

INSECT PESTS AND EVOLUTION

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INTRODUCTION

Insect pests have been with us for a long time. As early as 10,000 years ago, farmers in primitive agricultural societies in areas of the Near and Middle East already had to reckon with insect pest problems to increase harvest (Jones, 1973). Tremendous efforts and expenses have been put into containment of insect pests throughout human history, and some significant successes were made in this century (Klassen, 1989). For the last 50 years, although such alternate approaches as biological control have been promoted, control and management strategies for insect pests have relied heavily on chemical pesticides. Despite control efforts directed against many serious insect pests, no single insect pest species has been completely eradicated. Insect pest problems are still here and will remain with us indefinitely. Insect pest problems have become increasingly more complicated and difficult to deal with because of the burdens of immigrant species (Kogan, 1982; Horsfall, 1983; CAST, 1987), pesticide resistance (NRC, 1986), economic factors (Southwood and Norton, 1973), and environmental degradation (NRC, 1986; Green et al., 1990). These may become further aggravated by the global climate changes.

Insect pests are a dynamic group of organisms with a long evolutionary history. They continue to evolve in response to changing environmental conditions, particularly of anthropocentric origin. However, the pest concept is a human construct: the problem of insect pests is defined by a value judgement and cultural criteria (Southwood and Norton, 1973). Insect pests counter new strategies as they are introduced. The fate of DDT was a case in point. DDT, which was discovered in 1939 and hailed as the "ultimate" weapon against insect pests in the 1940s, was banned by the 1960s because of the environmen-

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tal and public health problems that it caused. By then, many insect pests had already developed a resistance to DDT and many other pesticides. Subsequent pest management technologies, such as integrated pest management (IPM), still do not consider evolutionary dynamics of pest species; rather, they rely on contemporary ecology and anthropocentric criteria. Rational solutions to the problem of insect pests must be based on knowledge of genetics and evolutionary strategy as much as on biology and ecology of pest species (Stenseth, 1987).

Insects as Pests

Insects, the most abundant group of organisms, are widely distributed throughout the world. They inhabit diverse habitats and serve many important functional roles in ecosystems. Their small size and high mobility enable long-distance dispersal and invasion of new territories and habitats (Wilson and Graham, 1983; Ehrlich, 1986). Insects are able to resist substantial environmental changes and yet, under certain conditions, are highly adaptable to changing environmental conditions (Parsons, 1983, 1987, 1991; Hoffmann and Parsons, 1991).

Insect pest fauna consists of both endemic and exotic species. Endemic species may become pests when a new crop species or variety is planted in an area (Elton, 1958), whereas immigrant species may become pests after they have successfully colonized the new territory (Wilson and Graham, 1983; Pimentel, 1986). Indigenous insects, either endemic or immigrant species, that have been established for a long time in the territory but not are directly associated with human enterprise or are of minimal economic importance can become major pests following environmental perturbation (Gould, 1991; Hoffman and Parsons, 1991).

The insect pest fauna has become more homogeneous throughout the world by introductions, accidental or intentional. Highly mobile insects persistently move about between the nations through international traffic and commerce (Sailer, 1978, 1983; Kim, 1983), and continue to invade new territories and habitats, particularly those modified by human disturbance (Wilson and Graham, 1983; Margolies, Chapter 6; Pimentel, Chapter 8; Andow et al., Chapter 11; Rauscher, Chapter 13 in this book). For example, the North American insect fauna contains approximately 2,000 immigrant species (Kim and Wheeler, 1991), which constitute about 40% of the North American agricultural insect pests (Pimentel, 1986). Many of these introduced species are the most serious agriculture pests (Sailer, 1983; Lattin and Oman, 1983).

Of the major arthropod pest species, approximately 64% have a worldwide distribution (Pimentel, 1986). For example, most animal pests were introduced with the importation of livestock; cattle lice and hog lice are now distributed throughout the world. Many phytophagous and vector species have a worldwide or transoceanic distribution, such as the European corn borer, *Ostrinia nubilalis*

(Hübner) (Showers, Chapter 14 in this book), and yellow fever mosquito, *Aedes aegypti* (Linnaeus) (Tabachnick, Chapter 21 in this book). They show an extensive geographic variation (Gould and Johnston, 1972; Parsons, 1983; Brussard, 1984; Futuyma and Peterson, 1985).

Insect Pests Evolving

Through a long evolutionary process, insects have developed the ability, dynamic genetic norms of reactions, to adapt to changing environmental conditions (Hedrick et al., 1976; Hoffmann and Parsons, 1991; Parsons, 1991). As described in this book, a wide range of genetic diversity is shown in major insect pests; for example, European corn borer, by Showers et al. (1975) and Shower (Chapter 14 in this book); Colorado potato beetle, *Leptinotarsa decemlineata* (Say), by Hsiao (1985); alfalfa weevil, *Hypera postica* (Gyllenhal) by Hsiao (Chapter 15 in this book); Mexican bean beetle, *Epilachna varivestis* Mulsant, by Saks (Chapter 16 in this book); yellow fever mosquito, *Aedes aegypti* (Linnaeus) by Tabachnick (Chapter 21 in this book); Greenbug, *Schizaphis graminum* (Rondani), by Beregovoy and Starks (1986) and Inayatullah et al. (1987); and pear psylla, *Cacopsylla pyricola* Forester, by Unruh (1990).

Insect pests are evolving rapidly with much higher genetic variability under stressed environmental conditions (Parsons, 1983, 1987, 1988; Croft and Dunley, Chapter 7 in this book; Krysan, Chapter 18 in this book), created by anthropogenic factors such as pesticide application, habitat degradation, and environmental pollutions.

In this chapter, the theme of the book, patterns of genetic variation and evolution of insect pests, is defined, and the biological nature of insect pests is discussed as background for the synthesis of succeeding chapters.

THE NATURE OF INSECT PESTS

The Concept of Pest

The *Random House Dictionary* defines *pest* as a destructive or troublesome organism; any species of insects is a potential pest. Insects become pests when they compete with humans for the common resources or their activity interferes with human interests. In other words, the state of being a pest is a human construct, and insect pest problems are defined by anthropocentric criteria.

The degree of insect pest problems is defined by specific economic criteria and cultural value systems, including the nuisance level. For example, although it may not be a big problem to the indigenous people of the Ethiopian highland, the human body louse, *Pediculus humanus* Linnaeus, is a serious pest and is important to Americans and Europeans as a potential disease vector. Evaluation of the impact or damage of a pest species by the measure of economic threshold may also differ by the type of crop species and local value criteria.

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Origin of Insect Pests

Insect pests have a diverse origin, which involves endemics, immigrants, and mutants. Indigenous insects consist of endemic species and those of foreign origin that are well established in a region. An indigenous species that feeds on native plants may become a serious pest when a preferred crop species is introduced to the agroecosystem. For example, the Colorado potato beetle (CPB), which is native to the semiarid region of eastern and southern Colorado and fed on the sandbur (*Solanum rostratum*), colonized potato (*Solanum tuberosum*) when this plant was first introduced into the southwestern United States, perhaps 135 years ago (Riley, 1877; Tower, 1906). Since then, CPB has extended its range throughout the United States (Hsiao, 1985) and has become the most serious pest of potato. Similarly, sugarcane has a local set of pest species unique to each region in which it is grown, because indigenous insect species have become associated with the crop (Strong et al., 1977).

Insect pest and host plant, both of exotic origin, may become associated in a new territory (Rausher, Chapter 13; Saks, Chapter 16 in this book). For example, corn (*Zea mays*) was originally introduced into the United States from tropical America, whereas the European corn borer came from central and southern Europe. The European corn borer became one of the most serious pests of corn in north-central North America (Hudon et al., 1989). Similarly, Hessian fly, *Mayetiola destructor* (Say), introduced into North America from Europe around 1779, became one of the most destructive pests of wheat, which originated in the Middle East (Allan et al., 1959).

Immigrant pest species may come from either the original species distribution or its secondary range. For example, the Mediterranean fruit fly, *Ceratitidis capitata* (Wiedmann), found sporadically in southern California, may come from Sub-Saharan Africa, the original distribution, or from Latin America or the Mediterranean, secondary distribution areas.

A major category of insect pests that are directly related to anthropogenic environmental perturbances are indigenous species that were not considered economically important or were associated with cultivated crops and have become serious pests under stressed or perturbed environmental conditions (Kennedy, Chapter 22 in this book). For example, the sweetpotato whitefly, *Bemisia tabaci* (Gennadius), which has been in California since the 1920s but was not considered a pest of field-grown crops (Byrne et al., 1990), has become a destructive pest of many field crops since 1981 because of intensive pesticide application.

INSECT PEST FAUNA

Most important pests are of exotic origin, but insect pests constitute a small part of the larger insect fauna of a region (Sailer, 1983; Lattin and Oman, 1983). The North American insect fauna contains approximately 2,000 immigrant spe-

cies, which is equivalent to about 2% of the total diversity (Kim and Wheeler, 1991). Of the 148 major insect pest species, about 40% are introduced species and are among the most serious pests in North American agriculture (Pimentel, 1986).

North American Fauna

The known diversity of North American insects consists of approximately 91,800 species, which represent perhaps 50% of the extant fauna (Kosztarab and Schaefer, 1990); Coleoptera is the largest order, with more than 23,600 species (Arnett, 1990), followed by Diptera, 19,562 species (Thompson, 1990); Hymenoptera, 17,429 species (Masner, 1990); and Lepidoptera, 11,233 species (Covell, 1990).

The North American fauna has changed since Columbus's 1492 discovery of the Americas. The magnitude of human effects on the natural environment of North America are comparable to those of the Pleistocene glaciations (Howden, 1969). One of the most important effects is the introduction of numerous insects into the New World. With continued immigration and commerce from around the world, the entry of exotic species from other continents has been constant, despite all measures taken to prevent their entry (Herrick, 1929; Kim, 1983). These invaders have caused major losses to agricultural production and forests (Pimentel et al., 1980; Pimentel, 1986; Klassen, 1989) and also have had a detrimental effect on environmental quality, human health, and aesthetics (Reynolds et al., 1982).

During colonial times, many European insects managed to become established in North America, such as the Hessian fly, *Mayetiola destructor* (Say), Angoumois grain moth, *Sitotroga cerealella* (Olivier), and codling moth, *Laspheyresia pomonella* (Linnaeus). Pierce (1917) listed 103 important foreign insects introduced into the United States, although about four times that number had already become established (Sailer, 1983). In the 1920s, 81 species of the 182 (44.3%) most economically important insect plant pests were of definite foreign origin (Smith, 1929). Recent assessment of the North American fauna for nonindigenous insects recorded 1,115 (McGregor, 1973), 1,385 (Sailer, 1978), and 1,683 species (Sailer, 1983). The most recent study revealed over 2,000 exotic species (Kim and Wheeler, 1991).

Distribution of Nonindigenous Insects

The geographical distribution of our nonindigenous insects is not even. The Hawaiian Islands, for example, having no history of a continental connection, are characterized by an immigrant biota (Elton, 1958; Carlquist, 1981). In continental North America, three principal areas are considered historically to be centers of introduction: the Canadian Maritime Provinces, the seaports of the Northeastern states, and the Pacific Northwest. For example, the carabid fauna

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of Newfoundland now contains 14.5% European species (Larson and Langor, 1982) and its leafhopper fauna has 17.2% introduced species (Hamilton and Langor, 1987). California and Florida are probably characterized by a relatively high proportion of immigrant taxa (Frankie et al., 1982; Dowell and Gill, 1989; Ewel, 1986), and the Great Lakes region also seems vulnerable to invasion by exotic species (Davis, 1962).

Habitats and disturbed sites made by humans, such as railroad and highway rights-of-way, contain an unusually high percentage of immigrants (Elton, 1958). Eurasian weeds in many disturbed areas, now well established among the native biota, are fed on by various Old World insects. For example, noxious weeds like Canada thistle and spotted knapweed are attacked by accidentally introduced generalist and specialist herbivores and also by a suite of biocontrol species deliberately introduced (Kelleher and Hulme, 1981; Wheeler, 1985, 1988; Wheeler and Whitehead, 1985). A similar pattern is also found in agroecosystems (Pimentel and Wheeler, 1973). Because about 99% of the cultivated area in North America is planted with introduced crops, this agroecosystem is usually vulnerable to immigrant pests (CAST, 1987). However, few immigrant species may be found in natural plant communities other than in areas modified by humans (Elton, 1958; McGregor, 1973), and annual field crops appear relatively less vulnerable to successful colonization by immigrant pests than perennial plants (Kogan, 1982).

GENETIC VARIATION

Genetic variation provides the basis for evolutionary change, and the genetic structure of populations is shaped by natural selection through the interaction of genetic forces and changing environments in space and time. Thus, the primary force in maintaining and structuring the genetic diversity in natural populations is environmental heterogeneity (Nevo, 1988). In a constantly changing environment, molecules, chromosomes, and morphological traits evolve at very different rates (Beaverstock and Adams, 1987), and evolutionary rates are not related to the population size and the mutation rate (Gillespie, 1985; Nevo, 1988). Molecular evolution is closest to being constant in time (Beaverstock and Adams, 1987) and protein evolution usually follows a specific model of the evolutionary process (Gillespie, 1985; Nevo, 1988), whereas chromosomal and morphological evolution vary greatly with time (Beaverstock and Adams, 1987).

Genetic differentiation between populations largely depends on the interacting balance between gene flow (homogenizing force) and genetic drift and natural selection (diversifying mechanism) (Futuyma and Peterson, 1985). Although natural selection directly acts on phenotypes, it is a major factor causing genetic differentiation at the protein and DNA levels within and between populations (Gillespie, 1985).

Genetic Diversity

Genetic diversity in insects is highly polymorphic (Selander, 1976) and genetic variation is expressed in numerous biological (e.g., Denno and Dingle, 1980; Tauber et al., 1986; Taylor and Karban, 1986; Hudon et al., 1989) and genetic traits (e.g., Lewontin, 1974; Nevo et al., 1984), and genetic diversity in natural populations is well documented for diverse groups of organisms by biochemical analyses of allozymic (Lewontin, 1974, 1985; Powell, 1975; Nevo, 1983a, 1983b; Steiner, Chapter 2 in this book) and DNA diversity (Nevo, 1988) and morphometric analyses (Daly, 1985). Diverse biological traits involved include the following: morphological, sexual behavior, geotactic behavior, developmental rate, fecundity, dispersal ability, seasonal adaptation such as diapause, feeding preference, host plants, resistance to pesticides and other toxins, and chromosomal such as crossover and inversion rates, and genic traits like allozyme polymorphism and DNA sequence.

The following examples illustrate a diversity of genetic variation in insect and acarine pests.

Electrophoretic Studies on Allozymes

ACARI

Ixodidae: *Boophilus microplus* (Canestrini) (Sattler et al., 1986)

COLEOPTERA

Chrysomelidae: *Leptinotarsa decemlineata* (Say) (Jacobson and Hsiao, 1983; Zehnder et al., 1992)

Curculionidae: *Hypera postica* (Gyllenhal) (Hsiao and Stutz, 1985; Hsiao, Chapter 15 in this book)

DIPTERA

Culicidae: *Aedes triseriatus* (Say) (Matthews and Craig, 1980)

Aedes aegypti (Linnaeus) (Wallis et al., 1984; Tabachnick and Wallis, 1985; Tabachnick, Chapter 21 in this book)

Tephritidae: *Rhagoletis pomonella* (Walsh) (McPheron et al., 1988)

HOMOPTERA

Aphididae: *Macrosiphum rosae* (Linnaeus) (Rhombert et al., 1985)

Myzus persicae (Sulzer) (May and Holbrook, 1978; Wool et al., 1978; Tomiuk and Wohrmann, 1983; Brooks and Loxdale, 1987)

Rhopalosiphum padi Linnaeus (Martinez et al., 1992)

Schizaphis graminum (Rondani) (Beregovoy and Starks, 1986)

Psyllidae: *Cacopsylla pyricola* (Foerster) (Unruh, 1990)

LEPIDOPTERA

Gelechiidae: *Pectinophora gossypiella* (Saunders) (Bartlett, 1981)

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Geometridae: *Alsophila pometaria* (Harris) (Mitter et al., 1979)

Noctuidae: *Heliothis zea* (Boddie) (Sell et al., 1975)

Spodoptera (den Boer, 1978; Pashly et al., 1985)

Chromosomal Studies

COLEOPTERA

Curculionidae: *Hypera postica* (Hsiao and Hsiao, 1984)

DIPTERA

Culicidae: *Anopheles* (Tadei, 1982)

Drosophilidae: *Drosophila* (Parsons, 1988)

Phenotypic Studies

COLEOPTERA

Chrysomelidae: *Diabrotica* (crop rotation; Krysan et al., 1986; Krysan, Chapter 18 in this book)

DIPTERA

Calliphoridae: *Calliphora* (diapause; Vinogradova, 1986)

Culicidae: *Wyeomyia smithii* (Coquillett) (development rate; Istock, 1980)

Tephritidae: *Rhagoletis pomonella* (Walsh) (seasonal asynchrony; Smith, 1988)

HOMOPTERA

Aleyrodidae: *Bemisia tabaci* (Gennadius) (morphometry; Bethke et al., 1991)

Aphididae: *Schizaphis* (three biotypes; Inayatullah et al., 1987)

LEPIDOPTERA

Pyralidae: *Ostrinia nubilalis* (Hübner) (morphometry, diapause, development, seasonal biology; Hudon et al., 1989; Showers, Chapter 14 in this book)

Genetic variation is expressed in specific traits by different species, depending upon the forces that direct natural selection in the changing environment. The greenbug, *S. graminum*, corn leaf aphid, *Rhopalosiphum maidis* (Fitch), and Hessian fly, *M. destructor*, the three major cereal pests, show genetic variation in different biological traits. Three biotypes of the greenbug differ in their ability to live on and damage varieties of wheat, barley, and sorghum, whereas the corn leaf aphid, another sorghum pest, has four or more biotypes that differ in fecundity or survival capacity on different host plants. Hessian fly biotypes interact differently with varieties of wheat (Gallun et al., 1975).

Genetic variation between populations at molecular levels differ by species. Local populations may not have differentiated, and yet a significant allele frequency between different populations does exist. For example, sexual forms

of *Alsophila pometaria* Harris (fall cankerworm) show no allozyme differences, while parthogenetic forms show a variety of genetic differences in emergence and hatching time among local populations (Mitter et al., 1979). Populations of *Pectinophora gossypiella* (pink bollworm) are highly polymorphic, with a high heterozygosity, and yet are not genetically isolated (Bartlett, 1981). *Rhagoletis pomonella* (apple maggot) does not show genetic isolation between host-associated fly populations (hawthorn and apples), although a significant allele frequency exists between fly populations (McPheron et al., 1988), and temporal asynchrony and seasonal genetic divergence may restrict gene flow between apple and hawthorn host races (Smith, 1988).

Populations of the sweetpotato whitefly, *Bemisia tabaci*, on cotton have a larger body length for 1–4 instars, a longer and wider pupal case, and lower fecundity, while nymphal instars of the poinsettia populations are smaller with a high fecundity (Bethke et al., 1991). It is likely that these differences are genetically fixed.

Geographic Variation

Geographic variation, which represents a wide range of variation, both ecological and genetic, is found in almost all species of insects. Every species has a different degree of variation by location and time. There is a considerable body of literature on geographic variation (e.g., Gould and Johnston, 1972; Powell and Taylor, 1979; Slatkin, 1985; Futuyma and Peterson, 1985; Nevo, 1988; Steiner, Chapter 2 in this book). Geographic variation between central and marginal populations is well documented in terms of gene and chromosomal polymorphisms in *Drosophila* (Parsons, 1983, 1991).

Geographic variation is developed by local evolutionary processes that involve interactions of genetic mechanisms and environmental processes (see Chapters 4–13 in this book). Local populations evolve as those forces interact within the range of genetic variability (“norm of reactions”) of the species. Genetic forces such as mutation and genetic drift interact with natural selection favoring adaptation to local environmental conditions, leading a genetic differentiation of local populations, whereas the force of gene flow opposes such differentiation (Slatkin, 1985, 1987). A significant genetic bottleneck likely occurs when an expanding population colonizes a new locality, and the short-term effects of a genetic bottleneck are a modest reduction of overall heterozygosity and a loss of rare alleles (Nei et al., 1975). In this process, environmental diversity leads to genetic variation with little genetic load (Parsons, 1983). In other words, the degree of genetic variation in local populations is a balance of the intensity of these forces, and it is expressed in biological characteristics of local populations that affect fitness, such as morphology, physiology, behavior, life history traits, and gene frequency (Barker and Thomas, 1987). The taxonomic status of local populations, such as Rassenkreis, Artenkreis, biotype, ecotype, and variety, is the manifestation of such evolutionary processes (Endler, 1977).

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Among widespread species, the genetic variability levels differ by local populations. In *Drosophila*, central populations in the range of species distribution are contiguous at high density and show high levels of genetic and phenotypic variation, whereas populations on the margin usually are small and isolated with monomorphic chromosomes but no reduction in allozyme heterozygosity (Brusard, 1984). Heterozygosity is correlated positively with environmental heterogeneity and habitat unpredictability (Nevo, 1976), and high genic heterozygosity is found among marginal populations (Lewontin, 1974). Although there is no reduction in electrophoretic polymorphisms, most marginal populations show a reduction of chromosomal polymorphisms and also a reduction of lethal and semilethal alleles (Parsons, 1983). Yet, the pattern of DNA polymorphism is similar to that of protein diversity (Nevo, 1988).

The pattern of geographic variation greatly varies and is not necessarily similar between closely related species. The fall armyworm, *Spodoptera frugiperda* (J. E. Smith), shows a significant heterogeneity in allozymes among different populations that are related to host associations (Pashley et al., 1985; Pashley, Chapter 17 in this book), whereas the related African armyworm, *Spodoptera exempta* (Walker), shows practically no heterogeneity in 17 population samples (den Boer, 1978). Natural populations of tree-hole mosquito, *Aedes triseriatus* (Say), showed a high genetic variation with average heterozygosity of 21.5% (Matthews and Craig, 1980), and, similarly, another mosquito, *Anopheles darlingi* Root, was highly polymorphic in inversion frequency, with a high heterozygosity (Tadei, 1982). However, many other species are monomorphic or have relatively low polymorphism in space and time: *Heliothis zea* (Boddie) (Sell et al., 1975); *Boophilus microplus* (Canestrini) (Sattler et al., 1986); *Schizaphis graminum* (Rondani) (Beregovoy and Starks, 1986); *Myzus persicae* (Sulzer) (May and Holbrook, 1978; Wool et al., 1978; Tomiuk and Wohrmann, 1983; Brooks and Loxdale, 1987); *Macrosiphum rosae* (Linnaeus) (Rhombert et al., 1985).

Geographic variation appears in both phenotypic and genotypic systems in most species; phenotypic characters generally include structure/function and behavior. For example, the European corn borer, *O. nubilalis* (Hübner), whose three ecotypes are defined by diapause-based responses (Showers et al., 1975; Showers, 1981; Showers, Chapter 14 in this book), differ among geographic populations by host plant preference (Hudon et al., 1989), development and seasonal biology (diapause) (Beck, 1989), and morphology (Kim et al., 1967; Chiang et al., 1970). These variations, however, are not necessarily expressed similarly in both phenotypic and genotypic systems. In *Schizaphis graminum*, three biotypes (B, C, E) show distinct morphometric differences (Inayatullah et al., 1987) but not enzyme patterns (Beregovoy and Starks, 1986). In the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), which is widely distributed in North America and continental Europe and feeds both on potatoes and alternate solanaceous plants, different populations show considerable difference in ecological adaptation and host plant relationships. However, of 12 different populations studied, all populations were alike in genetic diversity, except the southern Mexican populations, which are very different from all others, with

moderately high genetic variability (Jacobson and Hsiao, 1983; Hsiao, 1985). Similarly, geographic variation among the alfalfa weevil (*Hypera postica*) populations were not very extensive in allozyme patterns, karyotype, chiasmata frequency, and Giemsa C-banding pattern (Hsiao and Hsiao, 1984; Hsiao and Stutz, 1985; Hsiao, Chapter 15 in this book).

Phenotypic variation involves both genetic and environmental components that closely interact. These factors may compete to produce a selected level of phenotypic variance (Bull, 1987), as the direction and degree of responses to environmental factors are genetically variable (Gupta and Lewontin, 1982). A genotype may express an individual character differently in response to different environments (evolutionary plasticity) (Bradshaw, 1985), whereas at another level a genotype may produce more than one alternative phenotype, such as structure/function, physiological state, and behavior, in response to environmental conditions (phenotypic plasticity) (West-Eberhard, 1989). Phenotypic plasticity is one of the most common types of variability influenced by local environmental conditions and subjected to natural selection and evolutionary change (Williams, 1966). Thus, phenotypic variation is selectively maintained in a population by one of the two components; selection may favor maintaining only the environmental component, only the genetic component, or may be indifferent to the composition of the variance (Bull, 1987).

EVOLUTION OF INSECT PESTS

Insect pests are by definition associated with anthropogenic environments; they no longer live in natural ecosystems. Natural ecosystems are rapidly transformed into human ecosystems, the environments strongly impacted by human enterprise, in which insect pests must adapt to the changing environmental conditions for survival. Insect pests have a great innate capacity to adapt to environmental stress (Hedrick et al., 1976; Hoffmam and Parsons, 1991; Parsons, 1991).

Stressed Environments

Transformation of nature into human ecosystems is continually accelerated by rapid increase in the global human population, urbanization, and economic development. The effects of global changes are environmental stresses to insects as well as to humans. In a stressed environment, anthropogenic input, such as pesticide application, habitat destruction, acid rain, and climatic changes, is the *stressor*, while *stress*, which is defined as a detrimental or disorganizing influence, is the *output* or *response*. Odum (1985) identified 18 trends expected in stressed ecosystems, of which 5 components likely occur at the community level: (1) r-strategists increase proportionally; (2) organisms get smaller; (3) life spans decrease; (4) energy flow at high trophic levels reduces and food chains shorten; and (5) if original diversity is high, species diversity declines and dominance increases (Woodwell, 1983).

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At the ecosystem level, the trends include (1) community respiration increases; (2) nutrient turnover increases with more nutrient loss (Mooney and Godron, 1983); (3) resource use becomes less efficient; (4) parasitism and other negative interactions increase, but positive interactions, such as mutualism, decrease (Axelrod and Hamilton, 1981); and (5) functional properties, such as community metabolism, are more robust than structural properties, such as species composition (Odum, 1985). As we, the human species, must adapt to the human ecosystem, insect pests are forced to cope with anthropogenic stresses.

Differentiation of Populations

Local populations have adapted uniquely to their habitats, and their differentiation is shaped by the interaction between gene flow and genetic drift and/or mutations and natural selection (Nevo et al., 1984; Futuyma and Peterson, 1985; Parsons, 1991). Genetic divergence can come about by changes in environment or genetic system (Kirkpatrick, 1982). For example, as landscape or environmental condition changes, the equilibrium between genetic and environmental systems sustained by the population under an initial environment becomes unstable and deterministic selection pressure will force the population to adapt to the new environment (Templeton, 1980).

The differentiation of populations involves both genetic and environmental systems. However, the process is ultimately genetic, even though natural selection acts on phenotypes (Barker and Thomas, 1987). Populations of a species can be differentiated genetically by one of the following events: (1) colonization of a new habitat (habitat, hosts) (Bartlett and Richardson, 1986; Holt, 1987; Rice and Salt, 1988); (2) colonization of a new territory or region (founder effect) (Barton and Charlesworth, 1984; Carson and Templeton, 1984; Bartlett and Richardson, 1986); (3) landscape changes (bottleneck effect) (Nei et al., 1975; Hedrick, 1986); (4) genetic changes by stochastic events, such as genetic drift and mutation (Templeton, 1980; Bush, 1981) or natural selection (directional and disruptive) (Rice, 1987; Barker and Thomas, 1987).

Barton and Charlesworth (1984) summarized potential mechanisms that drive genetic divergence for major speciation models. They include (1) drift with background homozygosity (peripatric model) (Mayr, 1954), relaxation of selection (founder-flush model) (Carson, 1968, 1975), and deviation from Hardy-Weinberg Law (genetic transience) (Templeton, 1980); (2) accumulation of mutations and changing selection (allopatric speciation) (Mayr, 1963); (3) spatial variation in selection (parapatric model) (Endler, 1977); (4) drift and meiotic drive (stasipatric model) (White, 1968, 1978); (5) drift and fluctuations in the adaptive landscape (shifting-balance model) (Wright, 1932); (6) disruptive selection (sympatric speciation model) (Maynard-Smith, 1966). However, the level of differentiation differs for individual local populations because of varying interactive forces of genetic and environmental systems, and the differentiation of populations does not necessarily lead to speciation. As a result, these processes

will produce diverse infraspecific taxa that have been classified as biotype, ecotype, formenkeris, rassenkreis, race, or subspecies, based on the degree of genetic and phenotypic divergence.

The differentiation of populations by colonization involves niche shift, invasion of disturbed or newly created habitats by humans or immigration and founder effect (Parsons, 1983). Successful colonizers are usually generalists with the following attributes: (1) widely distributed and abundant in the original range of distribution, (2) polyphagous, (3) having a short generation time, and (4) possessing a wide range of genetic and phenotypic variability, which allows them to function in a wide range of physical conditions (Ehrlich, 1986). Local populations may be differentiated by habitat specialization (Rice, 1987; Rice and Salt, 1988) or host shift (Bush, 1981; McPherson et al., 1988; and Kaneshiro, Chapter 4; Tauber and Tauber, Chapter 5; Margolies, Chapter 6; Inmentel, Chapter 8; Rausher, Chapter 13 in this book).

Populations of a species may simply be subdivided by establishment of a new population from founder individuals (Carson and Templeton, 1984). After the successful founder event, the populations go through genetic changes (recombination) and produce descendent populations that are well adapted to the local environment. In this process, the genetic system interacts with the environment, and this causes gradual genetic changes over many generations (Carson and Templeton, 1984). At this time, a genetic bottleneck may occur, resulting in modest reduction of overall heterozygosity and a loss of rare alleles (Nei et al., 1975). At a locality, the populations may be drastically reduced in size by landscape changes, such as flooding, drought, and other natural factors, or by environmental changes in the habitat. Here, the surviving individuals essentially become a random sample of the original population in which a genetic bottleneck likely occurs (Nei et al., 1975).

Genetic changes may occur in populations by stochastic events in the genetic system, such as genetic drift or mutation (Lewontin, 1974; Templeton, 1980; Bush, 1981), and, similarly, genetic divergence may develop by natural selection (directional and disruptive), such as the constant application of chemical pesticides (Rice, 1987; Barker and Thomas, 1987; Shelton and Wyman, 1991; Croft and Dunley, Chapter 7 in this book). For example, the sweetpotato whitefly (*Bemisia tabaci*), which has been in California since the 1920s, has become highly resistant to most chemical pesticides widely used in agriculture. Thus, its pest status in field crops has increased since 1981 (Byrne et al., 1990). In the last three years, this species has been a serious threat to California agriculture, and it is now perhaps the most damaging pest of field crops in that state.

Evolution in the Stressed Environment

The level of stress that insects must face in stressful environments is much greater than in natural ecosystems. In stressed environments, insect pests must continually adapt to severe environmental conditions for survival. As stress and variability are correlated, genotypic and phenotypic variabilities under severe

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environmental stress are usually much higher than in stable environments, particularly for those traits that are important in determining survival (Parsons, 1987, 1991).

Under stressed environments, additive genetic variability for recombination is higher than in constant environments, such as laboratory conditions, and substantial recombination can be induced under the combination of karyotype and environments (Parsons, 1988). For example, in *Drosophila*, the genetic system of recombination rapidly reorganized and recombination increased in the chromosomes 2 and 3 when subjected to selection for resistance to DDT (Laurie-Ahlberg and Merrell, 1979; Flexon and Rodell, 1982), for variable temperature stress (Zhuchenko et al., 1985), and for nutritional and behavioral stress (Parsons, 1988). Chromosomal mutation rates also are known to vary considerably over time and space within species (Bush, 1981).

Insect pests have rapidly evolved and are evolving at an unprecedented rate as they are subjected to stressed environments. Although no direct experimental evidence exists as yet, insect pests are forced to evolve rapidly to counter anthropogenic stresses, such as pesticides, temperature, and habitat degradation. Despite all the efforts invested for controlling insect pests for this century, no single species of insect pest has ever been completely eradicated.

Some insect pest species are resistant to most pesticides ever used (NRC, 1986); for example, *Tetranychus urticae* Koch, *Psylla pyricola* Foerster, phytoseiid mites, and many tortricoid moths (Croft and Dunley, Chapter 7 in this book). The populations of pest species that were introduced and established in the United States for a long time are no longer the same organisms as their ancestral populations. For example, European corn borers today are different from the populations that existed in 1930, even at the same locality, and are certainly different from those in Iowa and Minnesota in many biological traits (Hudon et al., 1989). This genetic differentiation has developed in less than 50 generations. Today's Hessian fly is not the same species as that first brought into the United States during colonial times (Gallun et al., 1975). The poinsettia population of the sweetpotato whitefly no longer behaves as did its ancestral population of many years ago (Bethke et al., 1991).

CONCLUSION AND SUMMARY

Insect pests are species of insects closely associated with anthropogenic activities. They are groups of dynamic organisms with a powerful genetic system and evolutionary strategy that have developed through a long evolutionary process. Insect pests are highly polymorphic and have broad genetic diversity, expressed in a multitude of biological traits.

Geographic variation is found in almost all species of insect pests, and populations of every species have different degrees of variation in space and time. The pattern of geographic variation greatly varies among species, and geographic variation appears in both phenotypic and genetic characters.

Human ecosystems are stressed environments for insect pests. In stressed environments insect pests are forced to evolve rapidly in response to anthropogenic stress, such as pesticides and environmental degradation. Insect pests have evolved at an unprecedented rate and are also rapidly evolving as they are subjected to stressed environmental conditions. Local populations of many insect pests have been differentiated, and some are recognized as genetically distinct infraspecific taxa.

The concept of pest is a human construct, and the problem of insect pests is defined by specific economic criteria and a cultural value system. However, pest management strategy should not be based on anthropocentric criteria, because insect pests are dynamic organisms with the genetic capacity to adapt rapidly to changing environments.

Conventional pest control practices, based primarily on shortsighted economics and a heavy use of diverse chemical pesticides, resulted in rapid adaptations of insect pests to diverse local environmental conditions and the anthropocentric control measures, such as DDT and crop rotations. Enormous efforts to contain insect pests have not succeeded in permanently eradicating a single species of insect pest. Genetic variation is important in determining the pest status and evolutionary response of various insect species (Kennedy, Chapter 22 in this book). Thus, sound pest management strategies must be based on the knowledge of genetic mechanisms and evolutionary strategies of the pest species.

REFERENCES

- Allan, E. R., E. G. Heyne, E. T. Jones, and C. O. Johnson. 1959. Genetic analysis of ten sources of Hessian fly resistance, their interrelationships and association with leaf rust reaction in wheat. *Bull. Kans. Agric. Expt. Sta.* 104.
- Arnett, R. H., Jr. 1990. Present and future of systematics of the Coleoptera in North America. Pages 165–173 in Kosztarab, M., and C. W. Schaefer (eds.), *Systematics of the North American Insects and Arachnids: Status and Needs*. Va. Agric. Exp. Sta. Infor. Ser. 90–1. Blacksburg, Va.: Va. Polytech. Inst. St. Univ.
- Axelrod, R., and W. D. Hamilton. 1981. The evolution of cooperation. *Science* 211: 1390–1396.
- Barker, J. S. F., and R. H. Thomas. 1987. A quantitative genetic perspective on adaptive evolution. Pages 3–23 in Loeschcke, V. (ed.), *Genetic Constraints on Adaptive Evolution*. Berlin: Springer-Verlag.
- Bartlett, A. 1981. Isozyme polymorphisms in populations of the pink bollworm. *Ann. Entomol. Soc. Am.* 74:9–13.
- Bartlett, D. C. H., and B. J. Richardson. 1986. Genetic attributes of invading species. Pages 21–33 in Groves, R. H., and J. J. Burdon (eds.), *Ecology of Biological Invasions*. Cambridge: Cambridge Univ. Press.
- Barton, N. H., and B. Charlesworth. 1984. Genetic revolutions, founder effects and speciation. *Annu. Rev. Ecol. Syst.* 15: 133–164.

18 Insect Pests and Evolution

- Beaverstock, P. R., and M. Adams. 1987. Comparative rates of molecular, chromosomal and morphological evolution in some Australian vertebrates. Pages 175–188 in Campbell, K. S. W., and M. F. Day (eds.), *Rates of Evolution*. London: Allen & Unwin.
- Beck, S. D. 1989. Developmental and seasonal biology of *Ostrinia nubilalis*. Pages 45–82 in Russell, G. E. (ed.), *Biology and Population Dynamics of Invertebrate Crop Pests*. Andover, Hampshire: Intercept, Ltd.
- Beregovoy, V. H., and K. J. Starks. 1986. Enzyme pattern in biotypes of the greenbug, *Schizaphis graminum* (Rondani) (Homoptera: Aphididae). *J. Kan. Entomol. Soc.* 59(3):517–523.
- Bethke, J. A., T. D. Paine, and G. S. Nuessly. 1991. Comparative biology, morphometrics, and development of two populations of *Bemisia tabaci* (Homoptera: Aleyrodidae) on cotton and poinsettia. *Ann. Entomol. Soc. Am.* 84(4):407–411.
- Bradshaw, A. D. 1985. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* 13:115–155.
- Brooks, C. P., and H. D. Loxdale. 1987. Survey of enzyme variation in British populations of *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) on crops and weed hosts. *Bull. Entomol. Res.* 77:83–89.
- Brussard, P. F. 1984. Geographical patterns and environmental gradients: The central and marginal model in *Drosophila* revisited. *Annu. Rev. Ecol. Syst.* 15:25–64.
- Bull, J. J. 1987. Evolution of phenotypic variance. *Evolution* 41 (2):303–315.
- Bush, G. L. 1981. Stasipatric speciation and rapid evolution in animals. Pages 201–218 in Atchley, W. R., and D. S. Woodruff (eds.), *Evolution and Speciation in Honor of M. J. D. White*. Cambridge: Cambridge Univ. Press.
- Byrne, D. N., T. S. Bellows, Jr., and M. P. Parrella. 1990. Whiteflies in agricultural systems. Pages 227–261 in Gerling, D. (ed.), *Whiteflies: Their Bionomics, Pest Status and Management*. Andover, Hampshire: Intercept.
- Carlquist, S. 1981. Chance dispersal. *Am. Sci.* 69:509–515.
- Carson, H. L. 1968. The population flush and its genetic consequences. Pages 123–137 in Lewontin, R. C. (ed.), *Population Biology and Evolution*. Syracuse, N.Y.: Syracuse Univ. Press.
- . 1975. The genetics of speciation at the diploid level. *Am. Nat.* 109:73–92.
- Carson, H. L., and A. R. Templeton. 1984. Genetic revolutions in relation to speciation phenomena; the founding of new populations. *Annu. Rev. Ecol. Syst.* 15:97–131.
- Chiang, H. C., K. C. Kim and B. W. Brown. 1970. Morphometric variability related to ecological conditions of three biotypes of *Ostrinia nubilalis* in North Central United States. *Ann. Entomol. Soc. Am.* 63:1013–1016.
- Council for Agricultural Science and Technology (CAST). 1987. *Pests of Plants and Animals: Their Introduction and Spread*. Report 112. 40 pp.
- Covell, C. V., Jr. 1990. The status of our knowledge of the North American Lepidoptera. Pages 211–230 in Kosztarab, M., and C. W. Schaefer (eds.), *Systematics of the North American Insects and Arachnids: Status and Needs*. Va. Agric. Exp. Sta. Infor. Ser. 90–1. Blacksburg, Va.: Va. Polytech. Inst. St. Univ.
- Daly, H. V. 1985. Insect morphometrics. *Annu. Rev. Entomol.* 30:415–438.
- Davis, L. G. 1962. The need for pest detection follow-ups. *Bull. Entomol. Soc. Am.* 8:59–62.

- den Boer, M. H. 1978. Isoenzyme and migration in the African armyworm, *Spodoptera exempta* (Lepidoptera: Noctuidae). *J. Zool.*, London 185:539–553.
- Denno, R. F., and H. Dingle (eds.). 1980. *Insect Life History Patterns*. New York: Springer-Verlag.
- Dowell, R. V., and R. Gill. 1989. Exotic invertebrates and their effects on California. *Pan-Pac. Entomol.* 65:132–145.
- Ehrlich, P. R. 1986. Which animal will invade? Pages 79–95 in Mooney, H. A., and J. A. Drake (eds.), *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen.
- Endler, J. A. 1977. *Geographic Variation, Speciation, and Clines*. Princeton: Princeton Univ. Press.
- Ewel, J. J. 1986. Invasibility: Lessons from South Florida. Pages 214–230 in Mooney, H. A., and J. A. Drake (eds.), *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag.
- Flexon, P. B., and C. F. Rodell. 1982. Genetic recombination and directional selection of DDT resistance in *Drosophila melanogaster*. *Nature* (London) 298:672–674.
- Frankie, G., W. R. Gill, C. S. Kochler, D. Dilly, J. O. Washburne, and P. Hamman. 1982. Some considerations for the eradication and management of introduced insect pest in urban environments. Pages 237–255 in Battenfield, S. L. (ed.), *Proceedings, Symposium Imported Fire Ant*, Atlanta, Ga., June 7–10, 1982. USEPA & USDA, APHIS, Washington, D. C.
- Futuyma, D. J., and S. C. Peterson. 1985. Genetic variation in the use of resources by insects. *Annu. Rev. Entomol.* 30:217–238.
- Gallun, R. L., K. J. Starks, and W. D. Guthrie. 1975. Plant resistance to insects attacking cereals. *Annu. Rev. Entomol.* 20:337–357.
- Gillespie, J. H. 1985. The interaction of genetic drift and mutation with selection in a fluctuating environment. *Theor. Popul. Biol.* 27:222–237.
- Gould, F. 1991. The evolutionary potential of crop pests. *Amer. Sci.* 79:496–507.
- Gould, S. J., and R. F. Johnston. 1972. Geographic variation. *Annu. Rev. Ecol. Syst.* 3:457–498.
- Green, N. G., H. M. LeBaron, and L. W. K. Moberg. 1990. *Managing Resistance to Agrochemicals: From Fundamental Research to Practical Strategies*. Washington, D. C.: American Chemical Society.
- Gupta, A. P., and R. C. Lewontin. 1982. A study of reaction norms in natural populations of *Drosophila pseudoobscura*. *Evolution* 36:934–948.
- Hamilton, K. G. A., and D. W. Langor. 1987. Leafhopper fauna of Newfoundland and Cape Breton Islands (Rhynchota: Homoptera: Cicadellidae). *Can. Entomol.* 119:663–695.
- Hedrick, P. H. 1986. Genetic polymorphism in heterogeneous environments: A decade later. *Annu. Rev. Ecol. Syst.* 17:535–566.
- Hedrick, P. W., M. E. Ginevan, and E. P. Ewing. 1976. Genetic polymorphism in heterogeneous environments. *Annu. Rev. Ecol. Syst.* 7:1–32.
- Herrick, G. W. 1929. The procession of foreign insect pests. *Sci. Mon.* 29:269–274.
- Hoffmann, A. A., and P. A. Parsons. 1991. *Evolutionary Genetics and Environmental Stress*. Oxford: Oxford Univ. Press.

20 Insect Pests and Evolution

- Holt, R. D. 1987. Population dynamics and evolutionary process: The manifold roles of habitat selection. *Evol. Ecol.* 1:331-347.
- Horsfall, J. G. 1983. Impact of introduced pests on man. Pages 1-13 in Wilson, C. L., and C. L. Graham (eds.), *Exotic Plant Pests and North American Agriculture*. New York: Academic Press.
- Howden, H. F. 1969. Effects of man on the Ontario insect fauna. *Proc. Entomol. Soc. Ont.* 99:51-53.
- Hsiao, T. H. 1985. Ecophysiological and genetic aspects of geographic variations of the Colorado potato beetle. Pages 63-77 in Ferro, D. N., and R. H. Voss (eds.), *Proceedings, Symposium on Colorado Potato Beetle, XVIIth International Congress of Entomology*. Amherst, Mass.: Mass. Agric. Exp. Sta. Res. Bull. No. 704.
- Hsiao, C., and T. H. Hsiao. 1984. Cytogenetic studies of alfalfa weevil (*Hypera postica*) strains (Coleoptera: Curculionidae). *Can. J. Genet. Cytol.* 26:348-353.
- Hsiao, T. H., and J. M. Stutz. 1985. Discrimination of alfalfa weevil strains by allozyme analysis. *Entomol. Exp. Appl.* 37:113-121.
- Hudon, M., E. J. LeRoux, and D. G. Harcourt. 1989. Seventy years of European corn borer (*Ostrinia nubilalis*) research in North America. Pages 1-44 in Russell, G. E. (ed.), *Biology and Population Dynamics of Invertebrate Crop Pests*. Andover, Hampshire: Intercept.
- Inayatullah, C., W. S. Fargo, and J. A. Webster. 1987. Use of multivariate models in differentiating greenbug (Homoptera: Aphididae) biotypes and morphs. *Environ. Entomol.* 16:839-846.
- Istock, C. A. 1980. Natural selection and life history variation: Theory plus lessons from a mosquito. Pages 113-127 in Denno, R. F., and H. Dingle (eds.), *Insect Life History Patterns*. New York: Springer-Verlag.
- Jacobson, J. W., and T. H. Hsiao. 1983. Isozyme variation between geographic populations of the Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae). *Ann. Entomol. Soc. Am.* 76:162-166.
- Jones, D. P. 1973. Agricultural entomology. *Annu. Rev. Entomol.* 307-332.
- Kelleher, J. S., and M. A. Hulme. 1981. *Biological Control Programs Against Insects and Weeds in Canada 1969-1980*. Slough, England: Commonwealth Agricultural Bureaux, 410 pp.
- Kim, K. C. 1983. How to detect and combat exotic pests. Pages 261-319 in Wilson, C. L., and C. L. Graham (eds.), *Exotic Plant Pests and North American Agriculture*. New York: Academic Press.
- Kim, K. C., H. C. Chiang, and B. W. Brown, Jr. 1967. Morphometric differences among four biotypes of *Ostrinia nubilalis*. *Ann. Entomol. Soc. Am.* 60:796-801.
- Kim, K. C., and B. A. McPherson (eds.). 1993. *Evolution of Insect Pests: The Patterns of Variation*. New York: John Wiley & Sons.
- Kim, K. C., and A. G. Wheeler, Jr. 1991. Pathways and Consequences of the Introduction of Non-Indigenous Insects and Arachnids in the United States. Report to the U. S. Congress, Office of Technology Assessment, Washington, D. C. (unpublished).
- Kirkpatrick, M. 1982. Quantum evolution and punctuated equilibria in continuous genetic characters. *Am. Nat.* 119:833-848.
- Klassen, W. 1989. Eradication of introduced arthropod pests: Theory and historical practice. *Misc. Publ. Entomol. Soc. Am.* 73:1-29.

- Kogan, M. 1982. Impact and management of introduced pests in agriculture. Pages 226–235 in Battenfield, S. S. (ed.), *Proceedings of the Symposium on Imported Fire Ant*, Atlanta, Ga., June 7–10, 1982. USEPA & USDA, APHIS, Washington, D. C.
- Komai, T., N. Chino, and Y. Hosino. 1950. Contributions to the evolutionary genetics of the lady beetle, *Harmonia l.* *Genetics* 36:382–390.
- Kosztarab, M., and C. W. Schaefer (eds.). 1990. *Systematics of the North American Insects and Arachnids: Status and Needs*. Va. Agric. Exp. Sta. Infor. Ser. 90–1. Blacksburg, Va.: Va. Polytech. Inst. St. Univ.
- Krysan, J. L., D. E. Foster, T. F. Branson, K. R. Ostlie, and W. S. Cranshaw. 1986. Two years before the hatch: Rootworm adapt to crop rotation. *Bull. Entomol. Soc. Am.* 32:250–253.
- Larson, D. J., and D. W. Langor. 1982. The carabid beetles of insular Newfoundland (Coleoptera: Carabidae: Cicindellidae)—30 years after Lindroth. *Can. Entomol.* 114:591–597.
- Lattin, J. D., and P. Oman. 1983. Where are the exotic insect threats? Pages 93–137 in Wilson, C. L., and C. L. Graham (eds.), *Exotic Plant Pests and North American Agriculture*. New York: Academic Press.
- Laurie-Ahlberg, C. C., and D. J. Merrell. 1979. Aldehyde oxidase allozyme. inversion and DDT resistance in some laboratory populations of *Drosophila melanogaster*. *Evolution* 33(1):342–349.
- Lewontin, R. C. 1974. *The Genetic Basis of Evolutionary Changes*. New York: Columbia Univ. Press.
- . 1985. Population genetics. *Annu. Rev. Genet.* 19:81–102.
- McGregor, R. C. 1973. The Emigrant Pests: A Report to Dr. Francis J. Mulhern, Administrator, Animal and Plant Health Inspection Service, U. S. Dept. Agr. APHIS, Hyattsville, Md. 167 pp. (unpublished).
- McPheron, B. A., D. C. Smith, and S. H. Berlacher. 1988. Genetic differences between host races of *Rhagoletis pomonella*. *Nature* 336:64–66.
- Martinez, D., A. Moya, A. Latorre, and A. Fereres. 1992. Mitochondrial DNA variation in *Rhopalosiphum padi* (Homoptera: Aphididae) population from four Spanish localities. *Ann. Entomol. Soc. Am.* 85(2):241–246.
- Masner, L. 1990. Status report on taxonomy of Hymenoptera in North America. Pages 231–240 in Kosztarab, M., and C. W. Schaefer (eds.), *Systematics of the North American Insects and Arachnids: Status and Needs*. Va. Agric. Exp. Sta. Infor. Ser. 90–1. Blacksburg, Va.: Va. Polytech. Inst. St. Univ.
- Matthews, T. C., and G. B. Craig, Jr. 1980. Genetic heterozygosity in natural populations of tree-hole mosquitoes, *Aedes triseriatus*. *Ann. Entomol. Soc. Am.* 73:739–743.
- May, B., and F. R. Holbrook. 1978. Absence of genetic variability in the green peach aphid, *Myzus persicae* (Homoptera: Aphididae). *Ann. Entomol. Soc. Am.* 71:809–812.
- Maynard-Smith, J. 1966. Sympatric speciation. *Am. Nat.* 100:637–650.
- Mayr, E. 1954. Change of genetic environment and evolution. Pages 156–180 in Huxley, J. S., A. C. Hardy, and E. B. Ford (eds.), *Evolution as a Process*. London: Allen & Unwin.
- . 1963. *Animal Species and Evolution*. Cambridge, Mass.: Harvard Univ. Press.
- Mitter, C., D. J. Futuyma, J. C. Schneider, and J. D. Hare. 1979. Genetic variation and host plant relations in a parthenogenetic moth. *Evolution* 33(3):777–790.

22 Insect Pests and Evolution

- Mooney, H. A., and M. Godron (eds.). 1983. *Disturbance and Ecosystems*. Berlin: Springer-Verlag.
- National Research Council (NRC). 1986. *Pesticide Resistance: Strategies and Tactics for Management. Committee on Strategies for the Management of Pesticide Resistant Pest Populations*. Washington, D. C.: National Acad. Press.
- Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in population. *Evolution* 29: 1–10.
- Nevo, E. 1976. Adaptive strategies of genetic systems in constant and varying environments. Pages 141–158 in Karlin, S., and E. Nevo (eds.), *Population Genetics and Ecology*. New York: Academic Press.
- . 1983a. Population genetics and ecology: The interface. Pages 287–321 in Bendall, D. S. (eds.), *Evolution from Molecules to Men*. Cambridge: Cambridge Univ. Press.
- . 1983b. Adaptive significance of protein variation. Pages 239–282 in Oxford, G. S., and D. Rollinson (eds.), *Protein Polymorphism: Adaptive and Taxonomic Significance*. New York: Academic Press.
- . 1988. Genetic diversity in nature: Patterns and theory. *Evol. Biol.* 23:217–246.
- Nevo, E., A. Beiles, and R. Ben-Shlomo. 1984. The evolutionary significance of genetic diversity: Ecological, demographic and life-history correlates. Pages 13–213 in Mani, G. S. (ed), *Evolutionary Dynamics of Genetic Diversity*. Berlin: Springer-Verlag.
- Odum, E. P. 1985. Trends expected in stressed ecosystems. *Bioscience* 35(7):419–422.
- Parsons, P. A. 1983. *The Evolutionary Biology of Colonizing Species*. Cambridge: Cambridge Univ. Press.
- . 1987. Evolutionary rates under environmental stress. *Evol. Biol.* 21:311–347.
- . 1988. Evolutionary rates: Effects of stress upon recombination. *Biol. J. Linn. Soc.* 35:49–68.
- . 1991. Evolutionary rates: Stress and species boundaries. *Annu. Rev. Ecol. Syst.* 22:1–18.
- Pashley, D. P., S. J. Johnson, and A. N. Sparks. 1985. Genetic population structure of migratory moths: The fall armyworm (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 78:756–762.
- Pierce, W. D. 1917. *A Manual of Dangerous Insects Likely to Be Introduced in the United States Through Importations*. Washington, D. C.: Government Printing Office. 256 pp.
- Pimentel, D. 1986. Biological invasions of plants and animals in agriculture and forestry. Pages 149–162 in Mooney, H. A., and J. A. Drake (eds.), *Ecology of Biological Invasions of North America and Hawaii*. New York: Springer-Verlag.
- Pimentel, D., and A. G. Wheeler, Jr. 1973. Species and diversity of arthropods in the alfalfa community. *Environ. Entomol.* 2:659–668.
- Pimentel, D., D. Andow, R. Dyson-Hudson, D. Gallahan, S. Jacobson, M. Irish, S. Kroop, A. Moss, I. Schreiner, M. Shepard, T. Thompson, and B. Vinzant. 1980. Environmental and social costs of pesticides: A preliminary assessment. *Oikos* 34:127–140.
- Powell, J. R. 1975. Protein variation in natural populations of animals. *Evol. Biol.* 8:79–119.

- Powell, J. R., and C. E. Taylor. 1979. Genetic variation in ecologically diverse environments. *Amer. Sci.* 67:590–596.
- Reynolds, H. T., R. Clark, G. Frankie, F. E. Gilstrap, P. J. Hamman, M. Kogan, E. H. Smith, and D. E. Wiedhaas. 1982. Management of established vs. introduced pests. Pages 82–90 in Battenfield, S. L. (ed.), *Proceedings of the Symposium on Imported Fire Ant*, Atlanta, Ga., June 7–10, 1982. USEPA & USDA/APHIS, Washington, D.C.
- Rhomberg, L. R., S. Joseph, and R. S. Singh. 1985. Seasonal variation and clonal selection in cyclically parthenogenetic rose aphid (*Macrosiphum rosae*). *Can. J. Genet. Cytol.* 27:224–232.
- Rice, W. R. 1987. Speciation via habitat specialization. *Evol. Ecol.* 1:301–314.
- Rice, W. R., and G. W. Salt. 1988. Speciation via disruptive selection on habitat preference: Experimental evidence. *Am. Nat.* 131:911–917.
- Riley, C. V. 1877. *The Colorado Beetle*. London: George Routledge & Sons.
- Sailer, R. I. 1978. Our immigrant insect fauna. *Bull. Entomol. Soc. Am.* 24:3–11.
- . 1983. History of insect introductions. Pages 15–38 in Wilson, C. L., and C. L. Graham (eds.), *Exotic Plant Pests and North American Agriculture*. New York: Academic Press.
- Sattler, P. W., L. R. Hilburn, R. B. Davey, J. E. George, and J. B. Rajas Avalos. 1986. Genetic similarity and variability between natural populations and laboratory colonies of North American *Boophilus* (Acari: Ixodidae). *J. Parasitol.* 72(1):95–100.
- Selander, R. K. 1976. Genic variation in natural populations. Pages 21–44 in Ayala, F. J. (ed.), *Molecular Evolution*. Sunderland, Mass.: Sinauer Associates.
- Sell, D. K., G. S. Whitt, and W. H. Luckmann. 1975. Esterase polymorphism in the corn earworm, *Heliothis zea* (Boddie): A survey of temporal and spatial allelic variation in natural populations. *Biochem. Genet.* 13(11/12):885–898.
- Shelton, A. M., and J. A. Wyman. 1991. Insecticide resistance of diamondback moth (Lepidoptera: Plutellidae) in North America. *Proc. 2nd Internat. Diamondback Moth Workshops*. Taiwan.
- Showers, W. B. 1981. Geographical variation of the diapause response in the European corn borer. Pages 97–111 in Denno, R. F., and H. Dingle (eds.), *Insect Life History Patterns: Habitat and Geographic Variation*. New York: Springer-Verlag.
- Showers, W. B., H. C. Chiang, A. J. Keaster, R. E. Hill, G. L. Reed, A. N. Sparks, and G. J. Musick. 1975. Ecotypes of the European corn borer in North America. *Environ. Entomol.* 4:753–760.
- Slatkin, M. 1985. Gene flow in natural populations. *Annu. Rev. Ecol. Syst.* 16:393–430.
- . 1987. Gene flow and the geographic structure of a natural population. *Science* 236:787–792.
- Smith, D. C. 1988. Heritable divergence of *Rhagoletis pomonella* host races by seasonal asynchrony. *Nature* 336:66–67.
- Smith, H. S. 1929. On some phases of preventive entomology. *Sci. Mon.* 29:177–184.
- Southwood, T. R. E., and G. A. Norton. 1973. Economic aspects of pest management strategies and decisions. Pages 164–184 in Geier P. W., C. R. Clark, D. F. Anderson, and H. A. Nix (eds.), *Insects: Studies in Pest Management*. Ecol. Soc. Austr., Canberra-City.

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- Stenseth, N. C. 1987. Evolutionary processes and insect outbreaks. Pages 533–563 in Barbosa, P., and J. C. Schultz, *Insect Outbreaks*. New York: Academic Press.
- Strong, D. R., E. P. McCoy, and J. R. Rey. 1977. Time and the number of herbivore species. The pests of sugarcane. *Ecology* 58: 167–175.
- Tabachnick, W. G., and G. P. Wallis. 1985. Genetic structure of *Aedes aegypti* populations in the Caribbean: Ecological considerations. Pages 371–381 in Lounibos, L. P., J. R. Rey, and J. F. Frank (eds.), *Ecology on Mosquitoes: Proceedings of a Workshop*. College Park, Md.: Entomol. Soc. Am. Publ.
- Tadei, W. P. 1982. Biologia de anofelinos amazonicos. VII. Estudo da variacao de frequencias das inversoes cromossomicas de *Anopheles darlingi* Root (Diptera, Culicidae). *Acta Amazonica* 12(4):759–785.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. *Seasonal Adaptation of Insects*. New York: Oxford Univ. Press.
- Taylor, H., and R. Karban (eds.) 1986. *The Evolution of Insect Life Cycles*. New York: Springer-Verlag.
- Templeton, A. R. 1980. The theory of speciation via the founder principle. *Genetics* 94:1011–1038.
- . 1981. Mechanisms of speciation—A population genetic approach. *Annu. Rev. Ecol. Syst.* 12:23–48.
- Thompson, F. C. 1990. Biosystematic information: Dipterists ride the third wave. Pages 179–201 in Kosztarab, M., and C. W. Schaefer (eds.), *Systematics of the North American Insects and Arachnids: Status and Needs*. Va. Agric. Exp. Sta. Infor. Ser. 90–1. Blacksburg, Va.: Va. Polytech. Inst. St. Univ.
- Tomiuk, J., and K. Wohrmann. 1983. Enzyme polymorphism and taxonomy of aphid species. *Z. Zool. Syst. & Evolutionsforsch.* 21:266–274.
- Tower, W. L. 1906. An investigation of evolution in chrysomelid beetles of the genus *Lepitotarsa*. Washington, D. C.: Carnegie Institute.
- Unruh, T. R. 1990. Genetic structure among 18 West Coast pear psylla populations: Implications for the evolution of resistance. *Amer. Entomologist Spring* 1990: 37–48.
- Vinogradova, E. B. 1986. Geographical variation and ecological control by diapause in flies. Pages 35–47 in Taylor F., and R. Karban (eds.), *The Evolution of Insect Life Cycles*. New York: Springer-Verlag.
- Wallis, G. P., W. J. Tabachnick, and J. R. Powell. 1984. Genetic heterogeneity among Caribbean populations of the yellow fever mosquito, *Ades aegypti*. *Am. J. Trop. Med. Hyg.* 33:492–498.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Evol. Syst.* 20:249–278.
- Wheeler, A. G., Jr. 1985. Seasonal history, host plants, and nymphal descriptions of *Orthocephalus coriaceus*, a plant bug pest of herb garden composites (Hemiptera: Miridae). *Proc. Entomol. Soc. Wash.* 87:85–93.
- , Jr. 1988. An exotic honeysuckle aphid established in Pennsylvania. *Regul. Hortic.* 14(2):21–22.
- Wheeler, A. G., Jr., and D. R. Whitehead. 1985. *Larinus planus* (F.) in North America (Coleoptera: Curculionidae: Cleoninae) and comments on biological control of Canada thistle. *Proc. Entomol. Soc. Wash.* 87:751–759.
- White, M. J. D. 1968. Models of speciation. *Science* 158: 1065–1070.

- . 1978. *Modes of Speciation*. San Francisco: Freeman.
- Williams, G. C. 1966. *Adaptations and Natural Selections*. Princeton: Princeton Univ. Press.
- Wilson, C. L., and C. L. Graham (eds.). 1983. *Exotic Plant Pests and North American Agriculture*. New York: Academic Press.
- Woodwell, G. M. 1983. The blue planet: Of wholes and parts and man. Pages 2–10 in Mooney, H. A., and M. Godron (eds.), *Disturbance and Ecosystems*. Berlin: Springer-Verlag.
- Wool, D., S. W. Bunting, and H. F. Van Emden. 1978. Electrophoretic study of genetic variation in British *Myzus persicae* (Sulz.) (Homoptera: Aphididae). *Biochem. Genet.* 16:987–1006.
- Wright, S. 1932. The role of mutation, inbreeding, crossbreeding and selection in evolution. *Proc. 6th Int. Congr. Genet.* 1:356–366.
- Zehnder, G. W., L. Sandall, A. M. Tisler, and T. O. Powers. 1992. Mitochondrial DNA diversity among 17 geographic populations of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae). *Ann. Entomol. Soc. Am.* 85(2):234–240.
- Zhuchenko, A. A., A. B. Koral, and L. P. Kovtyukh. 1985. Changes for crossing over frequency in *Drosophila* during selection for resistance to temperature fluctuation. *Genetica* 67:73–78.