Insect Biotypes and Host Plant Resistance

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Abstract

The green plants and herbivorous insects are engaged in a constant struggle for dominance. Humans usually intervene in this struggle by developing pest-resistant genotypes and other pest management tactics. Upon failure of a previously successful tactic to which the insect population has apparently adapted, the latter is often considered to be a novel or distinct entity and termed as a "biotype." The success of host plant resistance (HPR) strategy is constantly challenged by the occurrence of resistance-breaking insect biotypes. In general, the term "biotype" usually designates an intraspecific group of organisms that are not morphologically distinguishable, but differ by a biological function. Variation among individuals within populations has always been the focus of population genetics. However, the term "biotype" includes the entities that are not consistent either within or between biotypes, and their underlying genetic composition and origins, while generally unknown, are likely heterogeneous within and variable between biotypes. Biotypes may differ in some biological parameters, including detoxification pathways, reproductive rate, dispersal, virus vectoriality, and capacity to damage plants, and are well defined by microsatellite polymerase chain reaction (PCR)-based DNA markers. Insect biotypes feeding on different species of host plants are particularly well documented. To slow down the process of biotype selection, crop cultivars with broad genetic bases are needed.

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The durability of host plant resistance can be enhanced by identifying a wide array of potential insect-resistant genes and ensuring their incorporation in commercially important cultivars.

Keywords
Insect biotype • Coevolution • Host plant resistance • Plant defenses • Biotype management

Plants defend themselves from herbivore damage through a plethora of structural and chemical defenses. These defenses may have exerted enormous selection pressure on the insects resulting in the evolution of counter-defenses (adaptations) in herbivorous insects. The process of plant defense and insect counter-defense is fast tracked in the agroecosystem where humans purposely select insect-resistant plants for cultivation. In this process, the eighteenth and early nineteenth centuries saw the development and cultivation of several insect-tolerant cultivars. However, with the discovery of Gregor Mendel's basic tenets of heredity and plant hybridization in the late nineteenth century, this approach of breeding of insect-resistant plants received scientific impetus. Host plant resistance (HPR) has become an important component of integrated pest management (IPM), and several scientists have tried to define it in their own words. Painter (1951) defined it as "the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect in the field." In practical agriculture, resistance represents the ability of a certain variety to produce a larger crop of good quality than do ordinary varieties at the same level of insect population. Panda and Khush (1995) further extended it as "any degree of host reaction less than full immunity." The breeding of resistant cultivars is a continuous process as genes for insect resistance in the cultivars may gradually be overwhelmed by the development of insect biotypes possessing essential genetic attributes of overcoming the corresponding properties of insect-resistance genes in plants.

13.1 Biotype Concept

Herbivorous insects are commonly known to escape the tactics deployed for their management. As per Downie (2010), when a previously known successful weapon for pest management fails, the insect population has apparently revamped itself to it and is often considered to be a new or distinct entity, given the nonformal category "biotype." It is a fact that the phenotypic variation is omnipresent in natural populations and interpretation of the nature of phenotypic distinctness requires an elucidation of the genetic and environmental variation that causes it, which requires a thorough understanding of the hierarchic structure of alleles within loci, genes within individuals, individuals within populations, and populations within species (Downie 2010).

The biotype concept has been reviewed by several authors over the years (Thorpe 1930; Smith 1941; Eastop 1973; Claridge and den Hollander 1983;

Diehl and Bush 1984; Saxena and Barrion 1987; Downie 2010). Printz (1937) and Painter (1941) applied the term "biotype" to situations where the insect response was indifferent to crop plants developed for their resistance to insect feeding.

Biotypes have been defined as populations within an arthropod species that show variations in their ability to effectively use a trait deployed by a plant cultivar (Gallun and Khush 1980; Wilhoit 1992; Pedigo 1999). A routine method of identifying biotypes is by exposing a set of plant cultivars, each possessing a different insect-resistant gene(s) that reacts differentially to a given insect biotype (Starks and Burton 1972; Saxena and Barrion 1983; Tomar and Prasad 1992; Ratcliffe and Hatchett 1997). Nielson et al. (1970) defined biotype as the populations that can reproduce and survive on cultivars developed for resistance to a particular insect or can resist insecticides. As per Gallun (1978), a biotype is an individual or a population whose phenotype is determined by the interaction between plants having different genes for resistance and the larvae's ability or inability to survive on and stunt the plant. However, Saxena and Barrion (1987) opined that the term biotype is an intraspecific category referring to insect populations of similar genetic composition for a biological attribute. The biotype populations may be partially and temporarily sympatric, allopatric, or parapatric with other compatible populations but differ in one or more biological attributes. Granett et al. (2001) have tried to clarify the concept of biotypes, strain, and host race: "strain designates a population arising from a single collection or clonal individual; biotype is a category designating shared phenotypic traits; host race is a biotype that is better adapted to a specific host than are other biotypes."

The gene-for-gene relationship between insect virulence genes and the genes for plant resistance is very much alike to that explained by Flor (1971) for the genes contributing pathogen resistance in plants and the corresponding genes for virulence in the pathogens. The virulence or avirulence of an insect biotype to a gene contributing to plant resistance depends on the extent of interaction between the resistance genes in the host plant and virulence genes in the insect. Upon recognition of the gene products of the avirulent insect by the defense system of the resistant plant, the insect finds it difficult to infest a resistant plant. On the other hand, when a resistant plant is unable to distinguish insect gene products, the virulent insect biotype overcomes the plant resistance gene(s). Puterka and Burton (1990) suggested that insect biotypes originate from a pre-existing variability for virulence or mutations resulting from sexual recombination or from the exposure to plant resistance gene selection pressure resulting in a variation in the insect virulence gene frequency. The level of resistance exerted by the plant resistance gene, the initial virulence gene frequency, and the extent of interaction between the genotype, the insect, and the environment decide the intensity and duration of virulence gene expression.

However, Claridge and Den Hollander (1983) opined that insects capable of reproducing parthenogenetically are different in kind to those reproducing bisexually. Many insects reproducing by means of parthenogenesis fall outside the scope of the biological species concept, because such organisms multiply without any exchange of genetic material with other organisms. With the passage of time, new mutants may evolve, resulting in new forms which may differ in some important traits, such as host or other habitat requirements. In pea aphid, *Acyrthosiphon pisum* (Harris), with the adaptation of parthenogenetic clones to different species of host plants, the new biotypes arise annually (Frazer 1972). According to Claridge and Den Hollander (1983), there is a little evidence to suggest that gene-for-gene relationship is usual or indeed common for insect-plant feeding relationships. The existence of a gene-for-gene relationship has been clearly established in case of Hessian fly, the only biparental species of insect.

Claridge and Den Hollander (1983) further argued to dispense away with the term "biotype" due to the confusion of two distinct schools of thought. The first concept applies both to individuals and to populations of a species which share certain biological characteristics, usually concerning virulence on different host varieties (synonymous with host race), with little or no knowledge of their genetic bases. The second is a very specific concept concerning the gene-for-gene relationship, in which a gene for virulence in a pest is known to correspond with a specific gene for resistance in the host plant. While considering the two schools of thoughts, the first one appears to be of little importance and may be potentially misleading as in case of the rice brown planthopper. However, the specific concept holds limited applicability since it is dependent upon the detailed genetic analyses which are available in very few cases.

Downie (2010) echoed the call given by Claridge and Den Hollander (1983) to dispense with the term and extended that the segregation of alleles and dynamics of gene frequencies (genotypic variation) should be the criteria for understanding the differences in virulence to host plant resistance and resistance should be deployed against genetically distinct populations not imagined homogenous "biotypes." The entities falling under the umbrella term "biotype" are not consistent either within or between biotypes, and their underlying genetic composition and origins, while generally unknown, are likely heterogeneous within and variable between biotypes.

The use of the term biotype suffers from some problems due to limited knowledge about the genetic makeup of different insect biotypes (Smith 2005). A major tenant of Flor's (1971) concept assumes that there exist single-gene relationships between the host plant and the pest. However, as per Wilhoit (1992), the insect biotypes may refer to populations expressing a particular set of virulence genes or to those insect populations reacting in the same fashion to a set of plant differentials with more than one gene. Mitchell-Olds and Bergelson (2000) suggested that the use of a gene-for-gene concept may be oversimplified due to the recent innovations in the field of plant genomics and that a "gene-for-genome" concept will allow simultaneous evaluation of several resistance genes involved in potentially overcoming a pest virulence gene. A thorough understanding of the genome-wide changes in the reaction of several plant resistance genes to an insect pest is required. For this to happen, the researchers must rely on existing gene models and a working definition of biotypes that include both individuals and populations that exhibit virulence to different genes in insect-resistant plant genotypes (Smith 2005).

13.2 Insect Biotypes in Important Crop Pests

The development of insect biotypes limits the prediction of their available host range, thus complicating the management strategies in different commercial crops. The biotypes may render the previously known resistant crop cultivars to succumb to insect injury, leading to economic losses. Continuous development of arthropod pest biotypes poses a continuous threat to the stability of resistant crop varieties as well as to the sustainability of the breeding programs focused on insect resistance. The development of abundant biotypes of rice insect pests hampered the progress of the breeding programs in several rice-growing countries in Asia (Saxena and Rueda 1982; Saxena and Barrion 1985).

Insect biotype development has been documented in several orders of insects (Thorpe 1930, 1940; Smith 1941). Classical cases of biotype development like in case of grape phylloxera, European corn borer, Hessian fly, corn leaf aphid, greenbug, and pea aphid (Painter 1951) laid the foundation for reorienting the breeding strategies in major crops. According to Pathak (1970), insect biotypes have been known to be developed in at least eight species of insect pests affecting agricultural crops. Saxena and Barrion (1987) documented biotypes to occur in 36 arthropod species belonging to 17 families from six orders. Aphids contribute almost half of these pest species with known biotypes.

Later, van der Arend (2003) listed biotype developments in several insect pests, majority of which overlapped with those documented by Saxena and Barrion (1987). It was Smith (2005), who updated this list of arthropod biotypes associated with plant resistance genes and gave a comprehensive overview of the existing biotypic diversity among arthropod pests in major crops like fruits, legumes, cereals (maize, rice, wheat), and several vegetables. Almost 18 different arthropod species belonging to orders Homoptera, Diptera, Acari, and one species of Coleoptera have been documented to develop virulent biotypes to plant resistance genes (Smith 2005). Parthenogenetic reproduction plays an immense role in contributing greatly toward the successful development of resistance-breaking biotypes in 10 of the 18 aphid species. Since aphids outnumber the entire documented cases of arthropod biotypes, the review by Smith and Chuang (2014) dealt in detail about the physiological, behavioral, genetic, and molecular cues regulating aphid host selection and the genetics and genomics of developed and deployed aphid-resistant cultivars. In their work, these authors documented 17 aphid species comprising more than 50% of all arthropod biotypes to demonstrate virulence. In some of these cases, the selection pressure exerted by the monogenic-based antibiosis resistance leads to the development of virulence in the aphid.

Many cases of emergence of several new resistance-breaking biotypes have been documented in several crop cultivars. Table 13.1 lists the documented cases of arthropod biotype development, till date, in various crop plants. About 50 arthropod species belonging to 20 families from seven orders have been so far documented to exist as biotypes in various agricultural crops across the globe. Majority of the arthropod biotypes have been documented to exist in the order Hemiptera (33) followed by Diptera (6), Coleoptera (4), Lepidoptera (3), Thysanoptera (2),

Table 13.1 Resistance-breaking arthropod biotypes documented in various agricultural crops

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
1	*Acyrthosiphon kondoi* Shinji	Blue alfalfa aphid	Hemiptera	Aphididae	Lucerne (*Medicago sativa*)	2	Frazer (1972) and Auclair (1978), Nielson and Lehman (1980) and Zarrabi et al. (1995)
2	*Acyrthosiphon pisum* (Harris)	Pea aphid	Hemiptera	Aphididae	Lucerne (*Medicago sativa*), dyer's whin (*Genista tinctoria*), winged broom (*G. sagittalis*), common sainfoin (*Onobrychis viciifolia*), and horseshoe vetch (*Hippocrepis comosa*)	15	Harrington (1943), Cartier et al. (1965), Auclair (1978), Frazer (1972) and Peccoud et al. (2015)
3	*Agromyza oryzae* (Munakata)	Rice leaf miner	Diptera	Agromyzidae	Rice (*Oryza sativa*)	2	Saxena and Barrion (1987)
4	*Amphorophora agathonica* Hottes	Large raspberry Aphid	Hemiptera	Aphididae	Red raspberry (*Rubus idaeus*)	6	Converse et al. (1971) and Dossett and Kempler (2012)

5	*Amphorophora idaei* (Born)	Large raspberry aphid	Hemiptera	Aphididae	Red raspberry (*Rubus idaeus*)	5	Panda and Khush (1995), Birch et al. (1996, 2002), Gordon et al. (1999), Jones et al. (2000), Jennings (1988) and Dossett and Kempler (2012)
6	*Amphorophora rubi* (Kaltenbach)	Raspberry aphid	Hemiptera	Aphididae	Red raspberry (*Rubus idaeus*)	4	Briggs (1959, 1965), Knight et al. (1960), Keep and Knight (1967), Keep et al. (1970) and Saxena and Barrion (1987)
7	*Aphis craccivora* Koch	Cowpea aphid	Hemiptera	Aphididae	Cowpea (*Vigna unguiculata*)	2	Ansari (1984), Kusi et al. (2010), Aliyu and Ishiyaku (2013), Jones (1967), Watson and Okusanya (1967), Jones (1967) and Saxena and Barrion (1987)
					Groundnut (*Arachis hypogaea*)	2	
					Bush sitao (*Vigna unguiculata sesquipedalis*)	5	
8	*Aphis fabae* Scopoli	Bean aphid	Hemiptera	Aphididae	Broad bean (*Vicia faba*)	2	Pathak (1970)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
9	*Aphis glycines* Matsumura	Soybean aphid	Hemiptera	Aphididae	Soybean (*Glycine max*)	3	Kim et al. (2008), Hill et al. (2010) and Michel et al. (2011)
10	*Aphis gossypii* Glover	Cotton or melon aphid	Hemiptera	Aphididae	Cotton (*Gossypium* spp.) and melon (*Cucumis melo*)	2	Wang et al. (2016), Vanlerberghe-Masutti and Chavigny (1998), Najar-Rodriguez et al. (2008), Xu et al. (2014) and Wang et al. (2004b)
11	*Aphis nasturtii* (Kaltenbach)	Buckthorn aphid	Hemiptera	Aphididae	Potato (*Solanum tuberosum*)	2	Saxena and Barrion (1987)
12	*Aulacorthum solani* (Kaltenbach)	Foxglove aphid	Hemiptera	Aphididae	Potato (*Solanum tuberosum*)	1	Saxena and Barrion (1987) and Miller et al. (2009)

13	*Bemisia tabaci* (Gennadius)	Sweet potato whitefly	Hemiptera	Aleyrodidae	Cotton (*Gossypium* spp.), okra (*Abelmoschus esculentus*), cassava (*Manihot esculenta*), squash (*Cucurbita maxima*), potato (*Solanum tuberosum*), sweet potato (*Ipomoea batatas*), tomato (*Solanum lycopersicum*)	34 cryptic species	Brown et al. (1995), Cervera et al. (2000), Nombela et al. (2003), Moya et al. (2001), De Barro et al. (2005), Dinsdale et al. (2010), De Barro et al. (2011) and Boykin and De Barro (2014)
14	*Brevicoryne brassicae* (Linnaeus)	Cabbage aphid	Hemiptera	Aphididae	Vegetables	2–4	Lammerink (1968) and Dunn and Kempton (1972)
15	*Callosobruchus maculatus* (Fabricius)	Cowpea weevil	Coleoptera	Chrysomelidae	Cowpea (*Vigna unguiculata*)	1	Shade et al. (1996)
16	*Chaetosiphon fragaefolii* (Cockerell)	Strawberry aphid	Hemiptera	Aphididae	Strawberry (*Fragaria ananassa*)	2	Saxena and Barrion (1987)
17	*Chlorops oryzae* Matsumura	Rice stem maggot	Diptera	Chloropidae	Rice (*Oryza sativa*)	2	Saxena and Barrion (1987)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
18	*Cydia* (*Laspeyresia*) *pomonella* (Linnaeus)	Coddling moth	Lepidoptera	Tortricidae	Apple (*Malus* spp.), plum (*Prunus domestica*), walnut (*Juglans regia*)	3	Phillips and Barnes (1975) and Saxena and Barrion (1987)
19	*Daktulosphaira vitifoliae* (Fitch)	Grape phylloxera	Hemiptera	Phylloxeridae	Grapes (*Vitus* spp.)	2	Granett et al. (1985), Williams and Shambaugh (1988), Song and Granett (1990), Omer et al. (1999) and Martinez-Peniche (1999)
20	*Dasineura* (*tetentsi*) *oxycoccana* (Johnson)	Blueberry gall midge	Diptera	Cecidomyiidae	Blackcurrant (*Ribes nigrum*)	2	Hellqvist (2001)
21	*Diuraphis noxia* (Kurdjumov)	Russian wheat aphid	Hemiptera	Aphididae	Wheat (*Triticum* spp.)	11	Kiriac et al. (1990), Shufran et al. (1997), Zsuzsa et al. (2001), Basky (2003), Haley et al. (2004), Smith et al. (2004), Merrill et al. (2014), Tolmay et al. (2007) and Jankielsohn (2011)

22	*Dysaphis plantaginea* (Passerini)	Rosy apple aphid	Hemiptera	Aphididae	Apple (*Malus* spp.)	3	Alston and Briggs (1977) and Rat-Morris et al. (1999)
23	*Eriosoma lanigerum* (Hausmann)	Wooly apple aphid	Hemiptera	Aphididae	Apple (*Malus* spp.)	3	Sen Gupta (1969), Gupta and Miles (1975) and Young et al. (1982)
24	*Frankliniella occidentalis* (Pergande)	Western flower thrips	Thysanoptera	Thripidae	Cucumber (*Cucumis sativus*)	2	De Kogel et al. (1997)
25	*Lepidosaphes ulmi* (Linnaeus)	Oystershell scale	Hemiptera	Diaspididae	Apple (*Malus* spp.)	2	Gharib (1978) and Saxena and Barrion (1987)
26	*Macrosiphum euphorbiae* (Thomas)	Potato aphid	Hemiptera	Aphididae	Tomato (*Solanum lycopersicum*)	2	Goggin et al. (2001) and Srinivasan and Alvarez (2011)
27	*Mayetiola destructor* (Say)	Hessian fly	Diptera	Cecidomyiidae	Wheat (*Triticum* spp.)	16	Gallun and Reitz (1971), Ratcliffe et al. (1994), Naber et al. (2000) and El Bouhssini et al. (2001)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
28	*Muellerianella fairmaire* (Perris)	Leafhopper	Hemiptera	Delphacidae	Common velvet grass (*Holcus lanatus*)	1	Drosopoulos (1976, 1977)
29	*Myzus persicae* (Sulzer)	Green peach aphid	Hemiptera	Aphididae	Tobacco (*Nicotiana tabacum*), cabbage (*Brassica oleracea* var. *capitata*), peach (*Prunus persica*)	3	van Emden et al. (1969) and Saxena and Barrion (1987)
30	*Nasonovia ribisnigri* (Mosley)	Currant-lettuce aphid	Hemiptera	Aphididae	Lettuce (*Lactuca sativa*)	2	van der Arend et al. (1999)
31	*Nephotettix cincticeps* (Uhler)	Green rice leafhopper	Hemiptera	Cicadellidae	Rice (*Oryza sativa*)	2	Sato and Sogawa (1981)
32	*Nephotettix virescens* (Distant)	Green leafhopper	Hemiptera	Cicadellidae	Rice (*Oryza sativa*)	3	Heinrichs and Rapusas (1985), Takita and Hashim (1985) and Panda and Khush (1995)
33	*Nilaparvata lugens* (Stal)	Brown planthopper	Hemiptera	Delphacidae	Rice (*Oryza sativa*)	4	Verma et al. (1979), Heinrichs (2001), Huang et al. (2001), Jena and Kim (2010) and Bhogadhi et al. (2015)

34	*Orseolia oryzae* (Wood-Mason)	Asian rice gall midge	Diptera	Cecidomyiidae	Rice (*Oryza sativa*)	11 (Indian-7, Chinese-4)	Heinrichs and Pathak (1981), Takita and Hashim (1985), Mohan et al. (1994), Rajyashri et al. (1998), Katiyar et al. (2000) and Vijaya Lakshmi et al. (2006)
35	*Ostrinia nubilalis* (Hubner)	European corn borer	Lepidoptera	Crambidae	Corn (*Zea mays*)	4	Kim et al. (1967), Chiang et al. (1968) and Saxena and Barrion (1987)
36	*Phaedonia inclusa* Stal	Soybean leaf beetle	Coleoptera	Chrysomelidae	Soybean (*Glycine max*)	1	Saxena and Barrion (1987)
37	*Rhagoletis cerasi* (Linnaeus)	European cherry fruit fly	Diptera	Tephritidae	Sweet cherry (*Prunus avium*), apple (*Malus* spp.)	2	Boller and Bush (1974), Prokopy et al. (1988) and Bush (1993)
38	*Rhopalosiphum maidis* (Fitch)	Corn leaf aphid	Hemiptera	Aphididae	Barley (*Hordeum vulgare*), corn (*Zea mays*), sorghum (*Sorghum bicolor*)	5	Cartier and Painter (1956), Painter and Pathak (1962), Singh and Painter (1964) and Wilde and Feese (1973)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
39	*Saissetia oleae* (Olivier)	Black scale	Hemiptera	Coccidae	Citron melon (*Citrullus lanatus* var. *citroides*)	1	Saxena and Barrion (1987)
40	*Schizaphis graminum* (Rondani)	Greenbug	Hemiptera	Aphididae	Barley (*Hordeum vulgare*), wheat (*Triticum* spp.), oats (*Avena sativa*), sorghum (*Sorghum bicolor*)	11	Curvetto and Webster (1998), Kindler and Hays (1999), Kindler et al. (2001), Porter et al. (2000), Harvey and Hackerott (1969), Kindler and Spomer (1986), Porter et al. (1982), Puterka et al. (1988), Teetes et al. (1975) and Wood (1961)
41	*Sitobion* (*Macrosiphum*) *avenae* (Fabricius)	English grain aphid	Hemiptera	Aphididae	Wheat (*Triticum* spp.)	3	Lowe (1981)
42	*Sitophilus oryzae* (Linnaeus)	Rice weevil	Coleoptera	Curculionidae	Split peas (*Pisum sativum*), adzuki bean (*Vigna angularis*)	2	Holloway (1984, 1985) and Holloway and Smith 1985

43	*Therioaphis maculata* (Buckton)	Spotted alfalfa aphid	Hemiptera	Aphididae	Lucerne (*Medicago sativa*)	6	Nielson et al. (1970), Nielson and Lehman (1980) and Panda and Khush (1995)
44	*Therioaphis trifolii forma maculata* (Buckton)	Spotted alfalfa aphid	Hemiptera	Aphididae	Alfalfa (*Medicago sativa*), clover (*Trifolium* spp.)	2	Nielson et al. (1970), Sunnucks et al. (1997b), Milne (1998a, b) and Saxena and Barrion (1987)
45	*Thrips tabaci* Lindeman	Onion thrips	Thysanoptera	Thripidae	Tobacco (*Nicotiana tabacum*), dead nettle (*Lamium purpureum*), onion (*Allium cepa*)	2	Zawirska (1976), Brunner et al. (2004), Toda and Murai (2007), Diehl and Bush (1984), Fekrat et al. (2014), Nault et al. (2006), Kobayashi and Hasegawa (2012), Jacobson et al. (2013), Westmore et al. (2013) and Saxena and Barrion (1987)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
46	*Trialeurodes vaporariorum* (Westwood)	Greenhouse whitefly	Hemiptera	Aleyrodidae	Vegetables	2	Lei et al. (1998)
47	*Tribolium castaneum* (Herbst)	Red flour beetle	Coleoptera	Tenebrionidae	Sorghum grain (*Sorghum bicolor*)	2	Coulibaly (1993)
48	*Yponomeuta padella* (Linnaeus)	Small ermine moth	Lepidoptera	Yponomeutidae	Hawthorn (*Crataegus monogyna*)	1	Raijmann (1992) and Saxena and Barrion (1987)
49	*Aceria tosichella* Keifer	Wheat curl mite	Acari: Prostigmata	Prostigmata	Goat grass (*Aegilops tauschii*)	6	Malik et al. (2003) and Harvey et al. (1995, 1997, 1999, 2001)
50	*Tetranychus urticae* Koch	Red spider mite	Acari: Trombidiformes	Tetranychidae	Tomato (*Solanum lycopersicum*)	1	Foster and Barker (1978)

Trombidiformes (1), and Prostigmata (1). Aphids continue to outnumber all other arthropod species as far as biotype development is concerned with as many as 24 species recorded on different host plants. Due to the enormous variations in aphid host plant specificity and reproductive biology, the avoidance of aphid virulence throws challenges to crop protection (Smith and Chuang 2014). However, enough evidence exists whereby the development of insect biotypes can be delayed or avoided through combined plant breeding and pest management efforts.

13.3 Factors Responsible for Biotype Evolution

The possible causes for biotype evolution have been reviewed by several workers (Ruggle and Gutierrez 1995; Porter et al. 1997; Birkle and Douglas 1999; Smith 2005; Michel et al. 2011). As per Xiang Dong et al. (2004), the insect biotypes have their genetic bases, including the mutation or change in the sequence of enzymes and chromosomes, assortive mating and genetic differentiation of population, and, of course, sexual reproduction. Puterka and Burton (1990) suggested several factors such as selection pressure exerted by the resistance genes, mutations, or preexisting differences in virulence; sexual recombinations may lead to the development of insect biotypes. However, the initial virulence gene frequency, the category of resistance exhibited by the plant resistance gene, and the interaction between the genotype, the pest, and the environment ultimately decide the intensity and duration of virulence gene expression.

There exists a direct correlation between the use of insect-resistant cultivars and the subsequent evolution of new insect biotypes. Biotype development in several insects is related to variations in the composition of the resistance genes in the deployed resistant cultivars. The question of how greenbug, *Schizaphis graminum* (Rondani), biotypes develop has been answered at the population, organism, and gene levels (Smith 2005). However, as per Porter et al. (1997), there exists no correlation between the occurrences of new greenbug biotypes with the deployment of greenbug-resistant wheat cultivars. Since the resistance in *Gb3*, *Gb4*, *Gb5*, and *Gb6* has never existed in a wheat cultivar in the field, therefore, the gene-for-gene relationship had no effect on the development of biotypes of *S. graminum*. In case of sorghum, the relationship between the use of resistant hybrids and the evolution of new biotypes has been established in only three of the 11 biotypes of greenbug. However, no clear relationship evidence has been established even within these three biotypes (Sharma 2009).

Biotype selection is also dependent upon the geographic extent to which resistant cultivars are planted throughout the insects' host range (Smith 2005). Besides, the selection of insect biotypes on previously resistant cultivars may also be attributed to improper insecticide application, lack of crop rotation, or improper management practices such as elimination of alternate (weed) hosts. Large-scale monoculture of same rice cultivars in several countries, as well as indiscriminate applications of insecticides for hopper control, leads to the evolution of hopper biotypes in Southeast Asia (Smith 2005). Planting of early *Mayetiola destructor* (Say)-resistant wheat cultivars over a wide geographical range may also contribute to the evolution of virulence (Smith 2005). Several non-crop cultivar factors have also been documented to play a likely role in the development of biotypes (Porter et al. 1997). Examples include non-crop host adaptation by *S. graminum* (Powers et al. 1989), large variations in *S. graminum* clonal diversity (Shufran et al. 1992; Shufran and Wilde 1994), and autumn sexual reproduction of the greenbug on cool season grasses, especially blue grass (Puterka et al. 1992). The greenbug summer populations on wheat die before sexual forms are produced, thereby eliminating the chances that individuals produced on summer crop plants result in biotypes (Smith 2005). This idea is well supported by the identification of a biotype on Western wheat grass (Anstead et al. 2003) with a unique virulence profile, thereby establishing the fact that noncultivated grasses are closely involved in the development of what have become recognized as *S. graminum* biotypes.

Michel et al. (2011) presented a comprehensive overview of the genetic basis for biotype development in homopterans, particularly aphids. In ecological levels, the natural enemies, the symbionts, the selection capacity to the host plants, and the resistance to insecticides are the possible reasons for the evolution of aphid host biotypes. Biotypes have been known to be intrinsically associated with host plant resistance, particularly many species within the family Aphididae (Smith 2005). Relationships between symbiotic bacteria and insects are well documented. Such intricate relationships are known to have a considerable effect on the host biology, can be obligatory or facultative for the host, and are known to be involved in host plant utilization, reproductive manipulation, nutrition, and ability to withstand environmental variations (Bourtzis and Miller 2006).

Many bacterial endosymbionts such as *Buchnera*, *Hamiltonella*, *Rickettsia*, *Arsenophonus*, *Regiella*, *Serratia*, etc. act as a source of essential amino acids to their carriers, the aphids, and may, therefore, be involved in aphid defense as well as biotype development (Ruggle and Gutierrez 1995; Birkle and Douglas 1999; Moran and Wernegreen 2000; Wille and Hartman 2009; Oliver et al. 2010). These endosymbionts have been documented to be involved with different insect biotypes, presumably because of the diversity in the nutrients and amino acids afforded by different host plants (Simon et al. 2003a; Chiel et al. 2007). For instance, it has been indicated that virulence to lucerne (alfalfa) varieties is symbiont based (Ruggle and Gutierrez 1995). There are several cases depicting the close associations between insects and their endosymbionts. These symbionts have been found to play a very crucial role in development, reproduction nutrition, speciation, and defense against natural enemies of their host insects (Baumann 2005; Douglas 1998; Gregory et al. 2000; Oliver et al. 2003; Stouthamer et al. 1999). There exists a large diversity of the bacterial microbes harbored by the brown planthopper, and the results of Tang et al. (2010) provide enough evidence of symbiotic relationships between specific bacterial microbes and biotypes of *N. lugens*. There are also evidences that some biotypes of *N. lugens* differ in DNA polymorphisms, isozymes, and small morphological features (Claridge et al. 1984; Latif et al. 2009; Shufran and Whalon 1995). However, the exact mechanism of conferring virulence in *N. lugens* biotypes is still not clear.

Studies conducted by Chiel et al. (2007) have revealed an interesting fact related to *Bemisia tabaci* B biotype and the bacteria it carries in Israel: all B biotype *B. tabaci* hosts *Hamiltonella*, but they have not been found to carry either *Wolbachia* or *Arsenophonus*. On the contrary, *Arsenophonus* and *Wolbachia* have frequent association with the Q biotype, with the latter having no association with *Hamiltonella* in Israel. Interestingly, *B. tabaci* Q biotype populations from other regions of the world showed infection with *Hamiltonella* and *Cardinium*, while only the A biotype showed infection with *Fritschea* in the United States (Baumann 2005). *Rickettsia* is the only symbiont that is commonly detected in both biotypes of *B. tabaci* and is also the only bacterium found in very high concentration throughout the insect body (Gottlieb et al. 2006, 2008), and being intracellular, this bacterium affects some biological aspects of the insect. Correlations between the symbiont profiles and biotypes of Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) and *S. graminum*, have recently been revealed (Pinheiro et al. 2014; Anathakrishnan et al. 2014), but their genetic underpinnings have not yet been explored.

Secondly, since most of the sap sucking insects feed exclusively on plant phloem, there is an induction of consistent responses within plants through interactions with aphid saliva (Mutti et al. 2008). Such responses highlight the role of the salivary glands in insect biotype adaptation (Michel et al. 2011). Specific factors found in aphid saliva play an immensely important role in biotype adaptation as has been implicated in earlier research. For instance, resistance breakdown in sorghum is a result of higher activity of pectin methylase in saliva of *S. graminum* biotypes (Dreyer and Campbell 1984). Furthermore, certain saliva-related proteins may be involved in *D. noxia* biotype adaptation against wheat (Lapitan et al. 2007).

Thirdly, the complex life cycle is the biggest factor which aids the aphids to develop into new biotypes (Michel et al. 2011). Most species are holocyclic (alternating between primary and secondary hosts) and heteroecious (undergoing sexual and asexual reproduction), although variations and phenotypic plasticity are common (Moran 1992; Blackman and Eastop 2000, 2007). Since the generation time is very short in aphids, any modification or adaptation that evolves during the asexual stage can quickly become common. However, very little information is available about the genetic mechanisms of biotype evolution in aphids, despite the frequency at which biotypes evolve. Only in a few studies (Dreyer and Campbell 1984; Lapitan et al. 2007) have mechanisms been explained, but the gene(s) involved remain elusive.

Based on analysis of these specific insect-plant interactions, future plant resistance programs should concentrate on the use of the most effective resistance genes irrespective of what effect these genes may have on insect population genetics. The evolution of insect biotypes with a high reproductive potential should be anticipated when developing plant resistance to insect pests. The high reproductive potential of aphids coupled with parthenogenetic mode of reproduction and clonal diversity suggests that new biotypes will continue to evolve in the future (Smith 2005). In a few cases, the development of insect virulence has also been promoted by the higher expression of genes controlling antibiosis.

13.4 Biotechnological Tools for Biotype Identification/Analysis

Morphology has been used historically to separate species when identifying and describing insect taxa. Among the many groups of insects, however, morphological characters can vary with respect to environmental factors within a single species or be as convergent and cryptic among closely related species as to be of limited usefulness (Calvert et al. 2005). The term "biotype" usually designates an intra-specific group of organisms that are not morphologically distinguishable but differ by a biological function (Eastop 1973). Although host plant response remains the main criterion for identification of insect biotypes, but it is often laborious and time-consuming. Therefore, other methods based on morphological characters (Starks and Burton 1977), isozymes (Abid et al. 1989), and mitochondrial DNA (Shufran et al. 2000) have been utilized to assess genetic relationships among biotypes or to develop alternative identification procedures. In such cases, studies of their biology and molecular profiles become essential to defining species and characterizing populations (Calvert et al. 2005). At the molecular level, protein and DNA polymorphisms can be combined with studies of biological characteristics by using experimental or technological approaches: electrophoresis of allozymes, analysis of randomly amplified polymorphic DNAs (RAPDs), and nucleic acid sequence comparisons of nuclear or mitochondrial DNA markers (Calvert et al. 2005). However, it has not been possible to fully distinguish all insect biotypes using these methods.

For solving routine taxonomic and ecological problems regarding biotype or cryptic status of insect, various molecular tools have been utilized. Various allozymes, RFLP, RAPD, microsatellite, and mtDNA-based markers have been used for differentiating biotypes and sympatric species (Laroche et al. 1996; Hoy et al. 2000; Hufbauer et al. 2004). For exploring the genetic differences between insect biotypes, DNA-based techniques are increasingly being applied (Birkle and Douglas 1999) and are particularly valuable for the study of aphids (Hales et al. 1997). For instance, consistent differences between greenbug, *S. graminum*, biotypes that use different sorghum cultivars have been revealed using restriction analyses of mitochondrial DNA (mtDNA) (Powers et al. 1989) and between alfalfa aphid, *Therioaphis trifolii* (Buckton), biotypes using different legume crops (Sunnucks et al. 1997b). Consistent differences in microsatellite profiles have also been unraveled in the English grain aphid, *Sitobion avenae* (Fabricius), collected from wheat and cocksfoot (De Barro et al. 1995; Sunnucks et al. 1997a). Furthermore, significant variations in ribosomal spacers have been detected for the large raspberry aphid, *Amphorophora idaei* (Born), infesting various raspberry cultivars (Birch et al. 1994).

Random amplified polymorphic DNA-polymerase chain reaction (RAPD-PCR) has been successfully applied to reveal distinctive patterns among some greenbug biotypes (Black et al. 1992; Aikhionbare et al. 1998; Lopes-da-Silva et al. 2004). Using several types of midge DNA analyses, biotypes of the Asian rice gall midge, *Orseolia oryzae* (Wood-Mason), have been identified. Based on DNA polymorphisms related to amplification by RAPD primers, Behura et al. (1999) developed a PCR-based assay to differentiate between the Indian *Orseolia* biotypes. The SCAR (sequence-characterized amplified region) primers could differentially amplify the DNA of the six Indian biotypes, as well as that of the African gall midge, *O. oryzivora* (Harris and Gagne). The AFLP (amplified fragment length polymorphism) cluster analyses have been utilized to closely evaluate the composition of the Chinese and Indian *O. oryzae* groups (Katiyar et al. 2000).

Molecular techniques and DNA-based markers have led to tagging of several plant resistance genes and mapping of virulence genes and their subsequent cloning for insect biotypes. The SCAR method has been utilized for the identification of the biotype of *O. oryzae* (Behura et al. 1999) and *Anopheles quadriannulatus* (Fettene and Temu 2003). It has been observed that the insecticide applications affect the balance of both B and Q biotypes of *B. tabaci* that have different inherent levels of resistance to insecticides (Horowitz et al. 2005). Therefore, to select a suitable strategy to manage different biotypes of *B. tabaci*, SCARs can play an integral role in the rapid identification of biotypes. So far, *B. tabaci* cryptic species have been distinguished using a variety of genetic markers (Gawel and Bartlett 1993; Wool et al. 1993; Cervera et al. 2000; De Barro 2005) with the recent focus shifting toward sequencing a portion of the mitochondrial cytochrome oxidase I (mt-COI) gene (Boykin et al. 2007; Dinsdale et al. 2010; De Barro et al. 2011). However, for species identification, the conventional molecular-based methods, such as polymerase chain reaction, require expertise in laboratory techniques and access to expensive laboratory equipment (e.g., thermocyclers), besides being time-consuming as well.

Among the molecular markers, RAPD-PCR is most commonly used to discriminate the *B. tabaci* biotypes. For successfully distinguishing *B. tabaci* B biotype and non-B biotypes, De Barro and Driver (1997) screened four random primers. For differentiating the B, Q, and newly found T biotypes distributed in Italy, Simon et al. (2003a) used methods such as RAPD-PCR, esterase electrophoresis spectra, and silverleaf symptom. The sequence analysis of DNA fragments in specific regions such as the mitochondrial cytochrome oxidase I (COI) and ribosome internal transcribed spacer 1 (ITS1) can also be used to distinguish *B. tabaci* biotypes (Frohlich et al. 1999; De Barro et al. 2000). For identifying insect species and biotypes, several studies on specific primer set applications are gradually becoming common (Behura et al. 1999; Kethidi et al. 2003; Wang et al. 2004a). Wang et al. (2004a) developed the specific primer set, Baf/Bar, for *B. tabaci* biotype B, through which it was indicated that *B. tabaci* biotype B existed in Taiwan. However, upon mitochondrial COI sequence analysis, it was revealed that in Taiwan, *B. tabaci* also included the An and Nauru biotypes, besides the biotype B (Hsieh et al. 2006). In order to rapidly amplify a target DNA sequence using four to six specially designed primers, Notomi et al. (2000) and Nagamine et al. (2002) used the loop-mediated isothermal amplification of DNA (LAMP) as one of the methods. Recently, LAMP assays have been used successfully to distinguish between Middle East-Asia Minor 1 (MEAM1) and Mediterranean (MED) regions' cryptic species of *B. tabaci* by two research groups (Adachi et al. 2010; Hsieh et al. 2012).

13.5 Management of Insect Biotypes

Host plant resistance is a cost-effective and sustainable approach to reduce insect damage and increase yield potential of plant varieties. Evolution of biotypes among insect populations is a potential threat to the durability of host plant resistance. Biotypes have long-lasting implications for pest management as the failure to identify distinct populations can have serious consequences (Bush and Hoy 1983). Large-scale cultivation of resistant cultivars exerts a constant selection pressure on insect populations, paving the way for the evolution of new biotypes (Kindler and Hays 1999; Naber et al. 2000). The successful utilization of certain insect-resistant varieties may be seriously constrained in time and space by the occurrence of new biotypes of the target pest. Hence, continuous and systematic evaluation of new germplasm must be explored to identify new genes for resistance (Sharma 2009). For conferring resistance to new insect biotypes, some of the known resistance genes could be pyramided and tested for efficacy. The pyramided major genes or quantitative trait loci (QTLs) may provide stable resistance and improve yield potential of cultivars. In such situations, one has to adopt the strategy of breeding crop cultivars for polygenic resistance or constantly search for new resistance genes followed by their introgression into high-yielding cultivars (Jena and Kim 2010). To delay or overcome the evolution of insect biotypes, cultivars with diverse mechanisms of resistance having stable expression against the prevalent insect biotypes should be utilized in a breeding program (Sharma 2009).

Still, much research is needed to determine the influence of emerging insect biotypes on resistant crop cultivars and to determine the relative frequencies and distributions of biotypes. Several methods have been suggested to maximize the use of host plant resistance to brown planthopper (and in general homopteran pests) in pest management. Sequential release of varieties with diverse resistance traits, the use of multilines with vertical resistance, and polygenic resistance with moderate resistance (horizontal resistance) received wide acceptability (Khush 1979;Panda and Khush 1995). However, these methods failed in practical applications, mainly due to the difficulties in developing a spectrum of activities that could satisfy the above criteria. In order to prevent the evolution of new biotypes in the field, gene pyramiding of known resistance genes in commercial rice varieties seemed to be insufficient unless the resistance-breaking mechanism of BPH to each resistance gene was considered (Horgan 2009; Chen 2009). Many doubts have arisen about the possibilities of developing high-yielding crop cultivars with the higher level of resistance to insect pests. This assumption is based on the fact that the energy and other resources that the plants divert for resistance would not be available for the growth and reproduction of the plant. For instance, van Emden (1991) concluded that partial host plant resistance was more important than the high level of resistance to insects.

Michel et al. (2011) suggested that the durability of host plant resistance can be preserved along with the management of evolution of insect virulence by introducing diverse soybean aphid-resistant genes and varieties. In addition, the possibility of gene pyramiding and geographically varying *Rag* (resistant to *Aphis glycines*

Matsumura) gene deployment may extend the life of host plant resistance (Porter et al. 2000; Smith 2005). The integration of all the tactics will be necessary to extend the durability of host plant resistance in soybean and slow the evolution of soybean aphid biotypes.

For biotype management, a thorough knowledge of the insect systematics and biology is a prerequisite. Such kind of information is absolutely required for both the establishment of management measures in the most severely affected areas and the prediction of risks associated with the insect pests. In order to characterize biotypes to map their occurrence, a comprehensive approach utilizing molecular tools and detailed morphological studies is absolutely necessary (Navia et al. 2013). This can be possible through the concerted efforts of researchers across regions, countries, and continents. A prior knowledge of the identity of the biotype in each geographical region would be very useful in integrated pest management practices. The use of biotype-specific SCAR primers in a single PCR with an unknown genomic DNA sample of a given biotype would enable entomologists and plant breeders to identify the biotype prevalent in that region in the shortest possible time and to avoid deploying any crop variety known to be susceptible to that biotype (Behura et al. 1999). Area-wide rigorous monitoring and surveillance programs should be initiated to detect and map the occurrence of insect biotypes. Improving pest prediction capabilities, cataloging the range of important host plant species, and establishing varietal impact under insect pressure are of utmost importance. In the newly affected areas, continuous screening of resistance of a commercial crop cultivar to this biotype should be taken on a priority basis.

Keeping into consideration the risks of biotype evolution, a single strategy of deployment of insect-resistant genotypes alone may be a risky proposition. For broadening the genetic base of resistance and enhancing its durability against different insect biotypes, the traditional breeding efforts need to be blended with alternative breeding strategies. For successful gene pyramiding, there is a need to explore new sources of resistance constantly, which can further be characterized and mapped using genetic markers (Dossett and Kempler 2012). Durable resistance will only come from combining multiple resistance sources, until strong sources of horizontal resistance are identified. For new sources to be efficiently combined to maintain their durability and prevent future breakdown of resistance, mapping studies will be necessary to identify markers and linkages for insect-resistant genes (Dossett and Kempler 2012). A comprehensive knowledge about the biology of resistance mechanisms will be imperative for judging how durable novel sources of resistance may be and how effective they will be at the objective of delaying the evolution of new insect biotypes. The risk of emergence of new biotypes could be reduced to a much greater extent by adopting well-planned monitoring strategy coupled with integrated biotype management practices that provide multiple selective pressures (Raffa 1989).

To avoid the selection of arthropod biotypes, an amalgamation of plant breeding and pest management practices is vital (Smith 2005). It has been observed that cultivars possessing tolerance mechanism against insects exert minimum selection pressure on pest populations to evolve virulence (Heinrichs 1986). On the contrary, those cultivars exhibiting antibiosis, where high levels of chemical and physical factors have resulted in selection for virulent individuals, are comparatively unstable than tolerant cultivars. Therefore, the utilization of a cultivar possessing moderate levels of antibiosis or with a blend of antibiosis, antixenosis, and tolerance could serve as an effective management practice (Smith 2005). This is further supported by the results of Basky (2003) which provide evidence that virulent *D. noxia* populations are unable to overcome tolerance but possibly overcome the antibiosis component of several different wheat resistance genes.

Development and adoption of improved arthropod pest management techniques can result in enhanced arthropod natural enemy fauna and delay the biotype development as has happened in the case of *N. lugens* (Smith 2005). To monitor the onset of new biotypes, surveillance and sampling programs should be initiated in different geographical locations and from diverse host plants. The method of differentiation of arthropod biotypes (host differentials or PCR-based assays) should be accurate and should give the most efficient differentiation of biotypes in an insect population. As per Smith (2005), a sound pest management approach aiming at slowing down the development of insect biotypes should focus on planting different genotypes with resistance genes to specific biotypes in different geographical areas. Smith (2005) and van Emden (2007) opined that the use of insect-resistant crop plants with horizontal resistance and moderate levels of resistance that blend well with other management strategies should be the key for all breeding programs focused on delaying the onset of insect biotypes. There is a dire need to identify new and diverse insect-resistant genes that express tolerance resistance or more moderate levels of antibiosis resistance in pest management.

13.6 Conclusions

Host plant resistance is an integral component of integrated pest management as well as varietal improvement programs. Continuous planting of crop cultivars with single major genes (R) may predispose them to certain virulent insect biotypes, thus limiting their sustainability and performance. Therefore, efforts should be oriented toward broadening the genetic base of resistance, both monogenic and polygenic. As biotype shifts may occur, rendering previously efficient genes, susceptible to the new biotypes, agricultural entomologists should undertake regular and systematic arthropod biotype surveillance programs that can help the plant breeders in evolving insect-resistant cultivars. Inability to recognize their existence in nature can have serious consequences in pest management programs (Diehl and Bush 1984). There are hundreds of insect-resistant genes deployed in improved cultivars globally, but the continual evolution of virulent biotypes dictates the need for the identification of new sources of resistance and for MAS systems to identify and track these genes. The refinement and increased use of MAS techniques and MAS centers should be encouraged to accelerate the rate and accuracy of breeding crop plants for insect resistance. From this increased understanding, there should emerge strategies to better manage these economically damaging pests in a sustainable manner.

References

Abid HS, Kindler SD, Jensen SG et al (1989) Isozyme characterization of sorghum aphid species and greenbug biotypes (Homoptera: Aphididae). Ann Entomol Soc Am 82:303–306

Adachi T, Umezawa T, Yamaguchi H et al (2010) Identification of Bemisia tabaci B and Q biotypes in Osaka Prefecture by DNA sequencing and a LAMP method. Annu Rep Kansai Pl Prot Soc 52:103–104

Aikhionbare FO, Pruess KP, Mayo ZB (1998) Greenbug (Homoptera: Aphididae) biotypes characterized using random amplified polymorphic DNA genetic analysis. Biomol Eng 14:105–108

Aliyu H, Ishiyaku MF (2013) Identification of novel resistance gene sources to cowpea aphid (Aphis craccivora Koch) in cowpea (Vigna unguiculata L.) Pak J Agric Sci 16(15):743–746

Alston F, Briggs J (1977) Resistance genes in apple and biotypes of Dysaphis devecta. Ann Appl Biol 87:75–81

Anathakrishnan R, Sinha DK, Murugan M et al (2014) Comparative gut transcriptome analysis reveals differences between virulent and avirulent Russian wheat aphids, Diuraphis noxia. Arthropod Pl Interac 8:79–88

Ansari A (1984) Biology of Aphis craccivora (Koch) and varietal resistance of cowpeas. Dissertation, The University of Reading, Reading

Anstead JA, Burd JD, Shufran KA (2003) Over summering and biotypic diversity of Schizaphis graminum (Homoptera: Aphididae) populations on non-cultivated grass hosts. Environ Entomol 32:662–667

Auclair J (1978) Biotypes of the pea aphid, Acyrthosiphon pisum, in relation to host plants and chemically defined diets. Entomol Exp Appl 24:212–216

Basky Z (2003) Biotypic and pest status differences between Hungarian and South African populations of Russian wheat aphid, Diuraphis noxia (Kurdjumov) (Homoptera: Aphididae). Pest Manag Sci 59:1152–1158

Baumann P (2005) Biology of bacteriocyte-associated endosymbionts of plant sap-sucking insects. Annu Rev Microbiol 59:155–189. doi:10.1146/annurev.micro.59.030804.121041

Behura SK, Sahu SC, Rajamani S et al (1999) Differentiation of the Asian rice gall midge, Orseolia oryzae (Wood-Mason) biotypes, by sequence characterized amplified regions (SCARs). Insect Mol Biol 8:391–398

Bhogadhi SC, Bentur JS, Durga Rani CV et al (2015) Screening of rice genotypes for resistance to brown plant hopper biotype 4 and detection of BPH resistance genes. Int J Life Sci Biotechnol Pharm Res 4(2):90–95

Birch ANE, Fenton B, Malloch G et al (1994) Ribosomal spacer length variability in the large raspberry aphid, Amphorophora idaei. Insect Mol Biol 3:239–245

Birch A, Geoghegan I, Majerus M et al (1996) Interactions between plant resistance genes, pest aphid populations and beneficial aphid predators. Scott Crop Res Inst Annu Rep:1–4

Birch A, Jones A, Fenton B et al (2002) Resistance-breaking raspberry aphid biotypes: constraints to sustainable control through plant breeding. Acta Hort 585:315–317

Birkle LM, Douglas AE (1999) Low genetic diversity among pea aphid (Acyrthosiphon pisum) biotypes of different plant affiliation. Heredity 82(6):605–612

Black WC, Duteau NM, Puterka GJ et al (1992) Use of random amplified polymorphic DNA-polymerase chain reaction (RAPD-PCR) to detect DNA polymorphisms in aphids (Homoptera: Aphididae). Bull Entomol Res 82:151–159

Blackman RL, Eastop VF (eds) (2000) Aphids on the world's crops: an identification and information guide, 2nd edn. Wiley, New York

Blackman RL, Eastop VF (2007) Taxonomic issues. In: van Emden HF, Harrington R (eds) Aphids as crop pests. CAB International, Cambridge, MA, pp 1–30

Boller EF, Bush GL (1974) Evidence for genetic variation in populations of the European cherry fruit fly, Rhagoletis cerasi (Diptera: Tephritidae) based on physiological parameters and hybridization experiments. Entomol Exp Appl 17:279–293

Bourtzis K, Miller T (2006) Insect symbiosis, vol 2. CRC Press, Boca Raton

Boykin LM, De Barro P (2014) A practical guide to identifying members of the Bemisia tabaci species complex: and other morphologically identical species. Front Ecol Evol 2:45. doi:10.3389/fevo.2014.00045

Boykin LM, Shatters RG Jr, Rosell RC et al (2007) Global relationships of Bemisia tabaci (Hemiptera: Aleyrodidae) revealed using bayesian analysis of mitochondrial COI DNA sequences. Mol Phylogenet Evol 44:1306–1319

Briggs JB (1959) Three new strains of Amphorophora rubi (Kalt.) on cultivated raspberry in England. Bull Entomol Res 50(1):81–87

Briggs JB (1965) The distribution, abundance and genetic relationships of four strains of the rubus aphid (Amphorophora rubi (Kalt.)) in relation to raspberry breeding. J Hort Sci 40:109–117

Brown JK, Frohlich DR, Rosell RC (1995) Silverleaf whiteflies: biotypes of Bemisia tabaci or a species complex? Annu Rev Entomol 40:511–534

Brunner PC, Chatzivassiliou EK, Katis NI et al (2004) Host-associated genetic differentiation in Thrips tabaci (Insecta: Thysanoptera), as determined from mtDNA sequence data. Heredity 93:364–370

Bush GL (1993) Host race formation and sympatric speciation in Rhagoletis fruit flies (Diptera: Tephritidae). Psyche 99:335–357

Bush GL, Hoy MA (1983) Evolutionary processes in insects. In: Huffaker B, Rabb RL (eds) Ecological entomology. Wiley-Interscience, New York

Calvert L, Villarreal N, Frohlich D (2005) Using molecular techniques to analyse whitefly species and biotypes in Latin America. In: Anderson PK, Morales FJ (eds) Whitefly and whitefly-borne viruses in the tropics: building a knowledge base for global action. Centro Internacional de Agricultura Tropical, CIAT Publication No. 341, pp 351

Cartier JJ, Painter RH (1956) Differential reactions of two biotypes of the corn leaf aphid to resistant and susceptible varieties, hybrids and selections of sorghums. J Econ Entomol 49:498–508

Cartier JJ, Isaak A, Painter RH et al (1965) Biotypes of pea aphid *Acyrthosiphon pisum* (Harris) in relation to alfalfa clones. Can Entomol 97:754–760

Cervera MT, Cabezas JA, Simon B et al (2000) Genetic relationships among biotypes of Bemisia tabaci (Hemiptera: Aleyrodidae) based on AFLP analysis. Bull Entomol Res 90:391–396

Chen YH (2009) Variation in planthopper–rice interactions: possible interactions among three species? In: Heong KL, Hardy B (eds) Planthoppers: new threats to the sustainability of intensive rice production systems in Asia. Los Ban˜os, IRRI, pp 315–326

Chiang HC, Keaster AJ, Reed GL (1968) Differences in ecological responses of three biotypes of Ostrinia nubilalis from the north central United States. Ann Entomol Soc Am 61:140–146

Chiel E, Gottlieb Y, Zchori-Fein E et al (2007) Biotype-dependent secondary symbiont communities in sympatric populations of Bemisia tabaci. Bull Entomol Res 97(4):407–413

Claridge MF, Den Hollander J (1983) The biotype concept and its application to insect pests of agriculture. Crop Prot 2(1):85–95

Claridge MF, Hollander JD, Haslam D (1984) The significance of morphometric and fecundity differences between the “biotypes” of the brown planthopper, Nilaparvata lugens. Entomol Exp Appl 36:107–114

Converse RH, Daubeny HA, Stace-Smith R et al (1971) Search for biological races in Amphorophora agathonica Hottes on red raspberries. Can J Pl Sci 51:81–85

Coulibaly CO (1993) Biotype variation in Tribolium castaneum (Herbst) from Mali. Dissertation, University of Leicester

Curvetto RO, Webster JA (1998) Resistance mechanisms of PI 240675 Rey to biotype F greenbug. Southwest Entomol 23:97–103

De Barro PJ (2005) Genetic structure of the whitefly Bemisia tabaci in the Asia-Pacific region revealed using microsatellite markers. Mol Ecol 14:3695–3718

De Barro PJ, Driver F (1997) Use of RAPD–PCR to distinguish the B biotype from other biotypes of Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae). Aust J Entomol 36:149–152

De Barro PJ, Sherratt TN, Brooks CP et al (1995) Spatial and temporal genetic variation in British field populations of the grain aphid Sitobion avenae (F.) (Hemiptera: Aphididae) studied by RAPD-PCR. Proc R Soc B 262:321–327

De Barro PJ, Driver F, Trueman JWH et al (2000) Phylogenetic relationships of world populations of Bemisia tabaci (Gennadius) using ribosomal ITS1. Mol Phylogenet Evol 16:29–36

De Barro PJ, Trueman JWH, Frohlich DR (2005) Bemisia argentifolii is a race of B. tabaci (Hemiptera: Aleyrodidae): the molecular genetic differentiation of B. tabaci populations around the world. Bull Entomol Res 95:193–203

De Barro PJ, Liu SS, Boykin LM et al (2011) Bemisia tabaci: a statement of species status. Annu Rev Entomol 56:1–19

De Kogel WJ, van der Hoek M, Mollema C (1997) Variation in performance of western flower thrips populations on susceptible and partially resistant cucumber. Entomol Exp Appl 83:73–80

Diehl SR, Bush GL (1984) An evolutionary and applied perspective of insect biotypes. Annu Rev Entomol 29:471–504

Dinsdale A, Cook L, Riginos C et al (2010) Refined global analysis of Bemisia tabaci (Hemiptera: Sternorrhyncha: Aleyrodoidea: Aleyrodidae) mitochondrial cytochrome oxidase 1 to identify species level genetic boundaries. Ann Entomol Soc Am 103:196–208

Dossett M, Kempler C (2012) Biotypic diversity and resistance to the raspberry aphid Amphorophora agathonica in Pacific Northwestern North America. J Am Soc Hort Sci 137(6):445–451

Douglas AE (1998) Nutritional interaction in insect-microbial symbiosis: aphids and their symbiotic bacteria Buchnera. Annu Rev Entomol 43:17–37

Downie DA (2010) Baubles, bangles, and biotypes: a critical review of the use and abuse of the biotype concept. J Insect Sci 10:176. doi:10.1673/031.010.14136

Dreyer DL, Campbell BC (1984) Association of the degree of methylation of intercellular pectin with plant resistance to aphids and with induction of aphid biotypes. Experientia 40:224–226

Drosopoulos S (1976) Triploid pseudogamous biotype of the leafhopper Muellerianella fairmairei. Nature 263:499–500

Drosopoulos S (1977) Biosystematic studies on the Muellerianella complex (Delphacidae, Homoptera Auchenorrhyncha). Meded Landbouwhogesch Wageningen 77:1–133

Dunn JA, Kempton DPH (1972) Resistance to attack by Brevicoryne brassicae among plant of Brussels sprouts. Ann Appl Biol 72:1–11

Eastop VF (1973) Biotypes of aphids. In: Lowe AD (ed) Perspectives in aphid biology. The Entomological Society of New Zealand Inc, Auckland, pp 40–51

El Bouhssini M, Hatchett JH, Cox TS et al (2001) Genotypic interaction between resistance genes in wheat and virulence genes in the Hessian fly Mayetiola destructor (Diptera: Cecidomyiidae). Bull Entomol Res 91(5):327–331

Fekrat L, Manzari S, Shishehbor P (2014) Morphometric and molecular variation in Thrips tabaci Lindeman (Thysanoptera: Thripidae) populations on onion and tobacco in Iran. J Agr Sci Tech 16:1505–1516

Fettene M, Temu EA (2003) Species-specific primer for identification of Anopheles quadriannulatus sp. B (Diptera: Culicidae) from Ethiopia using a multiplex polymerase chain reaction assay. J Med Entomol 40(1):112–115

Flor HH (1971) The current status of the gene-for-gene concept. Annu Rev Phytopathol 9:275–296

Foster GN, Barker J (1978) A new biotype of red spider mite (Tetranychus urticae (Koch)) causing atypical damage to tomatoes. Plant Pathol 27(1):47–48

Frazer BD (1972) Population dynamics and recognition of biotypes in the pea aphid (Homoptera: Aphididae). Can Entomol 104:1729–1733

Frohlich DR, Torres-Jerez I, Bedford ID et al (1999) A phylogeographical analysis of the Bemisia tabaci species complex based on mitochondrial DNA markers. Mol Ecol 8:1683–1691

Gallun RL (1978) Genetics of biotypes B and C of the Hessian fly. Ann Entomol Soc Am 71:481–486

Gallun RL, Khush GS (1980) Genetic factors affecting expression and stability of resistance. In: Maxwell FG, Jennings PR (eds) Breeding plants resistant to insects. Wiley, New York, pp 64–85

Gallun RL, Reitz LP (1971) Wheat cultivars resistant to races of Hessian fly. US Dep Agric Prod Res Rep 704–705

Gawel NJ, Bartlett AC (1993) Characterization of differences between whiteflies using RAPD-PCR. Insect Mol Biol 2:33–38

Gharib B (1978) On two new distinct biological races of Lepidosaphes ulmi L. (Homoptera, Coccoidea, Diaspidinae). Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences, D 286(18):1313–1314. (in French)

Goggin FL, Williamson VM, Ullman DE (2001) Variability in the response of Macrosiphum euphorbiae and Myzus persicae (Hemiptera: Aphididae) to the tomato resistance gene Mi. Environ Entomol 30:101–106

Gordon S, Woodford J, Williamson B et al (1999) Progress towards integrated crop management (ICM) for European raspberry production. Scott Crop Res Inst Annu Rep, pp 153–156

Gottlieb Y, Ghanim M, Chiel E et al (2006) Identification and localization of a Rickettsia sp. in Bemisia tabaci (Homoptera: Aleyrodidae). Appl Environ Microbiol 72:3646–3652

Gottlieb Y, Ghanim M, Gueguen G et al (2008) Inherited intracellular ecosystem: symbiotic bacteria share bacteriocytes in whiteflies. FASEB J 22:2591–2599. doi:10.1096/fj.07-101162

Granett J, Timper P, Lider LA (1985) Grape phylloxera (Daktulosphaira vitifoliae) (Homoptera: Phylloxeridae) biotypes in California. J Econ Entomol 78:1463–1467

Granett J, Walker MA, Kocsis L et al (2001) Biology and management of grape phylloxera. Annu Rev Entomol 46:387–412

Gregory DD, Jiggins HM, Jiggins FM (2000) Male-killing bacteria in insects: mechanisms, incidence, and implications. Emerg Infect Dis 6:329–336

Gupta GS, Miles P (1975) Studies on the susceptibility of varieties of apple to the feeding of two strains of woolly aphid (Homoptera) and relation to the chemical content of the tissues of the host. Crop Past Sci 26:157–168

Hales DF, Tomiuk J, Wohrmann K et al (1997) Evolutionary and genetic aspects of aphid biology: a review. Eur J Entomol 94:1–55

Haley SD, Peairs FB, Walker CB et al (2004) Occurrence of a new Russian wheat aphid biotype in Colorado. Crop Sci 44:1589–1592

Harrington C (1943) The occurrence of physiological races of the pea aphid. J Econ Entomol 36:118–119

Harvey TL, Hackerott HL (1969) Recognition of a greenbug biotype injurious to sorghum. J Econ Entomol 62:776–779

Harvey TL, Martin TJ, Seifers DL et al (1995) Adaptation of wheat curl mite (Acari: Eriophyidae) to resistant wheat in Kansas. J Agric Entomol 12:119–125

Harvey TL, Martin TJ, Seifers DL et al (1997) Changes in virulence of wheat curl mite on TAM 107 wheat. Crop Sci 37:624–625

Harvey TL, Seifers DL, Martin TJ et al (1999) Survival of wheat curl mites on different sources of resistance in wheat. Crop Sci 39:1887–1889

Harvey TL, Seifers DL, Martin TJ (2001) Host range differences between two strains of wheat curl mites (Acari: Eriophyidae). J Agric Urban Entomol 18:35–41

Heinrichs EA (1986) Perspectives and directions for the continued development of insect-resistant rice varieties. Agric Ecosys Environ 18:9–36

Heinrichs EA (2001) Development of multiple pest resistance crop cultivars. J Agric Ent 11:325–353

Heinrichs EA, Pathak PK (1981) Resistance to the gall midge, Orseolia oryzae (Wood-Mason) in rice. Insect Sci Appl 1:123–132

Heinrichs EA, Rapusas HR (1985) Cross-virulence of Nephotettix virescencs (Homoptera: Cicadellidae) biotypes among some rice cultivars with the same major-resistance gene. Environ Entomol 14:696–700

Hellqvist S (2001) Biotypes of Dasineura tetensi, differing in ability to gall and develop on black currant genotypes. Entomol Exp Appl 98:85–94

Hill CB, Crull L, Herman TK et al (2010) A new soybean aphid (Hemiptera: Aphididae) biotype identified. J Econ Entomol 103(2):509–515

Holloway GJ (1984) Genetic differentiation and life history variation in the rice weevil, Sitophilus oryzae. Dissertation, University of Reading

Holloway GJ (1985) An analysis of inherited factors affecting the sex ratio in the rice weevil, Sitophilus oryzae. Heredity 55:145–150

Holloway GJ, Smith RH (1985) Inheritance of the ability of Sitophilus oryzae (L.) (Coleoptera: Curculionidae) to feed and breed on yellow split-pea (Pisum sativum). Bull Ent Res 75:367–375

Horgan F (2009) Mechanisms of resistance: a major gap in understanding plantohopper–rice interactions. In: Heong KL, Hardy B (eds) Planthoppers: new threats to the sustainability of intensive rice production systems in Asia. Los Ban˜os, IRRI, pp 281–302

Horowitz AR, Kontsedalov S, Khasdan V et al (2005) Biotypes B and Q of Bemisia tabaci and their relevance to neonicotinoid and pyriproxyfen resistance. Arch Insect Biochem Physiol 58:216–225

Hoy MA, Jeyaprakash A, Morakote R et al (2000) Genomic analyses of two populations of Ageniaspis citricola (Hymenoptera: Encyrtidae) suggest that a cryptic species may exist. Biol Control 17:1–10

Hsieh CH, Wang CH, Ko CC (2006) Analysis of Bemisia tabaci (Hemiptera: Aleyrodidae) species complex and distribution in Eastern Asia based on mitochondrial DNA markers. Ann Entomol Soc Am 99:768–775

Hsieh CH, Wang HY, Chen YF et al (2012) Loop-mediated isothermal amplification for rapid identification of biotypes B and Q of the globally invasive pest, Bemisia tabaci, and studying population dynamics. Pest Manag Sci 68:1206–1213

Huang N, He G, Shu L et al (2001) Identification and mapping of two brown planthopper genes in rice. Theor Appl Genet 102:929–934

Hufbauer RA, Bogdanowicz SM, Harrison RG (2004) The population genetics of a biological control introduction: mitochondrial DNA and microsatellite variation in native and introduced populations of Aphidius ervi, a parasitoid wasp. Mol Ecol 13:337–348

Jacobson A, Booth W, Vargo EL et al (2013) Thrips tabaci population genetic structure and polyploidy in relation to competency as a vector of Tomato spotted wilt virus. PLoS One 8(1):e54484. doi:10.1371/journal.pone.0054484

Jankielsohn A (2011) Distribution and diversity of Russian wheat aphid (Hemiptera: Aphididae) biotypes in south Africa and Lesotho. J Econ Entomol 104:1736–1741

Jena KK, Kim SM (2010) Current status of brown planthopper (BPH) resistance and genetics. Rice 3:161–171. doi:10.1007/s12284-010-9050-y

Jennings DL (1988) Raspberries and blackberries: their breeding, diseases and growth. Academic, London

Jones MG (1967) Observations on two races of the groundnut aphid, Aphis craccivora. Entomol Exp Appl 10:31–38

Jones A, McGavin W, Birch A (2000) Effectiveness of resistance genes to the large raspberry aphid, Amphorophora idaei B¨orner, in different raspberry (Rubusidaeus L.) genotypes and under different environmental conditions. Ann Appl Biol 136:107–113

Katiyar SK, Tan Y, Nagaliyadde L et al (2000) Biodiversity of Asian rice gall midge (Orseolia oryzae Wood Mason) from five countries examined by AFLP analysis. Genome 43:322–332

Keep E, Knight RL (1967) A new gene from Rubus occidentalis L. for resistance to strains 1, 2, and 3 of the Rubus aphid, Amphorophora rubi Kalt. Euphytica 16:209–214

Keep E, Knight RL, Parker JH (1970) Further data on resistance to the Rubus aphid Amphorophora rubi (Kltb.) Rep East Malling Res Station for 1969:129–131

Kethidi DR, Roden DB, Ladd TR et al (2003) Development of SCAR markers for the DNA-based detection of the Asian long-horned beetle, Anoplophora glabripennis (Motschulsky). Arch Insect Biochem Physiol 52:193–204

Khush GS (1979) Genetics of and breeding for resistance to the brown planthopper: threat to rice production in Asia. Los Baños, IRRI, pp 321–332

Kim KC, Chiang HC, Brown JRBW (1967) Morphometric differences among four biotypes of Ostrinia nubilalis (Lepidoptera: Pyralidae). Ann Entomol Soc Am 60(4):796–801

Kim KS, Hill CB, Hartman GL et al (2008) Discovery of soybean aphid biotypes. Crop Sci 48(3):923–928

Kindler SD, Hays DB (1999) Susceptibility of cool-season grasses to greenbug biotypes. J Agric Urban Entomol 16:235–243

Kindler SD, Spomer SM (1986) Biotypic status of six greenbug (Homoptera: Aphididae) isolates. Environ Entomol 15:567–572

Kindler SD, Harvey TL, Wilde GE et al (2001) Occurrence of greenbug biotype K in the field. J Agric Urban Entomol 18:23–34

Kiriac I, Gruber F, Poprawski T et al (1990) Occurrence of sexual morphs of Russian wheat aphid, Diuraphis noxia, in several locations in the Soviet Union and the Northwestern United States. Proc Entomol Soc Wash 92:544–547

Knight RL, Briggs JB, Keep E (1960) Genetics of resistance to Amphorophora rubi (Kalt.) in the raspberry. II. The gene A_2-A_7 from the American variety, Chief. Genet Res 1:319–331

Kobayashi K, Hasegawa E (2012) Discrimination of reproductive forms of Thrips tabaci (Thysanoptera: Thripidae) by PCR with sequence specific primers. J Econ Entomol 105:555–559. doi:10.1603/ec11320

Kusi F, Obeng-Ofori D, Asante SK et al (2010) New sources of resistance in cowpea to the cowpea aphid (Aphis craccivora Koch) (Homoptera: Aphididae). J Ghana Sci Assoc 12(2):95–104

Lammerink J (1968) A new biotype of cabbage aphid (Brevicoryne brassicae (L.)) on aphid resistant rape (Brassica napus L.) NZ J Agric Res 11:341–344

Lapitan NLV, Li YC, Peng JH et al (2007) Fractionated extracts of Russian wheat aphid eliciting defense responses in wheat. J Econ Entomol 100(3):990–999

Laroche A, Declerck-Floate RA, Lesage L et al (1996) Are Altica carduorum and Altica cirsicola (Coleoptera: Chrysomelidae) different species? Implications for the release of cirsicola for the biocontrol of Canada thistle in Canada. Biol Control 6:306–314

Latif MA, Omar MY, Tan SG et al (2009) Interpopulation crosses, inheritance study, and genetic variability in the brown planthopper complex, Nilaparvata lugens (Homoptera: Delphacidae). Biochem Genet. doi:10.1007/s10528-009-9316-5

Lei H, Tjallingii WF, Lenteren JC (1998) Probing and feeding characteristics of the greenhouse whitefly in association with host-plant acceptance and whitefly strains. Entomol Exp Appl 88:73–80. doi:10.1023/A: 1003215227403

Lopes-da-Silva M, Tonet GEL, Vieira LGE (2004) Characterization and genetic relationships among Brazilian biotypes of Schizaphis graminum (Rondani) (Hemiptera: Aphididae), using RAPD markers. Neotrop Entomol 33:43–49

Lowe HJB (1981) Resistance and susceptibility to colour forms of the aphid Sitobion avenae in spring and winter wheats (Triticum aestivum). Ann Appl Biol 99:87–98

Malik R, Smith CM, Brown-Guedira GL et al (2003) Assessment of A. tauschii for resistance to biotypes of wheat curl mite (Acari: Eriophyidae). J Econ Entomol 96:1329–1333

Martinez-Peniche R (1999) Effet de differentes populations du phylloxera (Daktulosphaira vitifoliae Fitch) du sud de la France, sur l'expression de la resistance des port-greffes de vigne 41B et Aramon Rupestris Ganzin No.9. Vitis 38:167–178

Merrill SC, Randolph TL, Peairs FB et al (2014) Examining the competitive advantage of Diuraphis noxia (Hemiptera: Aphididae) biotype 1 over biotype 2. J Econ Entomol 107(4):1471–1475

Michel AP, Mittapalli O, Mian MR et al (2011) Evolution of soybean aphid biotypes: understanding and managing virulence to host plant resistance. In: Sudaric A (ed) Soybean – molecular aspects of breeding, InTech, Rijeka, pp 355–372

Miller GL, Favret C, Carmichael A et al (2009) Is there a cryptic species within Aulacorthum solani (Hemiptera: Aphididae)? J Econ Entomol 102:398–400

Milne WM (1998a) Comparative performance of two biotypes of Therioaphid trifolii (Monell) (Hemiptera: Aphididae) on clovers (Trifolium) and medics (Medicago). Aust J Entomol 37:350–355

Milne WM (1998b) Suitability of clovers (Trifolium species and cultivars) as hosts of spotted clover aphid, a biotype of Therioaphis trifolii (Monell) (Hemiptera: Aphididae). Aust J Exp Agric 38:241–245

Mitchell-Olds T, Bergelson J (2000) Biotic interactions: genomics and coevolution. Curr Opin Pl Biol 3:273–277

Mohan M, Nair S, Bentur JS et al (1994) RFLP and RAPD mapping of the rice Gm2 gene that confers resistance to biotype 1 of gall midge (Orseolia oryzae). Theor Appl Genet 87:782–788

Moran NA (1992) The evolution of aphid life cycles. Annu Rev Entomol 37:321–348

Moran NA, Wernegreen JJ (2000) Lifestyle evolution in symbiotic bacteria: insights from genomics. Trends Ecol Evol 15(8):321–326

Moya A, Guirao P, Cifuentes D et al (2001) Genetic diversity of Iberian populations of Bemisia tabaci (Hemiptera: Aleyrodidae) based on random amplified polymorphic DNA-polymerase chain reaction. Mol Ecol 10:891–897

Mutti NS, Louis J, Pappan LK et al (2008) A protein from the salivary glands of the pea aphid, Acyrthosiphon pisum, is essential in feeding on a host plant. Proc Natl Acad Sci USA 105:9965–9969

Naber N, El Boushssini M, Labhilili M et al (2000) Genetic variation among populations of Hessian fly, Mayetiola destructor (Diptera: Cecidomyiidae) in Morocco and Syria. Bull Entomol Res 90:245–252

Nagamine K, Hase T, Notomi T (2002) Accelerated reaction by loop-mediated isothermal amplification using loop primers 1. Mol Cell Probes 16:223–229

Najar-Rodriguez AJ, McGraw EA, Mensah RK et al (2008) The microbial flora of Aphis gossypii: patterns across host plants and geographical space. J Invertebr Pathol 100:123–126

Nault BA, Shelton AM, Gangloff-Kaufmann JL et al (2006) Reproductive modes in onion thrips (Thysanoptera: Thripidae) populations from New York onion fields. Environ Entomol 35:1264–1271. doi: 10.1603/0046-225x(2006)35[1264: rmiott]2.0.co;2

Navia D, de Mendonca RS, Skoracka A et al (2013) Wheat curl mite, Aceria tosichella, and transmitted viruses: an expanding pest complex affecting cereal crops. Exp Appl Acarol 59:95–143

Nielson M, Lehman W (1980) Breeding approaches in alfalfa. In: Maxwell FG, Jennings PR (eds) Breeding plants resistant to insects. John Wiley & Sons, Inc., New York, pp 277–311

Nielson MW, Harold D, Schonhorst MH et al (1970) Biotypes of the spotted alfalfa aphid in western United Sates. J Econ Entomol 63:1822–1825

Nombela G, Williamson VM, Muniz M (2003) The root-knot nematode resistance gene MI-1.2 of tomato is responsible for resistance against the whitefly Bemisia tabaci. Mol Pl Microbe Interact 16:645–649

Notomi T, Okayama H, Masubuchi H et al (2000) Loop-mediated isothermal amplification of DNA. Nuc Acids Res 28:e63

Oliver KM, Russell JA, Moran NA et al (2003) Facultative bacterial symbionts in aphids confer resistance to parasitic wasps. Proc Natl Acad Sci USA 100:1803–1807

Oliver KM, Degnan PH, Burke GR et al (2010) Facultative symbionts in aphids and the horizontal transfer of ecologically important traits. Annu Rev Entomol 55:247–266

Omer AD, Granett J, Kocsis L et al (1999) Preference and performance responses of California grape phylloxera to different Vitis rootstocks. J Appl Entomol 123(6):341–346

Painter RH (1941) The economic value and biologic significance of insect resistance in plants. J Econ Entomol 34:358–367

Painter RH (1951) Insect resistance in crop plants. Macmillan, New York

Painter RH, Pathak MD (1962) The distinguishing features and significance of the four biotypes of corn leaf aphid Rhopalosiphum maidis (Fitch). Proc XI Int Cong Entomol 2:110–115

Panda N, Khush GS (1995) Host plant resistance to insects. CAB International, Wallingford

Pathak MD (1970) Genetics of plants in pest management. In: Rabb RL, Guthrie FE (eds) Concepts of pest management. North Carolina State University, Raleigh, pp 61–81

Peccoud J, Mahéo F, de la Huerta M et al (2015) Genetic characterisation of new host-specialised biotypes and novel associations with bacterial symbionts in the pea aphid complex. Insect Conserv Divers 8(5):484–492

Pedigo L (1999) Entomology and pest management. Prentice Hall, Upper Saddle River

Phillips PA, Barnes MM (1975) Host race formation among sympatric apple, walnut, and plum populations of the codling moth, Laspeyresia pomonella. Ann Entomol Soc Am 68:1053–1060

Pinheiro P, Bereman MS, Burd J et al (2014) Evidence of the biochemical basis of host virulence in the greenbug aphid, Schizaphis graminum (Homoptera: Aphididae). J Proteome Res 13:2094–2108

Porter KB, Peterson GL, Vise O (1982) A new greenbug biotype. Crop Sci 22:847–850

Porter DR, Burd JD, Shufran KA et al (1997) Greenbug (Homoptera: Aphididae) biotypes: selected by resistant cultivars or preadapted opportunists? J Econ Entomol 90:1055–1065

Porter DR, Burd JD, Shufram KA (2000) Efficacy of pyramiding greenbug (Homoptera: Aphididae) resistance genes in wheat. J Econ Entomol 93:1315–1318. doi:10.1603/0022-0493-93.4.1315

Powers TO, Jensen SG, Kindler SD et al (1989) Mitochondrial DNA divergence among greenbug (Homoptera: Aphididae) biotypes. Ann Entomol Soc Am 82:298–302

Printz YI (1937) Contribution to the question of the changes in the virulence of Phylloxera of different biotypes. Plant Prot Lening 12:137–142

Prokopy RJ, Diehl SR, Cooley SS (1988) Behavioral evidence for host races in Rhagoletis pomonella flies. Oecologia 76:138–147

Puterka GJ, Burton RL (1990) Aphid genetics in relation to host plant resistance. In: Peters DC, Webster JA, Chlouber CS (eds) Proceedings aphid-plant interactions: populations to molecules. Okla Agric Exp Stn, MP 132:59–69

Puterka GJ, Peters DC, Kerns DL et al (1988) Designation of two new greenbug (Homoptera: Aphididae) biotypes G and H. J Econ Entomol 81:1754–1759

Puterka GJ, Burd JD, Burton RL (1992) Biotypic variation in a worldwide collection of Russian wheat aphid (Homoptera: Aphididae). J Econ Entomol 85:1497–1506

Raffa KF (1989) Genetic engineering of trees to enhance resistance to insects: evaluating the risks of biotype evolution and secondary pest outbreak. BioSci 39(8):524–534

Raijmann LEL (1992) Genetical population structure of small ermine mothYponomeuta padell. Proc Exp Appl Entomol 3:94–98

Rajyashri KR, Nair S, Ohmido N et al (1998) Isolation and FISH mapping of Yeast Artificial Chromosomes (YACs) encompassing an allele of the Gm2 gene for gall midge resistance in rice. Theor Appl Genet 97:507–514

Ratcliffe RH, Hatchett JH (1997) Biology and genetics of the Hessian fly and resistance in wheat. In: Bobdari K (ed) New developments in entomology. Research Signpost, Scientific Information Guild, Trivandrum

Ratcliffe RH, Safranski GG, Patterson FL et al (1994) Biotype status of Hessian Fly (Diptera: Cecidomyiidae) populations from the eastern United States and their response to 14 Hessian Fly resistance genes. J Econ Entomol 87:1113–1121

Rat-Morris E, Crowther S, Guessoum M (1999) Resistance-breaking biotypes of rosy apple aphid, Dysaphis plantaginea, on the resistant cultivar 'Florina. IOBC/wprs Bull 22(10):71–75

Ruggle P, Gutierrez AP (1995) Use of life-tables to assess host-plant resistance in alfalfa to Therioaphis trifolii f. maculata (Homoptera: Aphididae) – a hypothesis for the maintenance of resistance. Environ Entomol 24(2):313–325

Sato A, Sogawa K (1981) Biotypic variations in the green rice leafhopper, Nephotettix virescencs Uhler (Homoptera: Deltocephalidae). Appl Ent Zool 16:55–57

Saxena RC, Barrion AA (1983) Biotypes of the brown planthopper, Nilaparvata lugens (Stal). Korean J Pl Prot 22:52–66

Saxena RC, Barrion AA (1985) Biotypes of the brown planthopper Nilaparvata lugens (Stal) and strategies in deployment of host plant resistance. Insect Sci Applic 6:271–289

Saxena RC, Barrion AA (1987) Biotypes of insect pests of agricultural crops. Insect Sci Appl 8:453–458

Saxena RC, Rueda LM (1982) Morphological variation among three biotypes of the brown planthopper, Nilaparvata lugens, in the Philippines. Insect Sci Applic 3:193–210

Sen Gupta GC (1969) The recognition of biotypes of the woolly aphid, Erisoma lanigerum (Hausmann), in South Australia by their differential ability to colonise varieties of apple rootstock, and an investigation of some possible factors in the susceptibility of varieties to these insects. Dissertation, University of Adelaide

Shade RE, Kitch LW, Mentzer P et al (1996) Selection of a cowpea weevil (Coleoptera: Bruchidae) biotype virulent to cowpea weevil resistant Landrace TVu 2027. J Econ Entomol 89:1325–1331

Sharma HC (2009) Biotechnological approaches for pest management and ecological sustainability. CRC Press Taylor & Francis, Boca Raton

Shufran KA, Whalon ME (1995) Genetic analysis of brown planthopper biotypes using random amplified polymorphic DNA polymerase chain reaction (RAPD-PCR). Insect Sci Appl 16:27–33

Shufran KA, Wilde G (1994) Clonal diversity in overwintering populations of Schizaphis graminum (Homoptera: Aphididae). Bull Entomol Res 84:105–114

Shufran KA, Margolies DC, Black WC IV (1992) Variation between biotype E clone of Schizaphis graminum (Homoptera: Aphididae). Bull Entomol Res 82:407–416

Shufran KA, Burd JD, Webster JA (1997) Biotypic status of Russian wheat aphid (Homoptera: Aphididae) populations in the United States. J Econ Entomol 90:1684–1689

Shufran KA, Burd JD, Anstead JA et al (2000) Mitochondrial DNA sequence divergence among greenbug (Homoptera: Aphididae) biotypes: evidence for host-adapted races. Insect Mol Biol 9(2):179–184

Simon JC, Carré S, Boutin M et al (2003a) Host-based divergence in populations of the pea aphid: insights from nuclear markers and the prevalence of facultative symbionts. Proc Royal Soc London, B 270:1703–1712

Singh SR, Painter RH (1964) Effect of temperature and host plants on progeny production of four biotypes of corn leaf aphid, Rhopalosiphum maidis. J Econ Entomol 57:348–350

Smith HS (1941) Racial segregation in insect populations and its significance in applied entomology. J Econ Entomol 34:1–13

Smith CM (2005) Plant resistance to arthropods: molecular and conventional approaches. Springer, Dordrecht

Smith CM, Chuang WP (2014) Plant resistance to aphid feeding: behavioral, physiological, genetic and molecular cues regulate aphid host selection and feeding. Pest Manag Sci 70(4):528–540

Smith C, Havlickova H, Starkey S et al (2004) Identification of Aegilops germplasm with multiple aphid resistance. Euphytica 135:265–273

Song GC, Granett J (1990) Grape phylloxera (Homoptera: Phylloxeridae) biotypes in France. J Econ Entomol 83:489–493

Srinivasan R, Alvarez JM (2011) Specialized host utilization of Macrosiphum euphorbiae on a nonnative weed host, Solanum sarrachoides, and competition with Myzus persicae. Environ Entomol 40(2):350–356

Starks KJ, Burton RL (1972) Greenbugs: determining biotypes, culturing and screening for plant resistance. USDA-ARS Tech Bull No 1556, p 12

Starks KJ, Burton RL (1977) Greenbugs: determining biotypes, culturing, and screening for plant resistance with notes on rearing parasitoids. USDA Tech Bull 1556 US Government Print Office, Washington, DC

Stouthamer R, Breeuwer JA, Hurst GD (1999) Wolbachia pipientis: microbial manipulator of arthropod reproduction. Annu Rev Entomol 53:71–102

Sunnucks P, De Barro PJ, Lushai G et al (1997a) Genetic structure of an aphid studied using microsatellites: cyclic parthenogenesis, differentiated lineages and host specialization. Mol Ecol 6:1059–1073

Sunnucks P, Driver F, Brown WV et al (1997b) Biological and genetic characterization of morphologically similar Therioaphis trifolii (Monell) (Hemiptera: Aphididae) with different host utilization. Bull Entomol Res 87:425–436

Takita T, Hashim H (1985) Relationship between laboratory-developed biotypes of green leafhopper and resistant varieties of rice in Malaysia. Japan Agric Res Quart 19:219–223

Tang M, LV L, Shengli J et al (2010) Bacterial symbionts of the brown planthopper, Nilaparvata lugens (Homoptera: Delphacidae). Appl Environ Microbiol 76(6):1740–1745. doi:10.1128/AEM.02240-09

Teetes GL, Schaefer CA, Gipson JR et al (1975) Greenbug resistance to organophosphorous insecticides on the Texas High Plains. J Econ Entomol 68:214–216

Thorpe WH (1930) Biological races in insects and allied groups. Biol Rev 5:177–212

Thorpe WH (1940) Ecology and the future of systematics. In: Huxley JS (ed) The new systematics. Oxford University Press, New York, pp 341–364

Toda S, Murai T (2007) Phylogenetic analysis based on mitochondrial COI gene sequences in Thrips tabaci Lindeman (Thysanoptera: Thripidae) in relation to reproductive forms and geographic distribution. Appl Entomol Zoo 42:309–316

Tolmay VL, Prinsloo GJ, Lindeque RC (2007) Preliminary evidence of a resistance-breaking biotype of the Russian wheat aphid, Diuraphis noxia (Kurdjumov) (Homoptera: Aphididae), in South Africa. Afr Entomol 15:228–230

Tomar JB, Prasad SC (1992) Genetic analysis of resistance to gall midge (Orseolia oryzae Wood Mason) in rice. Plant Breed 109:158–167

van der Arend AJM (2003) The possibility of Nasonovia ribisnigri resistance breaking biotype development due to plant host resistance: a literature study. In: van Hintum TJL, Lebeda A, Pink D et al (eds) Eucarpia Leafy Vegetables 2003, Proceedings Eucarpia Meeting- Leafy Vegetables Genetics and Breeding, Noordwijkerhout

van der Arend AJM, Ester A, van Schijndel J (1999) Developing an aphid resistant butterhead lettuce 'Dynamite'. Eucarpia Leafy Vegetables '99, Proceedings Eucarpia Meeting- Leafy Vegetables Genetics and Breeding, Olomouc, pp 149–157

van Emden HF (1991) The role of host plant resistance in insect pest mismanagement. Bull Entomol Res 81:123–126

van Emden H (2007) Host-plant resistance. In: van Emden H, Harrington R (eds) Aphids as crop pests. CAB International, Wallingford/Oxfordshire, pp 447–468

van Emden HF, Eastop VF, Hughes RD et al (1969) The ecology of Mysus persicae. Annu Rev Ent 14:197–270

Vanlerberghe-Masutti F, Chavigny P (1998) Host-basic genetic differentiation in the aphid, Aphis gossypii Glover, evidenced from RAPD fingerprints. Mol Ecol 7:905–914

Verma SK, Pathak PK, Sing BN et al (1979) Indian biotypes of the brown planthopper. IRRN 4(6):7

Vijaya Lakshmi P, Amudhan S, Himabindu K et al (2006) A new biotype of the Asian rice gall midge Orseolia oryzae (Diptera: Cecidomyiidae) characterized from the Warangal population in Andhra Pradesh, India. Int J Trop Insect Sci 26:207–211

Wang CH, Ko CC, Liu CC et al (2004a) Development of rapid identification of Bemisia argentifolli (Hemiptera: Aleyrodidae) by PCR. Formos Entomol 24:229–246. (in Chinese)

Wang Y, Zhang P, Chen J et al (2004b) Host-preference biotypes of the cotton aphid, Aphis gossypii Glover and the behavioral mechanism in their formation[J]. Acta Entomol Sin 47(6):760–767

Wang L, Zhang S, Luo JY et al (2016) Identification of Aphis gossypii Glover (Hemiptera: Aphididae) biotypes from different host plants in North China. PLoS One 11(1):e0146345. doi:10.1371/journal.pone.0146345

Westmore GC, Poke FS, Allen GR et al (2013) Genetic and host-associated differentiation within Thrips tabaci Lindeman (Thysanoptera: Thripidae) and its links to tomato spotted wilt virus-vector competence. Heredity 111(3):210–215. doi:10.1038/hdy.2013.39

Wilde G, Feese H (1973) A new corn leaf aphid biotype and its effect on some cereal and small grains. J Econ Entomol 66:570–571

Wilhoit LR (1992) Evaluation of virulence in plant resistance: influence of variety mixtures. In: Fritz RS, Simms EL (eds) Plant resistance to herbivores and pathogens: ecology, evolution, and genetics. University of Chicago Press, Chicago, pp 91–119

Wille BD, Hartman GL (2009) Two species of symbiotic bacteria present in the soybean aphid (Hemiptera: Aphididae). Environ Entomol 38(1):110–115

Williams RN, Shambaugh GF (1988) Grape phylloxera biotypes confirmed by electrophoresis and host susceptibility. Ann Entomol Soc Am 81:1–5

Wood EA (1961) Biological studies of a new greenbug biotype. J Econ Entomol 54:1171–1173

Wool D, Gerling D, Bellotti AC et al (1993) Esterase electrophoretic variation in Bemisia tabaci (Genn.) (Hom., Aleyrodidae) among host plants and localities in Israel. J Appl Entomol 15:185–196

Xiang Dong L, Xiao XZ, Bao XP (2004) Host biotypes and their formation causes in aphids. Acta Entomol Sin:2004–2004

Xu TT, Ma TT, Liu XD (2014) How does the host-specialized aphid deal with food deficiency? Insect Sci 21:334–341

Young E, Rock G, Zeiger D et al (1982) Infestation of some Malus cultivars by the North Carolina woolly apple aphid biotype. HortScience 17:787–788

Zarrabi A, Berberet R, Caddel J (1995) New biotype of Acyrthosiphon kondoi (Homoptera: Aphididae) on alfalfa in Oklahoma. J Econ Entomol 88:146–1465

Zawirska I (1976) Untersuchungen uber zwei biologische Typen von Thrips tabaci Lind. (Thysanoptera, Thripidae) in der VR Polen. Arch Phytopath Pl Prot 12:411–422. doi:10.1080/03235407609431780

Zsuzsa B, Hopper KR, Jordaan J et al (2001) Biotypic differences in Russian wheat aphid (Diuraphis noxia) between south African and Hungarian agro-ecosystems. Agric Ecosyst Environ 83:121–128

Watson MA, Okusanya BAM (1967) Studies on the transmission of groundnut rosette virus by Aphis craccivora Koch. Ann Appl Biol 60:199–208