2005).

3.3.1.1. Plant structural traits

Plant structural defense is defined as "any morphological or anatomical trait that confers a fitness advantage to the plant by directly deterring herbivores from feeding on it" (Hanley et al., 2007). These plant morphological traits can be leaf surface wax, thorns, spines and trichomes that play an important role in plant resistance against insect herbivores. Morphological resistance factors are developed either constitutively or induced after herbivory (Dalin et al., 2008).

The plant cuticle, which is covered with epicuticular wax films and crystals, is one of plant resistance trait against insect herbivores (Howe and Schaller, 2008). For example, cabbage cultivars with more epicuticular wax were less preferred by flea beetles, *Phyllotreta* spp., cabbage stink bugs, *Eurydema ventrale* and onion thrips, *Thrips tabaci* as compared to varieties having less epicuticular wax (Žnidarčič et al, 2008). Pea leaf weevil and pea weevil inflicted higher damage on pea plants with reduced-wax as compared to normal-wax varieties (White and Eigenbrode, 2000; Chang et al., 2006). Nevertheless, on field pea accessions, pea aphids densities were lower on accessions with reduced wax as compared with standard/normal surface wax plants (White and Eigenbrode, 2000; Chang et al., 2006) suggesting that reduced-wax is not always advantageous for the host plant in terms of resistance to herbivores.

Trichomes which are found on different organs of plants such as stem, leaf, and fruit (Levin, 1973; Dent, 2000) have paramount importance for plant defense against insect herbivores (Wagner, 1991) and also protect the plant from abiotic stress such as extreme temperature (Peter and Shanowe, 1998). Trichomes are divided into two main groups, namely non-glandular and glandular. Non-glandular trichome mechanically hinder insect movement on plant surface, and also affect feeding and oviposition activities (Sadasivam and Thayamanavon, 2003; Glass, et al., 2012), whereas chemical substance produced by glandular trichomes such as sticky substance may impede insect movement and thereby deprive them from access of their food source (Bernays and Chapman, 1994; Dent, 2000).

3.3.1.2. Plant secondary metabolites

Unlike primary metabolites, secondary metabolites have no direct role in plant growth and development (Taiz and Zeiger, 2010). These secondary metabolites act as a direct defense against herbivores in different ways such as toxicant and repellent (Wu and Baldwin, 2010; Mithöfer and Boland, 2012). Plant secondary metabolites can be classified as (1) nitrogen-containing compounds, (2) terpenoids, (3) phenolic compounds and (4) acetylenic compounds (Schoonhoven et al., 2005).

Trichomes do not only contribute for direct plant resistance against insect herbivores, but also by secreting secondary metabolites which can be toxicant, repellent or trap insect herbivores (Bernays and Chapman 1994; Dalin et al., 2008). Given their ability to secrete and store various chemical metabolites (Wagner, 1991; Bernays and Chapman 1994; Glas et al., 2012), glandular trichomes received an increasing attention. Secondary metabolites produced by glandular trichomes such as terpenes, flavonoid, alkaloids play a role in plant-resistance against insect herbivores (Dalin et al., 2008; Glas et al., 2012). Several studies have shown the role of trichomes as a component of plant resistance against insect herbivorous (Levin, 1973; Glas et al., 2012; Dalin et al, 2008). In addition, some chemical substances produced by the plant can cause insect mortality due to toxic substances (Glas, et al., 2012) or may act as a repellent and inhibit oviposition by female insect (Peter and Shanower, 1998).

In general, plant secondary metabolites such as glucosinolates, cynogenic glucosides, alkaloids, terpenoids, phenolics, and proteinase inhibitors play a significant role in plant-resistance against insect herbivores (Bernays and Chapman, 1994; Kessler and Baldwin, 2002; Wu and Baldwin, 2010; Mithöfer and Boland, 2012).

1. Cyanogenic Glycosides

Cyanogenic glycosides are nitrogen containing secondary metabolites, which are widely distributed in plants such as legumes, sorghum, barley, cassava and clover (Bennett and Wallsgrove, 1994). Two enzymes, namely glycosidase and hydroxynitrile lyase, are responsible to hydrolyze cyanogenic compounds to release the toxic hydrogen cyanide (HCN) when the plant is attacked by herbivores (Taiz and Zeiger, 2010; Mithöfer and Boland, 2012). In order to avoid hydrolysis in intact plant, cyanogenic glycosides and these enzymes are stored in different cells, where hydrolysis occurs only upon damage of the plant by insect herbivores which cause the release of HCN (Taiz and Zeiger, 2010; Zagrobelny and Møller, 2011; Mithöfer and Boland, 2012). Cyanogenic glycosides act as feeding deterrents for generalist insect herbivores, while it serves as phagostimulants for specialist herbivores feeding on cyanogenic plants. Furthermore, these specialists can sequester the compounds, which then act as a defense for the herbivore against predators (Møller, 2010; Zagrobelny and Møller, 2011).

2. Glucosinolates

Glucosinolates (mustard oil glycosides) are sulphur and nitrogen containing compounds, which are found in several plant species in the family Brassicaceae such as broccoli, cabbage and oilseed rape (Bennett and Wallsgrove, 1994; Hopkins et al., 2009). Upon insect herbivory, glucosinolates hydrolyzed by enzymes thioglucosidase/myrosinase, and release toxic isothiocyanates, nitriles and oxazolidinethiones (Hopkins et al., 2009; Taiz and Zeiger, 2010). In intact plant glucosinolates and the enzymes are stored separately (Hopkins et al., 2009; Taiz and Zeiger, 2010). Nevertheless, for specialist insect herbivores of Brassicaceae family, they serve as feeding and oviposition stimulants (Schoonhoven et al., 2005). For example, isothiocyanates serve as attractants and oviposition stimulants for diamondback moth, *Plutella xylostella*, which is a pest of Brassica (Furlong et al., 2013). Furthermore, Kessler and Baldwin (2002) pointed out the indirect defense role of glucosinolates for host location of certain parasitoids.

3. Alkaloids

Alkaloids are one of the nitrogen containing secondary metabolites contributing in plant resistance against insect herbivores. Alkaloids are commonly found in several plant families such as Leguminosae, Liliaceae, Solonaceae, Amaryllidaceae, Asteraceae, Loganiaceae, Rubiaceae (Bernays and Chapman, 1994; Bennett and Wallsgrove, 1994; Mithöfer and Boland, 2012). Alkaloids contains different classes of compounds such as pyrrolidines, tropanes, pyrrolizidine, piperidines, indole, etc (Taiz and Zeiger, 2010). Alkaloids serves as feeding deterrents for generalist insects, where as the specialist insect uses them to locate their host plant as well as they sequester it for their own defense against predators (Bennett and Wallsgrove, 1994). For example, generalist herbivores are deterred by Pyrrolizidine alkaloids found in Senecio plant species, while it serves as a cue for specialist herbivores to find their host plant and for the defense against predators (Macel, 2011).

4. Terpenoids

Terpenoids is a highly diverse class of organic compounds found in various plant species. They play an important role in plant resistance against herbivores as toxicants and feeding deterrents (Taiz and Zeiger, 2010; Mithöfer and Boland, 2012). In addition, many plant species which are known to produce essential oils contain monoterpenes and sesquiterpenes (e.g. citral, menthol) which are repellent for some insect pests (Isman, 2010). Various studies reported the importance of terpenoids for defense of host plant against insect herbivores (e.g. Chen et al, 2002; Junker et al., 2011).

5. Phenolics

Phenolics is a highly diversified group of compounds, which include simple phenolic acids and their glycosides, flavonoids and their glycosides, coumarins, and polymers of phenols including tannins (Bernays and Chapman 1994). Several compounds found in the phenolic group serve as a defense against herbivores. They may act as feeding deterrents or toxicants against insect herbivores (Schoonhoven et al., 2005). Tannins, for example are feeding deterrents to many herbivores, while they act as feeding stimulants for specialist insect (Barbehenn and Constabel, 2011). Phenolics reported to be a resistance factor in mango against fruit fly, *Bactrocera dorsalis* (Verghese et al., 2012).

3.3.2. Indirect resistance

Herbivore induced plant volatiles (HIPVs) emitted upon damage caused by insect herbivores has been known to confer indirect resistance to the plant by attracting insect natural enemies (predators and parasitoids) and thereby reduce damage by herbivores (Kessler and Baldwin, 2001; Kessler and Baldwin, 2002; Schoonhoven et al., 2005). There are various studies which report the attraction of insect natural enemies to HIPVs (e.g. reviews of Kessler and Baldwin, 2002; Smith et al., 2012; McCormick et al., 2012). HIPVs are emitted not only after damage caused by feeding insect herbivores, but also after oviposition by female insects (review of Hilker and Meiners, 2006). For example, broad beans leaves, *Vicia faba* emitted VOCs upon oviposition of bug, *Nezera viridula* that attracts egg parasitoid *Trissolcus basalis* (Colazza et al., 2004).

Herbivore induced plant volatiles can be lost during plant breeding program aiming with development of certain traits such as yield and quality. For example, Tamiru et al. (2011) reported the loss of oviposition induced plant volatiles in commercial hybrid maize varieties, while the landrace varieties emitted HIPVs upon oviposition by stem borer moths (*Chilo partellus*) that attract egg (*Trichogramma bournieri*) and larval parasitoids (*Cotesia sesamiae*).

Furthermore, certain type of field pea genotypes known as neoplastic pod (*Np*), form neoplasm (tumor like growth) on pod surface. Such neoplasm express on the pod either when the plant is growing in the green house (UV repressed) or due to pea weevil oviposition on pods. In the later case, neoplasm inducing compounds (bruchins) which was identified from pea weevil serves as oviposition induced resistance in pea weevil (Doss et al., 1995; 2000). Such a neoplastic growth on pods either pushes out the eggs from pod surface or hinder larval entry to the pod (Muttall and Lyall, 1964; Doss et al., 1995; 2000).

4. Insect herbivores of field pea, *Pisum sativum*

Over 15 insect pests are known to feed on field pea (Table 2), however only a few of these insect herbivores are known to cause a considerable amount of losses in field pea production. The magnitude of the problem may vary from place to place, production systems, etc. (Clement et al., 1994; French, 2004; Sharma et al., 2010). Seedling, vegetative and reproductive parts of field pea plant are known to be attacked by different insect herbivores.

4.1. Pea weevil, *Bruchus pisorum* (Coleoptera: Bruchidae)

Distribution and biology

Although the exact origin of pea weevil is not yet known it is a cosmopolitan pest which is currently prevalent in almost all countries where field pea is grown (Fig. 2) (Plantwise, 2014). Pea weevil spread from one country to another mainly through weevil-infested seed materials, export trade, germplasm exchange, etc. In Ethiopia, for example this pest was accidentally introduced around the mid 1970s where it was first noticed in Amhara Regional State and then it has spread to other field pea growing areas of the country mainly through infested seed materials (Abate, 2006; Ali et al., 2009).

Pea weevil attacks seeds of growing crops, but not dried or stored seeds. It is the larval stage which inflicts losses in crop yield and quality by consuming the seed. In addition, infested seeds have lower seed viability and germination. Losses also occur due to shattering during threshing/harvesting (Brindley et al., 1956; Baker, 1998; Armstrong and Matthews, 2005). Pea weevil inflicts considerable amount of seed damage, for example in Australia, where it causes crop losses of 10.6-71.5% (Horne and Bailey, 1991); in Spain 12.2 – 25.7% (Marzo et al., 1997) and in USA up to 64% (Pesho et al., 1977). Studies conducted in the northern part of Ethiopia indicated 8% – 17% seed weight loss, and 48– 83% seed infestation (Teka, 2002). In addition, in some hot spot areas such as Sekota up to 85% yield losses was recorded (Ali et al., 2009).

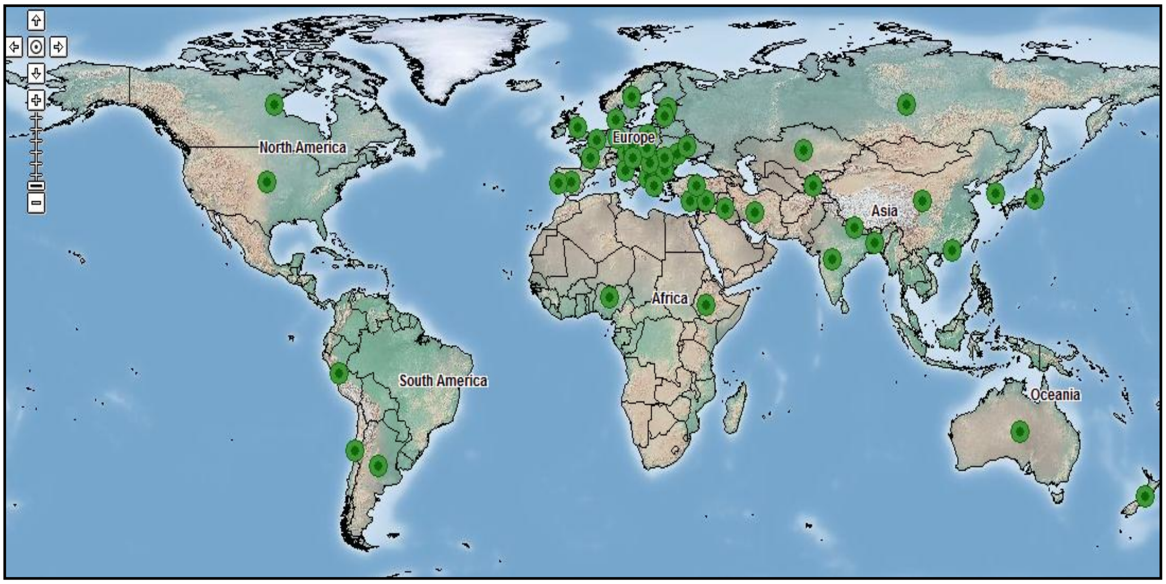

Figure 2. Distribution map of pea weevil, *Bruchus pisorum* (with kind permission from CABI). Source: http://www.plantwise.org/KnowledgeBank/Map/GLOBAL/Bruchus_pisorum/.

Pea weevil is a univoltine insect and a specialist of field pea (Fig. 3) (Brindley et al., 1956). When pea weevils emerged from hibernation sites, male insects are sexually mature, while females are sexually immature and need to feed on pollen before being sexually mature (Pesho and Van Houten, 1982). Although it was reported that pollen from other plant species such as *Lathyrus tingitanus* can promote ovarian development (Annis and O'Keeffe, 1984), pea weevil complete its life cycle only on field pea. Pea weevil use environmental factors (Brindley et al., 1956) and scent of pea flowers (McDonaled, 1995) to locate the pea field upon emergence from hibernation site.

Figure 3. Adult pea weevil, *Bruchus pisorum*. Photo (E. Mendesil).

Although female pea weevil oviposits on green pods of any size (Brindley et al., 1956; McDonaled, 1995), flat and swollen pods are preferred for oviposition as they probably increases the chance of larval survival (Hardie and Clement, 2001). The incubation period of the eggs is 4-14 days, and upon hatching the larvae bore directly into the seed inside the pod (Fig. 4a). The larvae feed and develop inside seeds for about 4 to 8 weeks. Before pupation, the last instars larva makes a thin translucent opening hole or "window" for adult exit (Fig. 4b). Then the larva pupates for about 12 to 14 days (Brindley et al., 1956).

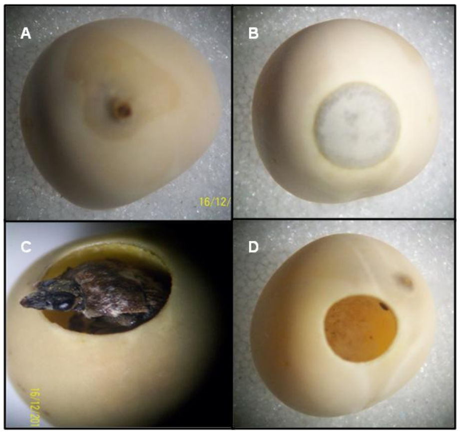

Figure 4. Damage symptoms of *B. pisorum* on field pea seeds (A) 'Sting', (B) 'window', (C) adult weevil emerging from the seed hole, and (D) adult exit hole. Photo (E. Mendesil).

4.2. Pea leaf weevil, *Sitona lineatus* L. (Coleoptera: Curculionidae)

Distribution and biology

The pea leaf weevil, *Sitona lineatus* L is one of the major pest of field pea and faba bean (Fig. 5) (Alford, 1999), which occurs in Africa, Europe and North America (Vankosky et al., 2009; Cárcamo and Vankosky, 2011). Although both adult and larval stages are considered as a pest, damage caused by adult is less important as compared to larval stage that causes a considerable amount of yield loss (Alford, 1999). This is attributed to damage of root nodule by larvae, which results in a considerable decrease in nitrogen fixing capacity of the plant and thereby reduction in yield (Johnson and O'Keeffe, 1981; Cárcamo and Vankosky, 2011).

Figure 5. The pea leaf weevil, *Sitona lineatus* L
Source: Pest and Diseases Image Library, Bugwood.org.
http://www.insectimages.org/browse/detail.cfm?imgnum=5321094

The pea leaf weevil is a univoltine insect, where the adult weevil undergoes overwintering in sheltering areas which protect the insect from harsh weather. The female insect oviposit on leaves and soil surface, and the eggs hatches 2-3 weeks after oviposition. Larva feed directly on the root nodule. The larval period lasts for 6 weeks. It pupates in the soil (Alford, 1999; Cárcamo and Vankosky, 2011).

4.3. Pea aphid, *Acyrthosiphum pisum* (Hemiptera: Aphididae)

Distribution and biology

The pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae) (Fig. 6) is distributed worldwide. The main host plants of pea aphid are found in Fabaceae which include field pea, alfalfa and clovers. Other legumes, such as lentils, faba beans, vetches, sweet clover, sweet peas, trefoil and dry beans also serve as hosts of this insect (Hill, 1994; van Emden, 2007). During feeding activities, pea aphid suck plant sap which results in damage symptoms such as leaf rolling, bending, and leaf yellowing (Hill, 1983; Alford, 1999). Heavy infestation often results in a considerable yield reduction of field pea. Furthermore, the pea aphid is also as a vector of more than 30 viral diseases, such as bean leaf roll virus (van Emden, 2007).

Figure 6. Pea aphid, *Acyrthosiphum pisum* [Photo courtesy of UC statewide IPM project] http://www.discoverlife.org/nh/tx/Insecta/Hemiptera/Sternorrhyncha/Aphididae/Acyrthosiphon/pisum/

Pea aphid overwinters in the egg stage on plants such as clover and trefoils. Eggs hatch in spring where asexual winged and wingless females are formed. Winged aphids migrate to the pea and bean field in summer. During autumn, sexual wingless females and sexual males (winged/wingless) are formed (Hill, 1994; Alford, 199; Brisson and Davis, 2008).

4.4. Pea midge, *Contarinia pisi* (Diptera: Cecidomyiidae)

Distribution and biology

Pea midge is a pest of peas mainly in Russia, UK, Scandinavia, France, Holland and other European countries (Biddle and Cattlin, 2007). Pea midge feeds on flower, flower buds and causing abortion of flower and it may also cause abnormal development of pods (Alford, 1999).

Figure 7. Pea midge, *Contarinia pisi* https://www.syngenta-crop.co.uk/insecticide/pea-and-bean-pests.aspx

The adult pea midge is about 2mm long and grey-brown in color (Fig. 7) (Biddle and Cattlin, 2007). Female pea midge lays its eggs on the flower buds and inside the shoots of field pea. After four days of incubation period, the larvae feed on young tissues of the plant. It takes about ten days to complete its development. Pupation takes place in the soil inside the cocoons to overwinter, while some of the larvae develop to second generation of adults after two weeks (Hill, 1987; Alford, 1999).

4.5. Pea Moth, *Cydia nigricana* (Lepidoptera: Tortricidae)

Distribution and biology

The pea moth, *Cydia nigricana* is widely distributed oligophagous pest which cause a considerable damage on field pea (Fig. 8). The larvae bore into developing pea pods and eat the seeds, causing a significant loss in yield and quality of crop (Alford, 1999; Kimber, 2013).

Figure 8. Pea moth, *Cydia nigricana* on pea leaf
http://www7.inra.fr/hyppz/IMAGES/7031500.jpg

Pea moth has only one generation per year. Female moth lays its eggs on the plant leaf and stipules. After about one week incubation period, the emerged larvae bore into the pod and feed the seed inside the pod. When fully develop, the larvae move out of the pod to overwinter inside the cocoon in the soil. Pupation takes place in the spring or early summer (Hill, 1987).

4.6. African Bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae)

Distribution and biology

The African bollworm, *Helicoverpa armigera* is a cosmopolitan pest which is distributed in Africa, Asia, Europe and Australia. It is a polyphagous pest which attacks about 60 species of cultivated plants and several wild hosts. Field pea is one its host plants. The larva, which is responsible to cause damage, cut a circular hole on the surface of field pea pod and feed the seed directly, which sometimes cause total damage of the seed (Fig. 9) (Hill, 1994; Cherry et al., 2003).

Figure 9. African bollworm**,** *Helicoverpa armigera* feeding on peas.
A. M. Varela, icipe, http://www.infonet-biovision.org/default/ct/181/crops

African bollworm is a large brown moth which measures about 14 to 18mm and is a strong flier. Eggs are laid on the plant surface and takes about 1-5 days to hatch. Larvae vary in color; however they have a distinctive light strip along each side of the body (Fig. 9). The larvae undergo six instars and it takes about 14-60 days to complete its development. Then fully developed larvae pupate inside the soil or plant debris for about 10-14 days. In general, the life cycle of African bollworm takes 30 days in warmer conditions (Hill, 1987; Abate and Ampofo, 1996).

Table 2. Insect pests of field pea (Modified from Hill, 1983; French, 2004; Sharma et al., 2010).

Common name	Scientific name	Occurrence
Pea aphid	*Acyrthosiphon pisum*	Worldwide
Blue aphid	*A. kondoi*	Australia
Cowpea aphid	*Aphis craccivora*	Worldwide
Thrips	*Thrips* spp. & *Frankliniella* spp.	Worldwide
	Caliothrips indicus	Worldwide
Stem fly	*Ophiomyia phaseoli*	Asia, Africa, Australia, Europe
	O. centrosematis	Asia, Africa, Australia
Pea midge	*Contarinia pisi*	Europe
Pea leaf weevil	*Sitona lineatus*	North America, Europe
Pea weevil	*Bruchus pisorum*	Most pea growing regions
Bruchid	*Callasobruchus chinensis*	Worldwide
Pea moth	*Cydia nigricanus*	North America, Europe
Cotton bollworm	*Helicoverpa armigera*	Asia, Australia, Africa
Australian bollworm	*H. punctigera*	Asia, Australia, Africa
Spiny pod borer	*Etiella zinckenella*	Asia, Africa, America
Lucerne seed web moth	*E. behrii*	Australia

5. Integrated pest management strategies for field pea insect pests with a focus on semiochemicals and host plant resistance

There are different definitions of integrated pest management (IPM). According to Dent (1995) "Integrated pest management is a pest management system that in the socioeconomic context of farming systems, the associated environment and the population dynamics of the pest species, utilizes all suitable techniques in as compatible manner as possible and maintains the pest population levels below those causing economic injury." Due to adverse effects of dependence on chemical insecticides coupled with public awareness about environmental protection, there is an increasing interest in developing IPM strategies for major insect pests.

Although the magnitude of pest problems may vary from place to place, year to year, and cropping systems, there is considerable information on biology, and pest management practices of major insect pests of field pea. Different pest management methods such as cultural practices, host plant resistance, semiochemicals, and biological control can be used for the development of IPM for field pea insect pests.

5.1. Semiochemicals

Semiochemicals are divided into two major groups (pheromones and allelochemicals) based on who "sends" a message and who "receives" it: Pheromones mediate interactions between two individuals of the same species, while allelochemicals is interactions between two individuals of a different species (Cork, 2004; Norin, 2007). Allelochemicals further divided into allomones, Kairomones, synomones and apneumones. Pheromones are subdivided into sex pheromones, alarm, trail pheromones and aggregation pheromones (Fig. 10) (Cork, 2004; Norin, 2007).

Unlike chemical insecticides, semiochemicals offers sustainable and environmentally friendly pest management options. As a result there is an increasing interest in research and development of semiochemicals based management methods of agricultural pest insects. Semiochemicals can be used in mass trapping, detection and monitoring of insect pests, and thereby contribute to minimize dependence on synthetic chemical insecticides (Pickett et al., 2006; Cook, et al., 2007; Cork et al., 2009; Witzgall et al., 2010).

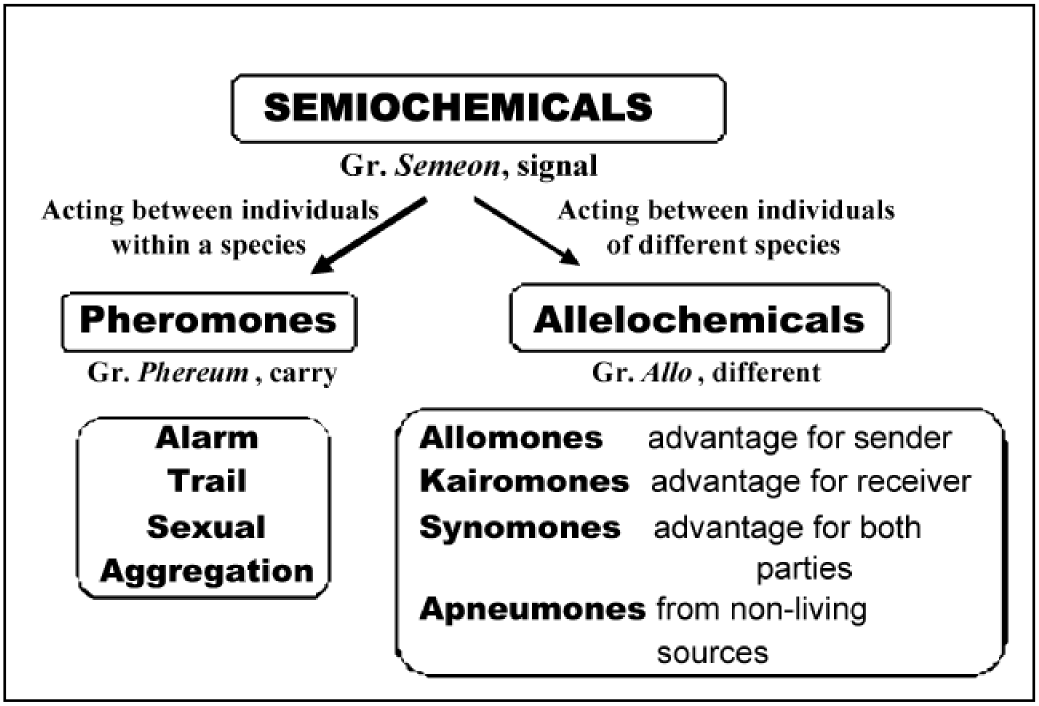

Figure 10. Terms commonly used for various semiochemicals (chemical signals) (Norin, 2007).

Furthermore, semiochemicals can be used in push-pull system which contribute for population reduction and thereby minimize damage inflicted by herbivores. For example, a successful push-pull systems been developed for insect pests such as cotton bollworm on cotton crop, Lepidopterous stem borers on maize and sorghum crop, pollen beetle on oil seed rape (Cook et al., 2007).

Semiochemicals viz. kairomone and pheromone have been identified for some economically important pest insects of field pea (Table 3). For example, the sex pheromone of *Contarinia pisi* is a blend of (2S11S)-diacetoxytridecane, (2S12S)-diacetoxytridecane and 2-acetoxytridecane (Hillbur et al., 1999; Hillbur et al., 2000). On the other hand, in spite of its economic importance to date there is still no identified kairomone and pheromone of *B. pisorum*.

Table 3. Semiochemicals of some field pea insect pests.

Insect species	Pheromone	Kairomone
Pea leaf weevil (*Sitona lineatus*)	4-methyl-3, 5-heptanedione Blight & Wadhams (1987)	cis-3-hexen-1-yl acetate Landon et al. (1997)
Pea aphid (*Acyrthosiphum pisum*)	E-beta-farnesene Pickett & Griffiths (1980); Francis et al. (2005)	
Pea aphid (*Acyrthosiphum pisum*)		Phagostimulant Valine, leucine, diphenylamine, tryptophan Srivastava & Auclair (1974)
African Bollworm (*Helicoverpa armigera*)	Saturated aldehyde (16:Ald), (Z)-9-hexadecenal (Z-9–16:Ald), (Z)-11-hexadecenal (Z-11–16:Ald), hexade-canol (16:OH) and (Z)-11-hexadecenol (2–11–16:OH) Wu et al. (1997)	
Pea midge (*Contarinia pisi*)	(2S11S)-diacetoxytridecane (2S12S)-diacetoxytridecane 2-acetoxytridecane Hillbur et al. (1999); Hillbur et al. (2000)	
Pea Moth (*Cydia nigricana*)	(E,E)-8,10- dodecadien-1-yl acetate (E8,E10-12:Ac)Witzgall et al. (1993)	
Pea weevil (*Bruchus pisorm*)	Not identified	Not identified

However, semiochemicals (sex pheromone and kairomones) have been identified for some other important bruchid beetles attacking stored legumes (Table 4).

Table 4. Semiochemicals of some important bruchid beetles (Bruchidae).

Insect Species	Type of semiochemicals	References
Callosobruchus analis	sex pheromone	Cork et al. (1991); Phillips et al. (1996)
C. maculates	sex pheromone	Cork et al. (1991); Phillips et al. (1996)
C. subinnotatus	sex pheromone	Shu et al. (1996)
C. chinensis	sex pheromone, attractant & repellent	Tanaka et al. (1981); Babu et al. (2003); Shimomura et al. (2008)
C. subinnotatus	sex pheromone	Shu et al. (1999)
Bruchus rufimanus	Attractant & sex pheromone	Bruce et al. (2011)
Acanthoscelides obtectus	Oviposition repellent	Nazzi et al. (2008)

5.2. Host plant resistance

Breeding for insect resistance in grain legumes in general has made little progress (Edwards and Singh, 2006). Nevertheless, plant resistance against economically important pest insects of field pea such as *A*. *pisum*, *B*. *pisorum*, *S*. *lineatus*, *C*. *nigricana* and *C*. *horticola* has been reported (Clement et al., 1994). Being one of the major pest insect of field pea, there were various attempts in search for host-plant resistance against *B. pisorum* (e.g. Pesho et al., 1977; Hardie et al., 1995; Clement et al., 2002) although results showed the absence of *B. pisorum* resistance in the *P*. *sativum* gene pool (Clement et al., 2009). However, breeding of *P*. *sativum* with wild pea, *P*. *fulvum* against *B*. *pisorum* showed a promising result (Clement et al., 2002; Byrne et al., 2008; Clement et al., 2009). On the other hand, genetically modified field peas which showed resistance against *B. pisorum* (Schroeder et al., 1995; De Sousa-majer et al., 2007), has been rejected due to problem of allergic asthma (Lee et al., 2011).

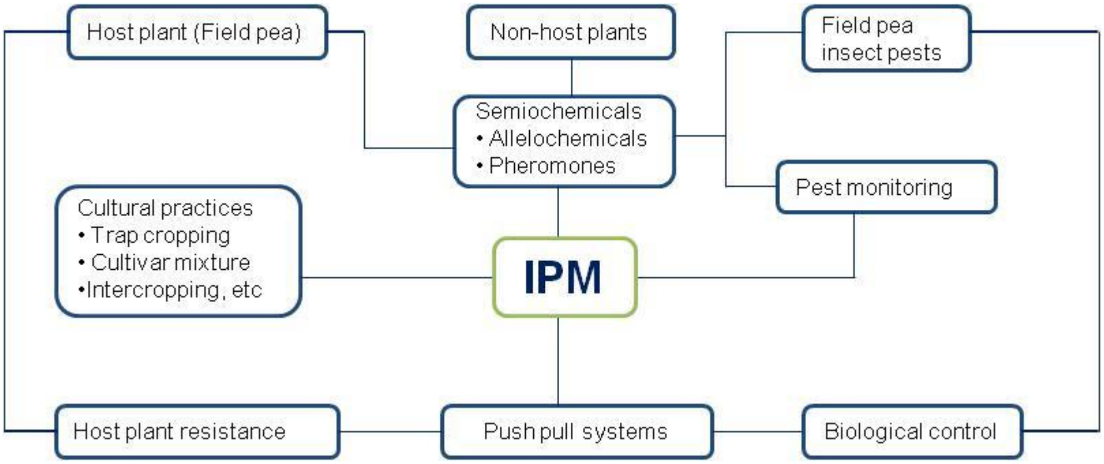

Figure 11. Schematic view of IPM approaches for field pea insect pests.

5.3. Cultural practices

Cultural practice mainly involve manipulation of cropping systems/agronomic practices which are not only contribute for suppression of pest population, but also enhance the activities of natural enemies by creating favorable conditions (Bajwa and Kogan, 2004). Cultural methods of pest control include: crop rotation, intercropping, trap cropping, clean seed, phytosanitation, planting date, etc (Dent, 2000; Bajwa and Kogan, 2004). Such cultural methods are major components of pest management for small-scale African farmers (Abate et al., 2000) and also it plays a pivotal role in the development of IPM programs. Among cultural practices, trap cropping for example, showed a promising results for management of different insect pests (e.g. review of Shelton and Badenes-Perez, 2006). However, cultural practices alone may not suppress pest population below damaging level hence they should be combined with other pest management methods in the context of IPM (Dent, 2000). For field pea insect pest management, cultural methods have a paramount importance as a component of IPM (Fig. 11). For example, use of healthy (pea weevil free seeds), phytosanitory measures, and destruction of volunteer-field pea plant is recommended for control of pea weevil (Armstrong and Matthews, 2005).

In conclusion, control of field pea insect pests is mainly dependent on the use of chemical insecticides. It is thus imperative to develop IPM strategy for major insect pests of this crop for sustainable production. Host-plant resistance, use of semiochemicals, cultural and biological control could be integral part of an IPM programme to control these insect pests.

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