

Insects that feed on resistant crop varieties

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**Abstract:** This monograph summarizes the revision and book on the development of insect xenotypes in response to the extensive crops of resistant plant varieties and their importance for plant breeding published by the author (see in list of references).

**Keywords:** Insect biotypes, pest xenotypes, population variants, subpopulations,

Introduction

1. Terms used to refer to pest subpopulation variants

**PESTS** possess inherited variability, which is vital in crop breeding for resistance as forms evolve that damage previously resistant varieties. The terms used to describe pest variants are varied. Some of them are physiologic race, strain, biotype, pathotype, and variant. The latter is a very useful general term for describing different forms of a parasite. Physiologic race has been widely used, particularly for fungal pathogens with race-specific (vertical) types of resistance (Russell 1978). Pathotype reflects nematode specificity on a narrow range of host plants (Robinson 1969, Kort et al. 1977, Jones et al. 1981, Yeates 1987), and several nematode pathotypes may co-exist within a population.

Strain is a most common term for variants of plant pathogenic viruses (Matthews 1949, 1981, Hutton & Peak 1952, Russell 1978). For example, Hoffmann-Wolf et al. (1990) studied the symptoms and synergistic reactions between PVX and PVY in two tobacco, *Nicotiana tabacum* L., cultivars. The B, O, and P strains of PVX produced the same type of mosaic symptom, and occasionally tiny necrotic rings, but the difference was obvious between two PVY strains, a mild mosaic for PVY-1, whereas vein necrosis for PVY-N. Information on strains of potato, *Solanum tuberosum* L., viruses appears in Matthews (1949, 1981), and Hutton & Peak (1952). Villavaso et al. (1993) used 'strain' for a radiation-resistant subpopulation of the boll weevil (*Anthonomus grandis grandis* Boheman), and Webb et al. (1993) compared strains of a gypsy moth [*Lymantria dispar* (L.)] nuclear polyhedrosis virus.

There are either five or 36 'races' of the soybean cyst nematode, *Heterodera glycines* Ichinohe, in the US. Because of the current confusion in terminology, Dropkin (1988) recommended that nematologists drop the use of 'biotype', 'race', and 'strain', and instead use 'pathotype' to denote a subpopulation delimited by its performance in a differential plant host test.

Other terms which have been used to account for genetic and environmentally induced phenotypic variations are race (geographic, host, biological, physiological, etc.), ecotype, form, morph, variety, subspecies, semispecies, etc. (Claridge & Den Hollander 1983). Race implies some geographical or spatial separation from other variants (Gonzalez et al. 1979).

Some degree of continuous variation within populations will always be found. If this variation is under genetic control, it will be susceptible to evolutionary change, particularly by environmentally induced selection pressure. Besides continuous variation, genetically discontinuous variation determining forms or morphs within a population can also occur. Polymorphism includes morphological, physiological, ecological, behavioral, and other forms. Electrophoresis is used to recognize electromorphs (Claridge & Den Hollander 1983).

Morphs is a term used for individuals and not for populations, although populations may be characterized by patterns of polymorphisms (Claridge & Den Hollander 1983), are common for aphids species (e.g., Hille Ris Lambers 1966, Dixon & Glen 1971, Tatchell et al. 1988, McPherson 1989, Mittler & Wilhoit 1990, Tatchell & Parker 1990).

An example of a pest species with different forms during its life cycle is that of the pear psylla, *Cacopsylla pyricola* Foerster, a highly specialized pest that has two distinct morphs, a large and dark overwintering form, and a smaller,

light summerform (Horton & Krysan 1990). Winterforms would be dispersive (Fye 1983) and can feed on non-host plants (Kaloostian 1970), whereas summerforms may disperse considerably less and are thus less likely to encounter, and hence feed and lay eggs on nonpear species (Wilde 1963, 1966, Ullman & McLean 1988a, 1988b, Horton & Krysan 1990). Insecticide resistance of pear psylla has extended to all pyrethroid insecticides (Pree *et al.* 1990).

Besides conventional morphological systematics, enzyme electrophoresis can identify populations of related species. Unruth *et al.* (1989) used this method to evaluate the genetic relationships among 17 populations of *Aphidius* species that were collected from the pea aphid, *Acyrtosiphon pisum* (Harris), throughout the Holarctic region. Their results supported traditional systematics and allowed them to identify six distinct *Aphidius* spp., including a new species. Unruth *et al.* (1989) concluded that *A. ervi* represents a complex including highly differentiated allopatric populations as well as cryptic species.

Wellso *et al.* (1988) analyzed six biotypes and two geographic populations of the Hessian fly, *Mayetiola destructor* Say, at 15 presumptive genetic loci using starch gel electrophoresis. Fourteen of the 15 loci appeared monomorphic. One locus, Pgi, varied in biotypes B, E, and a population from Mason, Michigan. The levels of genetic variation among Hessian fly subpopulations were considered among the lowest reported for insects, ranging from a Nei's D of 0.000 to 0.002.

## 2. Meanings of the term biotype

Breeding for resistance is a potent tool for crop protection, and has proven the ability of pests to adapt to resistant plant hosts (Ortman & Peters 1980). Without genetic variability in the pest, breeding for resistance could potentially be easy, since a single form of resistance in any plant would last indefinitely. However, this is not the case. In as much as the genetic information in the pest changes because of mutations and recombination, biotypes evolve with new capacities to affect the hosts (Welsh 1981).

Benjamin Walsh (1864) would have been the first to seriously consider the status of insects that morphologically resemble one another so closely that they can only be distinguished on the basis of subtle biological traits such as preference for or the ability to survive on different hosts. The term biotype, however, has been used frequently with different meanings (Russell 1978). For example, color pattern analysis of *Aphidius ervi* (Hål.), hymenopterous parasitoids reared in Czechoslovakia from three host species, the pea aphid, *A. pisum*, the English grain aphid, *Sitobion avenae* (F.), and *Microlophium carnosum* (Buckton), caused Stary (1983a, 1983b) to suggest the existence of two biotypes for the parasitoid, one associated with the pea aphid and the English grain aphid, the other with *M. carnosum*. Furthermore, Nemeč & Stary (1983) and Stary *et al.* (1985) used the term biotype for variants of *A. ervi* on *A. pisum* and *S. avenae* maintained on different host plants. In Australia, field infestations of the pea aphid on alfalfa contain a sub-dominant variant resistant to some fungal pathogens of the genus *Erynia*. Two different variants called 'biotypes' by Hughes & Bryce (1984), coexist in field infestations. Also, Müller (1984) reported a red 'biotype' of the pea aphid in Germany. Reporting on the behavioral differences of subpopulations of the pea aphid when interacting with parasitoids and predators, McAllister *et al.* (1990) have referred to them as the coastal and interior 'biotypes', according to their collecting sites.

Ignoffo & Garcia (1985) referred to Ecuatorian and Mississippian strains of *Nomuraea rileyi* (Farlow) Samson, a fungus affecting lepidopterans, as 'geographical biotypes' varying in host spectrum and virulence. Geographical (allopatric) variants of the braconid parasitoid *Microctonus aethiopooides* Loan reared from alfalfa weevils, *Hypera postica* (Gyllenhal) from Europe and Morocco differ morphologically and morphometrically, and were called 'biotypes' by Adler & Kim (1985). When studying the behavior of *Rhagoletis pomonella* (Walsh), Prokopy and Papaj (1988) added still another meaning, when referring to apple fruit cultivars as 'biotypes'. Similarly, Pennacchio & Tremblay (1986) referred to two populations of *Aphidius ervi* parasitizing *A. pisum* or *Microlophium carnosum* as different biotypes, even though they concluded that these 'biotypes' are distinct species, based on morphological observations supported by discriminant analysis and by differences in the disposition of the meconial pellets inside the mummies after the emergence of the adult parasitoids. The 'biotype' parasitizing *M. carnosum* was named *Aphidius microlophii* sp. n.

Reduced susceptibility to phosphine fumigants, used widely to disinfest stored grains, is especially problematic (Taylor 1989), McFarlane *et al.* (1993) reported on 'biotype' differences affecting the pest status of stored-grain insects, although in their study they named such population variants as strains. Fischer & Ramírez (1993) even compared rice lines as different 'biotypes'.

Day & Hedlund (1988) reported on arrhenotokous and thelytokous<sup>1</sup> biotypes of *Mesochorus nigriceps* Ratz., a parasite of *Bathyplectes* spp., parasites of the alfalfa weevil *Hypera postica* (Gyllenhal).

Allopatric variants, 'biotypes' for Meyerdirk & Coudriet (1986), have been reported for *Euseius scutalis* (Athias-Henriot), a phytoseiid mite predator on the whitefly *Bemisia tabaci* (Gennadius). A Jordanian variant had higher fecundity, longer oviposition period, and life span when fed *B. tabaci* stages than a Moroccan variant. Use of the Jordanian mite for biological control appears promising against *B. tabaci* in California. Other 'biotypes' have been referred to as by Androsov & Lavrinenko (1985) for strains of the entomopathogenic bacterium *Bacillus thuringiensis* Berliner differing in lecithinase and hemolytic activity.

Differences in host use occur in two variants of the ichneumonid parasitoid *Bathyplectes curculionis* (Thomson), both of which were introduced in northern and southern California from Utah for biological control of alfalfa weevils, *Hypera* spp., and are now allopatric (Salt & van den Bosch 1967). These variants differ in susceptibility to encapsulation by host weevils. Virus-like particles in the ovaries of this species (Stolz & Vinson 1977) may suppress the host's immune response (Edson *et al.* 1981). Without further study it cannot be determined whether this geographic variation is due to a genetic change in the insect, its symbiotic virus, or both. In most cases, the evolutionary status of geographically isolated variants differing in host utilization or other traits cannot be determined with certainty (Diehl & Bush 1984).

The increased virulence of the b- or poinsettia strain of *B. tabaci* led researchers to establish the appearance of *B. argentifolii* Bellows & Perring, although the acceptance of the new species was debated by entomologists during a time period, with many arguing at first for the development of the biotype, until the evidence for the new species was sufficient for its establishment. For example, Costa *et al.* (1994) reported on high populations of *B. tabaci* biotype B in Hawaii, but added that currently the species was proposed by Bellows *et al.* (1994) to be the new species *B. argentifolii*<sup>2</sup>.

Attempts have been made to standardize the meaning and use of the term biotype (Claridge & Den Hollander 1983), but there is a lot of confusion (*e.g.* Berlocher 1979, Gonzalez *et al.* 1979, Mackenzie 1980, Maxwell & Jennings 1980, Claridge & Den Hollander 1983). This is inevitable until more is known on the nature of resistance to parasites and on the genetics of host-parasite interactions (Russell 1978).

Biotypes are defined as populations of insects capable of damaging and of surviving on plants heretofore known to be resistant to other populations of the same insect species (Kogan 1975). The identification of biotypes has strengthened the evolutionary concept of pest resistance. According to Scriber *et al.* (1985), allelochemicals are important factors in determining insect damage and geographical distribution of biotypes. For Diehl & Bush (1984), biotypes are entomophagous parasites or parasitoids distinguished by survival and development on a particular host or by host preference for feeding, oviposition, or both. They use 'insect biotypes' to refer to variants differing in diurnal or seasonal activity patterns, size, shape, color, insecticide resistance, migration and dispersal tendencies, pheromone differences, or disease vector capacities (see also Russell 1978, Dyer *et al.* 1982). A biotype may be classified into one or more of the following five categories (Diehl & Bush 1984): (a) nongenetic polyphenisms, (b) polymorphic or polygenic variation within populations, and (e) species. However, after proposing this classification, Diehl & Bush (1984) concluded that further use of the ambiguous and all-encompassing term 'biotype' should be discontinued or use provisionally for cases where biological differences have been observed between organisms, but where the genetic basis and evolutionary status of the differences have yet to be ascertained.

### 3. Xenotypes, a new term proposed for biotypes causing a diverse response on differential varieties

To end this confusion in the use of the term biotype, I herein propose a new name to refer just to those population variants (or biotypes) that cause a diverse response on differential varieties. Similarly to the suggestion of the term antixenosis to replace nonpreference as a type of insect-plant resistance by Kogan & Ortman (1978), I have proposed the term XENOTYPE to refer specifically to aggressive pest population variants capable of surviving and reproducing on varieties formerly known to be resistant. Using the same approach, those population variants with varying degrees of resistance to insecticides could be referred to as chemiotypes. Throughout this work, however,

<sup>1</sup> Thelytoky is the production of females from unfertilized eggs.

<sup>2</sup> More on this debate is presented by Araya (2019) in his book on xenotypes Chapter 2, Section 2.7 (The case history of the sweet potato and silverleaf whiteflies).

and to avoid further confusion, I will use both terms, xenotype, or biotype as used in the literature, but this last with a practical meaning restricted to differential susceptibility-resistant responses on a series of plant hosts.

#### 4. Some factors that contribute to the formation of insect xenotypes

Many insects reproduce by parthenogenesis. Such forms may show relatively little genetic variation between cycles, forming clones of genetically similar individuals. From time to time mutants may arise, resulting in new forms that may differ in attributes such as hosts or other habitat requirements. These new forms may be expected to reproduce clones with the new mutant characteristics which may flourish, and either replace the original forms or coexist with them (Claridge & Den Hollander 1983). Some of the xenotypes of aphid species represent such clones (Eastop 1973). Indeed, in some species, as in the pea aphid, *A. pisum*, perhaps new xenotypes may arise annually by adaptation of parthenogenetic clones to different species of host plants (Frazer 1972).

*Acyrtosiphon pisum* has a green colored body. However, Gyrisco & Smith (1979), Smith & Gyrisco (1980), and Kluger & Ratcliffe (1983) have reported a reddish form on alfalfa in Maryland. Of 19 alfalfa lines or cultivars tested by Kluger & Ratcliffe (1983) which had been classified as resistant to the green form, only two lines (BAA-15 and PA-1) and one cultivar ('CUF-101') were highly resistant to the red form.

Growing genetically uniform crops over large geographical areas is artificial and has a tremendous potential to cause large-scale destruction by an adapting pest (Ortman & Peters 1980). When large areas of a highly resistant crop are sown, natural selection of the pest occurs, so that any potential genetic change that could result in virulence (the ability to infest) has a high selective advantage. The result is an increase in the population of pest organisms that can damage the host crop. Because of this potential for variability and natural selection, pest resistance breeding programs are a continuous operation with levels of resistance or tolerance being only temporary (Welsh 1981).

Biotypes are natural products of a survival mechanism for insect species. They are often selected from a population by a cultivar developed for resistance and grown in areas where exposure to the insect is common. Biotypes are extremely important for developing insect resistant cultivars, in studies of the genetics of inheritance of virulence in insects and inheritance of resistance in plants, and for developing concepts of insect plant relationship and mechanisms of insect resistance (Nielsen & Lehman 1980).

Not all individuals within a biotype population are equally aggressive. More aggressive individuals might take less time to adulthood, lay more eggs, or have a greater proportion of hatching eggs. Differences in aggressiveness of plant pathogenic fungi are correspondingly viewed as increased infection efficiency, increased sporulation, or shortened time for each step in the progression of disease development. Two isolates of race 15B-3 of the rust *Puccinia graminis* Pers f. sp. *tritici* Eriks & E Henn may differ in the rate at which they cause disease. The overall effect is to increase the aggressiveness of that individual. Such differences in aggressiveness are attributes of a biotype (MacKenzie 1980). The appearance of biotype variants depends on the selection pressure applied to the insect population by the plant, the genetics of the host plant, and the genetics of the insect (Gallun 1972).

The development of insect biotypes capable of surviving on resistant cultivars limits their full potential in insect control. New biotypes may develop from a few individuals in natural populations that can survive on new resistant plants. If farmers intensively grow resistant hosts, such insects are selected and more likely to survive and breed than other insects. In time, the general population can shift to a new biotype. Biotypes may also arise through mutation (Pathak & Saxena 1980).

For nematodes, a species represents phenotypes of samples from a gene pool that has multiple alleles in most loci. Frequencies of particular alleles fluctuate through time and vary from one portion of the geographical distribution to the next. Some genes are adaptive and other are neutral. Mutation and genetic drift maintain diversity in the species, and gene flow operates at different rates among partly isolated nematode subpopulations. In nature, both hosts and parasites undergo co-evolution; plant breeders direct the evolution of plant hosts by incorporating genetic resistance from various sources into crops. Nematode pests soon respond to selection pressure and demonstrate their diversity (Dropkin 1988).

The environment is very important for the growth of a population. Under some environmental conditions some pest populations cease to increase. Such conditions are easily identified for the late blight disease of potato caused by *Phytophthora infestans* (Mont.) de Bary. Under a specific set of environmental conditions some individuals in a pest population will grow more than others. Greater relative reproductive success means a greater fitness. Groups of



isolates with different sensitivity to environmental factors have been termed 'environmental biotypes' (MacKenzie 1980, Diehl & Bush 1984). For example, the shapes of the frequency distributions for embryos and pupae of the western spruce budworm, *Choristoneura occidentalis* Freeman, are not unimodal, suggesting the presence of 'thermal biotypes' (Reichenbach & Stairs 1984). The solitary and gregarious 'phases' of several locust species whose extremely detrimental outbreaks have plagued agriculture since their earliest descriptions in The Old Testament are another case (Diehl & Bush 1984). The phases differ in color, morphology, and behavior. These differences are continuous, inducible, and partially reversible in the lifetime of a single individual, primarily by crowding but also by temperature and humidity (Uvarov 1966, Krebs 1978). Another case is the seasonal variation in ovipositor length, associated with the growing size of the galls caused by *Torymus* cynipids (Askew 1965).

The association of the sweetpotato whitefly *B. tabaci* with varied habitats may be related to the selection for dispersal polymorphism (Byrne & Houck 1990), yielding individuals that engage only in trivial flight (restricted to the local habitat) and those for which flight is mainly migratory (Southwood 1962). The phenomenon of partitioning the two functions of "host-remaining" and "host-finding" between two morphs is widely known among insects (Denno 1976, Denno & Grissell 1979, Harrison 1980). Certain insects in a population migrate to keep pace with changes in habitat quality, but migrants commonly postpone reproduction (Johnson 1969) or are less fecund (Denno & Grissell 1979), and die if they fail to find new hosts (Roff 1986). Discriminant function analysis of wing forms of *B. tabaci* by Byrne & Houck (1990) indicated subtle morphological differences within the same sex between the wings of migrators and those of individuals engaging only in trivial flight. Migratory forms recognized by morphological differences has been confirmed in other hemipterans (e.g., Dingle 1978, Harrison 1980, Kawada 1987). The whitefly *Aleyrodes proletella* (L.) presents behavioral differences in seasonal morphs; winter (diapausing) females are much more willing to fly than summer (non-diapausing morphs) (Iheagwam 1977).

The term biotype, as used in entomological literature, has the same meaning as the term race applied to pathogenic fungi. Both refer to supopulations that are normally distinguished by parasitic ability and other criteria. That is, a population of a species may belong to one biotype and another to a second one if there is a difference in the ability of the populations to parasitize a host (Gallun & Khush 1980).

Many nematodes show great diversity within species. For example, there are clear host 'races' of the stem nematode *Ditylenchus dipsaci* (Kuhn) Filipjev, e.g., oat race, tulip race, etc. (Dropkin 1988). Seinhorst (1957) reported 11 biological races on nine plant host species; Hesling (1966) listed 21 stem nematode 'races' or 'strains'. These strains are polyphagous, as indicated by tests on many plant species from different botanical families. Some hosts are susceptible to more than one strain (Eriksson 1974, Ladygina & Barabashova 1976, Southey 1978). Therefore, crop rotations must be based on the host range of the particular race of *D. dipsaci* in a field (Dropkin 1988).

Populations of the potato cyst nematode, *Globodera rostochiensis*, are mixtures of pathotypes (Kort *et al.* 1977). These pathotypes are classified on their ability to reproduce on differential clones that separate variants that differ in the frequency of phenotypes compatible with the phenotypes of some or all of the clones (Dropkin 1988).

Pathotypes of the cereal cyst nematode, *Heterodera avenae* Wollenweber, are identified by reproduction on cereals (O'Brien & Fisher 1979, Dropkin 1988). More differentials reveal more pathotypes (Mathur *et al.* 1974). A British pathotype is also morphologically distinct from two others (Cook 1976). Certain French pathotypes are distinct by their reproduction on barley cultivars, and by their physiology. According to Dropkin (1988), they represent ecotypes – populations adapted to ecological situations.

The soybean cyst nematode *Heterodera glycines* has a wide host range, mainly Leguminosae (Riggs & Hamblen 1962, 1966a, 1966b). A study of populations of *H. glycines* in the major US soybean producing areas and of several populations from Japan confirmed their great variability (Riggs *et al.* 1981). Differential hosts to identify 'races' of this nematode include the standard susceptible 'Lee' soybean used for comparisons with four resistant differentials. Reproduction is considered to fail when the number of cysts produced in one generation is  $\leq 10\%$  of the number on 'Lee'. Four 'races', and subsequently a fifth were found. An expanded set of differentials consists of 13 soybean hosts and five other host plants. Using this expanded set, Riggs *et al.* (1981) separated 36 'physiological strains' of the nematode.

In this monograph, the use of the term biotype, and specifically xenotype, is restricted to those subpopulations of insects of the same species which differ in virulence towards a similar set of host plant cultivars with a differential

range in their susceptibility-resistance response. This meaning is intended to facilitate a common understanding for plant breeders, biologists, entomologists, geneticists, and other specialists working on insect-plant relationships.

### 5. Brief history of the recognition of insect biotypes

Biotypes were noted by Reginald Painter in the 1930s when he observed that Hessian fly from western Kansas did not damage certain soft wheats, whereas the flies from eastern Kansas flourished on the same wheats (Painter 1930). Painter (1931) reported two Hessian fly 'races' (biotypes) in Kansas, which differed in their ability to infest wheat varieties. Cartwright & Noble (1947) found different races of the Hessian fly in California and Indiana. Later, Crow (1957) prepared a revision of the literature on insect strains that originated because of their resistance to chemical insecticides (called chemiotypes earlier in this section). Eastop (1973) reviewed the biotype concept with reference to aphids, and associated it with parthenogenetical clones. Pathak (1975) listed seven insect pest species with biotypes identified, five of them aphids with at least a parthenogenetic phase of reproduction. The other two species were the Hessian fly, and the rice brown planthopper *Nilaparvata lugens* (Stål).

Since the initial reports of Hessian fly races, more biotypes have been identified (Gallun *et al.* 1961, Hatchett 1969, Woottipreecha 1971, Gallun 1977, Sosa 1977), resulting in 16 theoretical biotypes based on the plant-insect interaction (Gallun 1977, Ortman & Peters 1980). Using biotypes of Hessian fly, Hatchett & Gallun (1970) extended the gene-for-gene concept for the first time to an insect-host system (Hessian fly-wheat) from that initially identified by Flor (1955, 1956) in flax, *Linum usitatissimum* L., and flax rust, *Melampsora lini* Desm., and later developed by van der Plank (1963). The essence of this hypothesis is that a single gene in the pathogen matches a corresponding gene in the host.

### 6. Geographic subpopulations or allopatric biotypes

Allopatric subpopulations (geographically or spatially isolated variants), as opposed to sympatric (local variants within a population), should be distinguished (Claridge & Den Hollander 1983, Diehl & Bush 1984). Sympatric biotypes with genetic variation within a population occur in the chestnut gall wasp, *Dryocosmus kuriphilus* (Yasumatsu) (Shimura 1972). Introduced from China to Japan, caused initially severe damage but later was handled by resistant varieties. The lifetime of this resistance was short, however, and new resistance-breaking biotypes soon developed. Another example may be the sessile black pineleaf scale, *Nuculaspis californica* (Coleman), which may be genetically adapted to variation in susceptibility-resistance among individual Ponderosa pines (Edmunds & Alstad 1978). Populations of these scales appear to have adapted to overcome the spectrum of defenses exhibited by their host tree.

Discrepancies in feeding preferences between allopatric variants of the European moth *Parapoinx stratiolata* L., studied as a biological control agent of the Eurasian water milfoil, *Myriophyllum spicatum* L. in the US, led Habeck (1983) to suggest the probable presence of (allopatric) 'biotypes' of *P. stratiolata*.

Allopatric biotypes adapt to local conditions, so that the existence of isolated races with distinct patterns of host plant preference and virulence would occur. Claridge & Den Hollander (1983) suggested that some forms that have been described as distinct biotypes, such as in the European corn borer, *Ostrinia nubilalis* (Hubner) in North America (Sparks *et al.* 1966, Kim *et al.* 1967, Chiang *et al.* 1968, 1970), the rice gall midge, *Orseolia oryzae* (Wood-Mason) in India, Indonesia and Thailand (Heinrichs & Pathak 1981), and the rice green leafhopper, *Nephotettix cincticeps* (Ühler) in areas of Japan (Sato & Sogawa 1981), are such allopatric races [or allopatric biotypes, as originally indicated for *O. nubilalis* by Beck & Apple (1961)]. The status of geographically isolated variants (semispecies or subspecies) is difficult to establish because the differences may or may not be sufficient to ensure reproductive isolation if the variants become sympatric (Diehl & Bush 1984).

### 7. Some examples of variation within species

In spite of the great variation within species, aphid researchers have mostly worked for years on single clones, and assumed their patterns to represent the species or biotype as well as of the individual clones (MacKay 1989). For example, Eisenbach & Mittler (1987) characterized the photoperiod responses of two biotypes of the greenbug, *Schizaphis graminum* (Rondani), in tests with one clone of each biotype. For at least some aphids, it is increasingly clear that it is misleading to assume that a field population of aphids can be accurately represented by the characteristics exhibited by a single clone from that population (e.g., Lamb & MacKay 1983, Subasinghe 1983, Weber 1985a). This is particularly illustrated with the photoperiodic responses of the green peach aphid, *M. persicae*,

where qualitative (Blackman 1971, 1974, Takada 1982, 1986) as well as quantitative differences (Takada 1982) in response to a single short photoperiod have been documented. MacKay (1989) compared the photoperiod responses of two clones of the pea aphid, *A. pisum*, collected on the same day in the same field in Glenlea, Manitoba, Canada. The clones differed not only in the photoperiods at which sexuals first appear, but also in the rate of transition from production of one morph to another. When these clones were compared with other pea aphid clones for which data on production of sexuals were available in the literature, further differences in pattern of production of sexuals became apparent. These comparisons further emphasize the need to observe a sample of clones when attempting to describe any aspects of the species characteristics of aphids.

The European corn borer has affected corn (*Zea mays* L.) since it was introduced to North America from Europe during the early XX century. Once established, populations in North America were found to differ in voltinism, diapause, and degree of polyphagy (Chiang *et al.* 1968, Showers 1981). Sparks *et al.* (1966) reported differences in adults emerged and diapausing larvae, and proportion of surviving forms that entered diapause. Kim *et al.* (1967) found that populations from Minnesota, Iowa, Missouri, and Ohio differed in the size of certain structures. The extent of these differences was related by Kim *et al.* (1967) to the distance between the origins of the populations. They concluded that *O. nubilalis* had differentiated and evolved morphometrically as well as ecologically. Chiang *et al.* (1968) showed that corn borer populations from Minnesota, Iowa, and Missouri varied in percentages survival, larvae entering diapause, number of tunnels per borer, rate of development, and survival to host-resistance factors. The Minnesota population was clearly different from the Missouri one, with the Iowa population intermediate. It seemed that the allopatric variant (called a biotype in the original article) which was adapted to warmer conditions stood better temperature changes than the variant adapted to cooler conditions. Also, the variant adapted to short days in Missouri was more sensitive to photoperiod changes than the variant adapted to long days in Minnesota. Morphometric variability was correlated with biotype grouping, but rearing geographically isolated variants under identical conditions revealed that much of this variability is environmentally induced (Chiang 1978). The feasibility of managing the corn borer by release of population variants with diapause genes that are maladaptive to the climate of the release area has been discussed by Showers (1981).

The European corn borer occurs in three genetically distinct pheromonal types that use different proportions of geometrical pheromone isomers (Klun & Maini 1979), and afford the possibility of carrying out intraspecific studies. Schwarz *et al.* (1989, 1990) studied the male sexual behavior-stimulating and inhibiting properties of a series of analogs of the corn borer sex pheromone in a flight tunnel. The response to analogs by two pheromone types of the borer, homozygous for Z- or E-female sex pheromone production genes (Klun & Huettel 1988), indicates that the pheromone receptor and catabolic systems are biochemically very different in the two types. The Z-type utilizes 97:3 (Z/E)-11-tetradecen-1-ol acetate as its pheromone, the E-type uses 3:97 Z/E. (see also Glover *et al.* 1990).

Patterns of geographical variation in host use have been reported for the North American native Colorado potato beetle, *Leptinotarsa decemlineata* (Say), that feeds on about ten solanaceous plant species and on the introduced potato crop. This beetle exhibits little variation in host use ability among 12 geographic variants, although it does differ latitudinally in its diapause (Hsiao 1982). Beetles from Arizona, however, are unique and feed on a local wild *Solanum* sp., and also has the best development when tested on seven other hosts (Futuyma 1983).

Southern pine beetles, *Dendroctonus frontalis* Zimmermann, collected at different geographic regions both within the contiguous range and from isolated populations in Arizona and Mexico are genetically different (Anderson *et al.* 1979, Namkoong *et al.* 1979). Vité *et al.* (1974) found substantial quantitative and qualitative differences in chemicals extracted from excised hind guts from southern pine beetles collected in Texas, Mexico, Honduras, and Guatemala. Anderson *et al.* (1983) found similar genetic differences among populations of the black turpentine beetle, *Dendroctonus terebrans* (Olivier), and the sixspined ips, *Ips calligraphus* (Germar), from the same areas. In laboratory bioassays by Berisford *et al.* (1990), *D. frontalis* exhibited regional differences in response to pheromones.; beetles from Georgia, Texas, and Virginia had significantly higher positive responses to pheromones from their own region.

Many authors have suggested that genetic subdivision within a population in a heterogeneous environment is more likely if individuals tend, through prior experience, to breed in the same habitat in which they developed. This was implied by Papaj & Prokopy (1988) for the apple maggot fly, an important pest of apple in North America (Schotzko 1982, AliNiasee & Westcott 1986, Anon. 1986).

With time, geographic isolation of populations of the same species will also cause differences in their genetic makeup. This can be implied from the study by Claridge *et al.* (1988) with *Nilaparvata lugens*, and McPheron *et al.*

(1988) with *R. pomonella*, a pest thought to have undergone sympatric divergence in host use (Prokopy & Papaj 1988). Claridge *et al.* (1988) reported two morphologically similar populations of *N. lugens* in Australia differing in characters of pulse repetition frequencies of acoustic courtship signals. These two host-derived subpopulations from rice, *Oryza sativa* L., and *Leersia hexandra* Schwartz mated freely in the laboratory, although they had very significant preferences for homogametic matings in mate choice experiments. No indication of field hybridization was found, so Claridge *et al.* (1988) concluded that the two morphologically inseparable populations represented sympatric biological species in Australia.

In an electrophoretic comparison of flies from Utah cherries with *R. pomonella* flies from Illinois hawthorns, *Crataegus mollis* (T. & G. Scheele), a native host within the native range of the fly, the Utah population (the fly had only recently been found in Utah infesting sour cherries) presented a marked reduction of genetic variability compared with the Illinois population (McPherson *et al.* 1988).

Oviposition and larval survival of *R. pomonella* varied significantly on fruit from 25 crab apple, *Malus* spp., and clones evaluated by Reissig *et al.* (1990) in the field and laboratory. Flies laid more eggs in lines with larger fruit, although this relationship was more clear in laboratory tests when fruit was infested by laboratory-reared flies than in field fruit infested by wild flies. Fruit of 'Aldenhamensis' (*Malus* x *purpurea*), 'Fuji' (*M. sieboldiia* (Regel) Rehd.), 'Vilmorin' (*M. yunnanensis* (Franch.) Schneid.), *M. zumi calocarpa* Rehd., and *M. hupehensis* (Pamp) Rehd. were not infested in the field, but flies oviposited in fruit of all 25 species and clones in laboratory choice tests. Eggs hatched but larvae did not survive in fruit of 'Henry F. DuPont' (*Malus* x *M. arnoldiana* x *M. purpurea* (Barbier Rehd), 'Frettingham' (PI 307689 from Holland), 'Fuji' (*M. sieboldiia* (Regel) Rehd.), 'Sparkler' (*M. pumila* Mill var. *niedswetskiana* Hopa OP), *M. zumi calocarpa*, and *M. hupehensis*. Larval mortality was very high in fruit from 'Vilmorin', 'Sparkler', 'NA 40298', 'Henrietta Crosby' (*Malus* x *M. arnoldiana* (Rehd.) Sarg. (bac x flor) x *M. pumila* var. *niedswetskiana*), 'Golden Gem' (*M. prunifolia* (Willd) Borkh.), 'Almey' (*M. baccata* (L.) Borkh. x *M. pumila* var. *niedswetskiana*), *M. baccata*, and *M. sikkimensis* (Hook.) Koehne.

Females of the apple maggot fly exposed by Prokopy & Papaj (1988) to apple or hawthorn in a field cage oviposited at a higher rate in test fruits than did inexperienced females. Females exposed to a particular fruit tended to remain longer in test trees harboring fruit of that species than did inexperienced females or females exposed to the other fruit species. Prior fly experience thus may alter two components of host preference in the fly: oviposition preference and habitat fidelity. The effect of experience on habitat preference should increase the likelihood that individuals mate assortatively and, may further increase the likelihood that apple maggot populations become genetically subdivided (Papaj & Prokopy 1988). Further studies indicate that females can also learn to differentiate characteristics of three different apple cultivars ('Early MacIntosh', 'Red Delicious', and 'Golden Delicious'), probably by discriminating among these cultivars on the basis of differences in chemical stimuli among cultivars (Prokopy & Papaj 1988).

The propensity of males to reside on a hawthorn or apple fruit is significantly modifiable through prior experience with the fruit, and hence involves learning. Host fruit learning in both sexes, in concert with genetic-based differences in host fruit residence and acceptance behavior between populations of flies from hawthorn and apple, could give rise to a reduction in gene flow between subpopulations of flies on these two host types (Prokopy *et al.* 1989). The phenotype differences seen in host response pattern between hawthorn and apple origin *R. pomonella* flies may have a genetic basis (Prokopy *et al.* 1988).

## 8. Cases of xenotypes in insect pests

Following an analysis of the speciation mechanisms that may play a role in the formation of xenotypes, and a discussion on the discriminating methods between closely related taxa, it follows an overview of the insect species that have developed xenotypes in response to the deployment of insect-resistant crop lines. The insects that have evolved to such population variants are presented in Table 1. Most species with xenotypes are homopterans, especially aphids, which is logical because of their parthenogenetic reproduction and short cycles. Some homopterans that have developed xenotypes are the alfalfa aphids *Acyrtosiphon pisum* (Harris) and *Therioaphis maculata* Shinji, the raspberry aphid *Ampborophora rubi* (Kaltenbach), the grape phylloxera *Daktulosphaira vitifoliae* (Fitch), the greenbug *S. graminum*, the green leafhopper *Nephotettix virescens* (Distant), and the brown planthopper. The last two species are important rice pests. Two dipterans have developed xenotypes, the Hessian fly on wheat, and the rice gall midge, *Orseolia oryzae* (Wood-Mason). Besides the 'biotypes' reported on other relationships between organisms which have caused confusion over the meaning of this term, some other aphid species have



truly insect xenotypes. The cabbage aphid, *Brevicoryne brassicae* L., the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), the English grain aphid, *Macrosiphum (Sitobion) avenae* (F.), the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), and the woolly apple aphid, *Eriosoma lanigerum* (Hausmann), for example, have developed, according to diverse authors, biotypical (=xenotypical) population variants. The development of xenotypes in these insect species, however, as well as the xenotype status of the alfalfa weevil, *Hypera postica* (Gyllenhal), had not generated enough research data to build separate sections in Araya (2001), and chapters in his further extensive book on insect xenotypes (Araya 2011).

**Table 1. Insect pest species that have developed xenotypes and selected references of literature1.**

Insect species	Xenotypes	Selected references
Blue alfalfa aphid, <i>Acyrtosiphon kondoi</i> Shinji	BAOK90	Zarrabi <i>et al.</i> 1995, 1998
Cabbage aphid, <i>Brevicoryne brassicae</i> (L.)	NZ-1; NZ-2	Lammerink 1968
	Local	Dunn & Kempton 1972
Chestnut gall wasp, <i>Dryocosmus kuriphilus</i> (Yasumatsu)	Chinese, Japanese	Shimura 1972
English grain aphid, <i>Macrosiphum (Sitobion) avenae</i> F.	5 color forms	Lowe 1981
	2 color forms	Araya <i>et al.</i> 1996
Corn leaf aphid, <i>Rhopalosiphum maidis</i> (Fitch)	KS-1 & KS-2	Cartier & Painter 1956
	KS-3 & KS-4	Painter & Pathak 1962
	KS-5	Wilde & Feese 1973
Greenbug, <i>Schizaphis graminum</i> (Rondani)	A & B	Wood 1961
	C	Harvey & Hackerott 1969a, 1969b
	D	Teetes <i>et al.</i> 1975B
	E	Porter <i>et al.</i> 1982, Puterka <i>et al.</i> 1982
	F	Kindler & Spomer 1986
	G & H	Puterka <i>et al.</i> 1988
	I	Harvey <i>et al.</i> 1991
Grape phylloxera, <i>Daktulosphaira vitifoliae</i> (Fitch)	Clinton&Concord (foliar)	Williams & Shambaugh 1988
	A & B (on roots)	Granett <i>et al.</i> 1985, 1987a, 1987b
Hessian fly, <i>Mayetiola destructor</i> (Say)	GP	Painter 1930, 1931
	A to D	Gallun <i>et al.</i> 1961
	E	Hatchett 1969
	F & G	Woottipreecha 1971, Gallun 1972
	L	Sosa 1977, 1978

	O	Kudagamage <i>et al.</i> 1990
Pea aphid, <i>Acyrtosiphon pisum</i> (Harris)	pea biotype	Harrington 1941, 1943, 1945, Migula 1986
	local biotypes	Cartier 1959, 1960, 1963, Cartier <i>et al.</i> 1965, Auclair & Aroga 1984, 1987
	several biotypes	Sohi & Swenson 1964, Thottappilly <i>et al.</i> 1977, Frazer 1972, Hübner-Dahl 1975, Auclair & Srivastava 1977, 1978, Müller 1980
	J, C, Lg, Lp	Auclair & Aroga 1987
Raspberry aphid, <i>Amphorophora rubi</i> (Kaltenbach)	2 allopatric races	Dicker 1940
	Variants 1 to 3	Briggs 1959a, Knight <i>et al.</i> 1960
	Variant 4	Briggs 1965a, 1965b
Rosy-leaf curling aphid, <i>Dysaphis</i> ( <i>Saphaphis</i> ) <i>devecta</i> (Walker)	3	Alston & Briggs 1977
Rice brown planthopper, <i>Nilaparvata lugens</i> (Stål)	1 to 5	Cheng 1975, Khush <i>et al.</i> 1977, Lakshminarayana & Khush 1977, Pathak 1978, Cheng & Chang 1979, Verma <i>et al.</i> 1979
Rice gall midge, <i>Orseolia oryzae</i> (Wood-Mason)	Local biotypes	Shastry <i>et al.</i> 1972, Israel 1974, Hidaka <i>et al.</i> 1977, Heinrichs & Pathak 1981, Shaw <i>et al.</i> 1981, Joshi & Venugopal 1985, Rao & Kittur 1989
Rice green leafhopper 1, <i>Nephotettix cincticeps</i> Uhler	2	Sato & Sogawa 1981
Rice green leafhopper 2, <i>Nephotettix virescens</i> (Distant)	2 allopatric races	Athwaletal. 1971, Karim & Pathak 1982
	Races adapted to resistant cultivars	Heinrichs & Rapusas 1985, Takita & Hashim 1985
Russian wheat aphid, <i>Diuraphis noxia</i> (Mordvilko)	Allopatric biotypes	Burd <i>et al.</i> 1990, Puterka <i>et al.</i> 1990, 1992
Spotted alfalfa aphid, <i>Therioaphis maculata</i> (Buckton)	ENT-B, ENT-A	Tuttle & Butler 1954
	A to H	Nielson <i>et al.</i> 1970a, 1970b, Nielson & Don 1974a, Manglitz <i>et al.</i> 1962, 1966, Nielson & Lehman 1980, MacKay & Lamb 1988
Woolly apple aphid, <i>Eriosoma lanigerum</i> (Hausmann)	Blackwood and Clare	Sen Gupta & Miles 1975

<sup>1</sup>This table updates one by Smith (1989) on insects forming 'biotypes' in response to plant resistance.

Today, control of crop pests through the use of resistant cultivars will be sustained and never ending. Given the low cost for selecting and breeding for resistance, compared with the cost of developing and releasing an insecticide, for example, and the absence of environmental constraints, plant resistance as a method for controlling insect pests will continue to develop in the future. This is particularly certain with the new genetic engineering methods becoming increasingly used in plant breeding (Araya 2011).

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